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Stem respiration of ponderosa pines grown in contrasting climates: implications for global climate change

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Abstract We examined the effects of climate and allocation patterns on stem respiration in ponderosa pine (*Pinus ponderosa*) growing on identical substrate in the cool, moist Sierra Nevada mountains and the warm, dry, Great Basin Desert. These environments are representative of current climatic conditions and those predicted to accompany a doubling of atmospheric CO_2, respectively, throughout the range of many western north American conifers. A previous study found that trees growing in the desert allocate proportionally more biomass to sapwood and less to leaf area than montane trees. We tested the hypothesis that respiration rates of sapwood are lower in desert trees than in montane trees due to reduced stem maintenance respiration (physiological acclimation) or reduced construction cost of stem tissue (structural acclimation). Maintenance respiration per unit sapwood volume at 15°C did not differ between populations (desert: 6.39 ± 1.14 SE μmol m^{-3} s^{-1}, montane: 6.54 ± 1.13 SE μmol m^{-3} s^{-1}, $P = 0.71$) and declined with increasing stem diameter ($P = 0.001$). The temperature coefficient of respiration (Q_{10}) varied seasonally within both environments ($P = 0.05$). Construction cost of stem sapwood was the same in both environments (desert: 1.46 ± 0.009 SE g glucose g^{-1} sapwood, montane: 1.48 ± 0.009 SE glucose g^{-1} sapwood, $P = 0.14$). Annual construction respiration calculated from construction cost, percent carbon and relative growth rate was greater in montane populations due to higher growth rates. These data provide no evidence of respiratory acclimation by desert trees. Estimated yearly stem maintenance respiration was greater in large desert trees than in large montane trees because of higher temperatures in the desert and because of increased allocation of biomass to sapwood. By analogy, these data suggest that under predicted increases in temperature and aridity, potential increases in aboveground carbon gain due to enhanced photosynthetic rates may be partially offset by increases in maintenance respiration in large trees growing in CO_2-enriched atmospheres.

Key words Climate change · Construction cost · Maintenance respiration · *Pinus ponderosa* · Stem respiration

Introduction

Future forest productivity and the potential role that forests will play in mitigating the impacts of increased atmospheric CO_2 concentrations (Post et al. 1990; Idso 1991; Cannell et al. 1996) will depend not only on the response of trees to CO_2-enriched atmospheres, but also on their response to changes in climate. A sustained temperature increase of as little as 1°C can alter the growth and regenerative capacity of trees (Cannell et al. 1996). Forest composition and productivity throughout North America may therefore change with the increase in mean annual temperature of 2–6°C expected as a result of doubling atmospheric CO_2 (Mitchell et al. 1990). No changes in mean annual precipitation are anticipated (Mitchell et al. 1990), and accordingly, atmospheric vapor pressure deficit is expected to rise.

A unique field laboratory for exploring these effects of increased temperature and vapor pressure deficit on the carbon budget of western conifers is found in the Great Basin Region of Nevada and on the adjacent eastern slope of the Sierra Nevada. In this area, ponderosa pine, *Pinus ponderosa* (and Jeffrey pine, *P. jef-*

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Table 1 Climate data for sites used in *Pinus ponderosa* stem respiration study. Values given are annual means

Site	Elevation (m)	Precipitation (mm year^{-1})	Temperature (°C)
Desert			
Peavine Mt.	1700	250	10.5
Desert Res. Inst.	1500	225	11.4
Montane			
Alpine County	2100	550	7.6
Virginia Mts.	2030	330	8.4

freyi) can be found growing both in the desert and on nearby Sierran slopes on patches of soil derived from hydrothermally altered bedrock (Billings 1950; DeLucia et al. 1988). The sites are very similar across environments with respect to nutrients, organic matter and other soil properties (*e.g.*, C, N, P, pH, Ca^{2+}, HCO_3–; Schlesinger et al. 1989). On patches of this substrate, low elevation desert *P. ponderosa* populations grow amidst Great Basin shrubs and high elevation montane populations grow among other Sierran conifers. The difference in mean annual temperature (3°C) between the Great Basin desert and Sierran montane populations (Table 1) is within the range of temperature change predicted to accompany a doubling of atmospheric CO_2 within the next century (Mitchell et al. 1990). Therefore, the desert populations are growing under conditions representative of the increase in temperature and vapor pressure deficit that Sierran conifers are expected to experience throughout much of their range under future atmospheric conditions.

