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Title

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Permalink

<https://escholarship.org/uc/item/8mc3s8hp>

Journal

Ecological Applications, 14(sp4)

ISSN

1051-0761

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Publication Date

2004-08-01

DOI

10.1890/01-6012

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Peer reviewed

RESPIRATION FROM A TROPICAL FOREST ECOSYSTEM: PARTITIONING OF SOURCES AND LOW CARBON USE EFFICIENCY

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Abstract. Understanding how tropical forest carbon balance will respond to global change requires knowledge of individual heterotrophic and autotrophic respiratory sources, together with factors that control respiratory variability. We measured leaf, live wood, and soil respiration, along with additional environmental factors over a 1-yr period in a Central Amazon terra firme forest. Scaling these fluxes to the ecosystem, and combining our data with results from other studies, we estimated an average total ecosystem respiration (R_{eco}) of $7.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Average estimates (per unit ground area) for leaf, wood, soil, total heterotrophic, and total autotrophic respiration were 2.6, 1.1, 3.2, 5.6, and $2.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. Comparing autotrophic respiration with net primary production (NPP) estimates indicated that only $\sim 30\%$ of carbon assimilated in photosynthesis was used to construct new tissues, with the remaining 70% being respired back to the atmosphere as autotrophic respiration. This low ecosystem carbon use efficiency (CUE) differs considerably from the relatively constant CUE of ~ 0.5 found for temperate forests. Our R_{eco} estimate was comparable to the above-canopy flux (F_{ac}) from eddy covariance during defined sustained high turbulence conditions (when presumably $F_{\text{ac}} = R_{\text{eco}}$) of 8.4 (95% CI = 7.5–9.4). Multiple regression analysis demonstrated that $\sim 50\%$ of the nighttime variability in F_{ac} was accounted for by friction velocity (u^* , a measure of turbulence) variables. After accounting for u^* variability, mean F_{ac} varied significantly with seasonal and daily changes in precipitation. A seasonal increase in precipitation resulted in a decrease in F_{ac} , similar to our soil respiration response to moisture. The effect of daily changes in precipitation was complex: precipitation after a dry period resulted in a large increase in F_{ac} , whereas additional precipitation after a rainy period had little effect. This response was similar to that of surface litter (coarse and fine), where respiration is greatly reduced when moisture is limiting, but increases markedly and quickly saturates with an increase in moisture.

Key words: ecophysiology; ecosystem model; forest dynamics; global carbon cycle; net ecosystem exchange; NPP/GPP ratio; rainforest; respiration; respiration photosynthesis ratio.

INTRODUCTION

Studies of net ecosystem production (NEP) are becoming an increasingly important area of applied ecological research because NEP quantifies the carbon source or sink strength of an ecosystem. This net exchange of carbon between ecosystems and the atmosphere can play a key role in regulating the human-induced increase in CO_2 and concomitant global changes predicted to result from this increase (Intergovernmental Panel on Climate Change [IPCC] 2001). Amazon forests play a particularly important role the atmospheric exchange of carbon, and the carbon balance of these ecosystems is a topic of active research.

Manuscript received 2 October 2001; revised 7 July 2002; accepted 22 July 2002; final version received 16 September 2002. Corresponding Editor: A. R. Townsend. For reprints of this Special Issue, see footnote 1, p. S1.

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Because NEP is the difference of two large fluxes of gross primary production (GPP) and ecosystem respiration (R_{eco}), quantifying NEP accurately is difficult. Nevertheless, a relatively small NEP flux of $0.5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, if scaled over the entire Amazon basin, results in a globally significant accumulative sink of about $0.2 \times 10^{12} \text{ g C/yr}$. Small NEP fluxes over large areas that are difficult to quantify accurately and precisely are of global importance.

Although respiration is of equal importance to photosynthesis in determining NEP, few studies (Goulden 1996, Lavigne and Ryan 1997, Law et al. 1999) have attempted to estimate total ecosystem respiration (R_{eco}). While photosynthesis is a distinct process, R_{eco} integrates a number of disparate processes, including autotrophic (R_{a} ; leaf, stem, root) and heterotrophic (R_{h} ; from litter and soil organic matter decomposition) sources. Adding to this complexity, R_{a} comprises mitochondrial, alternative-pathway, and futile cycles, and photorespiration, along with the numerous physiolog-

ical processes which demand respiratory support including growth, protein turnover, ion uptake, phloem loading, nitrate reduction, and maintenance of ion gradients (Amthor 2000, Cannell and Thornley 2000, Thornley and Cannell 2000). Measures of heterotrophic respiration integrate the activity of a wide variety of substrates and decomposers. Fungi, for example, are probably more important for decomposing surface litter, whereas bacteria are more important for decomposing mineral associated soil organic matter (SOM). Thus, while respiration is often measured as the integrated sum of many processes, to develop a more process level understanding, relating individual respiratory sources to factors that control variability is important.

