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Woody-tissue respiration for *Simarouba amara* and *Minquartia guianensis*, two tropical wet forest trees with different growth habits

Abstract We measured CO_2 efflux from stems of two tropical wet forest trees, both found in the canopy, but with very different growth habits. The species were *Simarouba amara*, a fast-growing species associated with gaps in old-growth forest and abundant in secondary forest, and *Minquartia guianensis*, a slow-growing species tolerant of low-light conditions in old-growth forest. Per unit of bole surface, CO_2 efflux averaged 1.24 $\mu mol\, m^{-2} s^{-1}$ for *Simarouba* and 0.83 $\mu mol\, m^{-2} s^{-1}$ for *Minquartia*. CO_2 efflux was highly correlated with annual wood production ($r^2 = 0.65$), but only weakly correlated with stem diameter ($r^2 = 0.22$). We also partitioned the CO_2 efflux into the functional components of construction and maintenance respiration. Construction respiration was estimated from annual stem dry matter production and maintenance respiration by subtracting construction respiration from the instantaneous CO_2 flux. Estimated maintenance respiration was linearly related to sapwood volume (39.6 $\mu mol\, m^{-3} s^{-1}$ at 24.6° C, $r^2 = 0.58$), with no difference in the rate for the two species. Maintenance respiration per unit of sapwood volume for these tropical wet forest trees was roughly twice that of temperate conifers. A model combining construction and maintenance respiration estimated CO_2 very well for these species ($r^2 = 0.85$). For our sample, maintenance respiration was 54% of the total CO_2 efflux for *Simarouba* and 82% for *Minquartia*. For our sample, sapwood volume averaged 23% of stem volume when weighted by tree size, or 40% with no size weighting. Using these fractions, and a published estimate of aboveground dry-matter production, we estimate the annual cost of woody tissue respiration for primary forest at La Selva to be 220 or 350 $g\,C\,m^{-2} year^{-1}$, depending on the assumed sapwood volume. These costs are estimated to be less than 13% of the gross production for the forest.

Key words Woody tissue respiration · Maintenance respiration · Tropical wet forest trees · Carbon balance

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Introduction

In forest ecosystems, autotrophic respiration may constrain productivity (Ryan 1991a) because forests contain much biomass in foliage, woody tissue, and roots. For example, the percentage of gross primary production used for plant respiration may differ for forests growing in different climates or in response to climate change because respiration rates are sensitive to temperature (Waring and Schlesinger 1985). Also, stabilization and subsequent decline of net primary production as stands age may be caused by the increased costs of woody-tissue respiration (Yoda et al. 1965; Whittaker and Woodwell 1967), although this hypothesis has been recently disputed (Ryan and Waring 1992). Rigorous tests of how autotrophic respiration affects forest productivity are rare (Jarvis and Leverenz 1983; Sprugel and Benecke 1991; Ryan and Waring 1992) and limited to temperate forests.

In forest ecosystems in the wet tropics, autotrophic respiration can consume more than 50% of gross primary production (Edwards et al. 1980). Because of the large amount of woody biomass in these ecosystems

and the warm temperatures under which they grow, a large fraction of the autotrophic respiration has been attributed to woody tissues (Müller and Nielson 1965; Yoda 1967; Whitmore 1984). These respiration estimates were developed using stem or branch diameter (Yoda 1967) or surface area (Odum 1970) to scale chamber measurements to the stand. However, direct measurements such as these can be highly variable due to differences in growth rate and proportion of living tissue in the organ being measured (Ryan 1990; Sprugel 1990). Therefore, diameter or surface area may be poor scalars for deriving stand estimates (Ryan 1990).

Recent studies (Ryan 1990; Sprugel 1990) have shown that it is possible to separate respiration in woody tissue into the functional components of construction (respiration used to build dry matter) and maintenance (respiration used to maintain ion gradients, replace enzymes, and repair membranes). The functional model recognizes that the energy from respiration is used for different purposes, even though it comes from the same biochemical pathways. Construction respiration will vary with the amount of tissue built and its chemical composition, while energy used for maintenance varies with temperature and perhaps with nutrition, water, atmospheric CO_2 concentration ($[CO_2]$), and pollutants (Amthor 1989). Using the functional model has furthered our understanding of pollutant effects (Amthor and Cumming 1988), differences in respiration costs between young and old forests (Ryan and Waring 1992), and the response of respiration to atmospheric $[CO_2]$ (Reuveni and Gale 1985; Amthor 1991; Amthor et al. 1992; Wullschleger et al. 1992). To our knowledge, maintenance respiration has never been estimated for woody tissue of trees in the wet tropics.

