

Wood CO₂ efflux in a primary tropical rain forest

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Abstract

The balance between photosynthesis and plant respiration in tropical forests may substantially affect the global carbon cycle. Woody tissue CO₂ efflux is a major component of total plant respiration, but estimates of ecosystem-scale rates are uncertain because of poor sampling in the upper canopy and across landscapes. To overcome these problems, we used a portable scaffolding tower to measure woody tissue CO₂ efflux from ground level to the canopy top across a range of sites of varying slope and soil phosphorus content in a primary tropical rain forest in Costa Rica. The objectives of this study were to: (1) determine whether to use surface area, volume, or biomass for modeling and extrapolating wood CO₂ efflux, (2) determine if wood CO₂ efflux varied seasonally, (3) identify if wood CO₂ efflux varied by functional group, height in canopy, soil fertility, or slope, and (4) extrapolate wood CO₂ efflux to the forest. CO₂ efflux from small diameter woody tissue (<10 cm) was related to surface area, while CO₂ efflux from stems >10 cm was related to both surface area and volume. Wood CO₂ efflux showed no evidence of seasonality over 2 years. CO₂ efflux per unit wood surface area at 25° (F_A) was highest for the N-fixing dominant tree species *Pentaclethra macroloba*, followed by other tree species, lianas, then palms. Small diameter F_A increased steeply with increasing height, and large diameter F_A increased with diameter. Soil phosphorus and slope had slight, but complex effects on F_A . Wood CO₂ efflux per unit ground area was $1.34 \pm 0.36 \mu\text{mol m}^{-2} \text{s}^{-1}$, or $508 \pm 135 \text{ g C m}^{-2} \text{ yr}^{-1}$. Small diameter wood, only 15% of total woody biomass, accounted for 70% of total woody tissue CO₂ efflux from the forest; while lianas, only 3% of total woody biomass, contributed one-fourth of the total wood CO₂ efflux.

Keywords: autotrophic respiration, branch respiration, canopy structure, carbon balance, plant functional group, seasonality, slope, soil phosphorus, tropical wet forest, woody tissue respiration

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Introduction

The balance between photosynthesis and plant respiration in tropical forest ecosystems has the potential to impact global carbon balance. Tropical forests account for more than one-third of global plant carbon uptake (Saugier *et al.*, 2001), and at least half of this carbon is released back into the atmosphere each year in plant respiration (Edwards *et al.*, 1981; Chambers *et al.*, 2004). The overall balance between carbon uptake and release remains unclear for tropical forests, because of inade-

quate knowledge of variation across landscapes and over time, and very limited measurements of respiration rates for tropical trees.

Woody tissue releases a proportion of total assimilated CO₂ back into the atmosphere, but estimates vary widely for tropical forests. The majority of recent estimates are in the range of 7–14% (Odum, 1970; Ryan *et al.*, 1994; Meir & Grace, 2002; Chambers *et al.*, 2004), while some earlier estimates are ~25% (Yoda, 1967; Whitmore, 1984), to as high as 50% (Müller & Nielson, 1965). Early wood CO₂ efflux studies performed in tropical rain forests were based on detached samples (Müller & Nielson, 1965; Yoda, 1967, 1983; Whitmore, 1984), which may have introduced errors associated

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with rapid diffusion of CO₂ upon excision (Teskey & McGuire, 2005), or other methodological biases. More contemporary studies in tropical forests measured wood efflux *in situ*, but only from lower boles (Ryan *et al.*, 1994; Nepstad *et al.*, 2002; Chambers *et al.*, 2004). Several authors have agreed on the importance of measuring branch CO₂ efflux high in the canopy (Sprugel, 1990; Ryan *et al.*, 1996; Damesin *et al.*, 2002; Vose & Ryan, 2002), but until now this has not been attempted in a tropical forest.

Many recent studies in temperate systems have estimated wood CO₂ efflux in terms of maintenance vs. growth respiration (Ryan, 1990; Ryan *et al.*, 1995; Sprugel *et al.*, 1995; Maier, 2001; Damesin *et al.*, 2002). Separating maintenance from growth respiration in tropical rain forests is difficult because they have no dormant season. Seasonality in wood CO₂ efflux has been found in tropical forests with distinct dry seasons (Nepstad *et al.*, 2002; Chambers *et al.*, 2004), but no seasonal study has yet been done in a tropical forest with a less pronounced dry season. We devised a novel approach to both measuring and extrapolating wood CO₂ efflux throughout the canopy, and also conducted a separate study to address the question of seasonality in woody tissue CO₂ for a tropical forest without a dormant season or a pronounced dry season.

Access has generally been the limiting factor for efforts to understand how woody tissue CO₂ efflux varies with canopy structure and across landscape gradients in tropical rain forests. This study presents results from an intensive 2-year field campaign where we measured bole and branch CO₂ efflux using a portable scaffolding tower to access wood from forest floor to canopy top across gradients of soil fertility and slope in a primary tropical rain forest in Costa Rica. We also were able to estimate small diameter wood biomass and surface area distribution using the wood harvested from the tower transects, which greatly improved our ability to extrapolate wood CO₂ efflux to the forest.

This study had four objectives. First, we sought to better understand the physiological sources of woody tissue CO₂ efflux by determining whether efflux measurements were related to wood volume or surface area. These units are also important for modeling exercises and extrapolation, because preferred units (volume or area based) determine what stand-level information will be needed in order to estimate wood CO₂ efflux for the forest. For the second objective, we investigated seasonal variation in wood CO₂ efflux, and whether or not this variation tracked changes in rainfall, temperature, or light. The third objective was to characterize the sources variation in wood CO₂ efflux. For this, we constructed competing analysis of covariance (ANCOVA) models with both structural variables (height, diameter,

plant functional group, branch, or stem) and landscape variables (slope, soil phosphorus). The final objective was to estimate net woody tissue CO₂ exchange for the forest with estimates of wood biomass, surface area, and CO₂ efflux rates stratified by canopy height, diameter, and plant functional group.

Materials and methods

Study site

La Selva Biological Station is located in the Caribbean lowlands of northern Costa Rica (10°20'N, 83°50'W), at 37–150 m above sea level. La Selva is classified as premontane tropical wet forest in the Holdridge life-zone system (Hartshorn, 1983). The mean annual rainfall is approximately 4 m, and the mean annual temperature is 26 °C. We sampled within La Selva's 515 ha of primary (old growth) forest. The average canopy height for the primary forest, including gaps, is approximately 20 m, and emergent trees range from 30 to 60 m (Clark *et al.*, 1996, 2004). The basal area of the primary forest is approximately 24 m² ha⁻¹, with about 500 trees ha⁻¹, and a quadratic mean diameter of 24 cm, based on an inventory of woody stems ≥10 cm in diameter (Clark & Clark, 2000a). Detailed information about La Selva soils and plant communities can be found in McDade *et al.* (1994).

Sample design: tower sites

We designed our study to test whether any landscape patterns in soil phosphorus or slope caused differences in woody CO₂ efflux. Phosphorus, rather than nitrogen, is likely limiting in this system (McDade *et al.*, 1994), and previous studies of the primary forest at La Selva found fewer and larger trees in fertile flat sites, while a higher density of smaller trees were found on steep slopes (Clark & Clark, 2000a). We used a stratified random sample to locate sites across the landscape, with three slope × three soil phosphorus classes. A soil phosphorus map of the primary forest area of La Selva with cells of 10 m × 10 m was created by krigging data of phosphorus concentrations from the top 10 cm of soil sampled at a resolution of 50 m × 100 m. A digital elevation map provided slope for the same 10 m × 10 m cells. The landscape was stratified into nine slope × phosphorus classes of equivalent area, using Arc's SLICE command (ArcGIS, Environmental Systems Research Institute, Redlands, CA, USA). Seventy-two possible tower sites were selected to the nearest meter using eight random coordinates from each of the nine classes, excluding swamps, permanent plots (to avoid disturbing long-term research), soils

near streams, and sites close to trails. The 72 randomly selected sites were visited to assess the feasibility of tower construction, and 27 of these were discarded, approximately half because of wet or rocky terrain, and half because of large stems [>10 cm diameters at breast height (DBH)] inside the tower footprint. Ultimately, 45 primary forest tower sites were selected in this manner, five sites in each of the nine slope \times phosphorus classes. Before each tower was constructed, we measured slope with a clinometer at the center of each tower site as the mean of two point measurements, taken 90° from one other. We used these slope data for all further analyses, rather than slope derived from the digital-elevation map.

Because our original stratification did not capture any forest gaps, we selected 10 of the original 45 sites as starting points for a procedure to locate 10 additional 'low canopy height' sites. At each of these 10 sites, we selected one low canopy height tower site as the first location along a randomly oriented 50 m transect that had vegetation less than 16 m in height. At each new site, we measured slope and used the krigged soil map to estimate soil phosphorus level.