Integrative studies of R_{eco} are quite limited for tropical forest ecosystems. Odum (1970) provided a comprehensive summary of extensive and detailed forest metabolism studies at El Verde, Puerto Rico (Odum et al. 1970, Odum and Jordan 1970), and many R_{eco} components were quantified. Additional studies have quantified R_{eco} or R_{a} for tropical forests (Müller and Nielsen 1965, Kira 1975, Yoda et al. 1983), although errors associated with harvested tissues, static (e.g., alkali trap) CO_2 flux chambers, and other methodological issues make an accuracy assessment of these pioneering studies difficult. Investigations of individual respiratory sources in closed-canopy tropical forests using more accurate dynamic chambers (Nay et al. 1994) are limited and include soil (Trumbore et al. 1995, Sotta 1998), live wood (Ryan et al. 1994, Meir and Grace 2002, Nepstad et al. 2002), leaf (Reich et al. 1991, Meir et al. 2001), and coarse litter (Chambers et al. 2001c) studies.

The eddy covariance (EC) method may provide a means for measuring R_{eco} at night. However, because nighttime atmospheric turbulence in the Amazon basin is often quite low (e.g., Trumbore et al. 1990), a significant amount of respired carbon can be trapped within the canopy leading to an accumulation of CO_2 below the EC measurement height (Grace et al. 1995, Goulden et al. 1996). This is often corrected by measuring the rate of CO_2 accumulation below the canopy (F_{bc} ; the storage flux), and the total ecosystem flux (F_{eco}) is estimated by summing F_{ac} and F_{bc} (Fan et al. 1990). However, there is some debate over what conditions allow the sum of F_{ac} and F_{bc} to be an unbiased estimate of R_{eco} . Several researchers acknowledge that under stable atmospheric conditions, some CO_2 may be not be captured by the eddy covariance method, leading to underestimates in R_{eco} (Goulden 1996, Malhi and Grace 2000). This potential bias may be corrected by removing (filtering) flux data when turbulence is low, although determining the appropriate threshold is a challenging task (Miller et al. 2004), and there is some debate over whether or not such a correction is needed (Araújo et al. 2002). To allow instructive comparisons

of EC and chamber data, it is important to determine under what conditions nighttime F_{eco} from EC data provides a reliable estimate of R_{eco} .

Accurately quantifying the relative importance of respiratory sources and pathways is an important first step to advance our understanding of R_{eco} . In addition, to move beyond simply quantifying fluxes, studies of factors controlling respiratory variability are needed, and are little understood for tropical forests. The overall objective of this study was to develop a better understanding of the components of R_{eco} for a tropical forest in the central Amazon. We accomplished this by (1) quantifying the contributions of leaf (R_{l}), live wood (R_{w}), soil (R_{s}), autotrophic (R_{a}), and heterotrophic (R_{h}) respiration to R_{eco} , (2) developing a methodology for estimating ecosystem-scale fluxes from limited chamber measurements, (3) quantifying how a number of environmental and ecological factors control variability in R_{eco} components, (4) comparing our scaled chamber data with nighttime EC data, and (5) evaluating R_{a} and net primary productivity (NPP) estimates to calculate a forest carbon use efficiency (CUE).

MATERIALS AND METHODS

Site characteristics

This study was carried out in the Central Amazon near the city of Manaus, Brazil, in collaboration with the National Institute of Amazon Research (Instituto Nacional de Pesquisas da Amazônia, INPA). Mean annual temperature is 26.7°C and rainfall varies throughout the year with distinct dry season during July, August, and September when there is usually <100 mm/mo (Fig. 1a). It is difficult to quantify average annual precipitation, with one record for Manaus showing a statistically significant increase from 1900 mm in 1910 to 2300 mm in 1980 (Fig. 1b). Precipitation measured at the ZF2 site base camp was 3550 mm in 2000 and 2380 mm in 2001. Vegetation is old-growth closed-canopy terra firme (nonflooded) forest. A total of 1176 tree species were identified in the nearby Ducke reserve (Ribeiro et al. 1999), and some trees can live for more than 1000 years (Chambers et al. 1998).

Investigations were carried out at an INPA reserve located along the ZF2 road on two 20×2500 m permanent forest inventory plots referred to as the Jacaranda plots ($2^\circ36' \text{S}$, $60^\circ12' \text{W}$). These long and narrow plots capture ecosystem variation associated with the undulating local topography. Mean elevation is ~ 100 m with ± 50 m between plateaus and valleys. Soils along a typical toposequence comprise Oxisols on plateaus, Ultisols on slopes, and Spodosols associated with small valley streams (Bravard and Righi 1989). Surface (to 5 cm) clay content decreases (from $\sim 75\%$ to 5%), and sand content increases (from $\sim 10\%$ to 85%), when moving from plateau to valley (Ferraz et al. 1998). Although soil characteristics vary continuously with slope, it is difficult to establish clear boundaries, and

