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Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO₂ and temperature regimes

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Abstract Increases in the concentration of atmospheric carbon dioxide may have a fertilizing effect on plant growth by increasing photosynthetic rates and therefore may offset potential growth decreases caused by the stress associated with higher temperatures and lower precipitation. However, plant growth is determined both by rates of net photosynthesis and by proportional allocation of fixed carbon to autotrophic tissue and heterotrophic tissue. Although CO₂ fertilization may enhance growth by increasing leaf-level assimilation rates, reallocation of biomass from leaves to stems and roots in response to higher concentrations of CO₂ and higher temperatures may reduce whole-plant assimilation and offset photosynthetic gains. We measured growth parameters, photosynthesis, respiration, and biomass allocation of *Pinus ponderosa* seedlings grown for 2 months in 2 × 2 factorial treatments of 350 or 650 μ bar CO₂ and 10/25° C or 15/30° C night/day temperatures. After 1 month in treatment conditions, total seedling biomass was higher in elevated CO₂, and temperature significantly enhanced the positive CO₂ effect. However, after 2 months the effect of CO₂ on total biomass decreased and relative growth rates did not differ among CO₂ and temperature treatments over the 2-month growth period even though photosynthetic rates increased ≈7% in high CO₂ treatments and decreased ≈10% in high temperature treatments. Additionally, CO₂ enhancement decreased root respiration and high temperatures increased shoot respiration. Based on CO₂ exchange rates, CO₂ fertilization should have increased relative growth rates (RGR) and high temperatures should have decreased RGR. Higher

photosynthetic rates caused by CO₂ fertilization appear to have been mitigated during the second month of exposure to treatment conditions by a ≈3% decrease in allocation of biomass to leaves and a ≈9% increase in root:shoot ratio. It was not clear why diminished photosynthetic rates and increased respiration rates at high temperatures did not result in lower RGR. Significant diametrical and potentially compensatory responses of CO₂ exchange and biomass allocation and the lack of differences in RGR of ponderosa pine after 2 months of exposure of high CO₂ indicate that the effects of CO₂ fertilization and temperature on whole-plant growth are determined by complex shifts in biomass allocation and gas exchange that may, for some species, maintain constant growth rates as climate and atmospheric CO₂ concentrations change. These complex responses must be considered together to predict plant growth reactions to global atmospheric change, and the potential of forest ecosystems to sequester larger amounts of carbon in the future.

Key words Biomass allocation · Climate change
CO₂ enhancement · Photosynthesis · Relative growth rate

Introduction

The concentration of CO₂ in the atmosphere has increased from ≈280 μ bar in the pre-industrial era to 353 μ bar currently and is continuing to increase at 1.8 μ bar per year (Watson et al. 1991). Increasing concentrations of CO₂ may enhance plant growth by increasing photosynthetic rates and water-use efficiency (Long 1991; Mooney et al. 1991). General circulation models predict that temperature will also increase 1.5–4.5° C in much of interior North America in response to a doubling of atmospheric CO₂ (Manabe and Wetherald 1987; Rind et al. 1990; Mitchell et al. 1990). Little is known about the interactive effects of CO₂ and temperature on plant growth (Eamus 1991; Farrar and Williams 1991). CO₂ fertilization typically increases photosynthetic rates (Eamus and Jarvis 1989; Mooney et al. 1991), and exposure to high

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concentrations of CO₂ under favorable conditions increases biomass accumulation for many C₃ plants (Cure and Acock 1986; Idso et al. 1987; Long 1991; Melillo et al. 1991). In general, larger increases in photosynthesis and growth occur when CO₂ fertilization is accompanied by increases in temperature (Long 1991).

In contrast to the majority of the literature, Norby et al. (1992) found that biomass of *Liriodendron tulipifera* saplings did not increase with long-term exposure to high CO₂ concentrations in the field even though photosynthetic rates were higher (also see Brown and Higginbotham 1986). Norby et al. (1992) attributed the lack of a growth response to reallocation of biomass from leaves to roots.