In this system, Callaway et al. (1994) demonstrated that for a tree of a given height or diameter, desert trees, grown under warmer temperatures and higher atmospheric vapor pressure deficits, allocate proportionally more of their aboveground biomass to sapwood and less to leaf area than their montane counterparts. Similar shifts in biomass allocation towards stems and branches in Scots pine (*Pinus sylvestris)* under warm, dry conditions have been found by Mencuccini and Grace (1995) and Berninger et al. (1995). These changes may function to provide more stable water potentials within tree stems in environments with different transpiration rates (Mencuccini and Grace 1995). However, the increase in non-photosynthetic biomass at the expense of photosynthetic biomass may decrease growth by increasing the carbon investment in constructing and maintaining proportionally more heterotrophic tissue (Poorter et al. 1990).

Stem CO_2 efflux is positively correlated with sapwood volume (Ryan 1990; Sprugel 1990) and with temperature (Penning de Vries 1975; Amthor 1994). Therefore, unless they have acclimated to growing in a high temperature environment, desert trees must expend more carbon than montane trees to maintain proportionally more sapwood. Based on the acclimation to temperature observed for other plants (Rook 1969; Strain 1969; Chatterton et al. 1970; Pearcy 1977; Criddle et al. 1994), we expected that respiration rates of desert trees would be lower at a given stem temperature. We measured maintenance respiration by gas-exchange when trees were dormant and construction cost of stem sapwood by calorimetry and chemical analysis to test the hypothesis that respiration rate of sapwood is lower in desert populations than in montane populations of ponderosa pine due to physiological or structural acclimation.

Materials and methods

Site description

Four locations representing two sites per environment (desert and montane) were chosen based on climatic characteristics. Desert sites were located at the Desert Research Institute and at the base of Peavine Mountain in Reno, Nevada. Montane sites were in the Virginia Foothills 30 km southwest of Reno, and in Alpine County, California, 6 km from Markleeville. Elevation and climate data for the sites are summarized in Table 1. Between 15 and 17 trees were selected at each site for gas-exchange measurements. Sample trees encompassed the range of diameters at breast height (DBH) present for mature trees with at least 0.5 m of branch-free bole between the ground and first branch (desert: 12–57 cm DBH; montane: 10–77 cm DBH). Sapwood cores were obtained from the four cardinal points of an additional 13 trees per site ranging in size from 9 to 56 cm DBH and 5 to 44 cm DBH, for desert and montane environments, respectively. Trees with crown damage or infection with dwarf mistletoe (*Arceuthobium campylopodum*, present only at the Alpine County site) were excluded from the sample population.

Gas-exchange measurements

Stem CO_2 efflux was measured in July and September 1993. The July mid-growing-season measurements represent maintenance and construction respiration combined. September measurements made when growth was slow or had ceased (Kramer and Kozlowski 1979; Ryan 1990) represent primarily maintenance respiration. Martin et al. (1994) observed an interaction between stem CO_2 efflux and transpiration which may lead to spurious estimates of stem respiration. Concurrent studies examining the potential interaction between rates of stem sapflow and CO_2 efflux in *Pinus ponderosa* revealed no interaction in this species (E. Carey, unpublished work). However, measurements were made in early morning, before sapflow started (determined by the use of sapflow probes), to ensure no interference.

Carbon dioxide efflux was measured from Plexiglas cuvettes attached to stems at DBH or below the lowest live branch. Cuvettes were sealed to the stems of trees (scrubbed and treated with 4% $CuSO_4$ several days prior to measurements to remove organisms on outer bark) with non-hardening sealant (Permagum) and were positioned on the northwest side of stems to minimize heat load in early morning. Gas-exchange measurements were made with an infrared gas analyzer operating as an open system (LI-6200, LI-COR, Lincoln, Neb., or ADC LCA-2, Analytical Development Co. Ltd., Hoddesdon, England). Air flow through the cuvettes was controlled by external pumps operating at rates between 0.6 and 1 l min^{-1}, and air inside of the cuvettes was well mixed with internal fans. Stem sapwood temperature was measured with a copper-constantan thermocouple inserted approximately 5 mm beneath the bark.