In practice, construction respiration has been related to dry matter production (Ryan 1990; Sprugel 1990) and its chemical composition (Vertregt and Penning de Vries 1987; Williams et al. 1987), and maintenance respiration to tissue nitrogen content (Ryan 1991a) and (for woody tissue) to sapwood volume (Ryan 1990; Sprugel 1990; Ryan et al. 1995). The use of the functional model of respiration can explain the variability in chamber measurements and the derived respiration rates can be directly incorporated into process-based models of forest growth [e.g., BIOMASS (McMurtrie et al. 1990), HYBRID (Friend et al. 1993), Forest-CENTURY (Sanford et al. 1991)].

To successfully model the productivity of tropical forests and the response to climate change, we need reliable models for respiration of the woody tissue of tropical forest trees. In this study, we measure stem respiration for two very different trees found in the wet tropics. We estimate maintenance respiration by subtracting construction respiration (estimated using stem growth) from measured CO_2 efflux, and determine if maintenance respiration is linearly related to sapwood volume. We also calculate an annual budget for woody-tissue respiration and compare it with other estimates.

Methods

Study area

We conducted our study at the La Selva biological station in Costa Rica (10° 26' N, 83° 59' W). This lowland forest reserve is located at the base of the continental divide on the coastal plain of the Sarapiqui River at an elevation of 50 m. Mean annual rainfall is 3880 mm with a moderately dry season from late January through April (Sanford et al. 1994). Mean monthly temperature varies from 24.7° C in January to 27.1° C in August with a mean annual temperature of 26.2° C. A water balance diagram for the site indicates a considerable excess of precipitation over potential evapotranspiration for every month except for February and March when values are about equal (Herrera 1985). Old growth vegetation at La Selva has been described as premontane tropical wet forest in the Holdridge life-zone system (Hartshorn 1983). A complete description of forest composition and soils is given in McDade et al. (1994).

CO_2 flux measurements

We measured CO_2 efflux from 18 stems of *Simarouba amara* Aubl. (Simaroubaceae), a fast-growing species that requires a high-light environment, and 18 stems of *Minquartia guianensis* Aubl. (Olacaceae), a slow-growing canopy species. Trees were selected from a long-term study of stem growth and tree population dynamics (Clark and Clark 1992), and were located in primary forest on upland sites. We selected trees with a wide variety of diameters (6–66 cm) and growth rates (0–2.1 cm year^{-1}) to help separate maintenance and construction respiration. For our sample, stem diameter and diameter growth averaged 27.0 cm (SD 16.2) and 9.7 mm (SD 5.1) for *Simarouba* and 21.6 cm (SD 15.0) and 1.7 mm (SD 1.7) for *Minquartia*.

CO_2 efflux was measured in October 1991 using an open system infra-red gas analyzer (LCA3, Analytical Development Company), with flow rates through the chamber of 273–342 μmol s^{-1}. We used three different chambers varying in size from 41 to 62 cm^2; chamber volume was less than 100 cm^3. Chambers were constructed of Lexan and a small fan stirred the air inside the chamber. Chambers were sealed to the bark surface with neoprene gasket and attached to the stems with elastic cord over the exact point where diameters were taken for the growth study (1.5–4 m above the ground). Reference air was drawn through a 20-l mixing chamber to maintain a stable reference CO_2 concentration. Flux data were recorded after the difference in $[CO_2]$ between reference and chamber had been stable for 3 min. We found no appreciable variation in CO_2 efflux from different positions around the circumference of the bole or in measurements repeated within 1 h at the same location on the bole. Therefore, we sampled most boles only once.

Estimating construction and maintenance respiration

In temperate forests, maintenance respiration for woody tissues has been estimated by measuring CO_2 efflux after growth ceased in autumn (Ryan 1990; Sprugel 1990; Sprugel and Benecke 1991). This approach could not be used where stem growth continues throughout the year. Therefore, we estimated maintenance respiration by subtracting construction respiration (estimated from stem growth and wood density) from measured CO_2 efflux.