Growth rate is determined by rates of photosynthesis and by allocation of fixed carbon to leaves versus allocation to non-photosynthetic tissues (e.g., branches, stems, roots, and reproductive parts). Poorter et al. (1990) found that, relative to changes in photosynthesis, small increases in biomass allocation to non-photosynthetic tissues profoundly decreased growth rate. Such offsetting influences of changes in CO₂ exchange and biomass allocation are common for plants under various growth conditions (Ågren and Ingestad 1987; Küppers et al. 1988; Mooney et al. 1988; Mooney and Winner 1991). These studies point to the importance of understanding the potential interactions between climate-driven changes in biomass allocation and physiology for predicting growth responses of plants in future climate regimes.

As in other ecosystems, the net effects of climate change and CO₂ fertilization are uncertain for western coniferous forests. Net photosynthetic rates of many western conifer species are relatively unresponsive to temperature (Larcher 1980; DeLucia and Smith 1987), but allocation of aboveground biomass varies substantially with moisture and temperature (Grier and Running 1977; Snell and Brown 1978; Gholz 1982; Pearsons et al. 1984; Waring and Schlesinger 1985). Comparisons along environmental gradients in the field provide an analog for changes that may occur in future climates. For example, Callaway et al. (1994) found large shifts in biomass allocation from leaves to sapwood in ponderosa pine (*Pinus ponderosa* Laws.) along a gradient of decreasing moisture and increasing temperature on mountain slopes of western Nevada. Thus shifts in biomass allocation in response to climate change could compensate for greater photosynthetic rates at high CO₂. We know of no study of the interactive effects of elevated CO₂ and temperature on biomass allocation and plant growth rate.

We measured growth, gas exchange, and biomass allocation of ponderosa pine seedlings grown in a 2 × 2 factorial experiment varying in CO₂ concentration and temperature in controlled growth-chambers. Based on biomass allocation patterns of ponderosa pine in response to climate in the field (Callaway et al. 1994) and biomass allocation patterns of seedlings of many plant species in response to CO₂ in laboratory experiments, we hypothesized that decreased allocation of biomass to leaves at high CO₂ concentrations and high temperatures

would at least partially offset potential growth enhancement due to CO₂-stimulation of photosynthesis.

Methods

We grew seedlings from seed from several open-pollinated trees at each of four isolated populations of ponderosa pine growing on soils derived from hydrothermally altered andesite near Reno, Nevada, USA. We selected two montane sites at Alpine County and Alum Creek, and two desert sites at Peavine Mountain, and Ramsey Mine (Table 1). Climate and soil chemistry are described in detail by Billings (1950), DeLucia et al. (1988), Schlesinger et al. (1989) and Callaway et al. (1994). Seedlings were grown in large 1.8-l PVC tubes, 35 cm deep, so as not to restrict root growth (see Thomas and Strain 1991) at the Duke University Phytotron. Pots contained steam-sterilized beach sand. After stratification at 5°C for 10 weeks, five seeds were planted per pot, and seedlings were thinned to one per pot after emergence. Seedlings were grown for 30 days in a greenhouse, then separated into four groups, each group containing 32 seedlings per population, and moved into four growth chambers with the following treatments: (1) 350 μ bar CO₂, 10° C/25° C night/day temperatures; (2) 350 μ bar CO₂, 15°/30° C; (3) 650 μ bar CO₂, 10°/25°; (4) 650 μ bar CO₂, 15°/30°. Low temperature treatments approximated mean growing season temperatures (May-June) at the sites, and high temperature treatments were based on the predictions of current climate models. Our choice of 650 μ bar as the high-CO₂ treatment was based on projected atmospheric concentrations of 575 μ bar by the year 2050 and 1330 μ bar by 2100, assuming a constant 2% per year increase in anthropogenic emissions (Watson et al. 1991). Throughout the 2 months in treatment conditions, seedlings were well-watered with half-strength Hoagland's nutrient solution and exposed to ≈ 1000 μ mol m⁻²s⁻¹ PAR on a 12/12 h day/night cycle. Relative humidity was maintained at 45% during the day. Prior to the treatments, each group of 32 seedlings was divided into 16 pairs ranked by size. One member of each pair was used for an initial harvest 30 days after the seedlings were moved to treatment conditions. Thirty days after the initial harvest the second group was harvested. The second harvest occurred over 4 days because of the time required for measuring CO₂ exchange.

