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Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO_2

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Summary To determine whether long-term growth in enriched CO_2 atmospheres changes the woody tissue respiration component of aboveground carbon budgets, we measured woody tissue respiration of stems of 3-year-old ponderosa pine (*Pinus ponderosa* Laws.) grown in ambient (350 ppm) or twice ambient (700 ppm) atmospheric CO_2 concentrations in open-top field chambers located in Placerville, CA. Total respiration rate was measured by gas exchange, and construction respiration was calculated from the construction cost, percent carbon of stem samples and relative growth rate. Maintenance respiration was determined as the difference between total and construction respiration. The Q_{10} of respiration was greater in stems grown in elevated CO_2 than in stems grown in ambient CO_2 (2.20 versus 1.67). As a result, mean daily respiration per unit volume of wood modeled for the month of September was greater in trees growing in elevated CO_2 than in ambient CO_2 (46.75 versus 40.45 mol m^{-3} day^{-1}). These effects of atmospheric CO_2 concentration were not the result of differences in relative growth rate. Calorimetric analyses of woody tissue construction cost indicated no difference between treatments; however, trees in the elevated CO_2 treatment showed a 1% lower carbon concentration than trees in the ambient CO_2 treatment. Estimates of construction respiration did not differ between treatments, confirming that the treatment differences in mean daily respiration rate were attributable to the maintenance component. Under future predicted atmospheric conditions, changes in the maintenance respiration of woody tissue may lead to an increase in the respiration component of whole-plant carbon budgets of ponderosa pine. Our results suggest that potential increases in the maintenance component of stem respiration should be considered when modeling the response of forest stand growth to enriched CO_2 atmospheres.

Keywords: construction cost, maintenance respiration, ponderosa pine, Q_{10}.

Introduction

Growth and maintenance respiration can consume more than 50% of the carbon fixed by plants in photosynthesis (Amthor 1989), and estimates of the contribution of stem respiration to total aboveground carbon budgets in mature forests range from < 13% (Ryan and Waring 1992) to as much as 42% (Waring and Schlesinger 1985). Therefore, as a conservative estimate, woody tissue respiration accounts for at least 25% of the aboveground respiratory budget of forests, and changes in this component in response to atmospheric CO_2-enrichment could have a significant effect on forest carbon budgets. Data on the effects of atmospheric CO_2 concentration on the structural component (wood) of woody plants are scarce (e.g., Wullschleger et al. 1995).

Leaf-level studies have shown that increasing the atmospheric CO_2 concentration results in direct, short-term, reversible decreases in leaf respiration (Reuveni and Gale 1985, Amthor et al. 1992, Ziska and Bunce 1994). Long-term exposure to CO_2-enriched atmospheres generally results indirectly in decreases in total respiration of leaves caused by compositional changes in tissue (Bunce 1992, Williams et al. 1992, Wullschleger et al. 1992*a*, Azcón-Bieto et al. 1994, Ziska and Bunce 1994). Leaf-level differences in the growth and maintenance components of dark respiration have also been demonstrated (Wullschleger et al. 1992*b*, Wullschleger and Norby 1992, Thomas et al. 1993, Ziska and Bunce 1993) with varying results in the direction of response to CO_2.

We measured stem maintenance and construction respiration in trees grown under relatively long-term elevated and ambient CO_2 conditions as a first step in determining whether growth in CO_2-enriched atmospheres results in changes in woody tissue respiration compared with trees growing in the current ambient atmosphere. We used a common model of respiration to partition total respiration into construction respiration (for producing new biomass and long-term storage) and maintenance respiration (involved in the upkeep and repair of existing tissue including protein turnover, phloem loading and translocation-related processes, and the maintenance of ion gradients) (Penning de Vries 1975, Amthor 1994). Several approaches have been used to partition total respiration into maintenance and construction components. In this study, total respiration was measured by gas exchange, and construction respiration was calculated from construction cost, carbon content and relative growth rate. Maintenance respiration was estimated as the difference between total and construction respiration. Understanding how these respiratory components, as well as growth rate, respond to the environment is a starting

point for understanding the overall responses of respiration to environmental change (Amthor 1994).