Stem growth had been measured to the nearest millimeter annually (in January or February) for the previous 6–8 years (Clark and
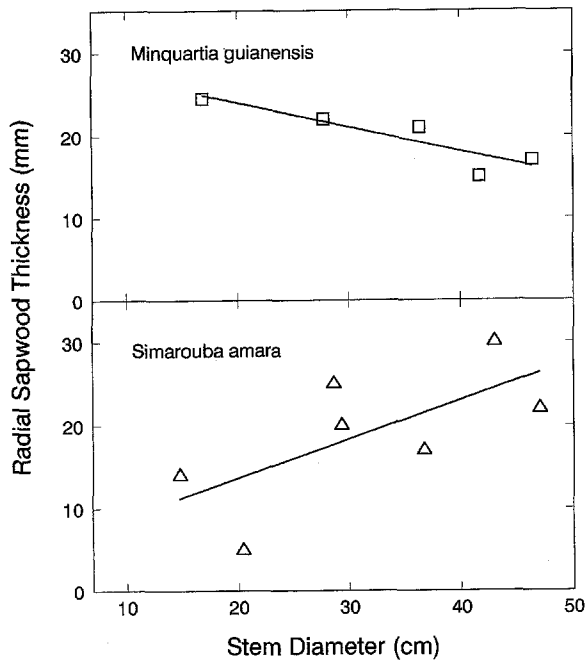
Fig. 1 Relationship between sapwood thickness and diameter for *Minquartia guianensis* and *Simarouba amara*. For *Minquartia*, sapwood thickness (mm) = 29.9 − 0.30 × bole diameter (cm), $r^2 = 0.81$. For *Simarouba*, sapwood thickness (mm) = 4.3 + 0.47 × bole diameter (cm), $r^2 = 0.46$. For the sample of trees where bole CO_2 efflux was measured, estimated sapwood thickness averaged 17 mm (SD 7.6) for *Simarouba* and 23 mm (SD 4.7) for *Minquartia*

Clark 1992), and year-to-year growth was highly correlated for the trees in our sample. We used stem growth for January–February 1991–1992 and calculated the volume of wood that grew under the chamber. Wood volume was converted to ash-free dry weight using ash content (0.7%) and specific gravity (0.36 g cm^{-3} for *Simarouba* and 0.74 g cm^{-3} for *Minquartia*). Ash content and specific gravity were measured for a sample of six increment cores per species on the same samples used for sapwood determination (see below).

To estimate construction respiration, we assumed (1) growth was constant throughout the year, (2) carbon content was 50% of ash-free dry weight (Edwards et al. 1980), and (3) construction cost for wood is 25% of the carbon content of new tissue (Penning de Vries 1975; Sprugel and Benecke 1991). The assumption of constant growth may cause errors in estimates, because bole growth for some tropical wet forest trees can vary seasonally (Hazlett 1987, Breitsprecher and Bethel 1990). For example, Breitsprecher and Bethel (1990) found that five of eight upland species measured at La Selva showed some seasonal pattern in bole production and the seasonal pattern was related to climate. However, Hazlett (1987) showed that bole production in October (the month of our measurements) averaged 7% of annual growth for *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae) and 9% of annual growth for *Goelthalsia meiantha* (D. Sm.) Burret (Tiliaceae). These values are very close to the 8.3% expected if annual growth were evenly distributed across months.

Because flux measurements were taken when stem temperatures were similar (about 25° C), and near the annual average air temperature, we did not correct for temperature. In equation form, construction respiration (R_c, in µmol m^{-2}s^{-1}) was estimated as:

$$R_c = 0.25 \rho V_G \left(\frac{0.5 \mathrm{gC}}{\mathrm{g\ Biomass}} \times \frac{10^6 \mu \mathrm{mole}}{12\ \mathrm{g\ C}} \times \frac{1}{365 \mathrm{days} \times 86400 \mathrm{s\ day}^{-1}} \right)$$ (1)

Table 1 Average total (R_t), construction (R_c) and maintenance (R_m) respiration rates (± SE) per unit of bole surface area for *Minquartia guianensis* and *Simarouba amara*. Stem temperatures averaged 24.6° C

Species	R_t	R_c	R_m
		µmol CO_2 m^{-2}s^{-1}	
Simarouba amara	1.24	0.57	0.66
	(0.11)	(0.07)	(0.08)
Minquartia guianensis	0.83	0.21	0.63
	(0.09)	(0.05)	(0.05)

where ρ is the specific density of new wood (g cm^{-3}) and V_G is the volume of annual wood growth under the chamber (cm^3 m^{-2}).