At each harvest plants were divided into roots, stems, and leaves, and each component was dried (70°C) and weighed. Harvest data were used to calculate relative growth rate (RGR), net assimilation rate (NAR) as g m⁻²day⁻¹, and leaf area ratio (LAR) as m²/g plant, from Evans (1972). Growth analysis was conducted on pairs of plants re-ranked by dry mass in each harvest after both harvests were complete. Determining RGR with post-harvest rankings greatly reduces variation within treatments and is more likely to yield significant results than other more conservative procedures. NAR was calculated on a total leaf area basis, and specific leaf area (SLA) as m²/g leaf, and leaf mass ratio (LMR) as g leaf/g plant, were calculated for each treatment. Leaf area for individual needles at each harvest was calculated from all leaf surface dimensions, and whole seedling leaf area was determined with leaf mass to leaf area regressions.

Table 1 Elevation, climate, soil characteristics for seed source populations of *Pinus ponderosa* on the east slope of the Sierra Nevada and adjacent Great Basin Desert

Site	Elevation (m)	Precipitation (mm/year)	Temperature ^a (°C)	Soil pH	Soil P (μg/g)
Alpine County	2100	950	11.5	4.7	19.2
Alum Creek	1800	350	12.1	4.0	5.0
Peavine Mt.	1700	240	13.1	4.1	13.8
Ramsey Mine	1750	200	14.0	3.5	2.0

^a Temperature is the daily mean for May

CO₂ exchange of shoots and roots was measured with a LI-COR 6200 closed gas analysis system on each of five plants per population per treatment 1–4 days prior to the final harvest (after 60–63 days of exposure to treatment conditions). Measurements were made under the growth conditions. Day and night shoot CO₂ exchange was measured once for each individual in a specially designed 1.2-l cuvette. Fan speed in the cuvette was adjusted to create a boundary layer resistance of $\approx 20.0 \text{ s m}^{-1}$ (see Smith 1980) which is appropriate for complex conifer shoots. Root respiration was measured during one day and one night in a 1.8-l cuvette that enclosed the open end of the PVC pot but excluded the shoot. CO₂ efflux from the soil was measured from the top and the bottom of the PVC pot and summed to calculate pot respiration. Efflux was measured over one-minute intervals at each end of the PVC pot. Respiration means of control pots for each treatment were subtracted from the pot CO₂ efflux to calculate respiration.

To estimate carbon lost as root exudation from seedlings we measured dissolved organic carbon (DOC) content of the sand in the pots and in leachate drained from the pots during the experiment. DOC was measured after the final harvest with a O.I. Model 700 Total Organic Carbon Analyzer (Chemical Analysis Laboratory, University of Georgia, USA). Sand and leachate DOC was measured in a subsample of eight pots per population per treatment. The volume of leachate collected over a 3-day period was measured for individual pots, and 2.5 ml of each sample per population per treatment was pooled for DOC analysis. DOC lost in leachate per seedling mass per day was calculated from pooled DOC measurements and leachate volumes for individual pots and converted to the mass of carbon lost per day.

Three-way analysis of variance was used to compare population, CO₂, and temperature effects on all dependent variables (SYSTAT; Wilkinson 1990). Independent variables were fixed in the ANOVA model. Dependent variables were normally distributed and did not require transformation.

Results

There were no significant effects or interactions of population, CO₂, or temperature on losses of DOC from the pots. DOC in the sand and leachate was estimated to be

less than 1% of the daily carbon budget of these seedlings. We concluded that carbon lost as DOC did not contribute significantly to the carbon budget of *P. ponderosa* seedlings over the duration of the experiment, and we have ignored the contribution of DOC to the seedling carbon budgets reported in this paper.

