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Woody tissue maintenance respiration of four conifers in contrasting climates

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Abstract We estimate maintenance respiration for boles of four temperate conifers (ponderosa pine, western hemlock, red pine, and slash pine) from CO_2 efflux measurements in autumn, when construction respiration is low or negligible. Maintenance respiration of stems was linearly related to sapwood volume for all species; at 10°C, respiration per unit sapwood volume ranged from 4.8 to 8.3 μmol CO_2 m^{-3} s^{-1}. For all sites combined, respiration increased exponentially with temperature (Q_{10} = 1.7, r^2 = 0.78). We estimate that maintenance respiration of aboveground woody tissues of these conifers consumes 52–162 g C m^{-2} y^{-1}, or 5–13% of net daytime carbon assimilation annually. The fraction of annual net daytime carbon fixation used for stem maintenance respiration increased linearly with the average annual temperature of the site.

Key words Maintenance respiration · Woody-tissue respiration · Carbon budgets · Temperature response

Introduction

In forests, autotrophic respiration has been reported to use 38–75% of gross photosynthesis (Edwards et al. 1980), with the remainder available for dry matter production. Environment may influence productivity by affecting the balance between photosynthesis and respiration, because these processes respond differently to temperature and water (Larcher 1983; Fitter and Hay 1987). However, despite the importance of respiration in forest carbon budgets, no study has demonstrated that environment can alter the annual carbon use efficiency (assimilation–respiration/assimilation) in forests. Indeed, a recent review of carbon balance studies (Ryan et al. 1994b) found no clear effect of climate on carbon use efficiency. To understand how carbon use efficiency might vary in forest stands will require complete carbon budgets in many stands. Producing these annual carbon budgets efficiently will require robust methods for extrapolating chamber measurements.

Woody-tissue respiration is an important component of the carbon balance of forests because of the fraction of assimilation used (e.g., Whitmore 1984) and because the amount of wood increases dramatically with stand development. For example, woody-tissue respiration has been estimated to use 11–33% of the annual total of net daytime carbon assimilation for a variety of conifer stands (Ryan et al. 1994b). The few studies that estimate annual budgets for woody-tissue respiration use a variety of approaches (e.g., surface area, Woodwell and Botkin 1970; biomass, Yoda 1967; sapwood volume and wood production, Ryan and Waring 1992), and no consensus exists about the correct approach. However, Ryan (1990) showed that because stem growth or the amount of living cells did not vary directly with surface area or biomass, these variables could produce incorrect stand-level estimates of woody-tissue respiration.

Partitioning respiration into the functional components of construction and maintenance is useful for modelling carbon balance (Amthor 1989), because maintenance respiration (R_m) varies with environment and protein content of tissue, while construction respiration varies primarily with the amount of growth (Ryan 1991). Estimating maintenance respiration correctly is critical, because most models calculate net production as the carbon remaining after subtracting R_m (e.g., BIOMASS,

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McMurtrie et al. 1990; Hybrid, Friend et al. 1993; Forest-BGC, Running and Coughlan 1988).

In this paper, we estimate maintenance respiration for stems of four conifers, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], red pine (*P. resinosa* Ait.), and slash pine (*P. elliottii* var. *elliottii* Engelm.), growing in contrasting climates. Our objectives are to determine (1) if a relationship developed elsewhere (sapwood volume, Ryan 1990; Sprugel 1990; Wullschleger et al. 1994) can be used to estimate stem R_m for these different species, (2) if rates for R_m and the response of respiration to temperature differ among species, and (3) if the fraction of assimilation used for R_m of woody tissue varies with the climate of a site. We accomplish objectives 1 and 2 by developing site-specific equations to estimate maintenance respiration from sapwood volume and temperature. Objective 3 is accomplished by estimating the annual flux of carbon from R_m of woody tissues in pure even-aged stands, and comparing this flux to assimilation estimated with models.

Method

Study sites

The study was conducted in pine plantations in Florida and Wisconsin, a pine forest in Montana, and a mixed western hemlock and Douglas fir forest in Oregon. These forests represent conifers growing in very different climates: short growing season, wet summer (Wisconsin) or dry summer (Montana); long growing season, wet summer (Florida) or dry summer (Oregon). At each site, stands were selected to represent the "stem exclusion" stage of stand development (Oliver 1981), characterized by a recently closed canopy, full use of resources, intense competition among individuals, and a lack of light that prevents younger stems from being established. Therefore, the developmental age of the stands was similar among the sites, even though the chronological ages differed. Site, climate, and stand characteristics are summarized in Tables 1 and 2.