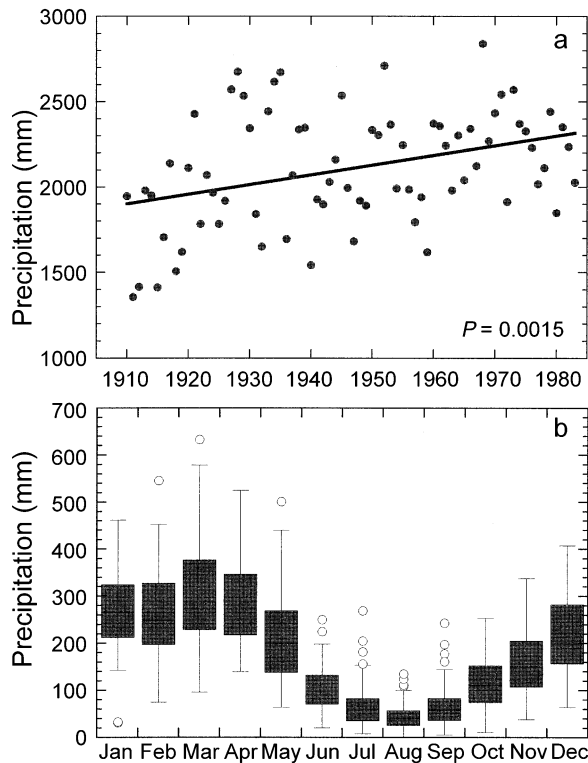


FIG. 1. (a) Annual and (b) monthly variability in precipitation for Manaus, Brazil from 1910 to 1983 (data from National Climatic Data Center, Asheville, North Carolina, USA). There was a significant increase in precipitation during the 20th century for the annual record. The monthly record shows that precipitation variability is always reduced during the dry season, whereas wet-season months are occasionally dry.

the landscape is approximately equally divided among plateau, slope, and valley forests.

Stem respiration

Fifty trees were selected from five relative growth classes using data collected during the first year of a seasonal tree growth study (Silva et al. 2002). Briefly, ~300 trees from the Jacaranda plots were randomly selected from three size classes. Each tree was outfitted with a dendrometer band used for measuring small changes in circumference (i.e., <0.05 mm). Using these increments, average woody tissue production (10 mo from September 1999 to July 2000) was estimated for all trees using an allometric model that predicts tree mass as a function of base diameter (D_b ; at 1.3 m height or above the buttresses) and expressed as mg growth·kg (dry mass) biomass⁻¹·d⁻¹ (Chambers et al. 2001b). Next, trees were classified into four classes each representing 25% of total wood production and a fifth class for trees that experienced no measurable growth during the 10-mo period. Ten trees were randomly selected from each of these five growth classes ($n = 50$) and woody tissue respiration (R_w) was quantified.

R_w was measured using an infrared gas analyzer (IRGA, LI 6252 with an LI-670 flow control unit; Li-Cor, Lincoln, Nebraska, USA) operated as a closed dynamic chamber (CDC) (Norman et al. 1997) with a flow rate of 1.0 L/min. Semicylindrical polyvinyl chloride (PVC) chambers (250–400 mL) were cinched to the base of the tree (at a height of $\sim D_b$, or ~ 1.3 m) using nylon straps. Closed-cell foam coated with silicon was glued to the rim of the chamber to provide a malleable seal that conformed to irregularities in the trunk. Leakage was checked by breathing around the chamber after each measurement. The measurement interval spanned ~ 1 –2 min. Flux from the base of each tree was quantified eight times between August 2000 and June 2001 at ~ 4 –6 wk intervals. We used multiple regression and ANOVA to test D_b , month, growth class (1–5), and stem surface temperature (T_s) as predictor variables. We hypothesized that R_w would vary seasonally and be positively correlated with growth rate, but due small temperature variations at 1.3 m height, would be independent of T_s .

Leaf respiration

Leaf respiration (R_l) measurements were made at ambient leaf temperature (T_l) using a LiCor 6400 (Li-Cor, Lincoln, Nebraska, USA) equipped with a blue/red LED light source turned off, creating a dark chamber. Measurements were logged only after the total coefficient of variation (a LiCor parameter) fell below 1%, and the IRGAs were “matched” prior to each measurement (4–8 min). Matching reroutes the outflow of the sample IRGA to the reference IRGA allowing calibration to an identical CO₂ source. R_l was measured at approximately hourly intervals over a combined 24-h period for the same leaf from a number of large trees (>14 m in height) located near three canopy access towers along the ZF2 road. Measurements were carried out from April to November 2001. These data were combined to test for hourly variation, and variation with T_l , using regression and ANOVA. We hypothesized that because all leaves were located high in the canopy, T_l would be an important factor controlling diurnal R_l variability. Due to the time consuming nature of this work, we did not attempt to quantify leaf respiration for trees <14 m in height, or to quantify within canopy variation for individual trees.

Our goal was to measure nonphotorespiratory mitochondrial CO₂ release (R_l). Although measuring this flux at night is relatively straightforward, there is growing evidence that, all other factors being equal, R_l in the light is lower than R_l in the dark (Graham 1980, Atkin et al. 1998, 2000a, Peisker and Apel 2001). Also, placing a sunlit leaf into a dark chamber introduces a number of artifacts including a postillumination CO₂ burst (PIB) and light enhanced dark respiration (LEDR), in addition to actual inhibition of R_l by light (Atkin et al. 2000b). Both PIB and LEDR are transient

phenomena that last for up to ~ 20 and 500 s, respectively, after the leaf is placed in a dark chamber (Atkin et al. 1998). Inhibition of R_1 by light is apparently continuous and results in an $\sim 40\%$ decrease in R_1 (Peisker and Apel 2001). Because we waited until the CO_2 flux from the leaf equilibrated (4–8 min), the effects of PIB and LEDR were minimized. However, to account for light inhibition of R_1 , we reduced our daytime flux estimates by 40%.