Because the trees we measured were part of a long-term study, and because we were concerned about the damage coring might cause, we did not extract cores to estimate sapwood thickness. Instead, we removed cores from several trees not in the sample to develop equations to predict sapwood thickness from stem diameter (Fig. 1) and estimate ash content and specific gravity. Sapwood was identified by staining fresh samples with 1% aqueous triphenyl tetrazolium chloride solution. Dehydrogenase in the cytoplasm of living ray cells in the sapwood reacts with the tetrazolium solution to form a red insoluble compound (Feist et al. 1971).

We correlated total CO_2 efflux from stems with stem diameter and annual diameter growth (expressed as g C year^{-1} under the stem chamber). We correlated estimated maintenance respiration with sapwood volume estimated from the regressions in Fig. 1. For all correlations, we tested whether the linear regression slopes differed between species (Steel and Torrie 1980) using the MANOVA procedure in SPSS/PC+ (Norusis 1988).

Response of CO_2 efflux to temperature

We measured two rapidly growing *Simarouba* trees located in the La Selva compound every 4–6 h for 48 h to determine diurnal temperature response. Temperatures during the 48-h period ranged from 21.4 to 28.0° C. Data from the two trees were fitted individually [using nonlinear regression analysis (Norusis 1988)] to the model:

$$\hat{R} = \beta_0 \exp(\beta_1 T)$$ (2)

where $\hat{R}$ is predicted respiration and β_0 and β_1 are regression coefficients. The change in respiration for a 10° C change in temperature (Q_{10}) is $\exp(10\beta_1)$.

Results

Average CO_2 efflux from stems was near 1 µmol m^{-2}s^{-1} for both *Minquartia guianensis* and *Simarouba amara* (Table 1). CO_2 efflux per unit of bole surface area varied from 0.30 to 2.05 µmol m^{-2}s^{-1}; the range of values was nearly as large for an individual species (Fig. 2). Stem diameter at the location of the CO_2 efflux measurements did not explain more than 43% of the variation in CO_2 efflux for either species or both species combined (Fig. 2). Stem diameter was significantly correlated with CO_2 efflux for *Simarouba* ($r = 0.65$, $P < 0.01$), but not for *Minquartia* ($r = 0.20$, $P = 0.42$).

Because of the faster growth rates of *Simarouba*, estimated construction respiration for that species
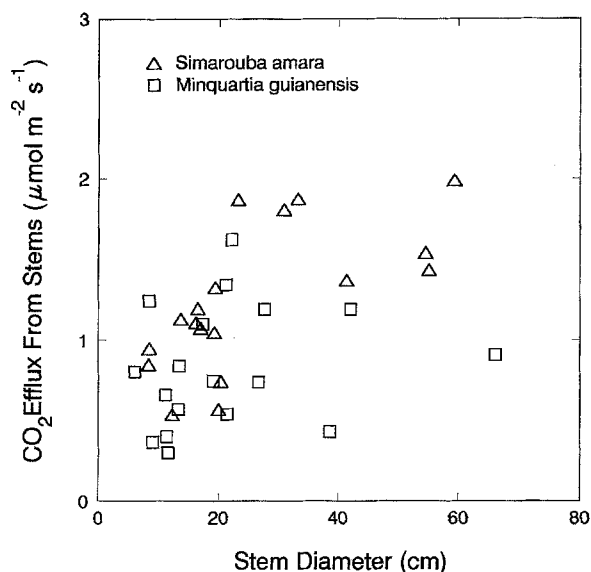
Fig. 2 CO_2 efflux from stems versus stem diameter for *M. guianensis* (*squares*) and *S. amara* (*triangles*). For both species combined, the relationship was significant ($r^2 = 0.22$, $P < 0.01$)