We relied on the wide diurnal variation in temperature to estimate the temperature-dependence of CO_2 efflux at each site. The increase in respiration rate accompanying a 10°C increase in temperature (Q_{10}) was calculated from the slope (β) of the relationship between the natural log of CO_2 efflux and temperature following the relationship $Q_{10} = \exp^{10\beta}$ (Ryan 1990). Continuous diurnal measurements of CO_2 efflux were made on one tree per site. The sample size for calculating Q_{10} was increased by measuring CO_2 efflux near the minimum and maximum daily stem temperature on between 12 and 18 trees per environment and calculating a slope from these data.

Comparisons of CO_2 efflux from trees at different sites and measured at different temperatures were facilitated by using the site mean Q_{10} to calculate respiration rates at several discrete temperatures. The rate of CO_2 efflux as a function of stem temperature was described by the relationship: $R_t = R_0[\exp(t \times \ln(Q_{10})/10)]$, 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 (Ryan 1990). This equation was used to calculate CO_2 efflux at 10, 15, 20, 25 and 30°C for each tree to verify that small (non-significant) variation in Q_{10} did not result in between environment differences in calculated CO_2 efflux rates, within the range of growing season temperatures.

Upon completion of the September measurements wood cores were taken from the area covered by the cuvette and stained with bromcresol green to delineate the heartwood-sapwood boundary. Sapwood volume was calculated as the difference between the total volume and heartwood volume of a sector with radius equal to 1/2 DBH. Correlation coefficients between temperature-adjusted CO_2 efflux rates and DBH, stem surface area, stem volume, and sapwood volume were determined using Proc Corr of SAS (Version 6.10, SAS Institute 1993). To compare CO_2 efflux among trees of various sizes, rates were expressed per unit sapwood volume as this was the variable with which it was most closely correlated (e.g., R_{20} for desert: July $r = 0.55$, September $r = 0.46$; montane: July $r = 0.56$, September $r = 0.73$; in all cases $P < 0.01$).

Construction cost of stem sapwood

Construction cost was determined for cores of sapwood (xylem) collected from the four cardinal points of another set of 13 trees per site. Oven-dry samples were ground to pass a 60-mesh screen with a Wiley Mill. Construction cost in grams of glucose per gram dry weight (DW) was calculated according to Williams et al. (1987), from the ash-free heat of combustion and the fraction of ash and organic nitrogen in the sample, based on the relationship: Construction cost = $[(0.0698\Delta H_c - 0.065)(1\text{-}A) + (k\mathrm{N}/14.0067)(180.15/24)](1/E_G)$; 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 nitrogen substrate (+5, assuming 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 samples in a microbomb calorimeter (Gentry Instruments, Aiken, N.C.). Ash content was determined by burning samples in a muffle furnace for 5 hours at 500°C, and total organic nitrogen content was determined by CHN analysis (Model NA1500, Carlo Erba, Milan, Italy). The coefficient of construction respiration (an estimate of grams carbon respired per gram carbon in tissue) was calculated from construction cost (grams glucose required to produce 1 g dry weight) by converting from units of glucose to units of CO_2 and subtracting the carbon content of the tissue (Nobel et al. 1992).

Statistical analysis

Initial comparisons between variables were made by both site and environment. No significant between site, within environment differences were found, therefore, only between environment comparisons are reported. Within environment by date comparisons of mean Q_{10} were done with t-tests (Proc Ttest). CO_2 efflux rates at various stem temperatures as a function of sapwood volume (R_t μmol m^{-3} s^{-1}) were natural log (ln) transformed to meet assumptions of normality, and covariance analysis (Proc GLM) with DBH as a covariable was used to test for between site differences in respiration rate as a function of stem diameter. Comparisons of mean percent ash, nitrogen content, heat of combustion, construction cost, and the growth coefficient of respiration were made using analyses of variance (Proc GLM). All data fit assumptions for models used. Analyses were performed using Statistical Analysis Software, Version 6.10 (SAS Institute 1993).

Estimates of yearly stem respiratory budgets

To compare stem respiratory carbon budgets for trees with different patterns of aboveground biomass allocation and in different environments, yearly estimates of maintenance (R_M), construction (R_C), and total respiration (R_T) were calculated. Annual maintenance respiration was estimated using a relationship derived by Ågren and Axelsson (1980) where maintenance respiration is a function of temperature and annual temperature is estimated by varying diurnal temperature sinusoidally about a sinusoidally-varying daily mean temperature: $R_y = R_0\ e^{\alpha \mathrm{Tm}}\ I_0(\alpha T_{ad}) I_0(\alpha T_{ay})$. We solved for R_y [annual maintenance respiration rate (μmol m^{-3} $year^{-1}$)] using R_0 [respiration at 0°C (μmol m^{-3} $year^{-1}$)] from our gas-exchange data, α (natural log of the Q_{10} of R_M measured in September), and site-specific temperature data (H. Klieforth, personal communication). T_{ad} is constant daily temperature amplitude, T_{ay} is yearly temperature amplitude, and I_0 is a modified Bessel function of zeroth order (Ågren and Axelsson 1980).