Soil respiration

To explore how R_s varies with changes in topography and soil texture, 54 PVC collars were equally distributed among plateau, slope, and valley soils along a portion of one Jacaranda plot, with each collar separated by 15 m. Chamber design and installation was analogous to Trumbore et al. (1995). The IRGA system and methodology was the same as used for stem respiration with the exception that the larger chamber (4.5–6.0 L) had a small pressure equilibration vent. Flux from each chamber was quantified eight times during the day (0800–1600 hours) between July 2000 and June 2001 at ~ 4 –6-wk intervals. Collars were installed about six months before the first measurement, and were kept in place between sampling dates. In conjunction with soil surface flux measurements, soil temperature (T_s) and soil volumetric water content (VWC) (TDR probes, HydroSense; Campbell Scientific, Logan, Utah, USA) were also measured. Relationships were explored using multiple regression and ANOVA. We hypothesized that the R_s vs. VWC relationship would be curvilinear, where respiratory activity from very dry and very wet soils would be reduced, and respiratory activity would peak at intermediate moisture contents. We also hypothesized that R_s would be independent of T_s due to small seasonal and daily changes in T_s .

Eddy covariance data

We used eddy covariance (EC) data collected from the ZF2-K34 tower from 31 August 1999 to 16 September 2000 (Araújo et al., *in press*). This tower is located within 2 km of the locations where chamber measurements took place. Although the chamber and EC data did not occur over the same interval of time, they both occurred during periods with relatively high precipitation. Annual precipitation measured at the ZF2 base camp beginning June 2000 was 2740 mm, whereas beginning August 1999 annual precipitation was 3190 mm (cf. Fig. 1).

We were interested in conditions where the EC flux was a reliable measure of R_{eco} , although these conditions are difficult to determine. The above-canopy EC flux (F_{ac}) is often corrected for the below canopy storage flux (F_{bc}) because CO_2 accumulates within the canopy when turbulence is low, and the total ecosystem (or biotic) flux (F_{eco}) is calculated as the sum of F_{ac}

and F_{bc} . Thus, most of F_{eco} is captured by F_{bc} during stable conditions, and most of F_{eco} is captured by F_{ac} during turbulent conditions. Malhi et al. (1998) found that the threshold between these two states at night occurred at a friction velocity (u^* ; a measure of atmospheric turbulence) of ~ 0.1 m/s. Ideally, the sum of F_{ac} and F_{bc} (F_{eco}) would be independent of changes in atmospheric turbulence, and F_{eco} would provide a continuous estimate of nighttime R_{eco} . However, Malhi et al. (1998) also found that F_{eco} varied with changes in meteorological conditions, suggesting difficulties when using F_{eco} to estimate R_{eco} . Thus, although F_{eco} may not provide a constant measure of nighttime R_{eco} , under conditions of sustained high turbulence (SHT), F_{eco} may provide a reliable estimate of R_{eco} (Goulden 1996). In addition, because F_{bc} approaches zero during SHT conditions, F_{ac} alone should provide an estimate of R_{eco} .

We selected a subset of the EC data for analyses. First, time of night was limited to 1900–0500 hours to avoid photosynthetic flux interference. In addition, at very low u^* , flux variability was greatly reduced, and the error model was fundamentally different than for higher u^* values, so we only considered data with u^* above 0.01 m/s. To ensure constant variance of the residuals, extreme outlier observations ($n = 63$) were also removed. Of a total of 4631 nighttime observations (half-hour averages), 4287 observations were considered. Due to negative fluxes (the CO_2 concentration decreased from one interval to the next), F_{ac} and F_{eco} were offset by the appropriate constants so that negative values could be included in the error model and allow transformation analysis of the response variable.

Our first goal was to determine the conditions under which F_{eco} and F_{ac} were independent of changes in u^* , and then estimate R_{eco} from the tower data under these conditions. To explore how F_{ac} and F_{eco} varied with changes in u^* , we used multiple regression analysis. Evaluated predictor variables were u^* (averaged every half hour) and the half-hourly change in u^* (Δu^*). Also, to explore how the long-term average u^* explained variation in F_{ac} and F_{eco} , a set of u^* averages varying from four (u_4^*) to eight (u_8^*) hours were calculated. SHT conditions under which F_{ac} and F_{eco} were no longer dependent on changes in u^* were then determined. A best estimate of R_{eco} was calculated as the average F_{ac} and F_{eco} under SHT conditions. Finally, we compared R_{eco} estimates from EC and scaled-chamber data to determine if they differ significantly.

Next, after accounting for variability in F_{eco} and F_{ac} due to turbulence, the effects of daily and seasonal variability in precipitation was explored. Evaluated precipitation variables were the 20-d average precipitation (Pr_{20}) and daily precipitation (Pr_{day}) preceding each EC observation. We employed the 20-d average because Toledo (2002) demonstrated that respiratory activity from fine surface litter was most strongly cor-

related with the 20-d average, as well as daily changes in precipitation. The respiratory flux from surface litter is susceptible to large variation with changes in moisture content (Chambers et al. 2001c, Toledo 2002), and is probably responsible for a considerable amount of daily and seasonal variability in R_{eco} .

Statistical analysis

All statistical analyses were performed using SAS (version 8.2) software. For ANOVA, data were transformed to ensure normality before testing for significant differences among means using Bonferroni's method. Transformations were tested using maximum likelihood analysis, and in some cases optimum power transformation was employed to explore transformation likelihood as a function of powers of the response variable. For multiple classification variables, interactions among variables were tested. When group variances were not equal (Brown-Forsythe test), variance weighted ANOVA results were used.

