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Estimates of species- and ecosystem-level respiration of woody stems along an elevational gradient in the Luquillo Mountains, Puerto Rico

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ABSTRACT

We measured CO_2 efflux from stems of seven subtropical tree species situated along an elevational gradient in the Luquillo Mountains, Puerto Rico and scaled these measurements up to the landscape level based on modeled and empirical relations. The most important determinants of ecosystem stem respiration were species composition and stem temperature. At a species scale, measured CO_2 efflux per unit bole surface area at a given temperature was highest in the early successional species *Cecropia schreberiana* and lowest in species that inhabit high elevations such as *Micropholis garciniifolia* and *Tabebuia rigida*. Carbon dioxide efflux rates followed a diel pattern that lagged approximately 6 h behind changes in sapwood temperatures. At an ecosystem scale, our simulation model indicates a decreasing trend of stem respiration rates with increasing elevation due to shifts in species composition, lower temperatures and reductions in branch surface area. The highest estimated stem respiration rates were present in the lowland tabonuco forest type and the lowest rates were present in the elfin forest type (mean 7.4 and 2.1 Mg C ha^{-1} yr^{-1}, respectively). There was slight temperature-induced seasonal variation in simulated stem respiration rates at low elevations, with a maximum difference of 19% between the months of February and July. Our results coincide well with those of Odum and Jordan [Odum, H.T., Jordan, C.F., 1970. Metabolism and evapotranspiration of the lower forest in a giant plastic cylinder. In: Odum, H.T., Pigeon, R.F. (Eds.), A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico. U.S. Atomic Energy Commission, Oak Ridge, TN, pp. I165–I189] for the tabonuco forest type and extend their work by presenting estimates and spatial patterns of woody tissue respiration for the entire mountain rather than for a single forested plot.

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1. Introduction

Since carbon fixation occurs in photosynthetic tissue only during daytime hours while respiration occurs continuously in all living tissues, trees release back into the atmosphere a large proportion of the carbon that they assimilate. Both the percentage of gross primary production used for respiration and the specific respiratory partitioning among leaves, wood, and roots may differ for forests growing in different climates (Waring and Schlesinger, 1985). For example, standing woody tissue respiration exceeded leaf respiration on a stand basis by a factor of more than 2.5 in a mature yellow poplar forest in Tennessee (Edwards et al., 1981), while the contribution of woody stem respiration to total autotrophic respiration was only 12% in sub-alpine *Pinus contorta* ssp. latifolia (Ryan and Waring, 1992). Despite the importance of stem respiration in calculating accurate carbon budgets, carbon fixation studies far exceed those focused on carbon loss, primarily because stem respiration is difficult to measure directly at the tree or ecosystem level. Therefore, measurements are often scaled up on the basis of surface area or volume to estimate respiration at these larger scales.

The vast majority of current stem respiration studies focus on conifers that are valuable as timber species (Lavigne, 1996; Lavigne et al., 1996; Carey et al., 1997; Maier, 2001; Xu et al., 2001), although stem respiration has been measured in species inhabiting other ecosystems including southern U.S. hardwood forests (Carter et al., 1973), mangroves (Lugo et al., 1975), tropical dry forests (Lugo et al., 1978) and cypress swamps (Brown, 1981). However, apart from the classic studies by Yoda (1967) in Thailand, stem respiration has been quantified for only a handful of tree species in the wet tropics (Müller and Nielson, 1965; Odum et al., 1970; Ryan et al., 1994). Therefore, one objective of this study was to quantify woody stem respiration rates for seven tree species in the Luquillo Mountains, Puerto Rico.

Efforts to model landscape-scale physiological processes tend to focus on total carbon budgets (Davi et al., 2005; Nalder and Wein, 2006; Adiku et al., 2006) rather than individual physiological processes. The single-process models that do exist tend to be geared towards photosynthesis, especially of agricultural crops (Jongschaap, 2007), or the temperature dependence of soil respiration (Qi et al., 2002; Tuomi et al., 2008). Even where large-scale estimates of stem respiration exist (Lugo et al., 1978; Brown, 1981), they are compared rarely among individual stands or forest types. In this study, we developed a spatially explicit simulation model that links site-specific physiological measurements with parameters of regional forest structure, then compared annual estimates of woody tissue respiration among forest types located along an elevational gradient in the Luquillo Mountains and with forest ecosystems located elsewhere.

Woody stems account for the largest portion of forest biomass, so estimates of stem respiration are essential for understanding the global carbon cycle and modeling the exchange of CO_2 between forests and the atmosphere. When stem respiration estimates are combined with other physiological measurements, it is possible to construct detailed carbon balance models for whole ecosystems, which can be used to estimate a system's potential for carbon sequestration or evaluate its response to scenarios of climate change, land use change or timber management.

2. Methods

2.1. Field methods

2.1.1. Study area

The Luquillo Experimental Forest (LEF, 18°N, 65°W) in northeastern Puerto Rico has been the site of forestry research for over 100 years. In 1988, the LEF became a Long-Term Experimental Research (LTER) site supported by the National Science Foundation. Today, data accumulates daily to produce a comprehensive record of meteorological and ecological information (see http://luq.lternet.edu). Elevations in the LEF range from about 100 to 1075 m above mean sea level (Brown et al., 1983), mean annual temperatures decrease from 23 °C in the lowlands to 19 °C at the mountain peaks (Weaver and Murphy, 1990) and annual precipitation increases from about 2330 mm at low elevations to about 4500 mm at upper elevations (Brown et al., 1983; García Martinó et al., 1996). Persistent cloud cover above the cloud condensation level at about 600 m elevation reduces annual solar radiation to approximately 63% of nearby coastal areas (Briscoe, 1966).

Climatic conditions that vary with elevation cause shifts in vegetation structure. As a result, there are four main forest types within the LEF that cover the subtropical wet, subtropical rain, lower montane wet and lower montane rain forest life zones in the Holdridge (1967) classification scheme (Ewel and Whitmore, 1973). Tabonuco forest is named for the dominant tree *Dacryodes excelsa* and is generally present below 600 m elevation. Palo colorado forest, named for the dominant tree *Cyrilla racemiflora*, occurs between 600 and 900 m. Elfin forest is restricted to mountain peaks and ridges above 750 m while palm brake forest, consisting largely of *Prestoea montana*, is widespread but dominates steeper slopes and areas with poor drainage and saturated soils. An isolated patch of ausubo forest, dominated by *Manilkara bidentata* trees, exists near sea level outside the forest boundary and falls in the subtropical moist forest life zone (Ewel and Whitmore, 1973). We chose to study trees in this forest type as well because this stand is comparable to the old growth forests that dominated lowland areas before widespread land use change took hold.