The red pine plantation was established in 1960 and is located 10 km north-west of Boulder Junction, Wisconsin (46°10′N, 89°40′W). Soil at the red pine site is classified as an Entic Haplorthod and developed on glacial outwash. The soil is often frozen to 50 cm between December and April despite a continuous snow pack. The red pine stand has no significant biomass in understory plants. Further description of the site can be found in Gower et al. (1993).

The slash pine plantation was planted in 1965 and is located 20 km north-east of Gainesville, Florida (29°44′N, 82°9′W). The soil is sandy and low in organic matter and nutrients and has a high water table. The predominant soil type is an Ultic Haplaquod. The slash pine stand has a substantial understory of palmetto (*Serenoa repens* Bartram) and galberry [*Ilex glabra* (L.) A. Gray]. Further description of the site and results from other studies conducted at the same location can be found in Cropper and Gholz (1991, 1993) and Gholz et al. (1991).

The ponderosa pine forest was regenerated from natural seed after a harvest in 1940 and is located at the University of Montana's Lubrecht Experimental Forest, 50 km north-east of Missoula, Montana (46°51′N, 113°29′W). Ponderosa pine made up >95% of the basal area of the plots. The soil developed on glacial till, is very shallow and rocky, and is classified as either a Dystric Eutrochrept or a Typic Eutroboralf (Nimlos 1986). There is negligible biomass in the understory, and further description of the site can be found in Gower et al. (1993).

The mixed western hemlock and Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] forest was regenerated from natural seed after a harvest in 1952. The site is located about 20 km east of Scio, Oregon (45°45′N, 122°35′W) at 800 m in elevation. Soils were derived from sandstones and volcanic basalts. The forest has virtually no understory vegetation. The site was part of a productivity transect used for other investigations (Runyon et al.

Table 1 Site and climate of conifer sites

Species	Location	Elevation (m)	Slope (%)	Air temperature (°C) Average January	Average July	Precipitation (mm)	Incident photosynthetically active radiation (MJ m^{-2} y^{-1})
Red pine	Wisconsin	500	0–5	−8.3	16.7	804	2281
Ponderosa pine	Montana	1250	0–10	−10.4	19.5	337	2807
Western hemlock, Douglas fir	Oregon	800	12	4.8	19.6	1180	2259
Slash pine	Florida	40	0	12.9	24.7	1320	2878

Table 2 Stand characteristics of conifer sites

Species	Location	Age in 1991 (year)	Basal area (m^2 ha^{-1})	Average diameter (cm)	Average height (m)	Leaf area Index [a]	Trees per ha	Above-ground woody biomass (Mg ha^{-1})	Sapwood volume (m^3 ha^{-1})
Red pine	Wisconsin	31	42.4	15.5	17	6.2	2106	65.5	283
Ponderosa pine	Montana	51	28.5	17.2	13.5	2.7	1152	52.6	189
Western hemlock, Douglas-fir	Oregon	39	43 [b] 24 [c]	29.1 [b] 38.7 [c]	30	8.7	870	393	770
Slash pine	Florida	24 [d]	26.1	17.3	15.5	2.2	1196	119	225

[a] Projected area of needles
[b] Western hemlock
[c] Douglas fir
[d] Age in 1989 when biomass and sapwood volume measured

1994). Western hemlock represented 64% of the basal area of the stand.

Respiration measurements

We estimated maintenance respiration for woody tissues by measuring CO_2 efflux from stems during the autumn, when growth and cell expansion had slowed or ceased. The method for measuring CO_2 efflux was similar to that described in Ryan (1990). We attached 10×25 cm aluminum plates to the bark with putty after removing loose bark and attached a plexiglass mixing chamber to the plate with a neoprene seal. Plates were located on the north side of the tree at 1.4 m above the ground. The chamber had a volume of 300 ml and was stirred continuously with a fan.

CO_2 efflux was measured with an open system (ADC LCA3, Analytical Development Company, Ltd., Hoddesdon, England) attached to a sampling manifold controlled by a datalogger (Campbell CR21X, Campbell Scientific, Logan, Utah, USA). Reference air entered a large 50-l mixing chamber and was continuously distributed to a maximum of eight stem chambers and to the reference loop of the gas analyzer. Air flow to and from the stem chambers was measured continuously with a turbine rotameter (McMillan Company, Copperas Cove, Texas, USA) and molar flow computed with corrections for temperature and atmospheric pressure. The manifold diverted each chamber's exhaust to the infrared gas analyzer approximately once every hour for 5–7 min; CO_2 concentration from the last minute was averaged, and the remaining data discarded. Sapwood temperature in the vicinity of the chamber was measured with a copper-constantan thermocouple inserted 1 cm into the sapwood.