For regression analysis, transformation of the response variable was carried out in the same manner as for ANOVA to ensure residuals were equally distributed about the regression line with constant variance (homoscedasticity). Outlier analysis was performed using Studentized residual analysis. Potential outlier observations ($P < 0.05$) were removed when it was clear that the data points were in error, or acted as leverage points. The amount by which the response variable changes when the continuous variable changes may be different within various groups defined by classification factors, or with levels of continuous variables. To account for these effects, all one-way interactions among predictor variables were tested for significance. In cases where only higher order terms were statistically significant, all lower order terms contained in these higher-order terms were also included (Aiken and West 1991). In some cases, data was constrained to a limited portion of the total range to avoid problems associated with nonconstant variance, and leveraging of the regression curve. In developing multiple regression and ANOVA models, we opted for first establishing the form of the relationship using single predictor (x) variables, then adding predictors and testing for interactions one at a time.

Scaling fluxes

When extrapolating results from a limited population towards developing an accumulative measure (e.g., from leaves to canopy), relationships that are not normally distributed can introduce bias. In some cases, the bias can be solved analytically. For example, the mean (y_{ave}) of a variable that is (natural) log-normally distributed is given by

$$y_{\text{ave}} = \exp(m + \text{SD}^2/2) \quad (1)$$

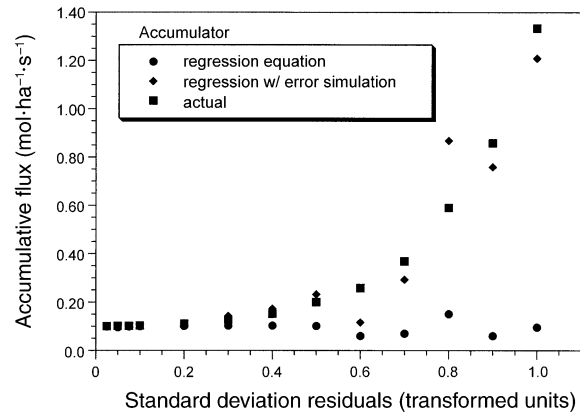


FIG. 2. A simulated data set demonstrates that extrapolating predictions from a regression equation with a transformed response variable can introduce bias when there is a large amount of unexplained variability (i.e., low r^2). The simulated data comprised soil respiratory flux from a 1-ha grid divided into 10 000 1-m² cells where the flux varied with changes in soil texture. Each cell was assigned a flux based on a random normal deviate (RND) drawn from a distribution with a mean of $\log(10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$ (1.0 in the transformed units), and a SD that varied from 0.25 to 1.0 in log units, along with a linear increase in flux with soil clay content.

where m is the mean and SD the standard deviation of the transformed data (Burlington and May 1970). In regression analysis with transformed data, additional problems arise. For example, if the y-axis is log transformed, a data point 1 SD above the regression line has more weight (in the original units) than a point 1 SD below the regression line, so the error model is not balanced in the original units. If the regression equation is used to calculate a summed measure (e.g., an accumulative flux), bias is introduced. As shown in Fig. 2 using simulated data, this bias can be particularly large when the correlation coefficient is small. One way to account for this bias is to use Monte Carlo randomization methods (Kalos and Whitlock 1986, Manly 1991) to account for error distributed about the regression line by creating bootstrap estimates (Manly 1991) using

$$y' = \text{RND}(y'_{\text{int}}, \text{SD}_{\text{res}}) + bx \quad (2)$$

where each prediction y' is estimated by drawing a random normal deviate (RND) from a distribution with a mean y'_{int} and SD of the residuals (SD_{res}) (in transformed units), and bx can be any number of regression variables and coefficients. Although Eq. 1 could be used to estimate an unbiased average in the case of a logarithmic transformation, Eq. 2 is more general and can be used when other transformations are employed, or when a number of explanatory variables vary continuously. The important point is that although residual error may be equally weighted about the regression line in the transformed units, when predictions from regression equations are scaled over a large number of

individuals, summed errors in the original units are not equally weighted about the regression line.

Scaling stem respiration

Scaling respiration measurements made at the base of the tree toward estimating whole-tree flux presents some difficulties. Some studies estimate the respiratory flux per unit live tissue volume, and then scale chamber values to whole trees by estimating the total amount of live tissue (Ryan and Waring 1992, Ryan et al. 1997, Law et al. 1999). This method has advantages because it allows a more physiological interpretation of flux variability (Amthor 2000). However, because growth respiration is primarily from cambium cells, and maintenance respiration is primarily from sapwood cells, the relationship between sapwood volume and R_w can vary with the growing season (Sprugel 1990). Edwards and Hanson (1996), for example, found that R_w was only related to sapwood volume during the dormant, not the growing season. Respiratory flux per unit sapwood volume can also vary between species or with height within the same individual (Yoda et al. 1983, Sprugel 1990, Ryan et al. 1996a) often related to variation in tissue nitrogen content (Maier et al. 1998, Stockfors and Linder 1998). Furthermore, based on preliminary investigations, we found that a standard method for estimating the volume of living cells (staining with tetrazolium) is difficult in tropical forests because many woods are very dense, dark or red in color (i.e., do not stain well), and the area stained is quite diffuse making volume estimates difficult.