2.1.2. Experimental design

In March 2005, we measured woody stem respiration (R_w) in 8–10 trees per species at various elevations in the Sonadora watershed of the Luquillo Mountains. Site locations were selected based on a digital map of forest types obtained from the Luquillo LTER database. We measured the dominant tree species in each forest type as determined from importance values in Brown et al. (1983) and selected trees to measure with a wide range of diameters (12.2–83.9 cm DBH) to capture variability in growth rates. We measured *Manilkara bidentata* in the ausubo forest type (15 m elevation); *D. excelsa* in the tabonuco forest type (378 m); *Cyrilla racemiflora* and *Micropholis garciniifolia* in the palo colorado forest type (606 m); *Prestoea montana* in the palm brake forest type (981 m); *Tabebuia rigida* in the

elfin forest type (1021 m); and *Cecropia schreberiana*, a pioneer species, from a disturbed site near the El Verde field station within the tabonuco forest type (366 m).

2.1.3. Respiration measurements

Rates of woody stem respiration were measured according to the methods of Xu et al. (2000) in which the soil chamber of a closed system, LI-6400-09 portable infrared gas analyzer (LI-COR, Lincoln, NE) was mounted horizontally on tree stems and CO_2 efflux per unit of surface area under the soil chamber was measured. Respiration chambers were constructed by cutting a 4-in. (10.1 cm) diameter, thin-walled PVC pipe crosswise into several rings, or collars, and all cut surfaces were sanded to a smooth finish. In the field, one side of each collar was cut on a curve to conform to the trunk surface to which it would be attached. Clear 100% silicone sealant (GE Silicone II) was used to glue the collars to trunk surfaces at or below breast height (1.4 m) in the direction that allowed an airtight seal to be made most easily, and to fill any gaps between chambers and trunk surfaces. A single respiration chamber was fit to each tree. Collars were secured tightly to trunk surfaces with nylon string until set (~24 h). If moss or other plant material grew on the stem at the point of measurement, it was brushed off carefully before collars were glued, and stem respiration measurements were recorded at least 24 h after this minor stem disturbance occurred.

During each measurement, a foam gasket was placed between collar and chamber to ensure an airtight seal. After measuring the CO_2 concentration of ambient air at the stem surface, the concentration of CO_2 in the chamber was pumped down with an internal CO_2 pump to 10 ppm below this measured value. Then, the CO_2 concentration was allowed to rise in the chamber to 10 ppm above the ambient value and the stem respiration value was calculated based on the rate of the CO_2 buildup curve within the chamber over time. We ran 3 measurement cycles (replicates) per chamber and calculated CO_2 efflux per chamber as the mean of these three values. Measurements for each stem collar were complete after approximately 5 min. Stem temperature was measured concurrently with stem respiration by inserting a digital temperature probe (Forestry Suppliers model #89102) adjacent to the stem collar and approximately 1 cm into the sapwood past the cambium. All measurements were completed between 800 and 1500 h except those collected to compute diel curves (described below). No stem photosynthesis was detected in any of the trees sampled; all collars were naturally shaded since the forest floor of a tropical rain forest is virtually always shady.

All measurements were recorded in the field using a chamber surface area of 80 cm^2. Data were then recomputed using the exact dimensions for each collar. The amount of stem surface area enclosed within each chamber was calculated using the following equation (Xu et al., 2000):

$$S = \frac{\pi^2}{720} D_c D_t \arcsin\left(\frac{D_c}{D_t}\right) \quad (1)$$

where S is stem surface area enclosed in the collar, D_c is the diameter of the PVC collar, and D_t is the diameter of the stem where the collar was attached.

Measurements were made using a chamber insertion depth of 0 cm, corresponding to a chamber volume of 991 cm^3 (specified in LI-6400 09 user's manual). The volume of the chamber was not adjusted to account for stem-specific geometry, but our calculations indicated that the air space between the flat surface of the chamber and each curved stem would have increased the chamber volume by less than 5% on average over all trees sampled.

To test for effects of temperature on respiration rate and to compute diel respiration curves, stem respiration rates were measured in a single *Manilkara bidentata* tree located in the vicinity of the El Verde field station (366 m elevation) once every 3 h over a 48-h period. Stem temperatures during the measurement period ranged from 19.3 to 25.0 °C. After preliminary analysis, a nonlinear regression model was chosen that is used commonly to represent respiration rate as a function of temperature (Ryan et al., 1994; Lavigne et al., 1996):

$$R_w = \beta_0 \exp(\beta_1 T) \quad (2)$$

where R_w is predicted woody stem respiration, T is the stem temperature 2 *measurement periods earlier* (there was no significant correlation between R_w and measured temperature, further explanation in Section 3 below), and β_0 and β_1 are regression coefficients. The change in respiration for a 10 °C change in temperature (Q_{10}) was calculated as (Ryan et al., 1994):

$$Q_{10} = \exp(10\beta_1) \quad (3)$$

2.2. Model description

After species-specific stem respiration rates were measured in the field, they were combined with forest structural data to extrapolate area-based stem respiration measurements to the landscape scale. A flowchart of the model is shown in Fig. 1. Stem respiration was driven in the model by both abiotic and biotic drivers (described below). Assumptions of the model are as follows: (1) the seven species measured in the field (or those modeled to exist at a given elevation) are representative of all those species that exist at that elevation; (2) respiration rates per unit of branch surface area and per unit of bole surface area are similar within a species; and (3) all CO_2 efflux originates from respiration of local tissues and escapes to the atmosphere through the bark.

2.2.1. Data inputs

The model requires a 30 m × 30 m resolution digital elevation model (DEM) of the LEF, parameters for the temperature regression (outlined in Table 1) and species-specific values for fresh leaf mass per unit leaf area (LMA) (listed in Table 2). The DEM was digitized from a 1:24,000 USGS Forest Service map and was used to derive slope and aspect values in a GIS (IDRISI, Clark University).