At each site, we measured six to eight trees that represented the range in stem diameter at the site; stem diameter for trees measured was 12.8–23.6 cm for red pine, 11.9–32.7 cm for ponderosa pine, 13.4–40.6 cm for western hemlock, and 12.0–24.5 cm for slash pine. CO_2 efflux from each stem was monitored continuously for 36–72 h. After sampling, we used increment cores to measure sapwood and heartwood thickness. Because the CO_2 flux chamber did not completely surround the bole, we had to estimate the amount of sapwood that contributed CO_2 to the chamber. We estimated this "chamber" sapwood volume by (1) calculating sapwood volume for the bole cylinder defined by the top and bottom of the chamber, and (2) multiplying this volume by the ratio of the surface area covered by the chamber to the surface area of the bole cylinder.

Because CO_2 efflux stabilizes when sapwood temperature is constant (e.g., Fig. 1), we used CO_2 efflux from periods when stem temperature was constant for 3–4 h to estimate a relationship

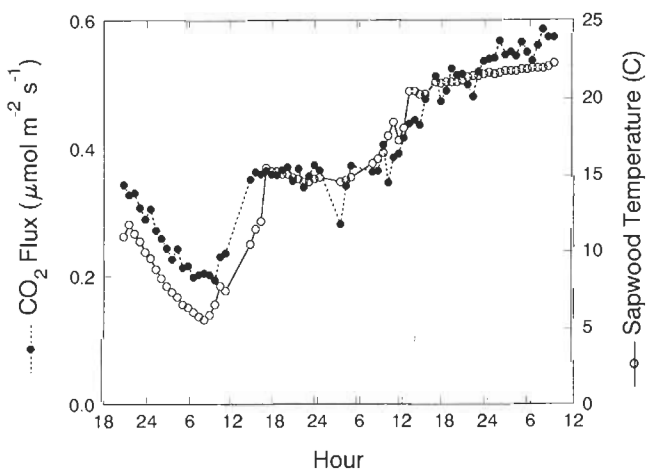

Fig. 1 CO_2 efflux (*solid symbols*) and sapwood temperature (*open symbols*) for a slash pine tree (diameter 22.3 cm). Chamber surface area was 250 cm^2

of CO_2 efflux and sapwood volume. Because the intercepts for a standard linear regression were nonsignificant ($P > 0.21$ for all species), zero-intercept regressions were fit to the two variables and r^2 for the regressions was calculated as $1-[\Sigma(Y_i-\hat{Y}_i)^2/\Sigma(Y_i-\bar{Y})^2]$ (Kvalseth 1985). To compare the relationship between CO_2 efflux and sapwood volume among sites, we adjusted CO_2 efflux to 10°C for each tree at each site, using a site-specific exponential temperature response derived from Eq. 1, below. Slopes for the zero-intercept regressions were compared using a likelihood ratio test (Bates and Watts 1988).

Temperature response

To compare the response of CO_2 efflux to temperature among trees and sites, we normalized the data for each tree by dividing measured flux by that tree's average flux between 9–11°C. Additionally, because wood and cambium have a high resistance to diffusion, sapwood temperatures measured at the time of the flux measurement may not reflect CO_2 evolution outside the bark (e.g., Fig. 1). We corrected for this effect by using sapwood temperatures measured earlier than the current flux measurement (i.e., lagged sapwood temperature). The appropriate lag time for each site was selected from the best fit to a nonlinear regression between normalized flux (N) and lagged sapwood temperature (T, °C) using the equation:

$$\hat{N} = \beta_0 \exp(\beta_1 T) \quad (1)$$

where β_0 and β_1 are regression coefficients. We explored lag periods of 0–7 h. Once the appropriate lag period was selected for each site, normalized flux was fit to lagged sapwood temperature for all sites combined. Regressions were fit using a Levenberg-Marquart algorithm with the NLR procedure of SPSS/PC+ (SPSS 1989); r^2 for the nonlinear regressions was calculated with the formula from Kvalseth (1985) given above for zero-intercept regressions. Differences in temperature response (β_1 in Eq. 1) among sites were tested with a likelihood ratio test (Bates and Watts 1988).