At the first harvest, elevated CO₂ had strong effects on total seedling mass and root:shoot ratios, but population effects were predominant for all biomass allocation variables (Table 2a, b).

Total seedling mass was 8% higher in the low temperature treatment and 29% greater at high temperature for plants grown at 650 μ l/l CO₂ compared to plants grown at 350 μ l/l CO₂, and the interaction term was highly significant. Although populations accounted for most of the variability of dependent variables at the first harvest, total seedling mass and biomass allocation did not vary consistently with respect to the two montane and two desert populations. For example, in the 350 μ bar low-temperature treatment, percent leaf allocation was highest for seedlings from the Ramsey Mine population and lowest for seedlings from Peavine Mountain, although both populations were from desert climates.

At the second harvest, CO₂ effects were much stronger on total seedling mass and biomass allocation than population effects, which became insignificant for total mass and stem allocation (Table 3a,b). At low temperatures, enhanced CO₂ increased total biomass 6% and at high temperatures 26% ($P_{\text{CO}_2 \times \text{temperature}} = 0.025$). Although the only significant effect of CO₂ or temperature on biomass allocation at the first harvest was for CO₂ and root:shoot ratio (Table 2b), by the time of the second harvest proportional allocation of biomass to roots, shoots, stems, and leaves was profoundly affected by CO₂ concentration, temperature, or both. The effect of

Table 2a Biomass allocation of *Pinus ponderosa* seedlings at the first harvest after 1 month at factorial treatments of high and low CO₂ and high and low temperatures. All populations were combined. Shared letters indicate no significant difference (Tukey, *post-ANOVA*)

	Low CO ₂ - low temp	Low CO ₂ - high temp	High CO ₂ - low temp	High CO ₂ - high temp
Root:shoot ratio	0.939±0.019 ^a	0.945±0.014 ^a	0.976±0.020 ^a	1.006±0.021 ^a
Stem allocation (% of total)	5.83 ±0.27 ^a	7.08 ±0.57 ^a	6.49 ±0.36 ^a	6.135±0.21 ^a
Leaf allocation (% of total)	47.69 ±1.85 ^a	45.02 ±1.12 ^a	45.13 ±0.99 ^a	44.95 ±1.26 ^a
Total seedling mass (g)	0.265±0.007 ^a	0.265±0.008 ^a	0.286 ±0.008 ^a	0.343±0.011 ^b

Table 2b ANOVA table for growth and biomass allocation variables after 1 month of treatment conditions

	df	Root/shoot			Stem allocation			Leaf allocation			Total mass		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
CO ₂	1	0.16	6.60	0.011	0.66	0.09	0.766	115.11	0.97	0.325	0.151	32.62	<0.001
Temp	1	0.02	0.90	0.343	11.29	1.51	0.221	126.76	1.07	0.302	0.050	10.72	0.001
Population	3	0.17	7.39	<0.001	47.86	6.40	<0.001	133.35	1.13	0.034	0.020	4.39	0.005
CO ₂ ×Temp	1	0.01	0.41	0.527	37.00	4.94	0.027	93.04	0.79	0.376	0.050	10.78	0.001
CO ₂ ×Population	3	0.06	2.50	0.060	21.03	2.81	0.040	18.35	0.16	0.926	0.004	0.89	0.447
Temp×Pop	3	0.13	5.34	0.001	55.63	7.43	<0.001	32.51	0.28	0.843	0.001	0.26	0.856
CO ₂ ×Temp×Pop	3	0.05	2.18	0.091	23.59	3.15	0.026	0.24	0.00	1.000	0.007	1.49	0.219
Error	237	0.02			7.48			118.26			0.005		

Table 3a Growth variables and biomass allocation of *Pinus ponderosa* seedlings grown for 2 months in factorial treatments of high and low CO₂ and low temperatures. All populations were combined. Shared letters indicate no significant difference (Tukey, post-ANOVA)