At each original and low canopy tower site, an aluminum walk-up scaffolding tower (Upright Inc., Dublin, Ireland) was constructed to the top of the canopy. These wood CO₂ efflux data represent sampling from 41 of the original 45 tower sites (including at least three towers in each of the nine slope \times phosphorus classes), and eight of the 10 low canopy height tower sites for a total of 49 towers. The wood biomass and wood surface area data used to estimate CO₂ efflux for the forest represent sampling from all 45 original tower sites, but no low canopy height sites, (because they did not represent the forest). While this paper focuses only on woody tissue net CO₂ exchange, the towers sampling design and construction were part of a larger project where we sought to characterize canopy structure and function in a tropical rain forest.

Towers were constructed one section at a time, and all biomass within a section was harvested as each tower was built. Each section was $2.45 \text{ m} \times 1.86 \text{ m} \times 1.86 \text{ m}$ (L \times W \times H), with a footprint area of 4.56 m^2 . The number of sections for each tower varied with canopy height, ranging from one section (1.86 m) to 24 sections (44.64 m). Harvested woody material was measured for length and diameter. After completing tower construction and harvesting, we measured CO₂ efflux on all intact woody species accessible from the side of the tower. Care was taken to avoid sampling near cut ends of stems or branches. We then dismantled the tower and moved it to the nearest preselected random site. Each tower site was sampled only once, and tower construction and sampling occurred continuously from June

2003 to June 2005. These data represent 1226 wood CO₂ efflux measurements: two replicate measurements each of 613 individual branches or stems. Efflux samples represent over 110 species, 90 genera, and 52 families. We separated woody species into four functional groups: trees, palms, lianas, and *Pentaclethra maculosa*, a leguminous tree species with 37% of the above-ground biomass (Clark & Clark, 2000a). Palm rachises measured in this study were woody and were included as branches.

The sampling scheme was not designed to take an unbiased sampling of wood biomass, surface area or CO₂ efflux for stems or branches >10 cm in diameter, because the tower could not be constructed within 1 m of large trees, or where large branches passed through the tower column. Therefore, large diameter stems and branches in the upper canopy were difficult to reach from the tower. To capture CO₂ efflux for large diameter wood, we measured efflux at approximately breast height on all woody stems surrounding the tower that had foliage represented anywhere in the tower footprint.

Sample design: seasonal measurements

To detect any seasonal changes in woody tissue net CO₂ exchange, an additional 10 trees (five from each of two plots), were selected from long-term 0.5 ha plots in the primary forest landscape of La Selva (Clark & Clark, 2000a). We randomly chose canopy-level trees that represented five families, five genera, and six species, with above-buttress diameters ranging from 34 to 56 cm (Table 1). These 10 trees were located in the same stand of primary forest, but were independent of the tower sampling sites. We sampled each tree once a month for 23 months from July 2003 to May 2005, with no measurements in December 2004 or January 2005 because of flooding. CO₂ efflux was measured in two locations on each tree, at heights ranging from 1.3 to 4.0 m, depending on buttress height.

CO₂ efflux measurements

Woody CO₂ efflux was measured using LCA-3 and LCA-4 open-system infrared gas analyzers (IRGA, Analytical Development Company, Hoddeson, UK). Woody tissue net CO₂ flux may be considered the sum of three terms: woody tissue respiration (+ flux), bark photosynthesis (–flux), and CO₂ dissolved in the xylem sap (+ if diffusing out, – if transported away; Cernusak & Marshall, 2000; McGuire & Teskey, 2004; Bowman *et al.*, 2005). We used unshielded clear polycarbonate custom-made chambers that allowed bark photosynthesis in an attempt to measure the sum of

Table 1 Species, family, and diameter of 10 trees measured each month for the stem CO₂ efflux seasonal study

| Species | Family | Above-buttress diameter (cm) | Number of trees measured |
|-------------------------------|----------------|------------------------------|--------------------------|
| <i>Virola sebifera</i> | Myristicaceae | 44.1 | 1 |
| <i>Virola koschnyi</i> | Myristicaceae | 34.6 | 1 |
| <i>Apeiba membranacea</i> | Malvaceae | 49.4 | 1 |
| <i>Cespedesia spathulata</i> | Ochnaceae | 46.7 | 1 |
| <i>Laetia procera</i> | Flacourtiaceae | 49.0 | 1 |
| <i>Pentaclethra macroloba</i> | Fabaceae | 36.7, 42.0, 49.4, 53.7, 55.6 | 5 |

Each tree was measured once a month for 23 months.

all three terms, throughout the vertical canopy transect. Chambers had neoprene gaskets and were clamped to stems or branches for measurements. Four chamber sizes were used, depending on the diameter of the woody material. Wood surface areas inside the four chambers were 7, 15, 16, and 22 cm², and sampled wood ranged from 0.7 to 90.0 cm in diameter. Chamber areas were calculated as the area enclosed by the neoprene gasket + half the area of the gasket (assuming half the CO₂ from the area under the gasket would diffuse inside the chamber and half would diffuse outside the chamber). Small 9 V battery-operated fans were installed to stir the air inside all but the smallest (7 cm²) chambers. Air-flow rates through the chambers ranged from 223 to 297 μmol s⁻¹ and chamber seals were checked with a flowmeter. Stable reference air CO₂ concentrations were maintained by drawing air through a 19 L mixing chamber. The difference in CO₂ concentration between the reference and the chamber was recorded after it had been stable for at least 2 min. We measured CO₂ efflux twice on each stem and branch, with measurements ~90° from one another, and replicates were averaged before analysis. Diameter was measured at the center point of chamber attachment.

At each CO₂ efflux measurement site, surface wood temperature was taken with a thermocouple thermometer. All fluxes were corrected to a reference temperature of 25 °C using a Q₁₀ of 2.0. Ryan *et al.* (1994) found stem respiration Q₁₀ values of 2.1 and 2.2 for two tree species at La Selva, and Meir & Grace (2002) found mean stem respiration Q₁₀ values of 1.6 and 1.8 for two tropical rain forests in Brazil and Cameroon.

We randomly selected subsamples of the harvested woody material for specific gravity measurements to calculate CO₂ efflux rates per unit biomass. Wood sample volume was measured by water displacement, and sample mass was measured after oven drying to constant mass at 60 °C. Stems measured for CO₂ efflux from the ground, where the wood was not representative of wood harvested in the tower footprint, were

assigned specific gravity based on published values by species (Hidayat & Simpson, 1994; Brown, 1997; Segura & Kanninen, 2005). When species were unknown or specific gravity values were not found in the literature for a particular species, a La Selva stand-level mean specific gravity was used, 0.53 g cm⁻³ (Muller-Landau, 2004).

Levy-Jarvis analyses: woody CO₂ efflux per surface area vs. volume

We used a graphical technique to discern the best units for expressing wood CO₂ efflux and for extrapolating to the forest (Levy & Jarvis, 1998). If the CO₂ efflux rate is proportional to surface area, measured CO₂ efflux per unit volume will be positively and linearly correlated with the reciprocal of diameter. If the CO₂ efflux rate is proportional to volume (or biomass), measured CO₂ efflux on an area basis should be positively and linearly correlated with diameter. We examined the volume vs. surface area components for four canopy height classes: bottom 2 m (0–2 m), lower canopy (2–15 m), mid canopy (15–25 m), and upper canopy (25+ m).

Statistical analyses: seasonal changes in wood CO₂ efflux

The 10 tree boles measured once a month for 2 years were analyzed with a repeated measures ANOVA in SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA) with individual tree as the 'subject.' We tested for differences in month, species, or their interaction on CO₂ efflux corrected to 25 °C. Monthly stem CO₂ efflux rates for individual species and averaged over all species were regressed against total monthly rainfall, mean monthly day and night temperature, and mean monthly photosynthetically active radiation (PAR) from the La Selva Biological Station long-term weather station data base (Organization for Tropical Studies; <http://www.ots.duke.edu/>).

Statistical analyses: sources of variation in CO₂ efflux across canopy and landscape gradients

We constructed an *a priori* set of candidate ANCOVA models with structural and environmental variables to describe both area-based wood CO₂ efflux corrected to 25 °C (F_A : $\mu\text{mol m}^{-2} \text{s}^{-1}$), and mass-based wood CO₂ efflux corrected to 25 °C (F_M : $\text{nmol kg}^{-1} \text{s}^{-1}$). Models were developed for two purposes: (1) to investigate the primary sources of variation in woody tissue CO₂ efflux and (2) to estimate efflux rates and errors for extrapolating rates to the forest. For each purpose, the most appropriate units were used as determined by the Levy–Jarvis analysis. The predictor variables considered were: natural log of diameter ($\ln D$: continuous variable, cm); slope (S : continuous variable, degrees); plant functional group (G : liana, *P. macroloba*, tree or palm); soil phosphorus class (P : low P range: 0.65–0.86 mg g⁻¹; medium P range: 0.88–1.11 mg g⁻¹; high P range: 1.12–1.57 mg g⁻¹); canopy height class (H : bottom 2 m = 0–2 m; lower canopy = 2–15 m; mid canopy = 15–25 m; upper canopy 25+ m); and wood type (WT: branch or stem). Diameter, F_A , and F_M were natural log-transformed to account for nonnormal distributions and heteroscedasticity in the residuals.