Annual estimates of woody-tissue R_m

We estimated the annual flux of CO_2 from maintenance respiration in woody tissue for each of the four stands sampled for stem respiration. The annual cost of woody-tissue R_m was calculated from stand sapwood volume and daily air temperature with a method similar to that described in Ryan and Waring 1992.

For the pine stands, sapwood volume was estimated from tree basal area using a site-specific allometric equation; sapwood volume was calculated for all of the trees in three 25×25 m plots and summed to give an areal estimate. For the red pine and ponderosa pine stands, the allometric equation for sapwood volume was given in Gower et al. (1993). For slash pine, >95% of the wood volume was sapwood, so sapwood volume was estimated as total volume using an allometric equation that estimated biomass from tree basal area (Gholz and Fisher 1982); biomass was converted to volume using measured specific gravity of wood (0.53 g cm^{-3}). For the Oregon western hemlock and Douglas fir stand, sapwood volume was calculated from sapwood basal area measured on twenty 50-m^2 plots, using a mean tree approach and generalized allometric equations given in Gholz et al. (1979). For the tree of average basal area, sapwood volume was estimated as the difference between total volume and volume estimated by subtracting mean sapwood basal area from mean total basal area. For all sites, branches were assumed to be 100% sapwood for all four conifer species. Branch biomass ranged from 5% of total biomass for the slash pine stand to 15% of the total biomass for the western hemlock and Douglas-fir stand.

Maintenance respiration was estimated daily from sapwood volume, daily mean air temperature, and a Q_{10} temperature-response function (Eq. 1) using either site-specific values for Q_{10},

Q_{10} equal to 2, or Q_{10} derived from data from all sites combined. Maintenance respiration per unit sapwood volume is described in this study and the coefficients were derived for each site. The coefficient for western hemlock was used for both western hemlock and Douglas-fir trees at the Oregon site. We assumed the respiration rate for branch sapwood was the same as for bole sapwood, which may underestimate branch respiration (Sprugel 1990). Ryan (1990) showed that the average of daily mean sapwood temperature was within 1.5°C of daily mean air temperature for a closed lodgepole pine forest. Therefore, we assumed daily sapwood temperature equaled daily air temperature. We corrected the daily estimates of respiration for bias caused by daily temperature fluctuations using an equation given in Ågren and Axelsson (1980). Daily mean temperature was measured on site at all the stands, except for the western hemlock and Douglas fir stand, where the weather station was located 5 km to the southwest of the site.

Annual estimates of net daytime carbon assimilation

We estimated the annual total of net daytime carbon assimilation for the red pine, ponderosa pine, and western hemlock and Douglas fir stands with a forest ecosystem simulation model (Forest-BGC, Running and Coughlan 1988). For the slash pine stand, we estimated the annual total of net daytime carbon assimilation with the site-specific SPM model (Cropper and Gholz 1993). To estimate assimilation, Forest-BGC requires site-specific structural values (e.g., leaf mass, snowpack, soil water content), model parameters (e.g., specific leaf area, soil water capacity, foliage N content, canopy light extinction), and daily weather data (maximum and minimum temperatures, relative humidity, total irradiance, precipitation). The complete list of coefficients is described in Running and Coughlan (1988); we obtained these characteristics and parameters as part of a larger study to compare the carbon budgets of these four conifer stands (S.T. Gower et al., unpublished work). The carbon balance simulations of Forest-BGC have been validated by Korol et al. (1991) and McLeod and Running (1988). Weather data for the Forest-BGC and SPM model runs was obtained at or near the sites. The Forest-BGC model was run with the respiration coefficients set to 0 to output net daytime assimilation.

The SPM model requires structural values (new and old foliage, stem, branches, coarse roots, fine roots in litter layer, fine roots in mineral soil, dead fine roots, soil organic carbon) and hourly air temperature and solar radiation. Precipitation and humidity effects were not modelled because (1) in their 2-year study pre-dawn water potentials remained high and relatively constant, (2) midday stomatal closure was not observed, and (3) assimilation was not related to vapor pressure deficit or leaf water potential (Cropper and Gholz 1993). The SPM model was developed specifically for the slash pine site and integrates the results of many studies (e.g., Cropper and Gholz 1991; Gholz et al. 1991).