An alternative method for scaling chamber flux measurements to whole trees is to estimate the stem surface area for the entire tree (Kinerson 1975), and then scale fluxes similar to using leaf area index (LAI) for scaling leaf respiration (e.g., Law et al. 1999). Although this method provides little insight into differences in R_w among individuals, it may be a more accurate method of scaling R_w to the ecosystem because estimating total surface area is more straightforward than estimating total sapwood volume, especially in a species-rich tropical forest. The main stem surface area can be estimated as a truncated cone (Yoneda 1993) and calculated by

$$A_{\text{bole}} = \pi(r_b + r_{\text{min}})\sqrt{h_b^2 + (r_b - r_{\text{min}})^2} \quad (3)$$

where r_b and r_{min} are radii at the base and top of the bole, and h_b is the height of the bole. Yoneda (1993) applied the pipe-model theory of Shinozaki et al. (1964) to the frequency distribution $\phi(d)$ of diameter (d) of tree branches, and found the relationship can be modeled by

$$\phi(d) = Kd^{-2} \quad (4)$$

where K is characteristic of each tree and given by

$$K = 4m_w/[\pi\rho(d_{\text{max}} - d_{\text{min}})] \quad (5)$$

and where m_b , ρ , d_{min} , and d_{max} are the dry mass of the branches, the wood density (kg dry mass/m³ fresh volume), and the maximum and minimum diameters of branches, respectively. Eq. 4 has been verified for trees in Pasoh, Malaysia (Yoda 1983), and Yamakura et al. (1987) demonstrated that the pipe model theory explained crown shape differences in Sebulu, East Kalimantan. Total surface area for branches derived from Eq. 4 is given by Yoneda (1993) as

$$A_b = \pi K \ln(d_{\text{max}}/d_{\text{min}}) \quad (6)$$

and total stem surface area (A_s) is given by the sum of Eqs. 3 and 6.

We estimated A_s for 315 trees harvested in a central Amazon forests (Chambers et al. 2001b) using the Eqs. 3 and 6. Values for r_b , h_b , and m_b were measured independently for each harvested tree. The radius at the top of the bole (r_{min}) was estimated using a taper equation in Chambers et al. (2000), and d_{max} was assumed to be equal to r_{min} . The minimum branch diameter (d_{min}) was assumed to be 2 mm based on the average value for broad-leaf trees (cited in Yoneda 1993). We then employed regression analysis to explore the relationship between D_b and A_s . Next, we applied this regression equation to each tree (>10 cm D_b) in the Jacaranda PFIPs (permanent forest inventory plots; 10 ha, 5823 trees), and calculated an average stem area index (SAI), analogous to leaf area index (LAI), which gives the total stem surface area per unit ground area.

Because the 50 trees sampled for stem respiration were selected from five unbalanced growth classes, these data could not be simply randomly applied to the entire forest. However, because the ~300 trees from the dendrometer study were selected randomly (Silva et al. 2002), we assumed that the distribution of the total number of trees in each relative growth (mg growth·kg⁻¹ biomass·d⁻¹) class for the entire forest would be the same as their distribution in the dendrometer study. Thus each tree from the Jacaranda plots ($n = 5283$) was randomly assigned a growth class based on their frequency in the dendrometer study. Respiration per unit area was then randomly assigned to each tree's surface area using the A_s vs. D_b relationship.

Scaling leaf respiration

Extrapolating leaf-level respiration measurements toward estimating ecosystem-scale fluxes using LAI is difficult. We adopted a unique approach that employs estimates of total leaf surface area for individual trees. Fifty trees were harvested in the central Amazon to quantify biomass, moisture, and nutrient contents (N. Higuchi, unpublished data). For each tree, leaf mass and leaf moisture content was measured. To calculate the total leaf surface area (A_l) for each of these trees, we needed the specific leaf area (SLA, cm² fresh volume/g dry mass) for each tree, but SLA had not been measured. To estimate SLA for these trees, three leaves

in different canopy positions were collected from the same 50 trees sampled for stem respiration, and SLA was measured for each leaf. We found a highly significant relationship between $\log(\text{SLA})$ and leaf moisture content (averaged for each tree, $r_{\text{adj}}^2 = 0.38$, $P < 0.0001$):

$$\log(\text{SLA}) = 1.47 + 0.868(M_1) \quad (7)$$

where M_1 is leaf moisture content (%). We then estimated SLA for the harvested trees by using leaf moisture content (which had been measured) as a predictor variable using Eq. 2 ($\text{SD}_{\text{res}} = 0.0849$) to account for variability. A_1 was then calculated for these 50 trees using our SLA estimate and measured leaf dry mass. Next we developed a regression relationship between A_1 and D_b , and used this equation to estimate A_1 for each tree in the Jacaranda plots. A_1 was then summed for each tree and averaged over the total area (10 ha) to estimate an ecosystem LAI (for trees >10 cm D_b).