The coefficient of construction respiration calculated above from construction cost and percent carbon, was adjusted to an annual basis by multiplying by the relative growth rate (R. Callaway, unpublished work) for the 5 years prior to measurements. Maintenance respiration was expressed in the same units as construction respiration by converting to grams of carbon respired and multiplying by density (0.459 g cm^{-3}) and percent carbon (see Results) of sapwood. Total respiration is the sum of the maintenance and construction components. Sapwood volumes of desert and montane trees were obtained from allometric equations given in Callaway et al. (1994). Whole tree estimates of total sapwood respiration, R_M, and R_C (g C g^{-1} C $year^{-1}$) were multiplied by total carbon mass in sapwood to compare wood respiration of desert trees with montane trees of equal heights and diameters.

Results

Gas exchange

The Q_{10} of respiration was the same for trees from both environments during both sampling periods. However, Q_{10} differed seasonally within environments between sampling periods (Fig. 1), with higher values in July corresponding with the period of greater metabolic activity. Stem CO_2 efflux rate (apparent stem respiration rate) per unit sapwood volume decreased significantly with DBH at all stem temperatures during both sampling periods ($P < 0.001$). The data plotted in Fig. 2 are for stem CO_2 efflux rate at 15°C (R_{15}) and are representative of the data at other stem temperatures. The DBH × Environment term in the model was not significant ($P > 0.20$). Therefore, respiration at any given stem temperature (R_t) did not differ between environments during either sample period, and the ln-transformed mean respiration rate $\ln(R_t)$ per unit sapwood volume was the same for both desert and montane trees. The difference between July and September measurements yielded no difference in construction respiration between populations ($P = 0.63$). For ease of compari-

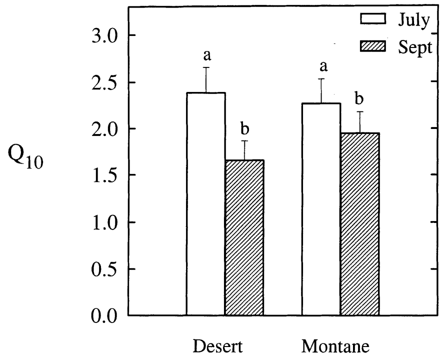

Fig. 1 Mean Q_{10} of respiration for *Pinus ponderosa* growing in desert and montane environments at two times of the year: July and September 1993. Each *bar* is the mean ± 1 SE for 12–18 trees per environment per sample date. Q_{10} did not differ between environments but differed within environment between sampling dates ($P < 0.05$). *Lower case letters* indicate seasonal differences

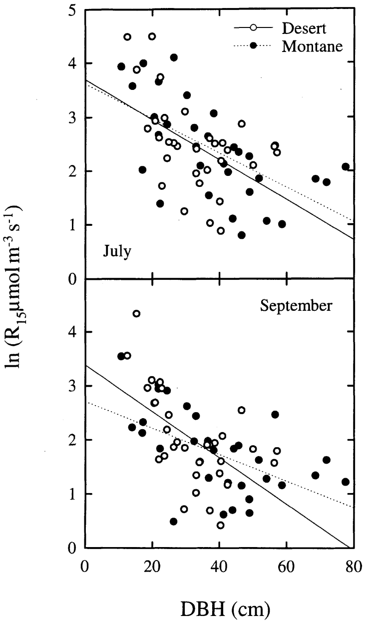

Fig. 2 Natural log (ln) of stem CO_2 efflux rate at 15°C (R_{15}) plotted as a function of diameter at breast height (DBH) for trees of desert (*open circles, solid lines*) and montane (*closed circles, dashed lines*) populations of *Pinus ponderosa* during July and September 1993. [*July*, desert: ln(CO_2 efflux) = 3.70–0.037(DBH), $r = 0.49$; montane: ln(CO_2 efflux) = 3.62–0.032(DBH), $r = 0.61$. *September,* desert: ln(CO_2 efflux) = 3.38–0.042(DBH), $r = 0.57$; montane: ln(CO_2 efflux) = 2.80–0.026(DBH), $r = 0.57$]. The decrease in ln(R_{15}) with DBH is significant in all cases ($P < 0.001$). Between environment differences were not significant, therefore the ln-transformed mean respiration rate per unit sapwood volume was the same for desert and montane trees within the range of the data