We evaluated competing models using Akaike's Information Criterion (AIC), which penalizes a model based on its number of parameters. The best statistical model minimizes the value of AIC (Burnham & Anderson, 1998). For each candidate model, maximum likelihood estimates of model parameters and AIC were calculated using Proc Mixed Method = ML in SAS Version 9.1 (SAS Institute Inc.). Normally distributed errors were verified by examining residuals after model fitting.

The best-fit models for both $\ln F_A$ and $\ln F_M$, as determined by the lowest AIC values, were used in all further analyses. Least-squares means for all interactions in the selected best-fit model were calculated for class variables and for specified values of continuous variables. Antilogs of least-squares means were plotted to make graphs easier to read, and only values within the range of diameters sampled for each class variable were plotted.

Estimating woody tissue CO₂ efflux for the forest

We estimated wood CO₂ efflux for wood <10 cm diameter using surface area, and for wood >10 cm using biomass, based on the results from the Levy–Jarvis analysis (Fig. 1). We used a two-part approach to assemble the biomass and surface area data needed for forest level estimates of wood CO₂ efflux, because the tower sampling was not designed to provide an unbiased estimate of wood >10 cm diameter (we could

not locate our tower over large stems). We used tower sample estimates of surface area for wood <10 cm diameter, and woody biomass from the eighteen 0.5 ha plots measured by Clark & Clark (2000a) for wood >10 cm in diameter. Biomass from the tower samples for wood <10 cm diameter was subtracted from the total biomass calculated from the 0.5 ha plot data to estimate biomass for wood >10 cm in diameter. We used mean wood CO₂ efflux rates for different diameter classes, height classes, and functional groups paired with the appropriate biomass or surface area estimates to calculate total flux per unit ground area. As wood CO₂ efflux rates differed little with slope and soil phosphorus, we did not use that information in our estimates.

For wood <10 cm diameter, CO₂ efflux per surface area (F_A) and wood surface area per ground area estimates were stratified by functional group (trees, lianas, palms and *P. macroloba*), height class (bottom 2 m, lower canopy, mid canopy, and upper canopy), and diameter class (0–2, 2–5, and 5–10 cm). Least-squares means and 95% confidence limits were calculated for each group, height class, and at diameters 1, 3.5, and 7.5 cm (class mid-points) using the best-fit model for F_A . Means and confidence limits were then back transformed and used with corresponding surface areas to estimate woody CO₂ for the forest for wood <10 cm diameter.

For wood >10 cm, CO₂ efflux per biomass (F_M) and biomass per ground area were estimated by diameter class (10–20, 20–30, 30–40, 40–60, 60–80, 80–100, and 100+ cm), and functional group (trees, lianas, palms, and *P. macroloba*). Height was not used for these estimates because almost all of the large diameter efflux measurements were taken in the first 2 m. Efflux rates for wood >10 cm were calculated for diameter class midpoints from the best-fit model for F_M in a similar manner to that used for wood <10 cm. Woody biomass was estimated from eighteen 0.5 ha plots, established through stratified random sampling in the primary forest of La Selva. Above-buttress bole diameters were measured on all trees ≥ 10 cm in diameter in each 0.5 ha plot in 2004 (for more information on how plots were designed and sampled, see Clark & Clark, 2000a). We calculated total biomass for each tree, palm and *P. macroloba* in the 18 plots using the following allometric equation from Chave *et al.* (2005):

$$\text{TAGB} = \rho \times \exp(-1.239 + 1.980(\ln D) + 2.207(\ln D)^2 - 0.0281(\ln D)^3), \quad (1)$$

where TAGB is the total above-ground biomass (kg), ρ the wood specific gravity (g cm^{-3}), and D the above-buttress diameter (cm). Specific gravity (ρ) used for trees = 0.53 g cm^{-3} (Muller-Landau, 2004), for *P. macro-*

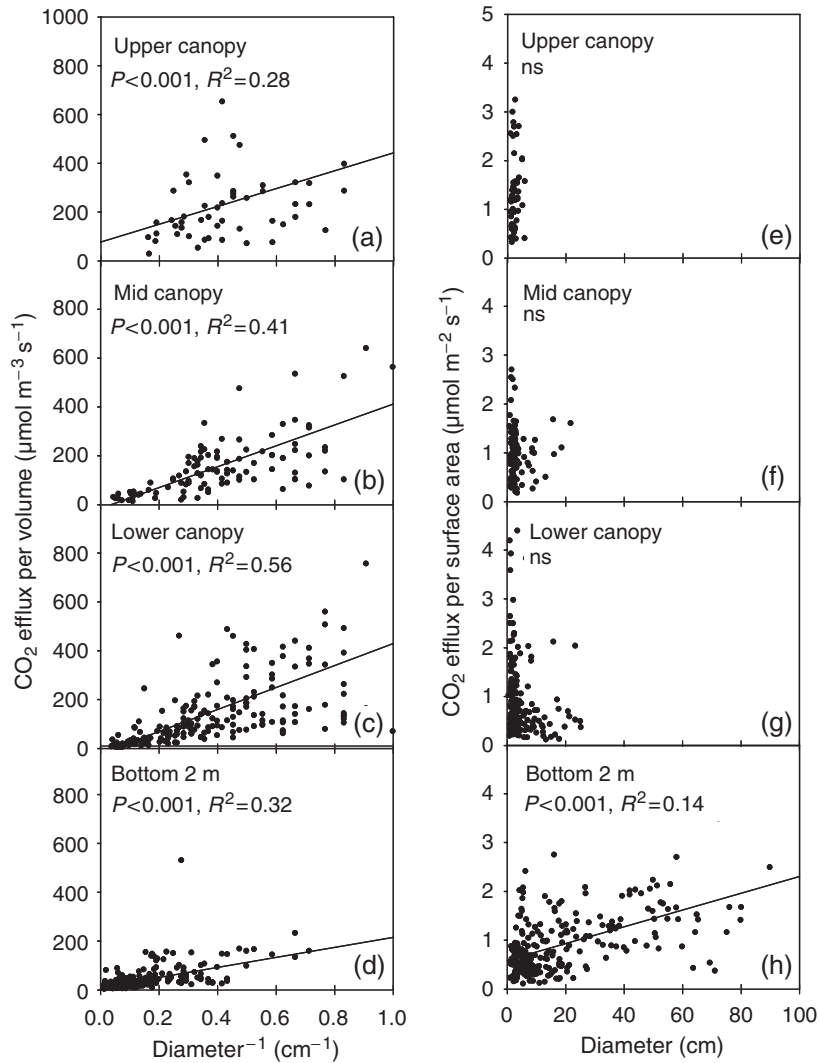


Fig. 1 In the upper, mid, and lower canopy, the relationship between the reciprocal of diameter and efflux per unit volume (a–c) and the lack of relationship between diameter and efflux per unit area (e–g) indicate that wood CO₂ efflux for all wood above 2 m was primarily dependent on surface area, and not volume. Unlike canopy rates, wood CO₂ efflux in the bottom 2 m was dependent on both volume and surface area (d and h). Wood CO₂ efflux measurements were corrected to 25 °C and expressed on a volume basis vs. the reciprocal of diameter (a–d), and on an area basis vs. diameter (e–h). Data are also separated by canopy class: upper canopy, mid canopy, lower canopy, and the bottom 2 m.

$loba = 0.60 \text{ g cm}^{-3}$ (Segura & Kanninen, 2005), and for palms = 0.31 g cm^{-3} (Baker *et al.*, 2004). We used a different allometric equation for lianas from Gehring *et al.* (2004)

$$\text{TAGB} = \exp(-7.114 + 2.276(\ln D)). \quad (2)$$

Mean plot total biomass (kg m^{-2}) estimates by group were assumed to include small branches, but not small stems (only stems ≥ 10 cm were measured in the 0.5 ha plots). We subtracted the small branch biomass estimated from the tower footprint data from total biomass for each group to get the percent of total biomass by

group that consisted of large diameter wood. Plot means and standard errors were calculated for large diameter wood biomass per ground area (kg m^{-2}) by plant functional group and diameter class.