Materials and methods

Total respiration

Gas exchange measurements were made (from September 10 to 15, 1994) on 3-year-old saplings of ponderosa pine (*Pinus ponderosa* Laws.) growing in open-top field chambers at the Institute of Forest Genetics in Placerville, CA. Treatment CO_2 concentrations within chambers were ambient (approximately 350 ppm atmospheric CO_2) and elevated (ambient + 350 ppm = approximately 700 ppm atmospheric CO_2). Seeds were planted in native soil in field chambers at the time of treatment initiation in May 1991. In September 1994, average sapling heights and diameters (above root collar) were 1.50 m and 4.93 cm and 1.72 m and 5.72 cm for the ambient and elevated treatments, respectively. Complete descriptions of experimental design and operation are given by Ball et al. (1992) and Johnson et al. (1994). Rate of total CO_2 efflux from stem cuvettes was measured by infrared gas analysis on nine to 12 trees per treatment. Clear Plexiglas cuvettes (6 cm in length) with compressed foam collars were attached with clamps to needle-free stem segments ranging in diameter from 2.7 to 5.5 cm. Cuvettes were covered with aluminum foil to minimize heating and prevent refixation of respired CO_2 by photosynthetically active bark. Surface stem temperatures inside the cuvettes were measured with copper-constantan thermocouples. Reference gases at approximately the same concentrations as the growth conditions were circulated through the cuvettes at 0.8 l min^{-1}. Total CO_2 efflux rate was measured as the difference in CO_2 concentration between gas entering and leaving the cuvette.

Measurements were made on trees from each treatment from before sunrise (0600 h) until late afternoon (1800 h) to maximize the temperature range over which data were collected. The response of CO_2 efflux rate to a 10 °C increase in temperature, Q_{10}, was calculated for each tree by plotting the natural log of CO_2 efflux rate as a function of the temperature over which the measurements were made, where $Q_{10} = \exp(10\beta)$, where β is the slope. Total CO_2 efflux rate was expressed on a per unit sapwood volume rather than surface area basis because total efflux was more highly correlated with the volume-based parameter ($r^2 = 0.61$, $P < 0.01$). The rate of CO_2 efflux as a function of stem temperature was described by Equation 1 (Ryan 1990):

$$R_T = R_0(\exp(T \ln(Q_{10})/10)), \quad (1)$$

where R_T is the total CO_2 efflux rate at stem temperature T, and R_0 is the rate at a stem temperature of 0 °C. Equation 1 was used to calculate CO_2 efflux at 10, 15, 20 and 25 °C for each stem. By calculating CO_2 efflux rates at these defined temperatures, we were able to calculate means for each treatment for data collected at disparate temperatures.

To determine the integrated effect of any temperature-dependent difference in respiratory CO_2 efflux rate over actual growth temperatures in the field, total respiration for the month of September was estimated. Total respiration (mmol CO_2 kg^{-1} h^{-1}) was calculated from Equation 1 using mean Q_{10}, respiration rate at 0 °C (R_0), and mean hourly predicted stem surface temperatures for each treatment. Mean hourly stem temperatures (y) were predicted from measurements of mean hourly air temperatures (x) for the month of September by a linear relationship derived from data collected on the sampling dates: $y = 0.66x + 4.22$ ($r^2 = 0.63$, $P < 0.01$).

Construction respiration

Estimates of wood (xylem) construction cost were determined from stems of 3-year-old trees harvested from the experiment chambers in July 1993, from which the bark, cambium and phloem had been removed. Oven-dry samples were ground to pass a 60-mesh screen with a Wiley Mill. The construction cost of wood in g glucose g^{-1} of tissue dry weight was calculated according to Williams et al. (1987) from the ash-free heat of combustion, ash content and total organic nitrogen, based on the relationship:

$$\text{Construction cost} = \left((0.0698\,\Delta H_c - 0.065)(1 - A) + \frac{k\text{N}}{14.0067}\,\frac{180.15}{24}\right)\frac{1}{E_G}, \quad (2)$$

where ΔH_c is the ash-free heat of combustion in KJ g_{DW}^{-1}, A is the ash content in g g_{DW}^{-1}, N is the organic nitrogen content in g g_{DW}^{-1}, k is the oxidation state of the nitrogen substrate (+5, assuming the substrate was nitrate N), and E_G is the growth efficiency of conversion (assumed to be 0.89). Ash-free heat of combustion was determined by combusting two 15–20 mg pellets of sample in a microbomb calorimeter (Gentry Instruments, Aiken, NC) and taking the average of the determinations. If the two determinations differed by more than 2%, a third sample was combusted. Organic nitrogen content was measured with a CHN analyzer (Model NA 1500, Carlo Erba, Milan, Italy), and ash content was obtained by combusting ground samples in a muffle furnace at 500 °C for 4 h.