RESULTS

Stem respiration

There was considerable variation in woody tissue respiration per unit stem surface area (R_w) ranging over two orders of magnitude from 0.027 to 3.64 $\mu\text{mol}\cdot\text{m}^{-2}$ (stem) $\cdot\text{s}^{-1}$ ($n = 391$ measurements). This variation was not simply due to differences among species, as within species variation is also quite high (J. Q. Chambers, unpublished data). R_w was highly correlated with D_b , month and growth class ($r_{\text{adj}}^2 = 0.35$, $P < 0.0001$) given by

$$\log(R_s) = -0.672 + \alpha(\text{class}) + \beta(\text{month}) + 0.0041D_b \quad (8)$$

where the coefficients for "class" were 1 = 0.516, 2 = 0.536, 3 = 0.317, 4 = 0.398, and 5 = 0; and the coefficients for "month" were 8 = -0.190, 9 = 0.000, 10 = -0.067, 11 = 0.0106, 2 = 0.0346, 3 = -0.135, 5 = -0.057, 6 = -0.111; and where 8 is August 2000, and 6 is June 2001. The fastest growing trees were class 1 and those showing no measurable growth were class 5. There was no relationship between R_w and stem surface temperature.

Leaf respiration

Leaf respiration (R_l) was measured on leaves from 20 canopy trees located near three access towers over 24-h periods ($n = 488$ measurements) and varied from a few small negative values to 6.1, and averaged 0.54 $\mu\text{mol}\cdot\text{m}^{-2}$ leaf $\cdot\text{s}^{-1}$. R_l was higher during the day than at night even after reducing daytime rates by 40% (see *Materials and methods*), although the difference was not statistically significant. The daytime increase was significantly correlated with changes in leaf temperature, although problems associated with calculating mi-

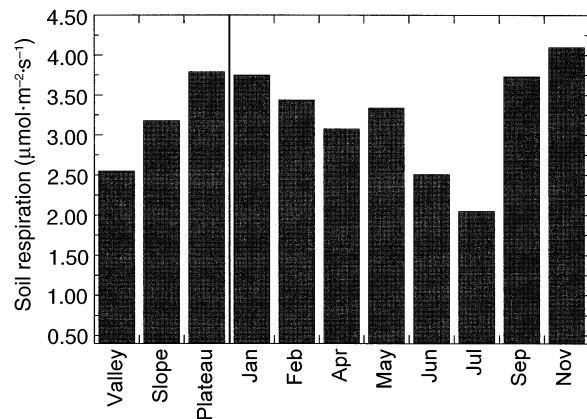


FIG. 3. Variation in ecosystem R_s (soil respiration) throughout the year and with topography. R_s increased from valley to slope to plateau forest, and monthly variability was probably the result of the interaction of a number of processes. R_s averaged 3.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ over the year for all topographic classes, and averaged 2.6, 3.2, and 3.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for valley, slope, and plateau forest, respectively.

tochondrial respiration during the day make interpretations of this response difficult.

Soil respiration

The respiratory flux from the soil was linearly correlated with soil temperature and curvilinearly correlated with soil VWC content, given by

$$\log(R_s) = -0.124 + 0.021T + 0.641M - 1.632M^2 \quad (9)$$

where M is VWC ($n = 422$ measurements). The mean response at varying levels of T and M were highly significant ($P < 0.0001$), although there was considerable unexplained variability ($r_{\text{adj}}^2 = 0.15$). There were few data with M less than about 0.20, so this model is only appropriate for relatively moist soil. 2000 and 2001 were La Niña years, when the central Amazon experienced some of the highest rainfall of the past century.

When "month" and "topography" were included as classification variables, M and T_s were no longer significant factors, suggesting that seasonal variability and landscape position were largely controlling variability in M and T_s . Multiple ANOVA with only "month" and "topography" as predictors, and \log -transformed R_s , explained 35% of the variability, suggesting that additional factors besides M and T_s were controlling variability in R_s . Calculating mean R_s for varying levels of "month" and "topography" using Eq. 1, assuming equal area for topographic classes, demonstrated that maximum monthly mean flux was about twice as high (4.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) as the minimum monthly mean flux (2.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and R_s for valley forest was significantly lower than slope or plateau (Fig. 3). Although it appears that the wet season flux was higher than the

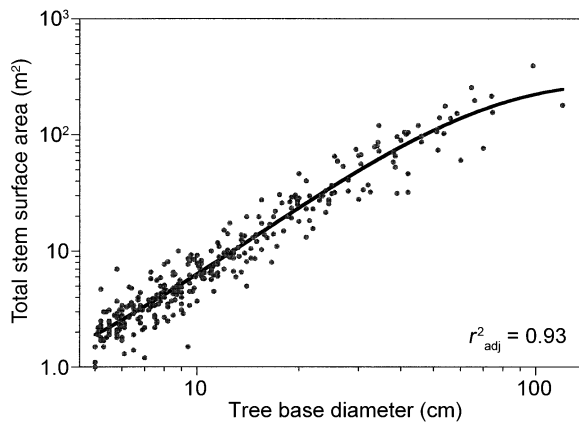


FIG. 4. Relationship between total stem surface area calculated using the Yoneda (1993) model and base diameter (D_b) for 315 harvested trees. Trunk and crown surface areas were estimated separately and then summed. This relationship was used to calculate a stem area index (SAI) of 1.7 using data from two 5-ha forest inventory plots.

dry season (Fig. 1) flux, based on average soil VWC, the wettest months were actually May, April, and June, and the driest months were November, September, and January. Averaged over the year assuming equal area in each topographic class, R_s was $3.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Scaling stem respiration

There was a strong functional relationship between total stem surface (A_s) area as calculated using Eqs. 1 and 4, and D_b (Fig. 4) given by

$$\log(A_s) = -0.105 - 0.686 \log(D_b) + 2.208 \log(D_b)^2 - 0.627 \log(D_b)^3 \quad (10)$$