	Low CO ₂ - low temp	Low CO ₂ - high temp	High CO ₂ - low temp	High CO ₂ - high temp
Relative growth rate (g g ⁻¹ day ⁻¹)	0.052±0.001 ^a	0.053±0.001 ^a	0.052±0.001 ^a	0.052±0.001 ^a
Net assimilation rate (g m ⁻² day ⁻¹)	0.5.91±0.26 ^a	5.83±0.29 ^a	6.18±26 ^a	6.48± 030 ^a
Leaf area ratio (m ² /g plant)	0.0094±0.004 ^a	0.0098±0.0004 ^a	0.0089±0.0004 ^a	0.0085±0.0003 ^a
Specific leaf area (m ² /g leaf)	0.0252±0.0005 ^a	0.0241±0.0004 ^{ab}	0.0255±0.0005 ^a	0.0229±0.0005 ^b
Leaf mass ratio (g leaf/g plant)	0.511±0.021 ^a	0.4900±0.016 ^a	0.501±0.019 ^a	0.483±0.014 ^a
Root:shoot ratio	0.825±0.017 ^a	0.795±0.014 ^a	0.884±0.020 ^b	0.878±0.021 ^b
Stem allocation (% of total)	5.32±0.21 ^{ac}	6.03±0.20 ^b	4.96±0.18 ^a	5.53±0.20 ^{ab}
Leaf allocation (% of total)	49.78±0.50 ^a	49.88±0.48 ^a	48.50±0.56 ^a	48.09±0.55 ^a
Total seedling mass (g)	1.66±0.07 ^a	1.70±0.08 ^a	1.76±0.07 ^a	2.15±0.09 ^b

Table 3b ANOVA table for biomass allocation variables after 2 months of treatment conditions

	df	Relative growth rate			Net assimilation rate			Leaf area ratio		
		MS	F	P	MS	F	P	MS	F	P
CO ₂	1	0.00000	0.16	0.687	13.54	2.88	0.091	0.00006	6.86	0.009
Temp	1	0.00002	0.85	0.358	0.67	0.14	0.706	0.00000	0.00	0.990
Population	3	0.00011	4.01	0.008	4.41	0.94	0.422	0.00002	2.50	0.061
CO ₂ ×Temp	1	0.00000	0.03	0.863	2.46	0.52	0.470	0.00001	1.25	0.264
CO ₂ ×Population	3	0.00025	9.55	<0.001	14.41	3.07	0.029	0.00001	1.80	0.148
Temp×Pop	3	0.00004	1.57	0.196	7.50	1.60	0.191	0.00002	1.92	0.126
CO ₂ ×Temp×Pop	3	0.00016	6.16	<0.001	16.28	3.47	0.017	0.00004	4.89	0.003
Error	237	0.00003			4.69			0.00001		
	df	Specific leaf area			Leaf mass ratio			Root:shoot ratio		
		MS	F	P	MS	F	P	MS	F	P
SO ₂	1	0.00001	0.61	0.436	0.024	1.19	0.276	0.351	16.86	<0.001
Temp	1	0.00020	15.91	<0.001	0.004	0.22	0.640	0.022	1.05	0.306
Population	3	0.00006	4.38	0.005	0.010	0.49	0.688	0.097	4.66	0.003
CO ₂ ×Temp	1	0.00003	2.55	0.112	0.000	0.00	0.979	0.010	0.46	0.498
CO ₂ ×Population	3	0.00001	0.72	0.542	0.001	0.07	0.976	0.018	0.85	0.469
Temp×Pop	3	0.00001	0.99	0.397	0.005	0.25	0.864	0.008	0.38	0.768
CO ₂ ×Temp×Pop	3	0.00003	2.04	0.109	0.003	0.15	0.927	0.011	0.52	0.668
Error	237	0.00001			0.020			0.021		
	df	Stem allocation			Leaf allocation			Total seedling mass		
		MS	F	P	MS	F	P	MS	F	P
CO ₂	1	16.34	5.75	0.017	157.07	9.33	0.003	4.68	12.61	<0.001
Temp	1	31.50	11.07	0.001	2.46	0.15	0.703	2.83	7.62	0.006
Population	3	0.42	0.15	0.932	76.51	4.54	0.004	0.68	1.84	0.140
CO ₂ ×Temp	1	1.15	0.41	0.525	2.87	0.17	0.680	1.90	5.12	0.025
CO ₂ ×Population	3	0.39	0.14	0.937	16.09	0.96	0.414	0.37	0.99	0.398
Temp×Pop	3	1.49	0.52	0.666	2.77	0.16	0.920	0.28	0.77	0.515
CO ₂ ×Temp×Pop	3	1.09	0.38	0.765	0.03	0.15	0.927	0.15	0.40	0.754
Error	237	2.85			16.84	0.15		0.37		