averaged greater than twice that of *Minquartia* (Table 1). Slopes for a linear regression of total CO_2 efflux and stem growth did not differ significantly between species ($P = 0.14$). Stem growth explained 65% of the variation in total CO_2 efflux from stems of both species combined (Fig. 3, $P < 0.01$). If percentages for the individual samples are averaged, construction respiration was 18% of annual CO_2 efflux from stems of *Minquartia* and 46% for *Simarouba*.
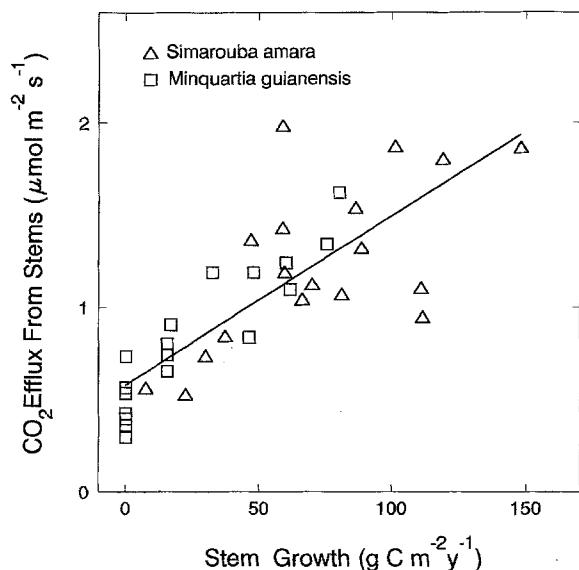

Fig. 3 CO_2 efflux from stems plotted against the carbon content of annual stem growth for *M. guianensis* (*squares*) and *S. amara* (*triangles*) ($r^2 = 0.65$, $P < 0.01$). The regression relationship is CO_2 efflux (in μmol m^{-2} s^{-1}) = 0.586 + 0.00912 × stem growth (in g C m^{-2} bole surface year^{-1})
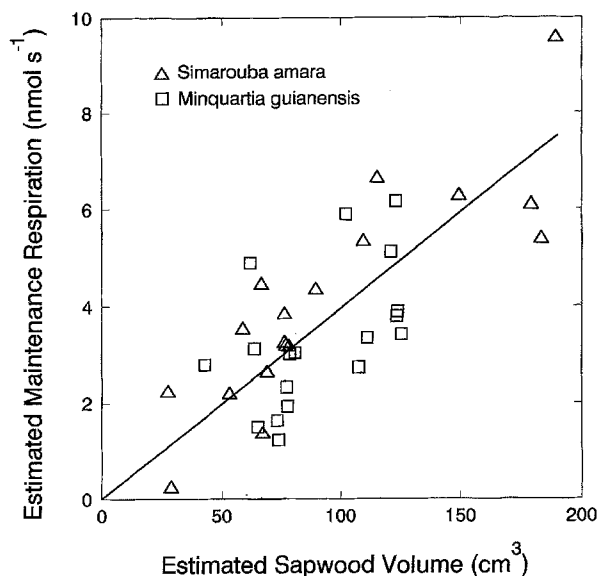

Fig. 4 Estimated maintenance respiration versus estimated sapwood volume for *M. guianensis* (*squares*) and *S. amara* (*triangles*). Maintenance respiration = 39.6 μmol m^{-3} s^{-1}, $r^2 = 0.58$

For our sample, the average of the estimated maintenance respiration rates were statistically identical ($P = 0.71$) for the two species (Table 1). Estimated maintenance respiration rates were linearly related to estimated sapwood volume ($P < 0.01$), and slopes for the linear regression did not differ significantly between species ($P = 0.47$). As the intercept in a linear model was not significantly different from 0 ($P = 0.49$), we estimated the slope from a zero-intercept regression. The relationship between maintenance respiration (R_m in μmol s^{-1}) and estimated sapwood volume (V_s in m^{-3}) for the two species was (Fig. 4):

$$R_m = 39.6 V_s \qquad (3)$$

The r^2 for Eq. 3, calculated as $1 - [\Sigma(Y_i - \hat{Y}_i)^2/\Sigma(Y_i - \overline{Y})^2]$ (Kvalseth 1985), was 0.58. For our samples, with each sample given equal weight, sapwood volume averaged 40% of stem volume. If weighted by tree size (larger trees represent most of the biomass at La Selva), sapwood volume averaged only 23% of stem volume.