Data from the Luquillo LTER database were also used to model the species distribution patterns illustrated in Fig. 2 (http://luq.lternet.edu/data, data collected by J. Barone). This dataset contains species and diameter at breast height (DBH) information for all trees >1 cm DBH situated along three transects of elevation in the LEF. Each transect consisted of 0.1 ha plots located at 50-m elevation intervals. For each plot in the

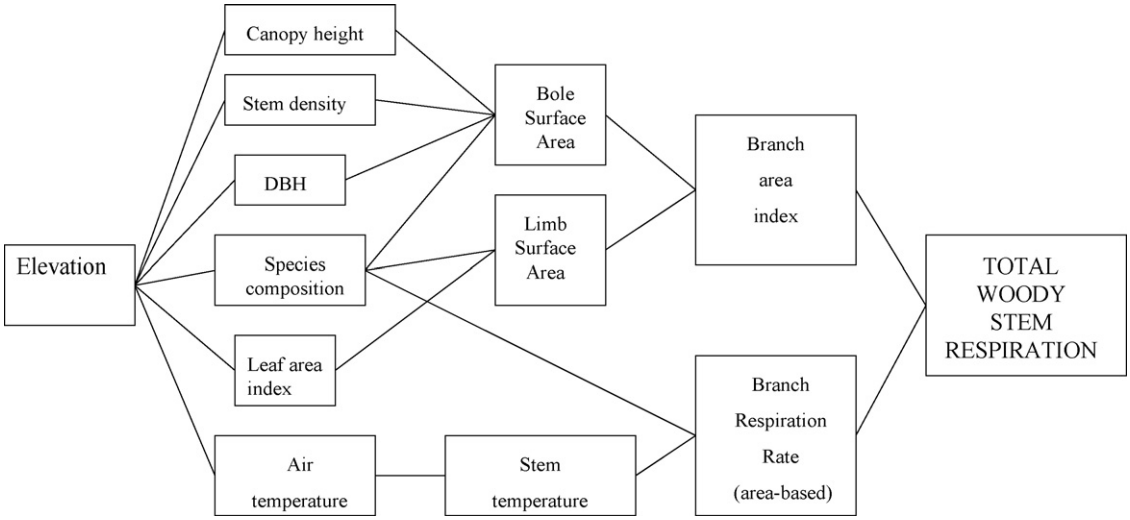

Fig. 1 – Diagram of model structure used to simulate branch area index and ecosystem woody stem respiration for the Luquillo Experimental Forest, Puerto Rico.

Table 1 – Air temperature (°C) vs. elevation (m) regression parameters for the LEF (Marley, 1998)

Month	Maximum air temperature (°C)			Minimum air temperature (°C)		
	Slope	Intercept	R^2	Slope	Intercept	R^2
January	−0.0083	27.580	0.83	−0.0044	21.211	0.88
February	−0.0080	28.253	0.80	−0.0043	21.079	0.84
March	−0.0091	29.024	0.85	−0.0050	21.533	0.89
April	−0.0090	29.232	0.92	−0.0045	22.111	0.83
May	−0.0091	29.517	0.93	−0.0054	23.286	0.90
June	−0.0082	29.599	0.87	−0.0049	23.680	0.93
July	−0.0091	29.949	0.82	−0.0057	23.896	0.95
August	−0.0089	30.322	0.90	−0.0050	23.832	0.97
September	−0.0065	29.200	0.36	−0.0043	22.959	0.60
October	−0.0087	29.622	0.89	−0.0051	23.633	0.87
November	−0.0082	28.793	0.82	−0.0042	22.281	0.83
December	−0.0087	27.574	0.83	−0.0047	21.766	0.89

Table 2 – Species-specific values of fresh leaf mass per area (LMA, g m^{-2}) for seven tree species in the Luquillo Experimental Forest, Puerto Rico

Species	Fresh LMA	N
Cecropia schreberiana	153	29
Cyrilla racemiflora[a]	511	160
Dacryodes excelsa	223	24
Manilkara bidentata	270	16
Micropholis garciniifolia	469	16
Prestoea Montana	236	34
Tabebuia rigida[b]	405	10

These values are used as parameters in the calculation of species-specific limb surface area (Eq. (7)).

[a] Data from A. Drew (unpublished results).

[b] Dry LMA = 192.7 g m^{-2} (Medina et al., 1981) converted to fresh LMA, using a fresh to dry weight ratio of 2.1 g fresh weight:1 g dry weight (Harris, unpublished data).

dataset, we estimated forest species composition based on the ratio of the basal area of each of our seven focus species to the total basal area of these seven species (Fig. 2). The tree species included in the analysis are the most (or second-most) dominant tree species in each respective forest type as indicated by their importance values (Brown et al., 1983; Frangi and Lugo, 1985). Additional forest structure data (total stem density and mean DBH at each plot) are illustrated in Fig. 3 and were obtained from J. Barone (LTER database).

2.2.2. *Abiotic (climatic) drivers*

Temperature has been shown to be the primary factor that influences respiration rates for a variety of organisms including trees (Amthor, 1984; Gillooly et al., 2001; Brown et al., 2004). Marley (1998) derived minimum and maximum daily air temperatures for the Luquillo Forest from a regression of temperature data from several meteorological stations located at different elevations in and around the LEF against each station's elevation (ranging from near sea level to 1059 m) (Table 1). Diel variation in air temperature was modeled after Parton and Logan (1981), where daytime temperatures are simulated as a modified sine function and nighttime