son with other studies, we expressed rates of stem CO_2 efflux at 15°C on a per unit sapwood mass and volume basis. The least-squares mean CO_2 efflux rates at 15°C for desert and montane sites respectively were: 10.69 ± 1.15 SE μmol m^{-3} s^{-1} and 11.87 ± 1.14 SE μmol m^{-3} s^{-1} (0.023 ηmol g^{-1} s^{-1} and 0.026 ηmol g^{-1} s^{-1}) in July; and 6.39 ± 1.14 SE μmol m^{-3} s^{-1} and 6.54 ± 1.13 SE μmol m^{-3} s^{-1} (0.014 ηmol g^{-1} s^{-1} and 0.014 ηmol g^{-1} s^{-1}) in September.

Construction cost of stem sapwood

Percent ash, heat of combustion (ΔH_C), and percent carbon of wood were the same for desert and montane trees (Table 2). Nitrogen content differed between environments, however, nitrogen content of xylem was so low (< 0.1%) that it did not result in significant differences in calculated construction cost or construction respiration (R_C). Construction respiration (g C g_{DW}^{-1}) was 0.153 ± 0.005 SE and 0.157 ± 0.005 SE for desert and montane trees, respectively.

Estimates of yearly stem respiratory budgets

Higher temperatures in the desert environment accounted for a 15% difference in annual maintenance respiration per unit sapwood (kg C m^{-3} $year^{-1}$) between populations. The annual rate was multiplied by the total amount of sapwood per tree to make comparisons of whole-tree sapwood respiration between desert and montane trees of equal diameters. At a diameter of 35 cm measured 1.4 m aboveground, the average desert tree is 30% shorter, but has only 9% less sapwood mass than the average montane tree of the same diameter (Callaway et al. 1994; Fig. 3). In desert trees, growth respiration was lower (47% for a tree of 35 cm DBH) than in montane trees due to a slower relative growth rate, and it contributed less to total respiration (19% vs. 34% on average for trees 5–60 cm DBH). In contrast, maintenance respiration per tree was greater (6% for a tree of 35 cm DBH) in the desert environment, accounting for 81% of total stem respiration on average. Total respiration was greater in montane trees as a result of more growth respiration. When expressed in proportion to leaf mass, to provide a measure of potential for carbon gain, differences in stem maintenance and total respiration between desert and montane trees were more pronounced. For example, in the 35 cm DBH trees in Fig. 3, maintenance respiration per unit leaf mass was

Table 2 Mean (± 1 SE) percent ash, percent organic nitrogen, ash free heat of combustion (ΔH_C), construction cost, percent carbon and construction respiration (R_C) of *Pinus ponderosa* sapwood from desert and montane environments (desert: $n = 25$, montane: $n = 26$). Significant treatment differences at $P < 0.05$ are indicated by *lower case letters*

	Desert	Montane
Ash (%)	0.44 (± 0.0001)	0.42 (± 0.0002)
Nitrogen (%)	0.09 (± 0.00004)[a]	0.07 (± 0.00002)[b]
ΔH_C (kJ g^{-1})	19.58 (± 0.12)	19.83 (± 0.11)
Construction Cost (g g^{-1})	1.46 (± 0.009)	1.48 (± 0.009)
Carbon (%)	50.54 (± 0.15)	50.91 (± 0.15)
R_C (mol kg^{-1})	6.40 (± 0.22)	6.72 (± 0.19)