CO_2 efflux increased exponentially with temperature for the two *Simarouba* trees measured for temperature response. Nonlinear regression estimated the temperature response coefficient (β_1 in Eq. 1) as 0.077 for tree 1 ($r^2 = 0.95$) and 0.073 for tree 2 ($r^2 = 0.99$). These coefficients correspond to Q_{10} values of 2.2 and 2.1.

Discussion

Flux rates for woody-tissue respiration

Variability in CO_2 efflux per unit stem surface was high for our samples (seven-fold for the two species), and flux was only weakly related to stem diameter. These
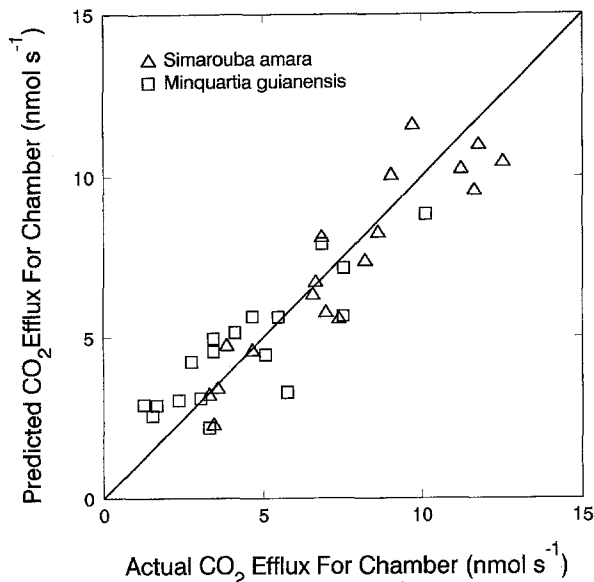
Fig. 5 CO_2 efflux for the measurement chambers predicted using Eqs. 1 and 3 versus actual CO_2 efflux. Predicted versus observed are compared with a *1:1 line*; r^2 for a linear relationship between predicted and actual CO_2 efflux is 0.85 (*squares M. guianensis, triangles S. amara*)

Table 2 Maintenance respiration rates (R_m) of woody tissue for different species. Rates are corrected to 20° C using a Q_{10} of 2, and expressed per m³ of sapwood volume

Species	R_m (μmol CO_2 $m^{-3}s^{-1}$)	Source
Minquartia guianensis	28.5	This study
Simarouba amara	31.1	This study
Pinus contorta	19.4	Ryan 1990
Abies amabilis	122	Sprugel 1990
Pinus resinosa	14.2	Ryan et al. 1995
Tsuga heterophylla	9.2	Ryan et al. 1995
Pinus elliottii	16.6	Ryan et al. 1995
P. ponderosa	16.0	Ryan et al. 1995
Quercus rubra	73.5	Gower et al. 1991
Acer saccharum	14.6	Gower et al. 1991

results are in contrast to Yoda et al. (1965) and Hagihara and Hozumi (1991), who describe methods for estimating the woody-tissue respiration of forest stands, based on relationships with diameter. Our results show that identifying the functional components of construction and maintenance respiration can explain much of the variability in CO_2 efflux from stems of tropical hardwoods. If we use the functional model and estimate construction respiration from annual wood growth (Eq. 1) and estimate maintenance respiration from sapwood volume (Eq. 3), we reliably predict CO_2 efflux from stems with diameters ranging from 6 to 66 cm and widely different growth rates (Fig. 5). Because of these results, we suggest that bole surface area and stem diameter may be inappropriate scalars for determining woody-tissue respiration for tropical forests.

The high correlation between CO_2 efflux and annual growth (Fig. 3) suggests strongly that the functional model is appropriate and that stem growth must be considered in estimates of woody tissue respiration. The correlation for *Minquartia* (0.92) was much greater than that for *Simarouba* (0.64), even though *Simarouba* trees had much higher growth rates. A possible explanation for the difference between species is that sapwood thickness and sapwood volume vary much less for *Minquartia* than for *Simarouba* (cf. Figs. 1 and 4).