Results and discussion

Bole respiration

Figure 2 shows the relationship of CO_2 efflux from stems at 10°C and sapwood volume under the chamber. Zero-intercept regressions with sapwood volume were significant for all species and r^2 ranged from 0.74 for western hemlock to 0.88 for red pine. At 10°C, respiration per unit sapwood volume was 8.3, 7.1, 8.0, and 4.8 μmol m^{-3} s^{-1} for slash pine, red pine, ponderosa pine, and western hemlock. CO_2 efflux per unit sapwood volume was statistically lower for western hemlock than for the pines ($P < 0.01$) and statistically lower for red pine than for ponderosa and slash pine ($P = 0.03$).

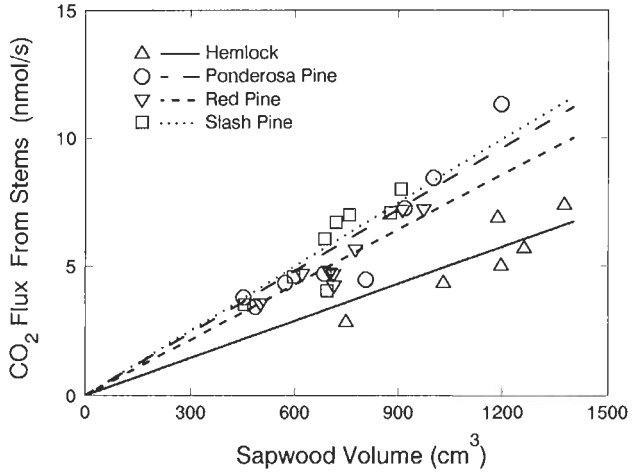

Fig. 2 CO_2 efflux from tree boles at 1.4 m (corrected to 10°C with site-specific equations for temperature response) versus sapwood volume for four conifers. *Points* represent CO_2 efflux for a single tree averaged over 3–4 h while sapwood temperature was constant. *Lines* are zero-intercept regressions; r^2 for the regressions was 0.75 for slash pine, 0.88 for red pine, 0.85 for ponderosa pine, and 0.74 for western hemlock. Sapwood density (g cm^{-3}) was 0.53 for slash pine, 0.35 for red pine, 0.44 for ponderosa pine, and 0.42 for western hemlock

These data show that CO_2 efflux from conifer stems is linearly related to sapwood volume after growth and cell expansion ceased in the autumn. Because the chambers enclosed the same bole surface area on each tree, variability in CO_2 efflux is clearly related to sapwood volume, not surface area. Therefore, sapwood volume is the appropriate scalar for R_m of the boles of these conifers.

Other studies have shown a linear relationship between sapwood volume (or the live cell content of sapwood volume) and R_m of woody tissues (Havranek 1981; Ryan 1990; Sprugel 1990). The rate of R_m for lodgepole pine (*P. contorta* var. *latifolia* Engelm.) was similar to that found for the pines in this study (Ryan 1990). Per unit sapwood volume, young stems of Pacific silver fir [*Abies amabilis* (Dougl.) Forbes] had R_m rates 6 times the value of the pines in this study (Sprugel 1990). However, if the rate is expressed per unit sapwood dry matter, the rate is twice that of the pines in this study (Sprugel et al. 1994).

Rates for R_m appear to be fairly conservative across species of pine: three different species of pine, growing in different climates had similar rates of R_m per unit sapwood. The rate of R_m for western hemlock was about 40% lower than the average rate of the pine, and was also lower than the pines when expressed per unit of sapwood biomass. Published differences in live cell content (Panshin and de Zeeuw 1970) of the sapwood did not explain the differences in R_m among species (suggested by Ryan 1990). For example, Panshin and de Zeeuw (1970) give ray volume in sapwood as 7.0% for red pine, 6.7% for ponderosa pine, and 11.7% for slash pine. However, this study found little difference in the temperature-corrected respiration rates per unit sapwood among the three pine species. In contrast, ray volume of western hemlock

Table 3 Characteristics of response of CO_2 efflux from stems to sapwood temperature. Q_{10} is the increase in respiration for a 10° C increase in temperature; β_1 is a coefficient that defines the exponential response of respiration to temperature (see Eq. 1)

Species	Number of trees	Temperature range	Lag period for best fit (h)	β_1	Q_{10}	r^2
Red pine	8	8–13	0	0.024	1.3	0.16
Ponderosa pine	8	3–12	5	0.032	1.4	0.20
Western hemlock	6	5–12	1	0.059	1.8	0.51
Slash pine	8	6–23	2	0.063	1.9	0.69