Construction cost estimates are based on the energy contained in chemical bonds of the tissue combusted. When expressed in units of glucose required for synthesis of an equal unit of dry weight, these estimates include both carbon incorporated structurally into the tissue and that respired during construction (Nobel et al. 1992). Construction respiration in mol CO_2 kg_{DW}^{-1} was calculated from construction cost in g glucose g^{-1} tissue by converting to units of CO_2 and subtracting the carbon fraction of the tissue (Nobel et al. 1992). Percent carbon in the tissue was measured by CHN analysis. Relative growth rates for the month of September were calculated as the slope of the natural log of average height multiplied by diameter, plotted over time from August through October. Construction respiration multiplied by relative growth rate (day^{-1}) was calculated as an estimate of construction respiration per day for September. Mean daily construction respiration was converted to a volume basis using the combined mean wood density (measured by volume displacement) of 318 kg m^{-3} (this value did not differ between treatments). Mean daily maintenance

respiration rate for September was taken to be the difference between the total and construction components.

Statistical analysis

Mean Q_{10} values were compared by analysis of covariance using the natural log of mean respiration rates (for 9 and 12 trees per treatment) at each of four selected stem temperatures and temperature as a covariable. The Q_{10} values were calculated from the slope of this relationship as for individual trees. Log transformed mean total respiration rates were compared using single degree of freedom contrasts. Differences in construction cost, construction respiration, ash-free heat of combustion, and percent ash, carbon and nitrogen were determined using the general linear models procedure of SAS (SAS Institute Inc., Cary, NC).

Results

Total respiration

The slope of the response of the natural log of CO_2 efflux rate to stem temperature, and therefore Q_{10}, differed significantly between treatments (ambient = 1.67, elevated = 2.20, $P < 0.05$) (Figure 1). At stem temperatures above the 15 °C isokinetic point for respiration (the intersection of the temperature relationships), trees grown in the elevated CO_2 treatment had higher rates of CO_2 efflux than trees grown in ambient CO_2, and the difference between treatments became significant at temperatures above 21 °C ($P < 0.05$).

For a representative cool day in September (Figure 2) when temperature ranged between 10 and 20 °C (e.g., September 10), modeled rates of integrated total daily respiration did not differ between treatments, but at higher temperatures on September 20 (between 20 and 25 °C), the differences in Q_{10} values resulted in as much as a 40% maximum difference in total respiration between the elevated and ambient CO_2 treatments. When integrated over the month of September, total respiration was 15% greater in the elevated CO_2 treatment than in the ambient CO_2 treatment, because stem temperatures remained above the 15 °C isokinetic point for respiration for most of the month.

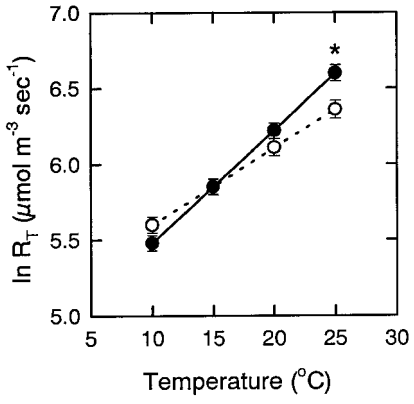

Figure 1. Natural log of total respiration rate (R_T) plotted as a function of temperature for ambient (○) and ambient + 350 ppm CO_2 (●) treatments. Each symbol represents the mean (± 1 SE) of n = 12 (ambient) and n = 9 (ambient + 350 ppm CO_2) trees per treatment. Treatment mean R_T was calculated for selected temperatures within the range of the data by substituting treatment mean Q_{10} values and respiration rate at 0 °C, R_0, into Equation 1 (see text). Significant differences in mean R_T between treatments at $P < 0.01$ are indicated by an asterisk.

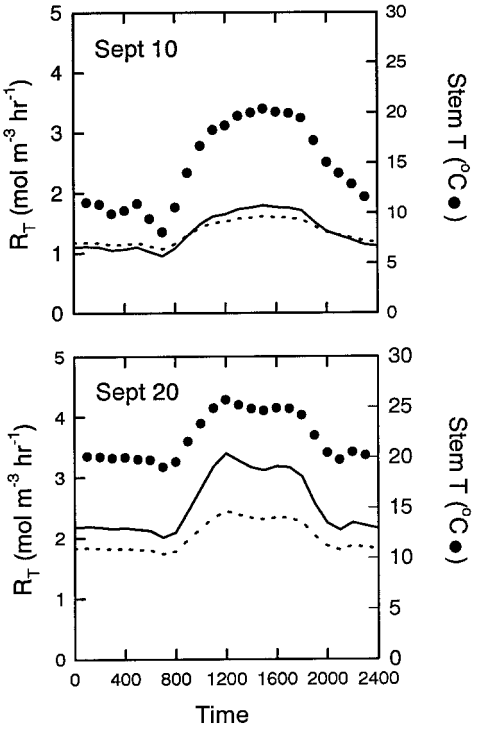

Figure 2. Predicted total respiration rate and stem temperature (●) on September 10 and September 20, 1994, for ambient (dashed line) and ambient + 350 ppm CO_2 (solid line) treatments.