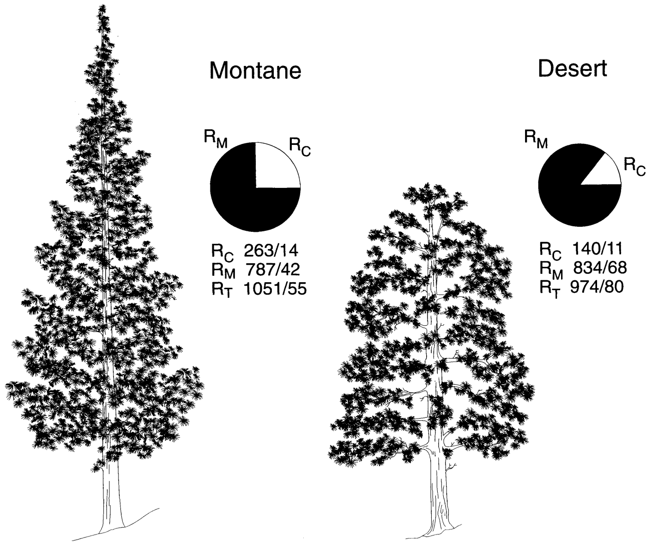

Fig. 3 Comparative morphology and stem respiration for ponderosa pine trees of equal diameter (35 cm) growing on the same substrate in desert and montane environments. Representations of trees are to scale. Values are for annual total (R_T), maintenance (R_M) and construction (R_C) respiration of stems on a whole-tree basis (g C year^{-1}) (*left-hand value*) and per unit leaf mass (g C g^{-1} C leaf mass year^{-1}) (*right-hand value*). Pie charts illustrate the contribution of R_C and R_M to R_T in each environment

64% greater and total respiration per unit leaf mass was 44% greater in the desert environment. The opposite was seen with respect to growth respiration (22% greater in montane trees) with the difference becoming smaller due to more leaf mass in the montane trees.

Modeling respiration over a range of stem diameters showed that in young trees (< 10 cm DBH), construction respiration was the larger component in montane trees and equal to maintenance in desert trees. In larger trees the relative contribution of maintenance to total respiration increased and accounted for approximately 75% and 85% of total respiration for montane and desert trees (> 25 cm DBH), respectively. These proportions remained relatively constant with increasing stem diameter.

Discussion

We found no differences in the temperature dependence of stem respiration (Q_{10}) nor in rates of maintenance stem CO_2 efflux per unit sapwood volume between desert and montane populations of ponderosa pine. Construction cost of stem sapwood was also similar for trees grown in desert and montane environments. Therefore our prediction that desert trees will minimize carbon loss through acclimation of respiration rate or through lowering the construction cost of structural tissue is not supported. Acclimation of respiration rate is a potentially important component of plant response to climate change (Ryan 1991; Larigauderie and Körner 1995), and although we did not see evidence for acclimation to temperature in stems, it may be an important component at the leaf level.

Although the Q_{10} of stem respiration did not differ between populations, it varied seasonally within both populations. In woody plants, Q_{10} is commonly highest in winter and decreases throughout the growing season as temperature increases (Hagihara and Hozumi 1991; Paembonan et al. 1991; Criddle et al. 1994). Higher temperatures during the September than the July sampling period may explain the low Q_{10} that we found late in the growing season. Seasonal fluctuations in Q_{10} influence carbon balance, calculations of R_M (because R_M is a function of temperature), and can also influence calculations of R_C (if calculated by subtraction, method 1 below).

Respiration can be partitioned into maintenance and construction components by a number of methods. For trees these include: (1) measuring total respiration during the growing season and subtracting R_M measured when trees are dormant to solve for R_C; (2) regressing total respiration (as measured by gas-exchange) against growth and biomass parameters and determining percent contribution to R_M and R_C from regression coefficients (Sprugel 1990); and (3) measuring R_M by gas exchange when trees are dormant and solving for R_C by biochemical pathway analysis as we did in this study. All three techniques rely on measurements of Q_{10} to make comparisons among gas-exchange rates measured at various stem temperatures. A potential problem with the first method is that when the same value for Q_{10} is used for all sample periods, estimates of R_C may be biased since Q_{10} varies seasonally. An additional complication with this method is the changing volume of wood during the course of the growing season. Computing growth respiration by chemical analysis and relative growth rate yields more conservative and more consistent estimates than those obtained by gas exchange (see Sprugel et al. 1995). For example, our estimates of construction respiration are within the range of values (0.15–0.65 g C g_{DW}^{-1}) derived from biochemical pathway analysis (Chung and Barnes 1977; Amthor 1994). When robust estimates of relative growth rate are available, this method provides a means to integrate over time intervals from months to years, however it is not effective for estimating instantaneous rates of growth and maintenance respiration. Our estimates of the relative contributions of R_M and R_C are comparable to those obtained by multiple regression by Sprugel (1990) for mature trees and by Wullschleger et al. (1995) for young trees.