Results

Levy–Jarvis analysis: CO₂ efflux per surface area vs. volume

In the upper, mid, and lower canopy, the analysis showed that CO₂ efflux was related to surface area (Figs 1a–c), and not to diameter (Figs 1e–g). In the

bottom 2 m, the analysis showed that CO₂ efflux was related to both volume and surface area (Figs 1d and h).

Seasonal changes in wood CO₂ efflux

Stem F_A did not vary with month ($P = 0.90$), species ($P = 0.18$), or their interaction ($P = 0.34$). Neither average F_A (Fig. 2a) nor F_A by species showed any trends with rainfall, temperature, or PAR (Figs 2b–d).

Model selection results

Six predictor variables and all of their interactions could yield hundreds of possible models, so we limited the set of candidates before model selection. Using a limited set of *a priori* candidate models also reduces the effects of

overfitting and erroneous correlations (Burnham & Anderson, 1998). Preliminary full-model fits showed five of the six predictor variables to be highly significant, therefore all subsequent candidate models contained these five variables ($\ln D$, G , P , H , and S); while WT was found to be redundant and dropped from further analysis. Both $\ln F_A$ and $\ln F_M$ were modeled with linear combinations of the following predictor variables: $\ln D$, G , P , H , and S ; the two-way interactions $\ln D \times G$, $\ln D \times P$, $\ln D \times H$, $\ln D \times S$, $G \times P$, $G \times H$, $G \times S$, $P \times H$, $P \times S$, and $H \times S$; and the three-way interactions $\ln D \times G \times P$, $\ln D \times G \times S$, and $\ln D \times P \times S$. The final *a priori* model set contained 143 models with 8–18 parameters. Surprisingly, the best-fit models with the lowest AIC values for predicting both $\ln F_A$ and $\ln F_M$ were exactly the same (Table 2). Model-derived least-squares means and 95% confidence limits of F_A and F_M are displayed for all height classes at five representative diameters (Table 3).

Sources of variation in wood CO₂ efflux

Because the Levy–Jarvis analysis showed that wood CO₂ efflux was related to surface area at all heights and diameters (Figs 1a–d), we used efflux per unit surface area to investigate variation across canopy and landscape gradients. F_A increased with increasing slope, with greater effect in small diameter wood (Fig. 3a) and low soil P (Fig. 3d). The dominant tree species of this ecosystem, *P. maculosa*, had the highest F_A at all diameters (Fig. 3b). Liana F_A sharply decreased with diameter, and the highest liana rates were comparable with high rates for *P. maculosa* at the smallest diameters (Fig. 3b). None of the lianas sampled were greater than 9 cm in diameter, and at this maximum diameter, lianas had lower F_A than all dicot tree species (Fig. 3b). Palms had the lowest overall F_A for all diameters, and showed little overall change in F_A with diameter (Fig. 3b). F_A of wood in the bottom 2 m increased with increasing diameter (Fig. 3c). F_A of small diameter wood in the canopy was much greater than F_A of small diameter wood in the bottom 2 m, and F_A of wood less than 15 cm in diameter increased sharply with height, given the same diameter (Fig. 3c). Our CO₂ efflux rates for large diameter wood could be biased toward lower heights because 82% of our CO₂ efflux measurements from wood greater than 10 cm, and 92% of measurements from wood greater than 20 cm were taken <2 m from the ground.

Small diameter wood biomass and surface area distribution

Biomass of all woody tissue <10 cm in diameter, including both branches and small stems, was 2.4 kg m⁻².

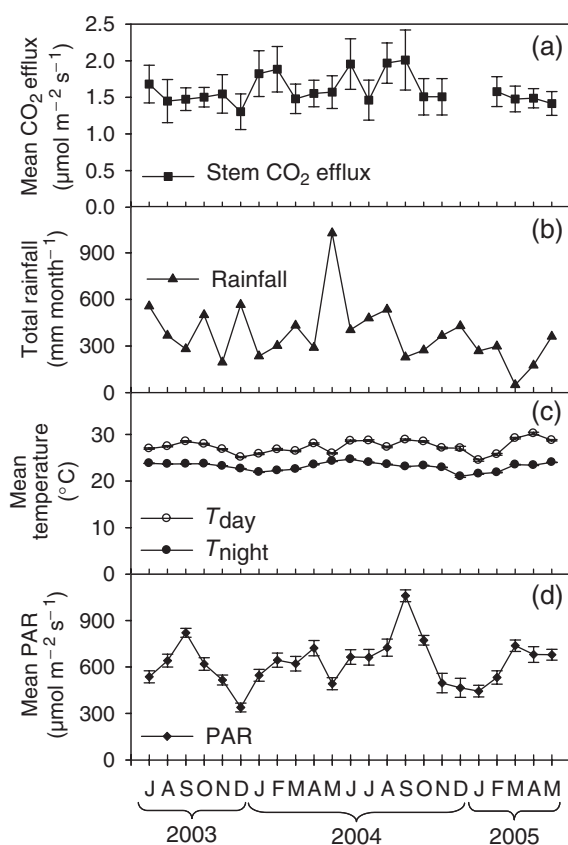


Fig. 2 No clear seasonality in wood CO₂ efflux is evident in this system. The effect of ‘month’ was not significant in a repeated measures ANOVA; and no correlations were found between monthly mean CO₂ efflux and rainfall, temperature or photosynthetically active radiation (PAR). Permanent plot mean monthly stem CO₂ efflux at 25 °C (a), total monthly rainfall (b), mean monthly daytime and nighttime temperatures (c), and mean monthly PAR (d) are shown over 23 months. Error bars represent standard error (some error bars may be hidden by symbols).

Table 2 Predictor variables, their *P*-values, and model *R*² values for the best-fit model predicting both the natural log of area-based woody CO₂ efflux at 25 °C (ln *F*_A), and the natural log of biomass-based woody CO₂ efflux at 25 °C (ln *F*_M)

| Predictor variable | Abbreviation | Coefficient <i>P</i> -values for model predicting ln <i>F</i> _A | Coefficient <i>P</i> -values for model predicting ln <i>F</i> _M | Factors or units (if applicable) |
|---|---------------------------|---|---|---|
| ln (diameter) | ln <i>D</i> | 0.10 | <0.0001 | Continuous (cm) |
| Plant functional group | <i>G</i> | 0.01 | 0.03 | <i>Pentaclethra. macroleoba</i> , tree, liana, palm |
| Soil phosphorus | <i>P</i> | <0.0001 | <0.0001 | Low P, medium P, high P |
| Height class | <i>H</i> | <0.0001 | <0.01 | Bottom 2 m, lower canopy, mid canopy, upper canopy |
| Slope | <i>S</i> | <0.0001 | <0.0001 | Continuous: degrees |
| ln (diameter) × group | (ln <i>D</i> × <i>G</i>) | 0.02 | 0.04 | NA |
| ln (diameter) × slope | (ln <i>D</i> × <i>S</i>) | 0.02 | 0.05 | NA |
| ln (diameter) × height | (ln <i>D</i> × <i>H</i>) | <0.0001 | <0.0001 | NA |
| Phosphorus × slope | (<i>P</i> × <i>S</i>) | <0.01 | <0.01 | NA |
| <i>R</i> ² of best fit model | | 0.29 | 0.75 | |

Table 3 Least-squares means, lower 95% confidence limits (LCL), and upper 95% confidence limits (UCL) for area-based (*F*_A, μmol m⁻² s⁻¹) and mass-based (*F*_M, nmol kg⁻¹ s⁻¹) CO₂ efflux rates corrected to 25 °C in four canopy height classes at each of five representative diameters

| Diameter (cm) | Bottom 2 m (0–2 m); <i>F</i> _A (LCL, UCL; μmol m ⁻² s ⁻¹) | Lower canopy (2–15 m); <i>F</i> _A (LCL, UCL; μmol m ⁻² s ⁻¹) | Mid canopy (15–25 m); <i>F</i> _A (LCL, UCL; μmol m ⁻² s ⁻¹) | Upper canopy (25+ m); <i>F</i> _A (LCL, UCL; μmol m ⁻² s ⁻¹) |
|------------------|---|--|---|---|
| 1 | 0.42 (0.33, 0.53) | 0.93 (0.77, 1.12) | 0.86 (0.68, 1.08) | 0.87 (0.58, 1.29) |
| 5 | 0.54 (0.48, 0.60) | 0.64 (0.57, 0.72) | 0.79 (0.67, 0.93) | 1.37 (0.98, 1.92) |
| 10 | 0.60 (0.53, 0.68) | 0.54 (0.46, 0.64) | 0.76 (0.58, 0.99) | 1.67 (0.93, 3.01) |
| 40 | 0.75 (0.59, 0.94) | – | – | – |
| 80 | 0.83 (0.62, 1.12) | – | – | – |

| Diameter (cm) | Bottom 2 m (0–2 m); <i>F</i> _M (LCL, UCL; nmol kg ⁻¹ s ⁻¹) | Lower canopy (2–15 m); <i>F</i> _M (LCL, UCL; nmol kg ⁻¹ s ⁻¹) | Mid canopy (15–25 m); <i>F</i> _M (LCL, UCL; nmol kg ⁻¹ s ⁻¹) | Upper canopy (25+ m); <i>F</i> _M (LCL, UCL; nmol kg ⁻¹ s ⁻¹) |
|------------------|--|---|--|--|
| 1 | 447 (350, 570) | 854 (701, 1041) | 784 (585, 957) | 669 (438, 1022) |
| 5 | 106 (94, 119) | 112 (99, 127) | 140 (118, 166) | 249 (175, 355) |
| 10 | 57 (50, 64) | 47 (39, 56) | 68 (52, 90) | 163 (88, 303) |
| 40 | 16 (13, 21) | – | – | – |
| 80 | 9 (6, 12) | – | – | – |

Least-squares means and confidence limits were calculated as the antilogs of values from best-fit model results. Means were not extrapolated beyond the diameters actually sampled in each canopy class, resulting in empty cells.