Table 4a Photosynthesis and respiration rates of *Pinus ponderosa* seedlings grown for 2 months in factorial treatments of high and low CO₂, high and low temperatures. All populations were combined. Shared letters indicate no significant difference (Tukey, post-ANOVA)

	Low CO ₂ - low temp	Low CO ₂ - high temp	High CO ₂ - low temp	High CO ₂ - high temp
Photosynthesis (μmol m ⁻² s ⁻¹)	51.4± 2.4 ^a	41.9± 2.6 ^b	54.7± 1.7 ^{ac}	49.8± 2.2 ^{ab}
Shoot respiration (μmol g ⁻¹ s ⁻¹)	0.0035± 0.0001 ^{ac}	0.0040± 0.0002 ^b	0.0033± 0.0001 ^a	0.0038± 0.0001 ^{bc}
Root respiration ¹ (μmol g ⁻¹ s ⁻¹)	0.016± 0.001 ^{ab}	0.017± 0.002 ^a	0.011± .001 ^b	0.012± 0.001 ^{bc}
Root respiration ² (μmol g ⁻¹ s ⁻¹)	0.027± 0.002 ^a	0.026± 0.002 ^a	0.019± 0.001 ^b	0.018± 0.002 ^b

¹ Night respiration

² day respiration

Table 4b ANOVA table for photosynthesis and respiration rates

	df	Photosynthesis			Shoot respiration			Root respiration (night)			Root respiration (day)		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
CO ₂	1	726.6	21.56	<0.001	0.01	0.02	0.878	0.00057	15.31	<0.001	0.00038	6.58	0.012
Temp	1	881.3	26.15	<0.001	3.69	6.82	0.011	0.00002	0.67	0.418	0.00001	0.13	0.719
Population	3	351.6	10.43	<0.001	2.29	4.24	0.008	0.00006	1.65	0.187	0.00006	1.05	0.375
CO ₂ ×Temp	1	151.5	4.50	0.038	0.99	1.83	0.181	0.00000	0.04	0.837	0.00005	0.87	0.353
CO ₂ ×Population	3	307.8	9.13	<0.001	3.65	6.75	<0.001	0.00001	0.29	0.829	0.00004	0.62	0.603
Temp×Pop	3	521.4	15.47	<0.001	6.01	11.11	<0.001	0.00006	1.59	0.201	0.00011	1.87	0.144
CO ₂ ×Temp×Pop	3	557.8	16.55	<0.001	5.85	10.82	<0.001	0.00002	0.47	0.703	0.00004	0.62	0.605
Error	63	33.7			0.54			0.00004			0.00006		

high CO₂ concentrations on root:shoot ratios was much larger after two months than after one month, and temperature effects remained insignificant. In the high temperature treatments stem biomass allocation increased 13% in low CO₂ concentrations and 11% in high CO₂ concentrations ($P_{\text{CO}_2 \times \text{temperature}} = 0.525$). Biomass allocated to leaves decreased significantly in response to elevated CO₂ in both temperature treatments.

Even though total seedling mass increased with high CO₂, and RGR was calculated using rankings most likely to produce treatment differences, we found no significant effect of CO₂ treatments on RGR (Table 3a,b). Population effects, however, were significant but did not vary consistently among montane and desert populations.