Maintenance respiration per unit sapwood volume decreased with increasing tree diameter in both desert and montane trees (Fig. 2). Yoda (1967) observed a similar decline in average respiration rate per unit mass as a function of stem diameter for total tree and woody organ respiration in a Thailand rainforest. This decrease in CO_2 efflux rate per unit mass or volume with age (DBH) could be attributable to fewer live cells per unit volume, decreasing Q_{10}, or increased resistance to diffusion of CO_2 across a greater sapwood width in larger trees. Percent nitrogen in sapwood did not decrease in a size-dependent manner in our study (data not shown); however, a more detailed investigation of either nitrogen distribution or live cell volume would be appropriate to identify whether structural (live cells), rather than physiological (Q_{10}) or physical (diffusion) processes are responsible. Most models of forest stand development calculate net production as the carbon remaining after subtracting R_M from gross productivity (Ryan et al. 1995). Failure to include a size-dependent decline in stem R_M per unit sapwood volume with age (as we found in this study) in models of forest growth could result in overestimation of respiration in older stands. This omission could potentially explain why estimates of low net primary productivity in mature forest ecosystems have been attributed to increasing woody tissue respiration (Kira and Shidei 1967).

The contribution of maintenance respiration to total respiration increases with tree size, and differences in biomass allocation between desert and montane-grown trees become more pronounced with increasing stem diameter. Large (> 50 cm DBH) desert trees are 30% shorter than montane trees of an equal diameter, but have 30% more sapwood mass and 30% less leaf mass (Callaway et al. 1994). As a result, the greatest between-environment difference in total respiration was for large trees (because there was no difference in the relationship of CO_2 efflux per unit volume as a function of stem diameter between desert and montane populations). The leaf:sapwood area ratio is greater in montane trees (Callaway et al. 1994). Stem respiration per unit leaf mass was much greater in desert trees suggesting that if photosynthetic carbon gain is the same in both environments then a larger proportion of carbon fixed is respired by stems in the desert environment. If we make the additional assumption that crown carbon accumulation does not increase with tree size in the desert and that root:shoot ratio remains constant, increased stem respiration in large desert trees could ultimately decrease growth. This prediction is currently under investigation.

When in situ rates of bole respiration are combined with climate-driven allometric relationships our data show that stem maintenance respiration accounts for a greater proportion of the aboveground carbon budgets in large desert trees as compared to large montane trees. By analogy, these data suggest that under predicted increases in temperature and aridity, potential increases in aboveground carbon gain due to enhanced photosynthetic rates are likely to be offset by increases in maintenance respiration in large trees growing in CO_2-enriched atmospheres. Further increases in woody tissue respiration can also be predicted based on increased branch volume (Callaway et al. 1994; Berninger et al. 1995) in warm, dry climates and higher rates of respiration from branches than boles (Sprugel 1990; Ryan et al. 1996). Respiration can account for between 50 and 80% of gross primary productivity in forests (Kira and Shidei 1967; Ryan 1991; Paembonan et al. 1992) and stem respiration alone can account for between 13 and 42% of carbon fixed (Waring and Schlesinger 1985; Ryan and Waring 1992). Maintenance respiration is the largest component of stem respiration in these populations, thus increases in this component in response to increased temperature could have a significant effect on forest carbon flux. Climate-driven allocation shifts from autotrophic to heterotrophic tissue may further reduce the potential role of forests as net carbon sinks in the future as photosynthetic gains are offset by decreased leaf area and increased respiration.

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References

Ågren GI, Axelsson B (1980) Population respiration: a theoretical approach. Ecol Model 11:39–54

Amthor JS (1994) Plant respiratory responses to the environment and their effects on the carbon balance. In: Wilkinson RE (ed) Plant-environmental interactions. Marcel Dekker, New York, pp 501–554

Berninger F, Mencuccini M, Nikinmaa E, Grace J, Hari P (1995) Evaporative demand determines branchiness of Scots pine. Oecologia 102:164–168

Billings WD (1950) Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecology 31:62–74

Callaway RM, DeLucia EH, Schlesinger WH (1994) Biomass allocation of montane and desert Ponderosa pine: an analog for response to climate change. Ecology 75:1474–1481