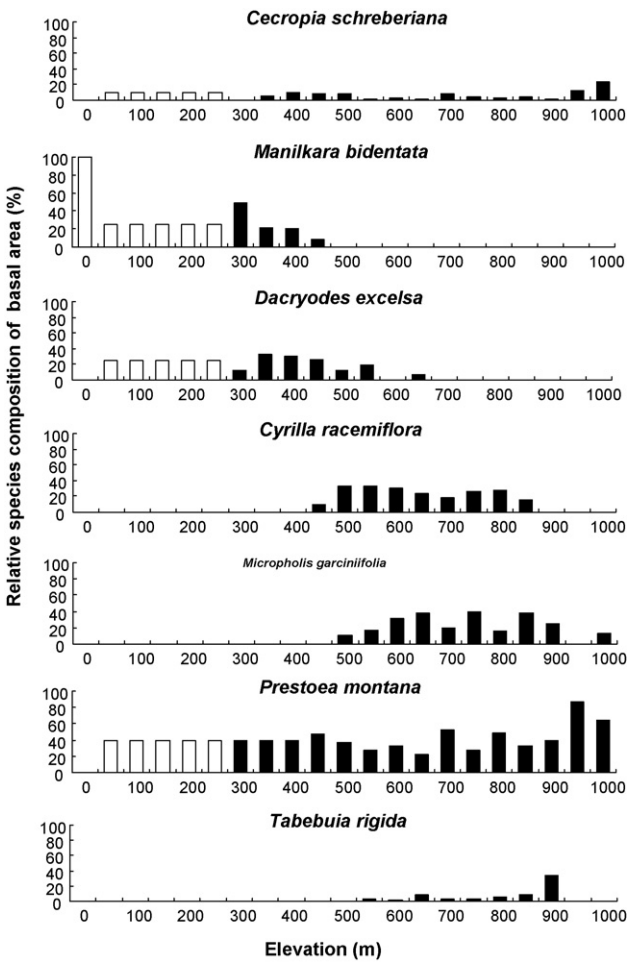

Fig. 2 – Species distribution patterns along an elevational gradient in the Luquillo Experimental Forest, Puerto Rico. Data collected originally by J. Barone and archived at http://luq.lternet.edu. The percentage of each species at a given elevation (y-axis) is represented on the basis of basal area, and percentages are relative among the seven species modeled. Species distribution patterns below 300 m were estimated (open bars).

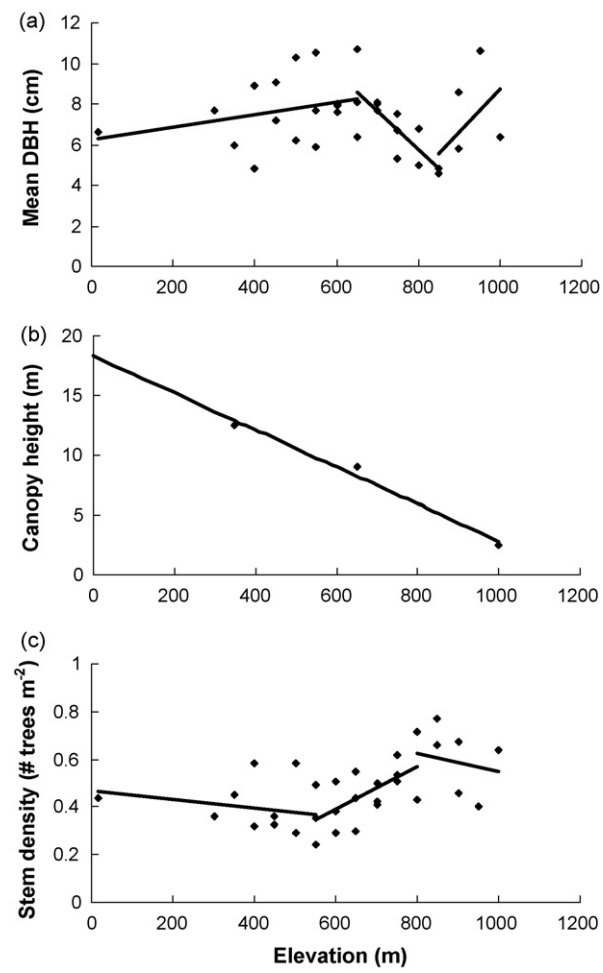

Fig. 3 – (a) Mean diameter at breast height, (b) canopy height and (c) stem density as functions of elevation in the Luquillo Experimental Forest, Puerto Rico. DBH and stem density data are based on measurements of all trees >1 cm diameter in 0.1 ha plots situated every 50 m elevation along three elevational transects. Canopy height data collected by N. Brokaw at three elevations representing three forest types (Brokaw and Grear, 1991). All data are archived at http://luq.lternet.edu except the lowest elevation plot, which were taken from Gould et al. (2006).

temperatures are simulated as an exponential decay function.

Stem temperature was related linearly to air temperature using the following equation derived from our empirical data (Fig. 4a):

$$T_s = (0.77 \times T_a) + 0.71; \quad R^2 = 0.66 \tag{4}$$

where T_s is stem temperature and T_a is air temperature, both in degrees Celsius.

Species-specific stem respiration rates were corrected to the same 25 °C stem temperature, and were then adjusted up or down based on the simulated stem temperature that varied throughout the day and year. This adjustment was based on a measured Q_{10} value of 1.5 ($\beta_1 = 0.0401$ in Eq. (2), see Section 3.2 below).

2.2.3. *Biotic (structural) drivers*

Leaf area index (LAI) is defined as the area of one-sided leaf surface (m^2) that occupies 1 m^2 ground surface. LAI decreases with elevation in the LEF and was modeled based on a linear regression of LAI against elevation that uses empirical data from four different elevations in the Luquillo Mountains (one from each of the four principal vegetation types). These data are summarized in Weaver and Murphy (1990) and Brown et al. (1983) and yield the following relation (Marley, 1998):

$$\mathrm{LAI} = (-0.0076 \times \varepsilon) + 9.4132, \quad R^2 = 0.98 \tag{5}$$

where ε is elevation in meters above sea level.

Mean DBH and stem density values were modeled as functions of elevation using data from the LTER database (Fig. 3).

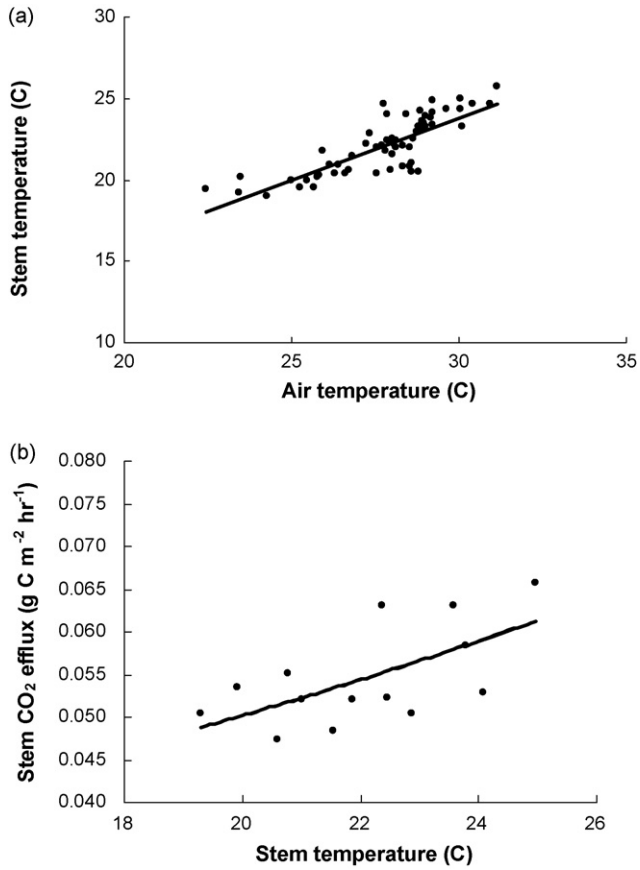

Fig. 4 – (a) stem temperature plotted against ambient air temperature, $R^2 = 0.66$, $P < 0.0001$ (b) stem CO_2 efflux plotted as a function of lagged temperature, i.e., the stem temperature present 6 h prior to when efflux measurements were made. The regression equation is $Y = 0.0225 \exp(0.0377X)$.