NAR (a component of RGR) tended to increase, but not significantly ($P_{\text{CO}_2} = 0.105$), in the high CO₂ treatments. Population effects on NAR were not significant. The relative contribution of photosynthesis and respiration to NAR varied among CO₂ treatments (Table 4a,b). Under elevated CO₂, net photosynthesis increased 6% and 19% in the low and high temperature treatments, respectively (Table 4, $P_{\text{CO}_2 \times \text{temperature}} = 0.038$). Shoot respiration was unaffected, but day and night root respiration decreased substantially in the high CO₂ treatments. Significant population effects occurred for photosynthesis and shoot respiration but differences were not consistent with respect to montane and desert populations.

Leaf area ratio (LAR), a second component of RGR, was reduced by high CO₂ concentrations, potentially compensating for the increases in CO₂ assimilation rates (Table 3a,b). LAR decreased 5% and 15% in the low and high temperature treatments respectively. However, we

did not detect significant changes in SLM or LMR, the factors determining LAR, in different CO₂ concentrations. Population effects were insignificant for NAR, LAR, and LMR.

As for CO₂, there were no significant effects of temperature on RGR (Table 3a,b). Additionally, temperature did not affect NAR or LAR even though SLA decreased 4% at low CO₂ concentrations and 10% at high CO₂ concentrations. CO₂ assimilation (the second component of NAR) was substantially reduced by elevated temperature, with 7–10% decreases in net photosynthesis and 14–15% increases in shoot night respiration (Table 4a,b). Root day and night respiration rates were not affected by temperature.

Interaction terms for CO₂ × temperature analysis of variance were insignificant for all dependent variables except for total seedling mass and photosynthesis at the second harvest, indicating that the effects of CO₂ concentration on respiration and biomass allocation, were consistent at both temperatures.

Discussion

Seedling biomass increased substantially under elevated CO₂ during the first month of the experiment. There was no further divergence in biomass among seedlings in the two CO₂ treatments by the second harvest, therefore CO₂ had no effect on RGR. During this second month, elevated CO₂ significantly altered the pattern of biomass allocation, shifting biomass from needles to stems and roots. Stimulatory effects of CO₂ on photosynthesis and inhibi-

tion of respiration measured at the end of the experiment appear to have been offset by these shifts in biomass allocation. Although significant population effects were found for photosynthesis and shoot respiration, differences in rates did not vary consistently with respect to the two montane and two desert populations.

Enhancement of net photosynthesis by elevated CO_2 at the whole seedling or leaf level and the large increases in biomass are consistent with most previous studies (see reviews by Long 1991; Mooney et al. 1991), including that of Surano et al. (1986) on ponderosa pine. Reported effects of elevated CO_2 on root respiration are inconsistent, but others have also found reduced root respiration at high CO_2 concentrations (Reuveni and Gale 1985; Bunce 1990). However, assimilation gains expected from increases in net photosynthesis and decreased respiratory losses were not manifested in higher growth rates during the second month of the experiment. We propose that the reallocation of photosynthate from autotrophic tissue to heterotrophic tissue at high CO_2 concentrations offsets assimilatory gains derived from changes in CO_2 exchange such as described by Norby et al. (1992). Not only did the relative effects of treatments on total seedling mass decrease over time in our experiments, population effects which were the primary source of variation at the first harvest, disappeared after 2 months of treatment conditions or were sharply reduced.

RGR is the product of NAR (mass accumulated per area of autotrophic tissue) and LAR (the area of autotrophic tissue displayed per seedling mass). Although this is mathematically correct only for instantaneous growth analysis, inferences about the relative contribution of the mean values of NAR and LAR to mean RGR are valid. NAR tended to increase (not significantly) as expected based on the positive photosynthetic responses, but LAR decreased significantly in elevated CO_2 . Thus photosynthetic and respiratory gains appeared to be offset by decreases in allocation to photosynthetic tissue. The decrease in LAR with increasing CO_2 was due to the reduced proportion of biomass allocated to leaf area rather than changes in SLM. The reallocation of biomass from shoots to roots in elevated CO_2 was also an important part of the whole-plant compensatory response, and greater root:shoot ratios have been observed for other conifer species in elevated CO_2 (Higginbotham et al. 1985; O'Neill et al. 1987; but see also Tolley and Strain 1984; Hollinger 1987). Biomass partitioning between root and shoot is generally thought to depend on nutrient status (Farrar and Williams 1991), with a decrease or no change in root:shoot ratios with elevated CO_2 when nutrients are not limiting (Eamus and Jarvis 1989). Our experimental seedlings experienced much higher water and nutrient availability than they would in natural field conditions. Nevertheless, we found large increases in root:shoot ratios in elevated CO_2 . Conifers growing in the field on altered andesite normally experience drought and very low nutrient availability in both montane and desert sites (DeLucia et al. 1988, Schlesinger et al. 1989); thus, extrapolation from our laboratory analyses