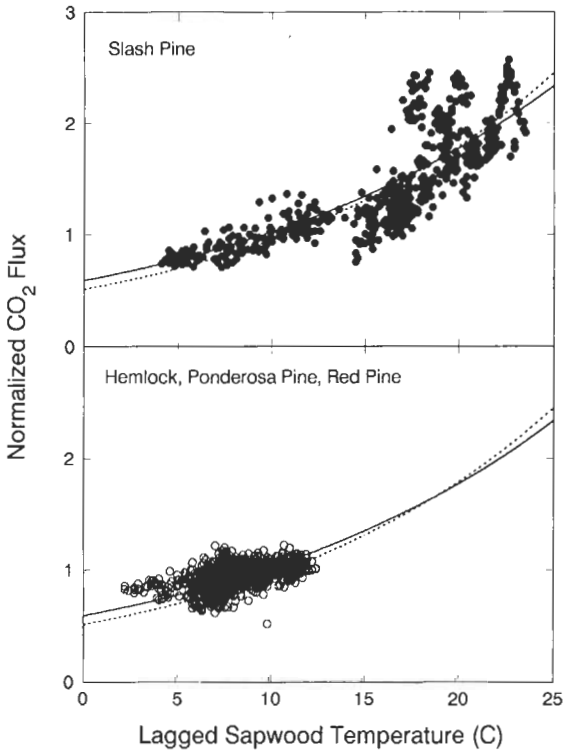

Fig. 3 Normalized CO_2 efflux from tree boles ($n = 30$) versus lagged sapwood temperature, shown separately for slash pine (*top panel*) and for western hemlock, ponderosa pine, and slash pine (*bottom panel*). The *solid line* is fit to all data ($\hat{N} = 0.591 \exp(0.0550T)$, $r^2 = 0.78$), and the dashed line is fit to slash pine only ($\hat{N} = 0.510 \exp(0.0628T)$, $r^2 = 0.69$)

sapwood was given by Panshin and de Zeeuw (1970) as 8% (similar to that of the pines), while the respiration rate per unit of sapwood of western hemlock was significantly lower than that of the pines.

Temperature response

CO_2 flux from stems varied strongly with sapwood temperature (see Fig. 1 for a sample trace), and an exponential model (Eq. 1) significantly fit the data for each site ($P < 0.01$). Temperature lags of 0–5 h provided the best fit to current CO_2 flux from stems (Table 3). Species with thicker bark (ponderosa pine and slash pine) had longer lag periods than species with thin bark (red pine and western hemlock).

The response of CO_2 efflux to lagged sapwood temperature varied by species; the likelihood ratio test showed that Q_{10} (the change in respiration with a 10°C change in temperature) differed for all species pairs ($P < 0.01$), except red pine and ponderosa pine ($P = 0.09$). Two species (ponderosa pine and red pine) showed unusually low values of Q_{10} (Table 3). These low values of Q_{10} may be an artefact either of the small temperature range over which these species were measured or of the poor fits of the data to the model. Overall, a model (Eq. 1) fit to the slash pine data, with a temperature range of 6–23°C, was very similar to the same model fit to data from all sites combined (Fig. 3). For all sites combined, Q_{10} was 1.73 ($r^2 = 0.78$).

Understanding the response of respiration to temperature is important to scaling instantaneous stem CO_2 efflux to an annual basis, because respiration rate is very temperature sensitive. While Q_{10} is often near 2 over physiologically relevant temperatures (Amthor 1989), Q_{10} can vary with season, growth temperature, measurement temperature, or acclimation. Additionally, a Q_{10} relationship may not be valid for plants that grow over a wide range of temperature (Criddle et al. 1991).

For woody tissue in conifers, many studies show Q_{10} is near 2 (Havranek 1981; Linder and Troeng 1981; Ryan 1990; Sprugel 1990), but can occasionally be greater (Ryan 1990). The temperature response of daily or weekly total respiration appears to be linear (Linder and Troeng 1981; Benecke 1985). For the aboveground parts of a whole tree, Paembonan et al. (1991) report Q_{10} decreases linearly with temperature from a high of about 3 during dormancy (air temperature 5°C) to a low of 1.5 in the middle of the growing season (air temperature 20°C). However, because they studied a small tree [*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.], CO_2 was likely primarily from foliage.