Estimating structural parameters such as mean DBH is not straightforward in the LEF, since variations in disturbance history and tree age may be large from point to point. Therefore, we plotted data from the three elevation transects, then created three breakpoints along the *x*-axis where the trend in the data switched from increasing to decreasing (or vice versa, Fig. 3).

Canopy height was estimated as a linear function of elevation, based on data from Brokaw and Grear (1991):

$$H = (-0.0236 \times E) + 27.991 \quad (6)$$

where H is canopy height in meters and E is elevation in meters above sea level. Height of palm trees was assumed to be 60% of this canopy height (Frangi and Lugo, 1985).

For all tree species except *Prestoea montana*, bole surface area of an average tree of each species (B_t) was modeled as the surface area of a cone, with base diameter equal to the mean DBH of all trees measured at that point along the elevation gradient (Fig. 3a) and canopy height (cone height) an inverse linear function of elevation (Eq. (4), Fig. 3b). Bole surface area of *Prestoea montana* trees was estimated as the surface area of a cylinder with base equal to the mean DBH and height equal to 60% of the full canopy height (Frangi and Lugo, 1985). The bole surface area of an average tree of each species was then multiplied by stem density values as a function of elevation (Fig. 3) and weighted by species (Fig. 2).

To model the surface area of limbs (defined as all twigs and branches up to 2.5 cm diameter), we used an empirical equation from Odum and Jordan (1970) developed from an experiment in which they enclosed a large area of tabonuco forest in a giant plastic cylinder to measure rates of forest metabolism and evapotranspiration. Limb surface area was related to leaf surface area by the following equation (Odum et al., 1970):

$$A_1 = \frac{L_{aw} \times LMA_f}{FL_m \times 10^4} \times LAI \quad (7)$$

where A_l is the limb area accompanying 1 m^2 of forest area ($m^2\,m^{-2}$), L_{aw} is the ratio of limb area to fresh-limb weight ($3.33\,cm^2\,g^{-1}$), FL_m is the ratio of fresh-leaf mass to fresh-limb mass (1.72 g leaves $(g\,limb)^{-1}$), LAI is the leaf area index ($m^2\,m^{-2}$) and LMA_f is the ratio of fresh-leaf weight to fresh-leaf area ($g\,m^{-2}$), which was measured for at least 16 leaves of each species modeled (Table 2). Limb surface area was set to zero for the palm species *Prestoea montana* (a monocot).

2.2.4. *Model output*

Our model combines species-specific, empirical rates of stem respiration ($g\,C\,m^{-2}\,stem\,h^{-1}$) with species-specific, modeled bole and limb surface area estimates and integrates computed values over both space and time. Model output includes hourly, daily, monthly and/or yearly estimates of woody stem respiration rates for all regions within the LEF. These estimates extend the work of Odum and Jordan (1970) by presenting estimates and spatial patterns of woody tissue respiration for the entire forested area rather than for a single forest plot.

3. Results

3.1. *Comparison of woody stem CO_2 efflux among species*

There were significant differences among species in rates of CO_2 efflux per unit bole surface area (one-way ANOVA, $F = 16.61$, $P < 0.0001$, Fig. 5). There was also a marked decrease in stem CO_2 efflux along the elevation gradient. Low elevation species *D. excelsa* and *Manilkara bidentata* had higher CO_2 efflux rates than the mid-elevation species *Cyrilla racemiflora*, while species that inhabit high elevations such as *Micropholis garciniifolia*, *Prestoea montana* and *T. rigida* had the lowest respiration rates. The pioneer species *Cecropia schreberiana* had the highest rates overall. Respiration rates were measured at ambient temperatures, but differences among species remained ($P < 0.0001$) when all rates were corrected to 25 °C using a Q_{10} value of 1.5 (see Section 3.2 below). The regression of CO_2 efflux vs. stem diameter at the point of measured CO_2 efflux was significant ($P = 0.0019$), but diameter explained less than 15% of the total variation in

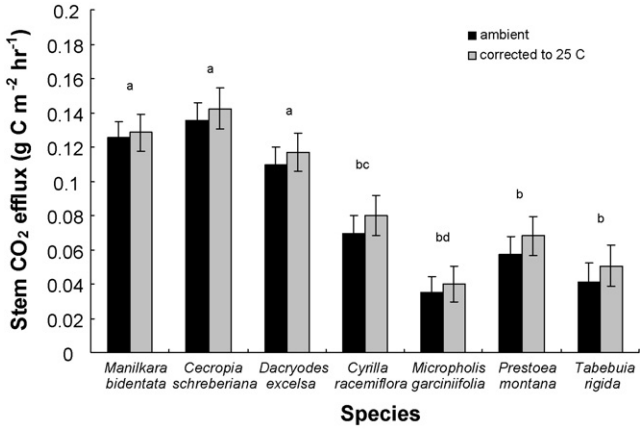

Fig. 5 – Mean (±1S.E.) stem respiration rates for seven tree species in the Luquillo Experimental Forest, Puerto Rico at ambient temperature (black bars) and corrected to 25 °C (gray bars). Species are oriented on the x-axis in order of increasing elevational position. Different letters indicate a significant difference at $\alpha = 0.05$ between species for temperature-corrected rates.

CO_2 efflux for all species combined. Furthermore, when an 84 cm outlier tree was removed, the correlation became non-significant.