to natural habitats is difficult. Under field conditions, however, we would expect even greater root:shoot ratios than in our experiments.

In natural conditions, ponderosa pine has relatively low stomatal conductances even when soil moisture is abundant (DeLucia et al. 1988), thus transpirational cooling in the humid conditions of the growth chamber may have been insufficient to keep leaves at optimum temperatures. Seedling growth was not limited by soil moisture in our experiment, but high temperatures depressed photosynthesis and increased shoot dark respiration, eliminating the positive effects of elevated CO_2 on biomass that were significant at low temperatures. Considering the large increases in shoot night respiration at high temperatures, temperature depression of net photosynthesis in our experiment may have been due to a disproportionate increase in day-time respiration in comparison to gross photosynthesis.

Callaway et al. (1994) found that the proportional allocation of biomass to leaves decreased and the allocation to whole-tree sapwood increased for sapling and mature ponderosa pine in warmer and drier climates. In this study we found that allocation of biomass to stems also increased significantly in seedlings grown at high temperature. High proportional allocation of biomass to stem sapwood appears to increase whole-plant water storage capacity in hot climates, reducing the impact of xylem cavitations induced by water stress (Tyree and Dixon 1986), and mitigating losses in sapwood permeability as water content of the bole decreases (Puritch 1971; Waring and Running 1978).

Ponderosa pine growing in xeric climates in the field appear to partially compensate for low leaf:sapwood biomass ratios by constructing leaves with higher area to mass relationships than conspecifics growing in more mesic climates (DeLucia and Schlesinger 1991; Callaway et al. 1994). In our greenhouse experiment in which seedlings were not water-limited, the opposite occurred, and ponderosa pine seedlings decreased in SLA at high temperatures. Rather than a response to ambient temperature, increased SLA in xeric climates in the field may be a functional response that maximizes photosynthetic capacity per leaf mass otherwise limited by water stress and by long periods of stomatal closure.

The prediction that CO_2 fertilization may improve the growth of plants in xeric climates is based on several lines of evidence. High concentrations of atmospheric CO_2 increase photosynthetic rates for many species (Acock and Allen 1985; Oechel and Strain 1985) and up to 84% for ponderosa pine in the field (Green and Wright 1977). Conifer seedlings and saplings, including ponderosa pine, are generally larger when grown in elevated CO_2 (Surano et al. 1986; Eamus and Jarvis 1989; Mooney et al. 1991), just as ponderosa pine seedlings did during the first month of our experiment. Historical patterns of annual growth in some subalpine conifers also suggest a positive whole-tree growth response to increasing atmospheric CO_2 concentrations at high elevations (Graybill 1987; LaMarche et al. 1984; Graybill and

Idso 1993). In contrast, our studies of greenhouse-grown seedlings and our observations of mature trees in the field (Callaway et al. 1994) suggest that biomass reallocation occurring very early in the development of ponderosa pine seedlings may offset later gains in net CO₂ assimilation resulting in a limited growth response to high concentrations of atmospheric CO₂. These results are consistent with Graumlich (1991), who reported no trend in the growth of western subalpine conifers during the past six decades attributable to higher atmospheric CO₂. If other conifer species reallocate biomass similarly to ponderosa pine, we suggest that western forests may not sequester substantial amounts of carbon as CO₂ concentrations continue to increase in the atmosphere.

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