A little over half of this total consisted of tree wood, while lianas, palms, and *P. macroleoba* contributed about 15% each (Figs 4a–d). Surface area of woody tissue <10 cm in diameter was 1.1 m² m⁻². Trees contributed a little less than half to the total surface area (Fig. 4f), lianas contributed almost one-third to the total (Fig. 4h), and palms and *P. macroleoba* contributed about 13% each

(Figs 4e and g). About 40% of tree small diameter biomass and surface area were in the lower canopy (2–15 m), with a fairly even distribution in the rest of the height classes (Figs 4b and f). Over three-fourths of both *P. macroleoba* and liana small diameter biomass and surface area were found above 15 m, in the mid and upper canopy (Figs 4a, e, d, and h), while palms accounted for

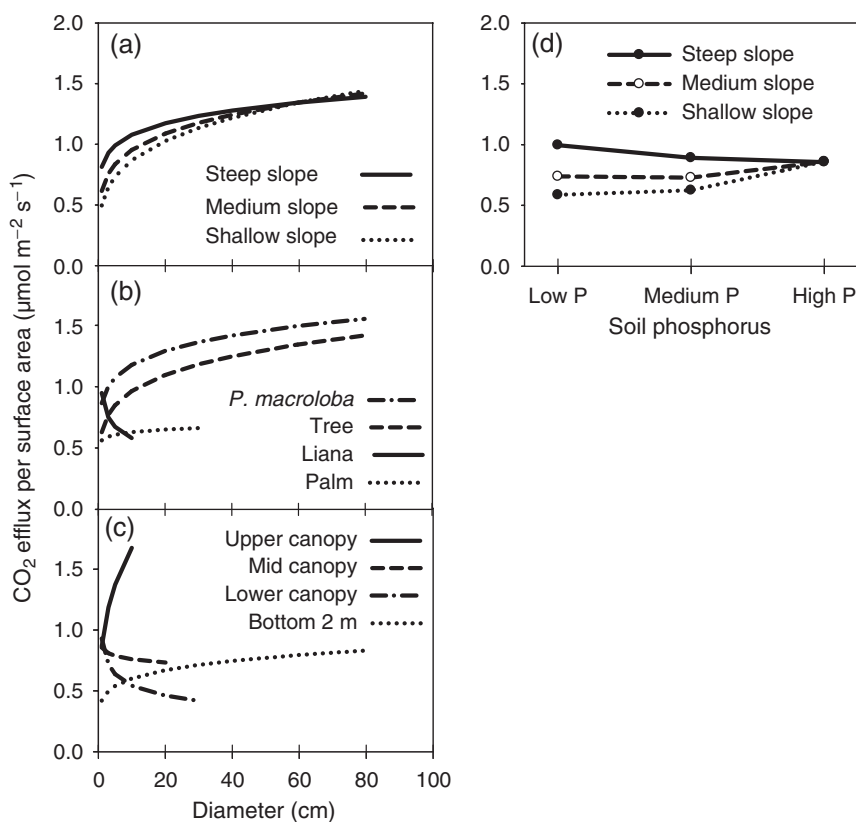


Fig. 3 The effect of increasing CO₂ efflux with increasing slope was greatest in small diameter wood (a), and at low soil P (d). CO₂ efflux increased with diameter for trees and *Pentaclethra macroloba* (b). For diameters less than 10 cm, CO₂ efflux increased steeply with height (c). Plots show least-squares means for significant interactions in the best-fit ANCOVA model (see Table 2) predicting wood CO₂ efflux per unit surface area at 25 °C in response to changes in diameter, plant functional group, soil phosphorus, slope, and canopy height. Antilogs of both ln (CO₂ efflux) and ln (diameter) are displayed. Least-squares means of interactions with slope (a and d) were calculated at the means of the upper-, middle-, and lower-thirds of the data set (steep slope = 23.1°; medium slope = 12.4°; shallow slope = 4.2°). Least-squares means of interactions with the variable diameter (a–c) were calculated for the range of the diameters observed for each specific category over a possible range of 1–80 cm.

virtually no biomass or surface area above 15 m (Figs 4c and g). Total biomass for all wood <10 cm was distributed evenly among diameter classes, with about one-third per class (Figs 4a–d). In contrast, the smallest diameter class (0–2 cm) accounted for 70% of the total <10 cm wood surface area (Figs 4e–h). Both total small diameter biomass and total surface area were distributed similarly by canopy height, with approximately 10% in the bottom 2 m, and about 30% in each of the lower, mid and upper canopy levels.

Large diameter wood biomass distribution

Small branches (<10 cm) were 11% of woody biomass for trees, 7% for *P. macroloba*, 17% for palms, and 49% for lianas, based on the small branches harvested from the tower transects and the 0.5 ha plot estimates of total woody biomass. Based on these percentages and the

total biomass calculated from the 0.5 ha plot data, the total aboveground biomass of wood >10 cm diameter was 13.8 kg m⁻². The contribution of trees to this total was 59%, while *P. macroloba* contributed 35%, palms only 6%, and lianas less than 1% (Fig. 5a). The largest proportion (31%) of woody biomass >10 cm was in the 40–60 cm diameter class (Fig. 5a). The rest of the diameter classes were fairly evenly distributed with about 15% of the biomass each, except for 80–100 cm and 100 + cm, which accounted for only about 5% of the total large diameter biomass each (Fig. 5a).

Forest estimates of wood CO₂ efflux

Wood CO₂ efflux per unit ground area for woody tissue <10 cm in diameter was $0.95 \pm 0.31 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($359 \pm 118 \text{ g C m}^{-2} \text{ yr}^{-1}$). Of this total, about 40% was from trees, 30% from lianas, 20% from *P. macroloba*, and