3.2. *Temperature responses*

No regression model (linear or nonlinear) was an appropriate fit to the data of stem CO_2 efflux vs. temperature. Fig. 6 shows stem CO_2 efflux rates and sapwood temperatures of a *Manilkara bidentata* tree measured over a 48-h period. Efflux rates and sapwood temperatures were better correlated when temperatures were plotted on a 6-h time lag than when both variables were plotted on the same time scale. After CO_2 efflux rates were plotted against stem temperatures present 6 h earlier (i.e., 2 measurement periods earlier), the nonlinear regression model in Eq. (2) became significant (pseudo-$R^2 = 0.39$, $P < 0.0001$, Fig. 4b) and the temperature response coefficient (β_1 in Eq. (2)) was estimated as 0.0401, corresponding to a Q_{10} value of 1.5.

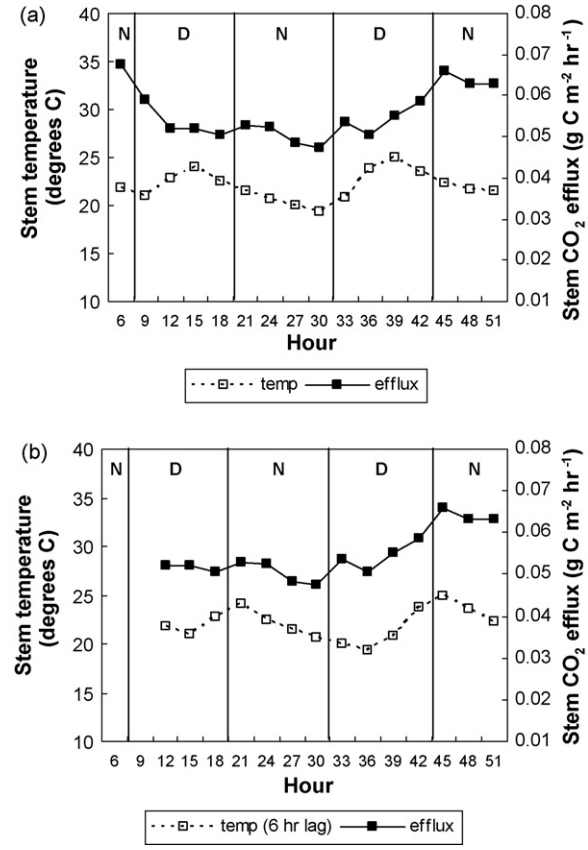

Fig. 6 – Relation between stem temperature (°C) and CO_2 efflux from stems per unit of stem surface area ($g\,C\,m^{-2}\,h^{-1}$) for a single *Manilkara bidentata* tree measured over a period of 48 h at El Verde Field Station, Puerto Rico. (a) Stem temperature measured concurrently with respiration, and (b) stem temperature observed 6 h earlier than respiration was measured. The letter 'D' corresponds to daytime hours and the letter 'N' to nighttime hours.

3.3. *Model results*

Our simulations indicate a general trend of decreasing annual stem respiration with increasing elevation (Fig. 7) due to

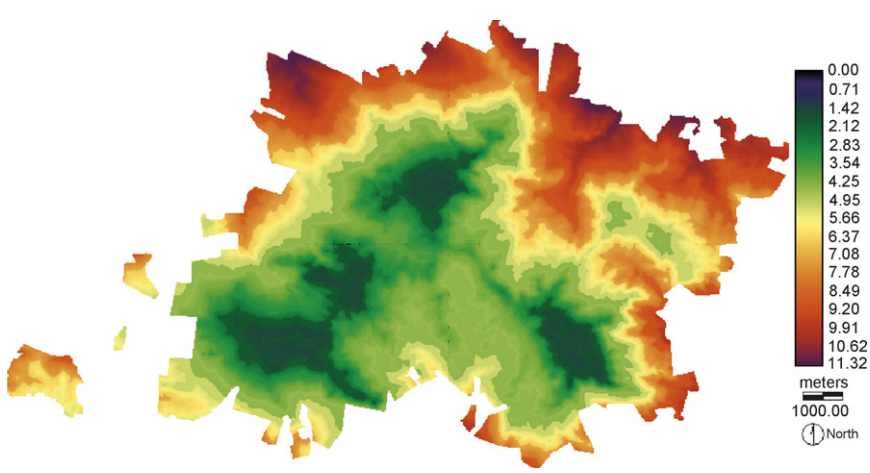

Fig. 7 – Simulated annual rates of woody stem respiration ($Mg\,C\,ha^{-1}\,yr^{-1}$) in the Luquillo Experimental Forest, Puerto Rico.

Table 3 – Mean rates of simulated woody stem respiration in each forest type

Forest type	Annual woody stem respiration ($Mg\,C\,ha^{-1}\,yr^{-1}$)
Tabonuco	7.37
Palo Colorado	3.80
Palm Brake	3.86
Elfin	2.14

Pixels in each forest type in the output map of Fig. 7 were averaged together to produce mean values.

shifts in species composition (Fig. 2), decreasing temperatures (Table 1) and decreasing stem surface area (Fig. 3). The highest respiration rates were present in the low elevation tabonuco forest type and the lowest rates were present in the high elevation elfin forest type (mean rates of 7.4 and 2.1 $Mg\,C\,ha^{-1}\,yr^{-1}$, respectively, Table 3, Fig. 7). There was slight seasonal variation in simulated stem respiration rates, with highest rates occurring in August and lowest rates occurring in February, but differences between consecutive months did not differ by more than 10%. Variation in species composition was the most influential factor in the model to explain the spatial variation of simulated woody stem respiration in the LEF. Our estimates of woody stem respiration represent approximately 10% of mean annual gross primary productivity (GPP) output values in the productivity model developed by Wang et al. (2003) for the LEF (forest-wide mean stem respiration = 5.5 $Mg\,C\,ha^{-1}\,yr^{-1}$, forest-wide mean GPP = 51.2 $Mg\,C\,ha^{-1}\,yr^{-1}$).

4. Discussion

4.1. *Species differences in stem respiration rates*

The range of stem respiration rates per unit bole surface area measured in this study (0.04–0.130 $g\,C\,m^{-2}$ stem h^{-1}) was higher than that of Odum et al. (1970) for trees of the same tree species (0.003–0.08, 0.006 and 0.02–0.06 $g\,C\,m^{-2}$ stem h^{-1} for *D. excelsa*, *Prestoea montana* and *Cecropia schreberiana*, respectively). Differences may be due to our measurement technique or to the fact that our measurements were recorded under relatively dry forest conditions. We measured 8–10 trees of each species of widely ranging diameters (and growth rates) while Odum et al. (1970) measured only 1–3 trees of each species with no diameter information given. Two hurricanes have passed through the forest since Odum's original measurements (Hugo in 1989 and Georges in 1998), and the higher stem respiration rates we measured may be a reflection of long-term forest recovery and growth.