A few studies have noted diurnal patterns in stem respiration that were not related to stem temperature. These patterns were attributed to (1) movement of CO_2 by the transpiration stream (Negisi 1975, 1981, 1982; Martin et al. 1994) or (2) diurnal variability in phloem sugar concentration (Edwards and McLaughlin 1978). In this study, variability in lagged sapwood temperature (driven by diurnal patterns in air temperature) accounted for most of the variability in CO_2 efflux for a given tree (Fig. 3). However, at temperatures >15°C, CO_2 efflux from slash pine stems deviated substantially from that estimated from the temperature model (Fig. 3). Normalized flux values substantially greater than the regression line were from three small-diameter trees during a warm, cloudy night. It is possible that the additional CO_2 flux for these trees was derived from CO_2 dissolved in the xy-

lem sap being released by warmer temperatures (cf. Willaman and Brown 1930; Stringer and Kimmerer 1993). Also, transpiration can remove CO_2 in the xylem stream and lower apparent respiration during the day in seedlings (Martin et al. 1994). However, it is unlikely that transpiration is a factor for these larger trees, because a recent experiment with ponderosa pine showed that severing xylem had no effect on bole CO_2 efflux over several days (E. Carey, unpublished work).

Annual estimate of woody tissue R_m

We used the relationships between respiration and sapwood volume and respiration and temperature described in previous sections to estimate daily CO_2 efflux for R_m of the aboveground woody tissues for these stands. The equation used was:

$$(R_m)_d = \frac{R_{10}}{e^{10\beta_1}} \times I_0(\beta_1 A_d) \times 86400 \times e^{\beta_1 T_d} \quad (2)$$

where $(R_m)_d$ is woody tissue maintenance respiration for day d in μmol m^{-3} day^{-1}, T_d is average daily air temperature for day d in degrees C, R_{10} is respiration at 10°C

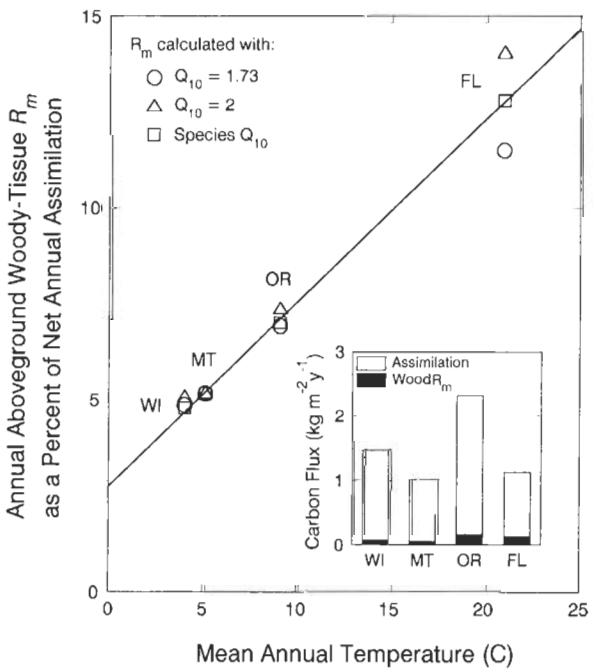

Fig. 4 Estimated annual cost of woody-tissue maintenance respiration for stands of four conifers in widely different climates as a fraction of estimated annual net assimilation (*MT* ponderosa pine, Montana; *WI* red pine, Wisconsin; *OR* western hemlock-Douglas fir, Oregon; *FL* slash pine, Florida). *Line* is fit to data calculated with species-specific values for temperature response ($y = 2.76 + 0.48x$, $r^2 = 0.99$). *Inset* shows annual totals for estimated net assimilation and woody tissue R_m calculated with species-specific values for temperature response. Values (in g C m^{-2} $year^{-1}$) for net assimilation are 1465 for WI, 1010 for MT, 2317 for OR, and 1140 for FL. Values (in g C m^{-2} $year^{-1}$) for woody tissue R_m calculated with species-specific values for temperature response are 70 for WI, 52 for MT, 162 for OR, and 146 for FL

(8.3, 7.1, 8.0, and 4.8 μmol m^{-3} s^{-1} for slash pine, red pine, ponderosa pine, and western hemlock), 86400 is seconds per day, and β_1 is the temperature response coefficient in Eq. 1. In Eq. 2, $I_0(\beta_1 A_d)$ is a function that adjusts for the effect of daily temperature amplitude (A_d) on daily respiration estimates (Ågren and Axelsson 1980). We estimated $(R_m)_d$ using three different temperature responses (β_1): (1) derived from all sites combined ($\beta_1 = 0.0550$), (2) for $Q_{10} = 2$ ($\beta_1 = 0.0693$), and (3) using site-specific values for β_1 (Table 3). Values for $(R_m)_d$ were summed for a year using T_d collected at or near the site.