For *Simarouba amara* and *Minquartia guianensis*, maintenance respiration calculated by subtracting estimated construction costs from total measured CO_2 efflux was linearly related to sapwood volume estimated from diameter. The unexplained variability in this relationship (Fig. 4) likely derived from our

methods and assumptions: (1) the estimation of sapwood volume from a relationship with other trees, (2) the variability in CO_2 efflux from point to point around the stem, and (3) the assumption of consistent growth through the year. The response of CO_2 efflux to temperature was similar to that reported for other woody tissue (Linder and Troeng 1981; Ryan 1990; Sprugel 1990).

Sapwood volume has been identified as a useful scalar for maintenance respiration in temperate species (Ryan 1990; Sprugel 1990; Ryan et al. 1995), but this paper represents the first test of this concept for tropical wet forest trees. Rates for maintenance respiration for the two tropical wet forest trees measured in this study were generally higher than rates found for temperate conifers (Table 2). The two tropical wet forest trees in this study had very different growth habits, yet had the same relationship between maintenance respiration and sapwood volume. This similarity suggests that sapwood volume may be a conservative estimator for maintenance respiration of tropical wet forest trees.

The amount of sapwood found in *Minquartia* and *Simarouba* is quite low compared with many temperate conifers, but similar to that found in white oak (*Quercus alba* L.). For example, in this study sapwood thickness varied from 5 to 30 mm, compared with nearly 3 times that amount for temperate conifers (M. G. Ryan, unpublished data). We also observed comparable sapwood thickness on the downed trees cut to clear paths at La Selva. Although it can be difficult to distinguish sapwood from heartwood in tropical species, many of the species found at La Selva have been reported to have thin sapwood (cf. Chudnoff 1980). If thin sapwood is common, annual estimates of maintenance respiration will likely be low.

Annual carbon costs for woody-tissue respiration

To make a first attempt at understanding the importance of woody-tissue respiration at La Selva, we estimated

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Table 3 Gross primary production (*GPP*) and annual carbon costs of woody tissue respiration (R_w) for five forests in the wet tropics. Woody biomass was assumed to be 50% carbon. We estimated gross production for the tropical wet forest at La Selva using a technique described by Ryan (1991b). Estimated gross production is the sum of aboveground wood production [from Lieberman et al. (1990)], aboveground foliage production [estimated from litter production (6.6 Mg ha^{-1} year^{-1}, R. L. Sanford Jr., unpublished data)], total belowground allocation (estimated from litter production), woody-tissue respiration (estimated from sapwood volume and respiration rates in this study), and foliage respiration. Foliage respiration was estimated from canopy biomass (8.5 Mg ha^{-1}, R. L. Sanford Jr., unpublished data) and average respiration rate (6.7 nmol g^{-1} s^{-1}, M. G. Ryan, unpublished data) for *Pentaclethra macroloba* foliage

Site	GPP	R_w	R_w/GPP	Woody biomass	R_w/ Woody biomass	Source
	g C m^{-2} year^{-1}			g C m^{-2}		
Tabonuco forest, Puerto Rico	5986	431	0.07	13 000	0.033	Odum 1970
Khao Chong rain forest, Thailand	6160[1]	1605[2]	0.26	20 000[3]	0.080	[1]Kira et al. 1967 [2]Yoda 1967 [3]Ogawa et al. 1965
Pasoh lowland evergreen rain forest, Malaya	4000	910	0.23	23 500	0.039	Whitmore 1984
Rain forest, Ivory Coast, Africa	2628	1314	0.50	13 000	0.101	Müller and Nielson 1966
Tropical wet forest, La Selva, Costa Rica	2700	220[4] −360	0.08 −0.13	12 450[5]	0.018 0.029	[4]This study [5]Lieberman et al. 1990

annual maintenance respiration from sapwood volume (this study) and construction respiration from the dry-matter production of aboveground biomass at three permanent plots at La Selva (Lieberman et al. 1990; Lieberman and Lieberman 1994).