Rates of stem respiration per unit stem surface area were lower in species that inhabit higher elevations, even when rates were corrected to the same 25 °C temperature. This suggests a basic difference in metabolic activity among different species and may be due to the different ecological characteristics to which each species is adapted. Leaf area index decreases with elevation in the LEF (Brown et al., 1983; Weaver and Murphy, 1990) and although the nitrogen concentration of the woody tissue sampled in this study was not measured, leaf nitrogen concentration has been shown to decrease with elevation in the LEF (Medina et al., 1981). Therefore, higher rates of stem respiration in trees growing at low elevations (such as *D. excelsa* or *Manilkara bidentata*) may be necessary to maintain the xylem and phloem tissues associated with additional leaf structure and/or to maintain a higher activity of respiratory enzymes. In addition, aerated soils and a greater atmospheric saturation deficit at low elevations may support more active transport of materials by the vegetation, leading to higher respiratory demands. In contrast, saturated soils at high elevations lead to reduced soil oxygen availability and an associated reduction in respiratory activity for plant roots at these locations (Silver et al., 1999). Stem anatomy (rather than temperature or soil saturation) may explain the low stem CO_2 efflux values measured in *Prestoea montana*, since transport tissues are diffuse rather than concentrated in rings.

Stem respiration rates were correlated only weakly to diameter at breast height. This finding is consistent with Ryan et al. (1994) but in contrast to Yoda et al. (1965) and Hagihara and Hozumi (1991), who describe methods for estimating woody tissue respiration of forest stands based on relationships with tree diameter. However, Yoda et al. (1965) and Hagihara and Hozumi (1991) calculated respiration rates per unit weight rather than per unit surface area. Another reason for the weak correlation between stem diameter and stem respiration rate may be that wood growth typically occurs after cell expansion, causing peaks in total stem respiration rates to lag behind peaks in diameter growth by 20–40 days, as was shown by Edwards and Hanson (1996).

4.2. *Model validation*

Our estimates of limb stem respiration rates (based on extrapolations to 30 m × 30 m) are virtually identical to those measured by Odum and Jordan (1970) for a cylinder of tabonuco forest (18.2 m across by 20.4 m high) located at 424 m elevation. Their independent estimates of daily limb respiration in late 1964 at 424 m elevation were 0.40 $g\,C\,m^{-2}\,day^{-1}$ while our estimate was 0.36 $g\,C\,m^{-2}\,day^{-1}$. However, our estimate of daily bole respiration for a day in December at 424 m elevation was 1.6 $g\,C\,m^{-2}\,day^{-1}$, vs. a 50% lower estimate by Odum and Jordan of 0.78 $g\,C\,m^{-2}\,day^{-1}$. Together, these estimates produce total woody stem respiration rates of 1.18 (Odum and Jordan, 1970) and 1.95 (this study) $g\,C\,m^{-2}\,day^{-1}$. This difference is most likely due to Odum and Jordan's lower estimate of stem surface area index (SAI) (0.97 $m^2\,m^{-2}$, comprised of 0.61 $m^2\,m^{-2}$ boles and 0.36 $m^2\,m^{-2}$ limbs). Our estimate of stem area index at this elevation was 10% higher (1.06 $m^2\,m^{-2}$), comprised of 0.89 $m^2\,m^{-2}$ boles and 0.16 $m^2\,m^{-2}$ limbs. The higher bole surface area in our model reflects actual data of stem density and diameter at breast height, while Odum and Jordan (1970)'s estimate was much more generic. Our estimate of limb surface area is influenced greatly by the inclusion of one tree species in our model (*Prestoea montana*), which is prominent at all elevations but does not possess limbs. Odum and Jordan (1970) also used a generic wood respiration rate of 0.046 $g\,C\,m^{-2}\,h^{-1}$ for their calculations based on the mean value of only eight measured trees. This rate is lower than many of the tree species mea-

sured in this study except those at the highest elevations (Fig. 5).

4.3. Comparisons with other forests

Stem respiration values per unit bole surface measured in this study were higher than those measured by Ryan et al. (1994) for *Simarouba amara* and *Minquartia guiarensis* (0.054 and 0.036 g C m^{-2} stem h^{-1}, respectively), two tropical tree species growing in Costa Rica. Respiration rates measured in this study were similar to those measured by Xu et al. (2001) in young ponderosa pine trees in California with rates ranging from 0.078 to 0.393 g C m^{-2} h^{-1} in November and August, respectively. Our measured Q_{10} value of 1.5 for stem respiration is at the low end of the range of Q_{10} values reported in previous studies (1.5–2.5, Ryan, 1991).

Our landscape-scale estimates of stem respiration in the LEF are lower than estimated rates for a forest in Japan measured by Yoda et al. (1965). Simulated stem respiration rates in the elfin forest, where soils are saturated, are similar to stem respiration rates of scrub cypress swamps measured by Brown (1981), which suggests that high soil moisture may be a primary inhibitor of stem respiration. Rates of ecosystem trunk respiration in the Guánica Forest, a subtropical dry forest in southwestern Puerto Rico, were estimated at 1.32 g C m^{-2} ground day^{-1} (Lugo et al., 1978), which are similar to daily total stem respiration estimates at mid-elevations in the Luquillo Forest (1.3 g C m^{-2} day^{-1}).

4.4. Lagged respiration responses to temperature

Total CO_2 efflux from the single *Manilkara bidentata* stem measured near El Verde field station showed a lagged response to stem temperature (Fig. 6), which is consistent with Ryan et al. (1995), Lavigne et al. (1996) and Kim and Nakane (2005), who showed similar patterns for conifer stands. This lag probably reflects the time required for a large enough concentration gradient to accumulate before respired CO_2 can diffuse from its origin to the atmosphere (Eklund and Lavigne, 1995). As temperature rises and drives a higher rate of CO_2 diffusion, it takes time for the internal concentration of CO_2 to increase sufficiently to drive this higher rate.