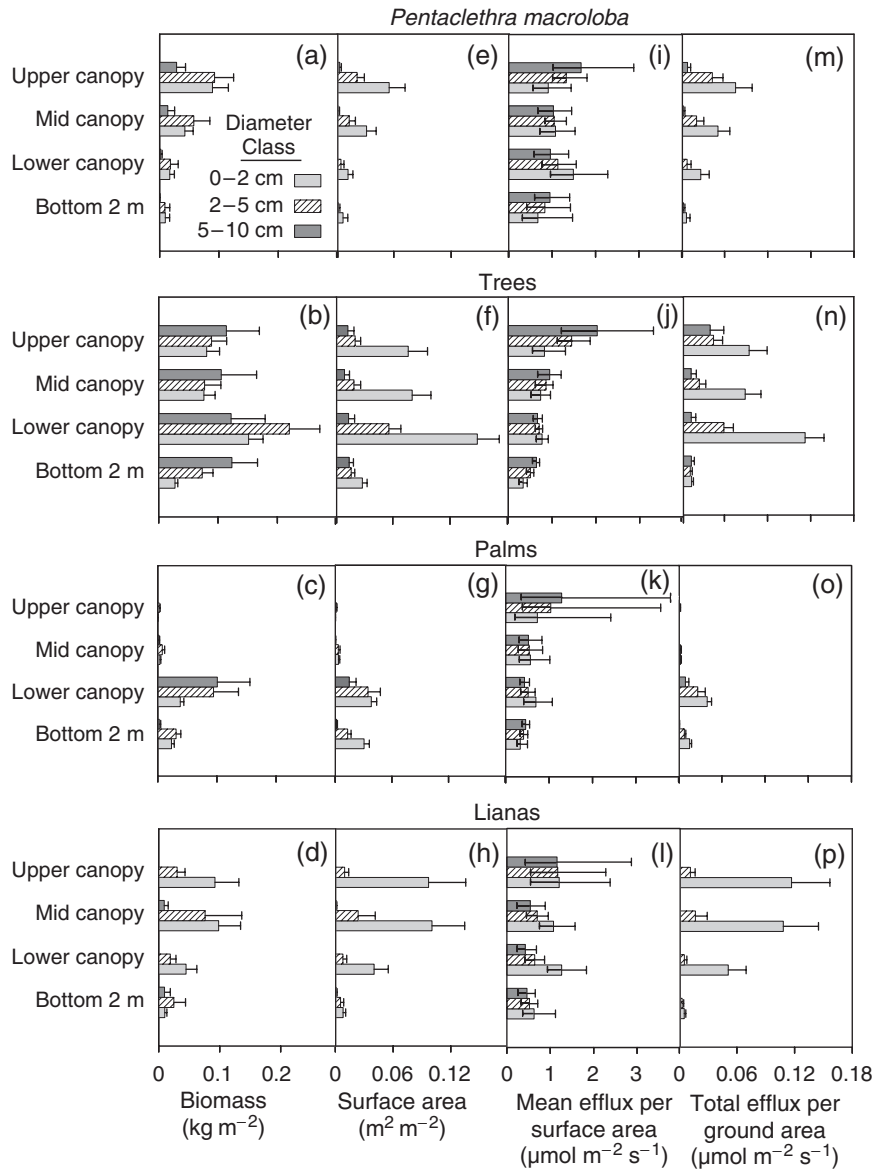


Fig. 4 Small diameter (<10 cm) wood biomass distribution (a–d), wood surface area distribution (e–h), mean CO₂ efflux rates at 25 °C per unit wood surface area (i–l), and total CO₂ efflux rates per unit ground area (m–p) by functional group, canopy height class, and diameter class. Lianas contributed a substantial portion of the total small diameter wood CO₂ efflux in the upper and mid canopy (p) because of their large surface area (h). The greatest proportion of tree biomass (b), surface area (f), and total CO₂ efflux (n) was in the lower canopy. Wood biomass and surface area per ground area were calculated as the mean tower small diameter wood biomass and surface area in each category. Error bars for (a–h) represent standard errors of the means among towers. CO₂ efflux per surface area values and errors were calculated as the antilogs of least-squares means and 95% confidence limits from the best-fit model, resulting in asymmetrical error bars for (i–l). Mean tower wood surface area per ground area and standard errors were multiplied by CO₂ efflux per surface area model-derived means to yield CO₂ efflux per unit ground area values and errors (m–p).

10% from palms (Figs 4m–p). The upper, mid and lower canopy height classes each contributed about 30% each, while only about 10% of the small diameter wood CO₂ efflux came from the bottom 2 m (Figs 4m–p). Over 70% of the CO₂ efflux for wood <10 cm came from the 0 to 2 cm diameter class, about 20% from the 2 to 5 cm class, and only about 10% from

the 5 to 10 cm class (Figs 4m–p). Because of their large surface area (Fig. 4h), lianas contributed a substantial portion of the total small diameter wood CO₂ efflux in the upper and mid canopy (Fig. 4p). The greatest proportion of tree biomass (Fig. 4b), surface area (Fig. 4f), and total CO₂ efflux (Fig. 4n) was in the lower canopy (2–15 m in height).

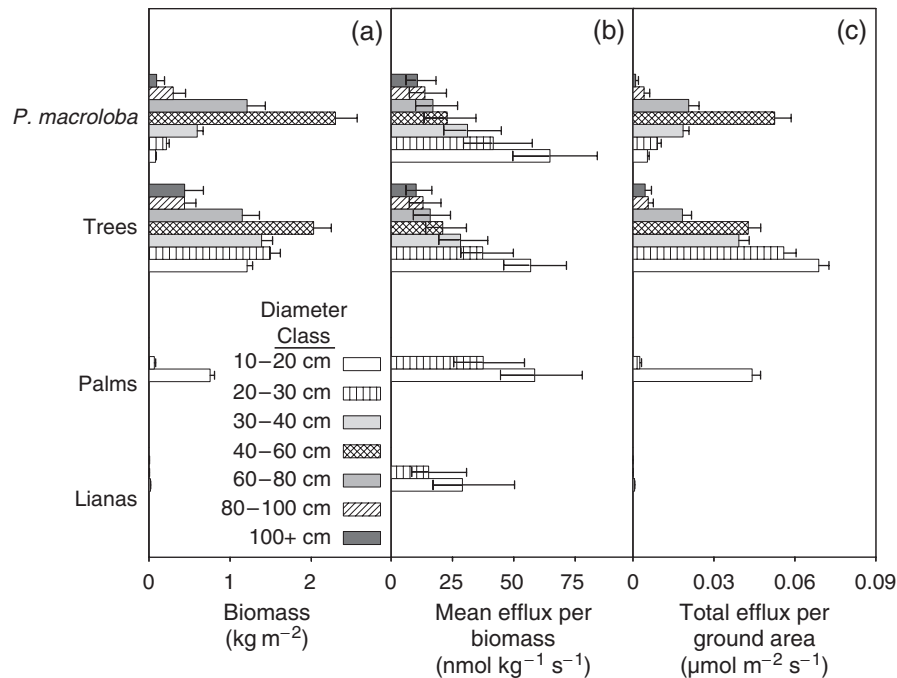


Fig. 5 Large diameter (>10 cm) wood biomass distribution (a), mean CO₂ efflux rates at 25 °C per unit biomass (b), and estimated CO₂ efflux rates per unit ground area (c) by functional group and diameter class. The largest proportion of *Pentaclethra macroloba* CO₂ efflux was from diameters in the 40–60 range, while the largest proportion of tree CO₂ efflux was from diameters in the 10–20 cm range (c). In the large diameter range, lianas contributed essentially no CO₂ efflux (c), because very few lianas were greater than 10 cm in diameter (a). Large diameter biomass was calculated as mean plot biomass per category from eighteen 0.5 ha plots, minus small diameter branch biomass per category as calculated from towers transects (error bars in (a) represent standard errors of the mean plot data). CO₂ efflux per surface area values and errors were calculated as the antilogs of least-squares means and 95% confidence limits from the best-fit model, resulting in asymmetrical error bars (b). Mean plot large diameter wood biomass area per ground area and standard errors were multiplied by CO₂ efflux per biomass model-derived means to yield CO₂ efflux per unit ground area values and errors (c). Means were not extrapolated beyond the diameters actually sampled for each functional group, resulting in empty cells for palms and lianas.

CO₂ efflux per unit ground area from wood >10 cm in diameter was $0.39 \pm 0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($149 \pm 17 \text{ g C m}^{-2} \text{yr}^{-1}$). Of this total, about 60% was from trees, 30% from *P. macroloba*, 10% from palms, and <1% from lianas (Fig. 5c). Diameter classes (in centimeters) and their approximate percent contributions to total large diameter wood CO₂ efflux per unit ground area were as follows: 10–20 = 30%, 20–30 = 15%, 30–40 = 15%, 40–60 = 25%, 60–80 = 10%, and the largest two classes had less than 2% each (Fig. 5c). The largest proportion of *P. macroloba* CO₂ efflux was from diameters in the 40–60 range, while the largest proportion of tree CO₂ efflux was from diameters in the 10–20 cm range (Fig. 5c).

Total wood (all diameters) CO₂ efflux per unit ground area for this system was $1.34 \pm 0.36 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($508 \pm 135 \text{ g C m}^{-2} \text{yr}^{-1}$). Trees contributed 47% of the total, *P. macroloba* contributed 20%, lianas contributed 24%, and palms only contributed 9% (Table 4). Wood that was <2 cm in diameter contributed half of the total efflux, and wood that was <10 cm accounted for 70% of total woody CO₂ efflux (Table 4). Less than 2% of the

total woody efflux was from wood that was >80 cm (Table 4).