Construction respiration

Construction respiration was calculated using percent carbon and construction cost. There was no difference in construction cost or its components between treatments (Figures 3A–D). Although statistically significant, the 1% difference in percent carbon between treatments did not significantly affect construction respiration (Figures 3E and 3F). Because relative growth rate was also the same in both treatments ($P = 0.46$), construction respiration (mol CO_2 m^{-3} day^{-1}) did not differ between treatments. The higher rates of stem respiration for trees grown in elevated atmospheric CO_2 than in ambient atmospheric CO_2 can therefore be attributed to an increase in maintenance respiration (Table 1).

Discussion

The response of stem respiration rate to temperature differed between trees in the elevated and ambient CO_2 treatments. A possible explanation for this difference is an interaction between transpiration rate (or sap flow rate) and CO_2 efflux rate.

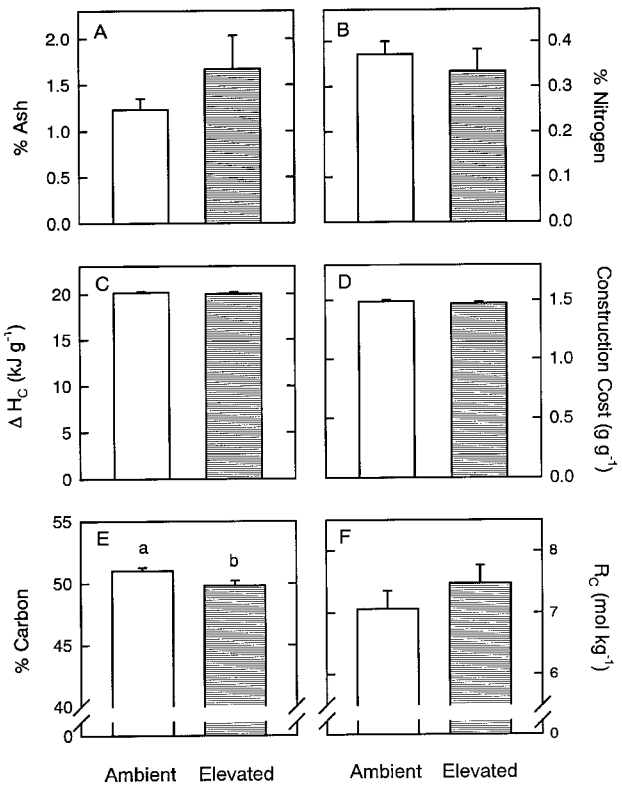

Figure 3. Effects of growth in ambient (about 350 ppm, open bars) and elevated (ambient + 350 ppm, cross-hatched bars) CO_2 on percent ash (A), percent organic nitrogen (B), ash-free heat of combustion (ΔH_c) (C), construction cost in g glucose g^{-1} (D), percent carbon (E), and construction respiration (R_c) in mol CO_2 kg^{-1} (F). Each bar is a mean (± 1 SE) (n = 8 for ambient, n = 6 for elevated), and significant treatment differences at $P < 0.05$ are indicated by lower case letters.

Table 1. Mean daily total, construction and maintenance respiration rates (mol CO_2 m^{-3} day^{-1}) for September 1994. Total respiration was estimated from treatment mean Q_{10}, R_0 and predicted hourly stem temperatures (see Equation 1). Construction respiration was calculated from construction cost, carbon content and relative growth rate. Maintenance respiration was estimated as the difference between total and construction respiration. Numbers in parentheses are percent of total respiration.

Respiration rate	Ambient CO_2	Elevated CO_2
Total	40.45	46.75
Construction	10.68 (21)	10.23 (17)
Maintenance	29.77 (79)	36.52 (83)

It has been proposed that a portion of the CO_2 respired from sapwood enters the transpiration stream and is carried upward in the xylem sap rather than diffusing outward through the bark (Negisi 1972, 1979, Sprugel 1990). This would result in greater underestimates of CO_2 efflux for the trees grown in ambient CO_2 because they are presumably transpiring at a faster rate than the more water conservative trees grown in elevated CO_2 (Eamus 1991). Consequently, a lower slope in the relationship between temperature and CO_2 efflux would result in a lower derived Q_{10}. Prior experimental manipulation of sap flow by cutting stems (thereby stopping sap flow) and bagging foliage (thereby decreasing vapor pressure deficit and thus decreasing sap flow) of similar sized ponderosa pine trees growing under natural conditions revealed no interaction between xylem sap flow rate and CO_2 efflux rate (Carey, unpublished data). The supposition that transpiration did not cause the observed differences in Q_{10} is also supported by the absence of hysteresis in plots of temperature versus CO_2 efflux rate and by the lack of any correlation between CO_2 efflux rate and relative humidity (data not shown). Although Q_{10} for respiration varies seasonally in plants (Paembonan et al. 1991, Criddle et al. 1994), the relative growth rates of trees in the two treatments were identical, and therefore, differences in total respiration cannot be attributed to differences in seasonality of growth.