4.5. Internal and external fluxes of CO_2

Our model assumes that all CO_2 efflux originates from respiration of local stem tissues and escapes to the atmosphere through the bark. However, several studies suggest that dissolved CO_2 can be transported in the xylem stream as well. Results from McGuire and Teskey (2004) indicate that during daylight hours when sap is flowing, most respired CO_2 in the stems is transported through the xylem stream while during nighttime hours, most respired CO_2 escapes to the atmosphere through the bark. Our time-course study of respiration (Fig. 7) partially supports this, as nighttime fluxes of CO_2 through the bark were higher, on average, than daytime fluxes, although the difference was not statistically significant. Regardless, our measurements may not account for all CO_2 produced by respiration and future studies may include CO_2 fluxes within the sap as well as fluxes to the atmosphere.

4.6. Estimating construction respiration

Energy obtained from woody tissue respiration can be separated conceptually into that used by the tree for construction (to accumulate new biomass) and that used for maintenance (e.g., for upkeep and repair of existing tissue, enzyme replacement, active transport, translocation-related processes such as phloem loading, etc.) (Penning de Vries, 1975; Amthor et al., 1994). In temperate forests, maintenance respiration for woody tissues is usually estimated by measuring CO_2 efflux after growth has ceased in autumn (Ryan, 1990; Sprugel and Benecke, 1991), but in tropical forests, growth continues throughout the year and so some other approach is required. We used the methods of Ryan et al. (1994) to estimate construction respiration for each species from stem growth and wood density data. The carbon allocated to stem maintenance was calculated as the difference between total CO_2 efflux from stems and estimated construction respiration.

To estimate construction respiration, we used the assumptions of Ryan et al. (1994) that (1) growth is constant throughout the year; (2) carbon content is 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).

In equation form, construction respiration (R_c, in μmol m^{-2} stem s^{-1}) was estimated as:

$$R_c = 0.25\rho V_G \frac{0.5\,\text{g C}}{\text{g Biomass}} \times \frac{10^6\,\mu\text{mol}}{12\,\text{g C}} \times \frac{1}{365\,\text{days}} \times 86400\,\text{s day}^{-1} \quad (8)$$

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

Specific density data were obtained from Baker et al. (2004) for palms and from Reyes et al. (1992) for all other species. Since growth bands were not attached to the specific trees measured, we estimated V_G (cm^3 m^{-2} stem) by multiplying chamber area (80 cm^2) by a range of species-specific annual radius increment values (1/2 × annual diameter increment, cm yr^{-1}) obtained from the literature (Table 4).

Estimated construction respiration values were a relatively small percentage of total CO_2 efflux from stems (Table 4). *D. excelsa* and *Manilkara bidentata* had the highest estimated construction costs (up to 16 and 27% of total stem respiration, respectively) while the species *Prestoea montana* had the lowest costs (<1.0–2.3% of total respiration). Construction respiration rates for the fast-growing pioneer species *Cecropia schreberiana* were 6–10% of total respiration (Table 4).

4.7. Scaling uncertainties

Previous studies have estimated stand-scale woody stem respiration on the basis of both surface area and sapwood volume. Sapwood volume has been related successfully to

Table 4 – Temperature-corrected rates of total woody stem respiration (R_w), separated into construction (R_c) and maintenance (R_m) respiration rates per unit of bole surface area for seven tree species in the Luquillo Experimental Forest, Puerto Rico

Species	Specific density[a] ($g\,cm^{-3}$)	ADI ($cm\,yr^{-1}$)	R_c ($g\,C\,m^{-2}\,h^{-1}$)	R_m ($g\,C\,m^{-2}\,h^{-1}$)	R_w ($g\,C\,m^{-2}\,h^{-1}$)	Maintenance (%)	Construction (%)
Cecropia schreberiana	0.36	0.36[b]–0.57[c]	0.009–0.015	0.128–0.133	0.142	90–94	6–10
Cyrilla racemiflora	0.53	0.09[d]–0.10[b]	0.003–0.004	0.076	0.800	95–96	4–5
Dacryodes excelsa	0.53	0.25[b]–0.48[e]	0.010–0.018	0.098–0.108	0.117	84–92	8–16
Manilkara bidentata	0.89	0.24[c]–0.55[e]	0.016–0.035	0.093–0.113	0.128	73–88	12–27
Micropholis garciniifolia	0.61	0.03[f]–0.07[g]	0.001–0.003	0.037–0.039	0.040	92–97	3–8
Prestoea montana	0.31[i]	0.01–0.07[h]	0.0004–0.002	0.067–0.068	0.068	98–100	0–2
Tabebuia rigida	0.52	0.03[f]	0.0009	0.050	0.051	98	2

Published values of specific density and annual diameter increment (ADI) for each species were used to estimate construction respiration.

[a] Reyes et al. (1992).
[b] Weaver (1983).
[c] LFDP dataset (http://luq.lternet.edu).
[d] Weaver (1986).
[e] Crow and Weaver (1977).
[f] Weaver et al. (1986).
[g] Weaver (2001).
[h] Lugo and Batlle (1987).
[i] Baker et al. (2004).

respiration rate in some forests where detailed information is available (Ryan et al., 1994; Lavigne et al., 1996; Lavigne and Ryan, 1997; Law et al., 1999), but sapwood volume is unknown in many tropical forests because of high species diversity, high variation among species, difficulty in sapwood-heartwood differentiation and, in some instances, coring difficulties due to excessive tree hardness (e.g., "hurricane wood"). Therefore, other scalars such as stem surface area have proved equally successful (Lavigne et al., 1996; Levy and Jarvis, 1998; Yokota and Hagihara, 1998). We chose to estimate woody stem respiration on a surface area basis so that we could compare our estimates directly against those of Odum and Jordan (1970) and because most ecosystem fluxes are expressed on an area basis.

5. Conclusions

Estimates of daytime carbon uptake are numerous, while those of carbon loss are scarce, especially for tropical regions. In this study, we showed that woody stem respiration rates vary among tree species located at different elevations in the LEF and showed that these differences remained when rates were corrected for temperature. Increases in stem respiration rates lagged behind increases in stem temperature by approximately 6 h. Simulated landscape-scale rates of woody stem respiration declined with elevation in the LEF and represented approximately 10% of estimated annual GPP in this forest. Construction costs were 2–27% of total stem respiration and varied by species. Woody stem respiration is a critical component of carbon flux estimates in tropical forests, and extrapolations of forest metabolism over large spatial regions are important for evaluating large-scale effects such as global climate change or other alterations to carbon cycling.

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