Using site-specific values of β_1, the annual total of R_m for aboveground woody biomass (from Eq. 2) ranged from 52 g C m^{-2} $year^{-1}$ for the ponderosa pine stand in Montana to 162 g C m^{-2} $year^{-1}$ for the western hemlock and Douglas fir stand in Oregon (Fig. 4). The annual cost for maintenance respiration of woody-tissues is comparable to carbon allocated to wood production in the slash pine stand, but 25% of aboveground wood production in the hemlock stand (S.T. Gower et al., unpublished work). Assuming the carbon content of wood is 50%, annual woody tissue R_m ranged from 1 to 1.4% of sapwood C for western hemlock, red pine and ponderosa pine, but was 2.5% of sapwood C for slash pine.

Surprisingly, use of different values for β_1 had little effect on the estimates of the annual total of woody-tissue respiration, except for the warm slash pine site (Fig. 4). This is because the estimate of the respiration rate at 0°C needed for the exponential response function [$R_{10}/\exp(10\beta_1)$ in Eq. 2] is higher with lower β_1, which compensates for the lower temperature response. For the warm slash pine site, temperature response clearly dominates: estimates of annual R_m for woody tissue (g C m^{-2} y^{-1}) were 131 with $Q_{10} = 1.73$ (all sites combined), 160 with $Q_{10} = 2$, and 146 with $Q_{10} = 1.93$ (Q_{10} for slash pine only).

Model estimates of the annual total of net daytime photosynthesis ranged from 1010 g C m^{-2} $year^{-1}$ for the ponderosa pine stand in Montana to 2320 g C m^{-2} $year^{-1}$ for the western hemlock and Douglas fir stand in Oregon (Fig. 4). The fraction of estimated net assimilation used by aboveground woody tissue R_m was low for all stands (<15%), but appeared to increase linearly with mean annual temperature of the site (Fig. 4). This linear relationship between mean annual air temperature and the fraction of assimilation used for R_m of aboveground woody tissues also describes carbon allocation in a young lodgepole pine stand for another study. For the lodgepole pine stand, Ryan and Waring (1992) report that R_m for aboveground woody tissue was 6% of annual net assimilation for a mean annual temperature of 4°C. However, in a premontane tropical wet forest (average mean air temperature of 24°C), estimated R_m for aboveground woody tissue was only 7–10% of annual net assimilation (Ryan et al. 1994a).

The models developed in this paper relating maintenance respiration to sapwood volume and temperature are difficult to test directly, because carbon fluxes for forests are difficult to determine absolutely. The success of these

models depends on (1) whether the rate for R_m estimated in the autumn applies to the entire year, and (2) whether the temperature response applies throughout the year.

Maintenance respiration cannot be measured directly for woody tissue during the growing season, because CO_2 efflux represent both growth and maintenance processes. However, periodic measurements for chambers can be compared to the sum of CO_2 efflux estimated from sapwood volume in the fall, plus growth respiration estimated from dry matter production and chemical content (e.g., Williams et al. 1987). Ryan (1990) showed that estimates of CO_2 efflux estimated with this method balanced over the course of the growing season for Engelmann spruce (*Picea engelmannii* Parry), but overestimated CO_2 efflux for lodgepole pine. Data from Sprugel (1990) for Pacific silver fir showed a reasonable balance between integrated measured and estimated CO_2 efflux.

It is also difficult to estimate the temperature response of woody-tissue R_m while the stem is growing. However, there is some evidence that temperature response for woody tissue *total* respiration is conservative throughout the year. For example, Linder and Troeng (1981) estimated Q_{10} was about 2 year-round from an intensive series of measurements on a single Scots pine (*Pinus sylvestris* L.) tree. Also, estimates of annual totals of woody-tissue maintenance respiration were fairly insensitive to the assumed temperature response in this study.

Conclusions

This study shows that rates of stem respiration when stem growth was not occurring were strongly related to sapwood volume and that the rates per unit sapwood were fairly conservative across species. CO_2 efflux varied exponentially with sapwood temperature with some differences in Q_{10} among sites. However, annual estimates for maintenance respiration of woody tissue were similar when calculated using either species-specific values of Q_{10}, $Q_{10} = 2$, or $Q_{10} = 1.73$ derived from data from all species combined.

The fraction of net assimilation used for woody-tissue respiration by young conifers growing in very different climates appears to increase linearly with mean annual site temperature. These results suggest that climate can affect carbon allocation to respiration.

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