Discussion

Levy–Jarvis analysis: CO₂ efflux per surface area vs. volume

The best units for expressing and extrapolating woody CO₂ efflux depend on whether the primary sources of CO₂ are surface area-based (Linder & Troeng, 1980; Matyssek & Schulze, 1988; Meir & Grace, 2002; Chambers *et al.*, 2004), or volume/biomass-based (Yoda, 1983; Ryan, 1990; Bowman *et al.*, 2005). Some studies conclude that a mixture of several units and extrapolating procedures may be desirable (Lavigne *et al.*, 1996; Damesin *et al.*, 2002). One of the main issues for the use of one method over another is the attempt to partition maintenance vs. growth respiration sources. Generally, growth respiration is estimated using stem diameter growth data, while maintenance respiration may be

Table 4 Total wood CO₂ efflux estimates (standard errors in parentheses) per unit ground area for the forest

| Total wood CO ₂ efflux | | Percent of total wood CO ₂ efflux from each category | | | | | |
|-----------------------------------|--|---|-----|----------------|-----|-----------|-----|
| Estimate ± SE | Units | Functional group | | Diameter class | | | |
| 1.34 ± 0.36 | μmol CO ₂ m ⁻² s ⁻¹ | Trees | 47% | 0–2 cm | 50% | 30–40 cm | 4% |
| 508 ± 135 | g C m ⁻² yr ⁻¹ | <i>P. maculoba</i> | 20% | 2–5 cm | 15% | 40–60 cm | 7% |
| | | Lianas | 24% | 5–10 cm | 5% | 60–80 cm | 3% |
| | | Palms | 9% | 10–20 cm | 9% | 80–100 cm | 1% |
| | | | | 20–30 cm | 5% | 100 + cm | <1% |

Percent contributions to efflux by functional group and diameter class are displayed. Small diameter wood (<10 cm) was only 15% of total woody biomass, but accounted for 70% of total woody CO₂ efflux. Lianas were only 3% of the total woody biomass, but contributed one-fourth of the total woody CO₂ efflux.

estimated using sapwood volume and/or measurements taken when trees are dormant (Ryan, 1990; Sprugel, 1990; Ryan & Waring, 1992; Ryan *et al.*, 1994, 1995; Sprugel *et al.*, 1995). These well-documented methods of measuring growth and maintenance respiration were not feasible in this study, because we had neither growth nor sapwood volume data.

According to Levy & Jarvis (1998), if the rate of CO₂ efflux is proportional to wood volume, efflux primarily reflects sapwood xylem parenchyma cell maintenance respiration; while a relationship with surface area reflects growth respiration of cambium and phloem cells. These divisions may not be useful for tropical forests, however, because separating growth vs. maintenance respiration is difficult when there is no dormant season. Therefore, an increase of CO₂ efflux with volume could result from faster growth of larger diameter wood and/or a larger sapwood maintenance component. Whether CO₂ dissolved in xylem sap diffuses radially out of the bark, or is transported up the xylem stream could also be affected by both xylem volume and surface area for diffusion (Teskey & McGuire, 2002). As a result of these confounding factors, we will discuss volume and surface area CO₂ efflux sources, but not infer growth or maintenance respiration from their source.

In the upper, mid, and lower canopy, the relationship between the reciprocal of diameter and CO₂ efflux per unit volume (Figs 1a–c) and the lack of relationship between diameter and efflux per unit area (Figs 1e–g) indicate that wood CO₂ efflux for all wood above 2 m was primarily dependent on surface area, and not volume. These results contradict the findings of Yoda *et al.* that respiration of small diameter wood was proportional to mass, while respiration of large diameter wood was proportional to surface area (Yoda *et al.*, 1965; Yoda 1967). Unlike canopy rates, wood CO₂ efflux in the bottom 2 m was dependent on both volume and area (Figs 1d and h). This is likely the result of the larger trees growing faster (Clark & Clark, 2000b)

and more sapwood volume in larger trees. By simple geometry, the proportion of sapwood volume per unit surface area in large diameter wood is much greater than that of small diameter wood. These patterns in volume vs. area-based measurements are consistent with other studies of large diameter wood measured near the ground (Damesin *et al.*, 2002; Meir & Grace, 2002).

Seasonal changes in wood CO₂ efflux

Woody CO₂ efflux has been shown to vary seasonally in temperate forests (Sprugel, 1990; Ryan *et al.*, 1997; Damesin *et al.*, 2002; Vose & Ryan, 2002), where there are definite growing season and dormancy dynamics. Increased rates of stem CO₂ efflux (Nepstad *et al.*, 2002; Chambers *et al.*, 2004) and ecosystem respiration (Goulden *et al.*, 2004) were found during the wet season in Brazilian rain forests, but the wet/dry season dynamics in our Costa Rican study site are not as pronounced. In the ecosystem of La Selva, there is documentation of seasonality in litterfall nutrient dynamics (Wood *et al.*, 2005), soil respiration (Schwendenmann *et al.*, 2003), and tree ring data (Fichtler *et al.*, 2003). Trees in this system grow year-round, and while some tree species show seasonal patterns in growth (Hazlett, 1987), the phenologies of all species are not synchronized the way they are in temperate forests or tropical forests with dry seasons. In this tropical rain forest, neither temperature, PAR, nor precipitation varied enough to affect woody CO₂ efflux rates of all species sampled. These results greatly simplify carbon balance modeling for this system.

Sources of variation in CO₂ efflux across canopy and landscape gradients

The best-fit model for ln F_M accounted for 75% of the variation in CO₂ efflux (Table 2), but this is likely

because F_M is autocorrelated with diameter (diameter is used to calculate F_M). The best fit model for $\ln F_A$ only accounted for 29% of the variation in CO₂ efflux (Table 2), likely because over 110 identified species and dozens more unidentified species were sampled. Nevertheless, we may still make general inferences based on the results of the models that will help us understand system processes, and how wood CO₂ efflux varies with canopy structure and landscape gradients.

Effects of slope and phosphorus

Initially, we believed woody CO₂ efflux would increase with increasing soil P, based on evidence that P is likely limiting in this system (McDade *et al.*, 1994) and the evidence that more nutrient-rich sites tend to have larger trees (Clark & Clark, 2000a). The situation is not this simple, however, as the effect of P seems to depend on slope, and the trend of higher F_A with higher slope (Figs 3a and 5d) is most likely confounded with nutrient availability. The shallow slopes at La Selva tend to be inceptisols with higher available soil P, and the steeper slopes tend to be more acidic ultisols with less P available (McDade *et al.*, 1994). At La Selva Biological Station, Schwendenmann *et al.* (2003) found higher rates of soil respiration where there were low levels of soil P, likely because more biomass of fine root mycorrhizae would be found in these sites, resulting in higher respiration rates from root/mycorrhizae complexes. Higher rates of tree root respiration where P is less available (steep, acidic ultisols) may have resulted in higher rates of measured aboveground woody CO₂ efflux. R. O. Teskey and M. A. McGuire (personal communication) recently found evidence that much of the CO₂ dissolved in stem xylem sap likely comes from root respiration and is transported upward in the xylem stream. The idea that tree root respiration rates affect aboveground woody CO₂ efflux rates is supported by the {slope × phosphorus} interaction plot, in which the slope effect is only at low total P, where the effect of pH on P availability is likely to be more biologically important (Fig. 5d).

Effects of functional group

Whatever competitive advantage that allows *P. macroloba* to be dominant in this extremely diverse system also likely contributes to higher growth rates and, thus, higher woody respiration rates. CO₂ efflux rates of *P. macroloba* and all other tree species increase with increasing diameter on average (Fig. 5b), probably because growth (Clark & Clark, 2000b), and likely growth respiration also increase with diameter in this ecosystem.

The decrease in liana CO₂ efflux rates with increasing diameter (Fig. 5b) could be the result of both higher growth rates and greater xylem CO₂ diffusion in liana branches, and lower maintenance respiration in liana stemwood. Lianas rely on the support of neighboring trees to reach the top of the canopy. Once there, they put proportionally more energy into producing leaf area than stem growth (Putz, 1983). Thus, growth respiration rates of fine liana branches would likely be higher than liana stem growth respiration rates. Lianas have larger diameter xylem vessels than trees on average (Ewers & Fisher, 1991; Fisher & Ewers, 1995), and have been documented to transport more water than trees of similar diameters (Restom & Nepstad, 2001). It would follow that lianas have the capacity to transport more dissolved CO₂ per unit surface area to the top of the canopy than the average tree, resulting in greater CO₂ diffusion out of small branches. Lianas also tend to have smaller stems than trees (Putz, 1983), and thus a smaller volume contribution of stem maintenance respiration. The high rates of small diameter liana branches would not have been revealed if only lower stem measurements had been taken.

Palms in this ecosystem are generally located in the lower canopy; they rarely reach the upper canopy, where the highest overall efflux rates were found (Fig. 5c). Slower growth rates would also likely lead to lower woody growth respiration rates. The lower CO₂ efflux rates for small diameter palm parts may be explained by the fact that measured palm 'branches' were actually palm frond rachises, which were usually green and, thus, likely refixing respired CO₂.

Effects of canopy position

WT (branch vs. stem) did not explain significant variation when both diameter and height were included in the model, indicating branches and stems of the same size and in the same location had similar CO₂ efflux rates. In this tropical forest, where most trees have deliquescent morphology, the concept of stem vs. branch is more of a continuum, and often difficult to determine. Although Sprugel (1990) asserts that branch respiration may be qualitatively different from stem respiration, our subjective decisions of stem vs. branch were not as important to CO₂ efflux rates as the diameter and height of the woody tissue itself.

Wood CO₂ efflux in the bottom 2 m, which increased with increasing diameter (Fig. 3c), largely consisted of stems. Large diameter stems likely have both greater growth respiration *and* greater maintenance respiration rates per unit surface area than smaller diameter stems. Several studies of tropical trees also found an increase of stem CO₂ efflux on a surface area basis with

increased stem diameter (Ryan *et al.*, 1994; Meir & Grace, 2002; Nepstad *et al.*, 2002).