In contrast to the results of leaf-level studies where elevated CO_2 decreased leaf respiration (Wullschleger et al. 1992*a*, Bunce 1992, Ziska and Bunce 1994, Azcón-Bieto et al. 1994), our results indicate that growth in elevated CO_2 concentrations resulted in increased stem respiration. When partitioned into construction and maintenance components, the greater total respiration in the elevated CO_2 treatment was attributable to an increase in maintenance respiration. It was not possible to make destructive harvests to determine the carbohydrate and nitrogen status of stems at the time of measurement; however, maintenance respiration rates are often correlated with tissue N content (Ryan 1991, Wullschleger et al. 1992*b*), and the nitrogen content of the xylem used to calculate construction cost was the same for both treatments (Figure 3B). Therefore, greater maintenance respiration in response to elevated CO_2 could be a result of a higher cost of maintaining proportionally greater protein concentrations in the cambium or phloem. This is consistent with the observation that whole-stem samples (xylem, cambium and phloem combined) from trees in the elevated CO_2 treatment had higher total N contents than trees in the ambient CO_2 treatment (Ball, unpublished data).

Neither construction cost nor construction respiration differed between treatments. Although published estimates of construction respiration vary based on the technique used, our estimates (0.16–0.17 g C respired g^{-1} C in tissue) were in the normal range for construction coefficients (Amthor 1994). However, they were lower than those computed for wood of *Quercus alba* L., *Pinus contorta* Dougl. ex Loud. and *Pinus radiata* D. Don (Wullschleger et al. 1995). This is partly because estimates of construction respiration obtained from chemical analysis are generally lower than those obtained by gas exchange techniques (Sprugel et al. 1995). Consequently, our estimates of maintenance respiration may be greater than expected from gas exchange techniques; however, they are within the range of those reported for saplings (Wullschleger et al. 1995). We were unable to make comparisons between methods because the climate is favorable for year-round growth of evergreen conifers, and therefore, we could not estimate maintenance respiration in the absence of growth by gas exchange techniques.

In leaves, construction costs and construction respiration either decrease (Wullschleger and Norby 1992, Wullschleger et al. 1992*b*, Griffin et al. 1993, Ziska and Bunce 1993) or remain the same (Thomas et al. 1993) in response to increasing atmospheric CO_2 concentration. Decreases in leaf construction costs and construction respiration may be associated with increasing carbon to nitrogen ratios and increased nitrogen use efficiency in plants grown in elevated CO_2 (Norby et al. 1986, Wullschleger et al. 1994). In addition to increased nitrogen concentrations, starch accumulation has also been shown to increase maintenance respiration rates in cotton leaves grown in elevated CO_2 (Thomas et al. 1993). In xylem, nitrogen content is low, and compositional changes caused by shifts in allocation to starch storage (lower carbon content) versus conducting tissue (higher carbon content) are difficult to detect without anatomical analyses. Similar to two previous studies (Rogers et al. 1983, Donaldson et al. 1987) and contrary to another (Conroy et al. 1990), we found no significant difference in wood density between treatments. However, carbon content differed by 1% between treatments, which may reflect differences in wood composition.

The pattern of greater total respiration rates at higher temperatures is similar to observations by Ziska and Bunce (1993, 1994), who found that decreases in maintenance respiration in response to elevated CO_2 were only significant at temperatures below 20 °C. Increases in respiration rate with increasing temperature are dependent on metabolic activity and may reflect temperature optima of other processes (e.g., photosynthesis). The finding of greater nitrogen concentrations in stems in the elevated CO_2 treatment combined with the observation of no difference in relative growth rate suggest that protein concentrations are likely to be higher in the phloem of stems in the elevated CO_2 treatment. These proteins, if present, presumably have important metabolic functions. Although our results for ponderosa pine saplings cannot be used to predict whole-stand responses to enriched CO_2 atmospheres, they do suggest that potential increases in the maintenance component of stem respiration should be considered when studying plant responses to climate change.

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