We estimated sapwood volume from the proportion of sapwood found in our samples. The proportion of sapwood volume in our samples averaged either 40% (each sample weighted equally), or 23% (if weighted by tree size). The 23% figure is likely more realistic, because large trees dominate at La Selva. For example, the quadratic mean diameter (the diameter of the tree of average basal area) for the Liebermans' plots in 1969 was 29.4 cm, but the quadratic mean diameter for our trees was 14.6 cm. The sapwood fraction can also be estimated for whole trees using an equation for stem biomass [$y = 0.89x - 136$, where y is biomass (kg) and x is stem basal area (cm^2); Lieberman et al. 1990] and estimating sapwood thickness from the equations given in Fig. 1. For a *Simarouba* or *Minquartia* tree of 29.4 cm diameter, we estimate the sapwood fraction to be 14.8% or 29.0%, respectively, with this method.

Over 13 years, aboveground biomass increment averaged 3.0 Mg ha^{-1} year^{-1} (Lieberman et al. 1990). In 1982, the permanent plots contained 249 Mg ha^{-1} in aboveground woody material (Lieberman et al. 1990). Because leaf biomass is a small proportion of the aboveground biomass in wet tropics, and the Liebermans' plots were located in primary forest where leaf area is expected to change little over time, we assumed that the biomass increment was strictly from wood production. To convert standing biomass to volume, we assumed the specific gravity of dry matter was 0.6 g cm^{-3}. Mean density for *Minquartia* and *Simarouba* was 0.55, and trees with wood of "intermediate density" were used to develop the equation used to estimate aboveground biomass from tree basal area (Lieberman and Lieberman 1994). We assumed construction respiration was 25% of the carbon content of dry-matter production (Penning de Vries 1975; Sprugel and Benecke 1991).

The aboveground wood production of 3.0 Mg ha^{-1} year^{-1} requires 40 g C m^{-2} year^{-1} for construction respiration. If sapwood volume for other species is similar to that for *Simarouba amara* and *Minquartia guianensis*, and if rates of CO_2 efflux we measured apply generally at La Selva, we estimate maintenance respiration for woody tissue as 320 g C m^{-2} year^{-1} for a sapwood volume 40% of total volume and 180 g C m^{-2} year^{-1} for a sapwood volume 23% of total volume. Adding together the estimates for construction and maintenance respiration, annual woody-tissue respiration at La Selva was either 360 or 220 g C m^{-2} year^{-1}, depending on assumed sapwood volume.

We found no evidence of substantially higher respiration rates for woody tissue for other species common at La Selva. CO_2 efflux from open-grown stems of *Pentaclethra macroloba*, a tropical hardwood which represents 14% of the trees on the sample plot, averaged 1.8 μmol m^{-2} s^{-1} and efflux from a tree-palm, *Welfia georgii* H. Wendl. (Palmae), averaged 0.7 μmol m^{-2} s^{-1} (M. G. Ryan and R. M. Hubbard, unpublished data). These rates are comparable to those we found for *Minquartia* and *Simarouba*. Also, we saw no evidence of greater sapwood volume in any of the downed trees near the paths at La Selva.

Our estimate of annual woody-tissue respiration is low (Table 3) compared with estimates from Yoda (1967), Müller and Nielson (1965), Whitmore (1984),

and Odum (1970). Relative to gross primary production (GPP) or woody biomass, our estimate is similar to that of Odum (1970) but lower than the others (Table 3). Despite the large uncertainty in our estimate for woody-tissue respiration, it is interesting to note that those studies that estimated high costs for woody-tissue respiration (Müller and Nielson 1965; Yoda 1967; Whitmore 1984) estimated rates from detached samples and used relationships with diameter or surface area to scale from samples to the stand. Odum (1970) directly measured flux (as in this study), but used surface area to scale.

Conclusions

CO_2 efflux from stems of two wet forest trees varied seven-fold, but was only weakly related to stem diameter. Our results show that partitioning CO_2 efflux into the functional components of construction and maintenance respiration can explain much of the variability in CO_2 efflux from stems of wet forest trees. CO_2 efflux was highly correlated with annual wood production, and estimated maintenance respiration was linearly related to sapwood volume. Maintenance respiration per unit of sapwood volume was similar for *Simarouba amara* and *Minquartia guianensis*, and the rate for these wet forest trees was roughly twice that measured for several temperate conifers. The amount of sapwood volume appeared low compared with many temperate species. The use of the functional model of plant respiration, together with respiration rates estimated in this study, yielded annual estimates for stand woody-tissue respiration considerably lower than most other reported values.

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