Cannell MGR, Cruz RVO, Galinski W, Cramer WP (1996) In: Watson RT, Zinyowera MC, Moss RH (eds) Climate change 1995 – Impacts, adaptations, and mitigation of climate change: scientific-technical analyses. Contribution of working group II to the second assessment report of the intergovernmental panel on climate change. Cambridge University Press, New York, pp 95–129

Chatterton NJ, McKell CM, Strain BR (1970) Intraspecific differences in temperature-induced respiratory acclimation of desert saltbush. Ecology 51:545–547

Chung HH, Barnes RL (1977) Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. Can J For Res 7:106–111

Criddle RS, Hopkin MS, McArthur ED, Hansen LD (1994) Plant distribution and the temperature coefficient of metabolism. Plant Cell Environ 17:233–243

DeLucia EH, Schlesinger WH, Billings WD (1988) Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. Ecology 69:303–311

Hagihara A, Hozumi K (1991) Respiration. In: Raghavendra AS (ed) Physiology of trees. Wiley, New York, pp 88–110

Idso SB (1991) The aerial fertilization effect of CO_2 and its implications for global carbon cycling and maximum greenhouse warming. Bull Am Meteorol Soc 72:962–965

Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jpn J Ecol 17:70–87

Kramer PJ, Kozlowski TT (1979) Physiology of woody plants. Academic Press, New York

Larigauderie A, Körner C (1995) Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. Ann Bot 76:245–252

Martin TA, Teskey RO, Dougherty PM (1994) Movement of respiratory CO_2 in stems of loblolly pine (*Pinus taeda* L.) seedlings. Tree Physiol 14:481–495

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol 15:1–10

Mitchell JFB, Manabe S, Tokioka T, Meleshko V (1990) Equilibrium climate change. In: Houghton JT, Jenkins GJ, Ephraums JJ (eds) Climate change: the IPCC scientific assessment. Cambridge University Press, New York, pp 131–172

Nobel PS, Alm DM, Cavelier J (1992) Growth-respiration, maintenance-respiration and structural-carbon costs for roots of three desert succulents. Funct Ecol 6:79–85

Paembonan SA, Hagihara A, Hozumi K (1991) Long-term measurement of CO_2 release from the aboveground parts of hinoki forest tree in relation to air temperature. Tree Physiol 8:399–405

Paembonan SA, Hagihara A, Hozumi K (1992) Long-term respiration in relation to growth and maintenance processes of the aboveground parts of a hinoki forest tree. Tree Physiol 10:101–110

Pearcy RW (1977) Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.). Plant Physiol 59:795–799

Penning de Vries FWT (1975) The cost of maintenance processes in plant cells. Ann Bot 39:77–92

Poorter H, Remkes C, Lambers H (1990) Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiol 94:621–627

Post WM, Peng TH, Emanuel WR, King AW, Dale VH, DeAngelis DL (1990) The global carbon cycle. Am Sci 78:310–326

Rook DA (1969) The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. NZJ Bot. 7:43–55

Ryan MG (1990) Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Can J For Res 20:48–57

Ryan MG (1991) Effects of climate change on plant respiration. Ecol Appl 1:157–167

Ryan MG, Waring RH (1992) Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100–2108

Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholtz HL, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 10:133–140

Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie, RE (1996) Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol 16:333–343

Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use efficiency of woody plants on contrasting soils in the Western Great Basin, Nevada. Ecology 70:105–113

Sprugel DG (1990) Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. Trees 4:88–98

Sprugel DG, Ryan MG, Brooks JR, Vogt KA, Martin TA (1995) Respiration from the organ level to the stand. In: Smith WK, Hinckley TM (eds) Resource physiology of conifers: acquisition, allocation and utilization. Academic Press, New York, pp 255–299

Strain BR (1969) Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. Ecology 50:511–513

Waring RH, Schlesinger WH (1985) Forest ecosystems concepts and management. Academic Press, New York

Williams K, Percival F, Merino J, Mooney HA (1987) Estimation of tissue construction cost from heat of combustion and organic nitrogen content. Plant Cell Environ 16:539–546

Wullschleger SD, Norby RJ, Hanson PJ (1995) Growth and maintenance respiration in stems of *Quercus alba* after four years of CO_2 enrichment. Physiol Plant 93:47–54

Yoda K (1967) Comparative ecological studies on three main types of forest vegetation in Thailand. III. Community respiration. Nat Life SE Asia 5:84–148