Wood in the upper canopy had much higher CO₂ efflux rates than wood of the same diameter lower in the canopy (Fig. 3c). Conversely, Yoda *et al.* (1965) found stems to have higher rates than branches, given the same diameter. Yoda *et al.* measured CO₂ efflux on detached wood in enclosed chambers, where the diffusion effect of dissolved CO₂ in the xylem would be negligible, as the xylem CO₂ had likely already escaped before measurement. Indeed, the rapid increase in woody CO₂ efflux after excision is likely the result of rapid diffusion, as opposed to an increased respiration rate from wounding (Teskey & McGuire, 2005).

Several possible driving mechanisms may be causing the trends of increasing CO₂ efflux with height for small diameter wood. First, within-tree woody respiration may increase closer to the leaves (higher in the canopy) because of the increased energy cost of both growing new cells, and loading and unloading carbohydrates into and out of the phloem from the xylem parenchyma cells (Sprugel, 1990). This effect may also be amplified by the fact that leaves in full sun (higher in the canopy) have higher photosynthetic capacity and net photosynthesis than shade leaves (Ellsworth & Reich, 1993; Dang *et al.*, 1997; Carswell *et al.*, 2000; Wilson *et al.*, 2000; Hubbard *et al.*, 2002). Second, wood respiratory potential, which is independent of xylem CO₂ diffusion, has been found to increase with increasing height in *Dacrydium cupressinum* (Bowman *et al.*, 2005) and *Pseudotsuga menziesii* (Pruyn *et al.*, 2002). A third possible explanation for higher CO₂ efflux rates of small branches high in the canopy is that they are growing faster. Small branches lower in the canopy may be older and have nearly stopped growing, while branches of the same size higher in the canopy may be younger and still growing rapidly. Finally, diffusion of CO₂ out of the xylem sap may also increase with increasing height and decreasing diameter as a result of the upward movement of dissolved CO₂ during the day and thinner bark closer to the leaves. In several studies, diffusion of CO₂ dissolved in the xylem stream was found to be the primary source of measured CO₂ efflux (Teskey & McGuire, 2002; McGuire & Teskey, 2004; Bowman *et al.*, 2005). Further study is necessary to tease apart all of these possible reasons as to why woody tissue CO₂ efflux rates are so high at the top of the canopy.

Wood surface area and biomass distribution

To our knowledge, no other dataset explores small diameter woody biomass and surface area distribution throughout the vertical canopy transect within a tropical rain forest. These data were crucial for extrapolating

small diameter wood CO₂ fluxes, as surface area high in the canopy had a large effect on our estimate of total efflux (Figs 4e–h and m–p).

The total woody biomass by our estimation was 16.2 kg m⁻², with wood >10 cm contributing 13.8 kg m⁻², and wood <10 cm contributing 2.4 kg m⁻². This corresponds almost exactly with a previous estimate of total aboveground biomass for the primary forest of La Selva, 16.1 kg m⁻² (Clark & Clark, 2000a). Perhaps this is not too surprising, considering the same eighteen 0.5 ha plot diameters were used in this study, however, Clark *et al.* used different allometric equations and did not take small vs. large diameter wood into account in their analysis.

Our study also provided a novel way to estimate total liana biomass: 0.44 kg m⁻², or 3% of the estimated total woody biomass. When using plot-level above-buttress stem diameter data that only included stems ≥10 cm to estimate biomass, lianas were essentially lost from the system (Fig. 5a). Using the same 0.5 ha plot data, Clark & Clark (2000a) estimated liana biomass as 0.06 kg m⁻², or only 0.4% of the total biomass, underestimating liana biomass sevenfold. In a lowland tropical rain forest in the Amazon, Phillips *et al.* (2005) accounted for all diameters and estimated total liana biomass as 1.43 kg m⁻². This estimate is over three times our estimate for a Costa Rican rain forest, possibly because the Amazonian forest had a much greater proportion of lianas that were ≥10 cm, which accounted for 80% of the total liana biomass (Phillips *et al.*, 2005).

Forest-level estimates of wood CO₂ efflux

Our estimate of total woody tissue CO₂ efflux rate (508 ± 135 g C m⁻² yr⁻¹), is approximately 40% of the estimated soil CO₂ efflux rate for the primary forest of La Selva (1027–1613 g C m⁻² s⁻¹, Schwendenmann *et al.*, 2003), and approximately 20–30% of the estimated nighttime CO₂ net ecosystem exchange (1741–2668 g C m⁻² s⁻¹), as estimated by the eddy covariance technique at La Selva from 1998 to 2000 (Loescher *et al.*, 2003). Our total woody tissue CO₂ efflux rate estimate for this stand is almost twice the previous estimate of woody CO₂ efflux at La Selva (Ryan *et al.*, 1994), which was only based two tree species. Our estimate is also about 20% higher than a recent estimate of woody tissue CO₂ efflux in an Amazonian tropical rain forest, which concluded that wood CO₂ efflux accounted for 20% of autotrophic respiration and about 14% of the total carbon assimilated by photosynthesis (Chambers *et al.*, 2004). Both of these woody tissue efflux estimates were extrapolated solely based on stem measurements taken from the ground. In our study, we would have missed a

large portion of CO₂ flux had we not measured small diameter wood high in the canopy, especially lianas. Small diameter wood (<10 cm) was only 15% of total woody biomass, but accounted for 70% of total woody CO₂ efflux (Table 4). Lianas were only 3% of the total woody biomass, but contributed one-fourth of the total woody CO₂ efflux (Table 4).

Uncertainties associated with these forest-scale woody CO₂ efflux estimates fall into two categories: uncertainties in the rates themselves and uncertainties in the data used to extrapolate these rates to the ecosystem. Three possible sources of error in the efflux rates per unit biomass or surface area are: (1) the lack of large diameter wood measurements high in the canopy, (2) the lack of a correction for seasonal temperature differences, and (3) the lack of nighttime measurements. The fact that we could not easily measure large branches or stems from the tower may not greatly bias our estimates of large diameter wood CO₂ efflux because, while small diameter wood efflux has been found to increase with height, efflux rates of large diameter wood tend to remain unchanged with height (Sprugel, 1990; Ryan *et al.*, 1996; Damesin *et al.*, 2002). The lack of a correction for seasonal temperature variation is also not likely to cause large errors, because the base temperature to which all CO₂ efflux rates were corrected (25 °C) was within a degree of the average annual temperature, and temperature shows only a small diurnal and seasonal amplitude (Ågren & Axelsson, 1980). If our measurements had been taken only at the bases of stems, we may have underestimated actual rates by 30% or more by only measuring during the day, because much of the respired CO₂ is transported up the xylem stream with the sapflow (Teskey & McGuire, 2002; McGuire & Teskey, 2004; Bowman *et al.*, 2005). In our study, we have attempted to capture this 'lost' respired CO₂ by measuring the full vertical transect of the canopy. During the day, when sapflow is at its peak, CO₂ in the xylem stream must eventually diffuse out of the tree, most likely high in the canopy where branch bark is thinnest.

Uncertainties in biomass and surface area estimates are likely to cause greater errors in ecosystem rates because of multiplicative effects and uncertainties in allometric equations. Even though our surface area estimates for all woody tissue <10 cm in diameter were based on direct harvesting rather than allometry, they still could lead to substantial error if our towers sampling scheme did not adequately represent the forest with respect to small diameter wood distribution. Of the original randomly located set of possible tower sites, 37% were discarded because of rocky terrain or large stems, therefore, it is reasonable to assume our tower sites are representative of at least 63% of the landscape. The allometric equations we used to estimate biomass

for wood >10 cm in diameter could also be large sources of error, especially in diameter ranges >80 cm (Clark & Clark, 2000a). Less than 2% of the total woody CO₂ efflux came from wood that was >80 in diameter, however (Table 4), so this is likely not a huge source of error in our ecosystem estimates of wood CO₂ efflux.

Main conclusions

- Stem CO₂ efflux showed no evidence of seasonality over a span of 2 years.
- Stem and branch CO₂ efflux rates per unit surface area at 25° (F_A) increased with woody tissue diameter for all dicot tree species, did not change with diameter for palms, and decreased with diameter for lianas.
- F_A was highest for the N-fixing dominant tree species *P. maculosa*, followed by other dicot tree species, lianas, and finally palms.
- Small diameter wood (<10 cm) F_A increased steeply with increasing canopy height.
- Total woody tissue net CO₂ exchange for this primary tropical rain forest was estimated as $1.34 \pm 0.36 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($508 \pm 135 \text{ g C m}^{-2} \text{yr}^{-1}$).
- Small diameter canopy wood is a substantial source of total woody CO₂ efflux, especially lianas.

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