This equation was used to estimate A_s for each tree from the Jacaranda plots ($n = 5283$). The 306 trees in the dendrometer study (Silva et al. 2002) were partitioned into relative growth classes as class 1, 3.3%; class 2, 6.9%; class 3, 13.7%; class 4, 52.0%; and class 5, 24.1%; with class 1 being the fastest growing trees, and class 5 showing no growth. These frequencies were used to randomly assign each tree in the Jacaranda plots a growth class. R_w was then assigned to each tree in the Jacaranda plots as a function of D_b , class, and month (Eq. 8), including random variability about the regression line using Eq. 2 ($\text{SD}_{\text{res}} = 0.271$). Summing R_w for each tree and averaging over the 10 ha of ground area provided estimates of R_w per unit ground area (R'_w), which varied from a high of $1.3 \mu\text{mol}\cdot\text{m}^{-2}$ ground $\cdot\text{s}^{-1}$ in December to a low of $1.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in June, with an overall mean of $1.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In addition, applying Eq. 10 to all trees from the Jacaranda PFIPs gave a stem area index (SAI) of 1.7, and an average R_w of $0.6 \mu\text{mol}\cdot\text{m}^{-2}$ stem $\cdot\text{s}^{-1}$.

Scaling leaf respiration

There was a strong relationship between $\log(A_l)$ and $\log(D_b)$ using the leaf mass data from the 50 harvested trees given by

$$\log(A_l) = -2.21 + 4.22 \log(D_b) - 0.918 \log(D_b)^2 \quad (11)$$

where $r^2_{\text{adj}} = 0.65$, $P < 0.0001$, and $\text{SD}_{\text{res}} = 0.304$ (Fig. 5). Thus, Eq. 11 estimates log-transformed average total leaf area for each tree as a function of D_b . Applying this equation to each of 5823 trees in the Jacaranda PFIPs, using Eq. 2 to account for variability, gave a mean LAI (for trees >10 cm D_b) of 4.7. Use of Eq. 2 was important since use of Eq. 11 without accounting for variability about the regression line gave a mean LAI of 3.7. Assigning R_l rates to each tree based on the hourly means and standard deviations (Eq. 2) from the LI-6400 chamber data demonstrated little diurnal variability in R_l per unit ground area (R'_l) (Fig. 6). The diurnal range of R'_l was 1.6 to $3.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, averaging $2.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or $0.55 \mu\text{mol}\cdot\text{m}^{-2}$ leaf $\cdot\text{s}^{-1}$.

Results from EC data

F_{ac} and F_{eco} were only independent of u^* variables during a very restricted set of conditions that for the purposes of this paper define sustained high turbulence (SHT). F_{eco} was independent of u^* when u^* was above 0.16 m/s and Δu^* was between -0.05 and 0.05 which occurred for 105 nighttime hours. F_{ac} was independent of u^* when u^* was above 0.21 m/s and Δu^* was between -0.05 and 0.05 which occurred for 53.5 nighttime hours. Since F_{ac} and F_{eco} during SHT conditions were approximately log-normally distributed, the mean flux during respective SHT conditions was calculated using Eq. 1 and averaged 8.8 (95% CI = 8.1–9.7)

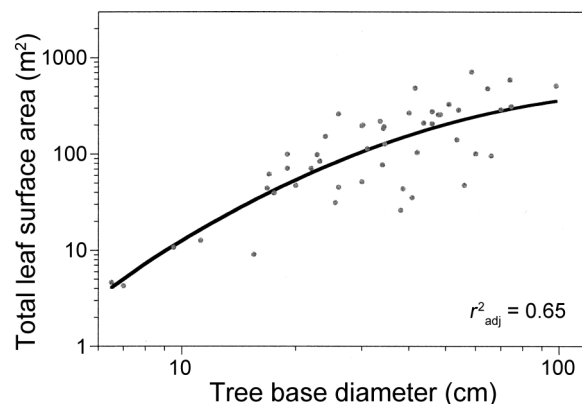


FIG. 5. Leaf mass and moisture content from 49 harvested trees were used to predict total leaf surface area (A_l), and A_l was correlated with tree base diameter (D_b). Extrapolating this model using D_b data from two 5-ha PFIPs (permanent forest inventory plots), and accounting for variability using Eq. 2, gave a leaf area index (LAI) of 4.7 for trees >10 cm in base diameter.

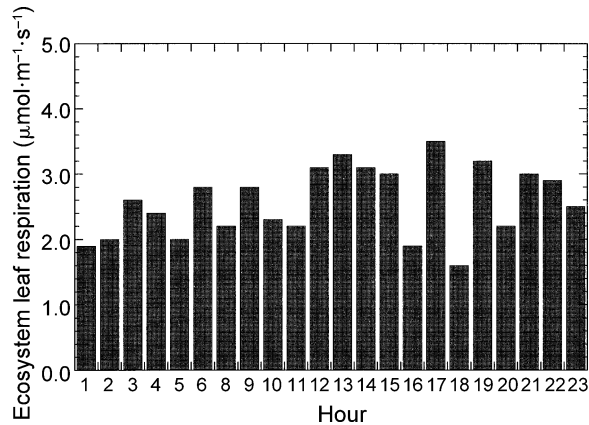


FIG. 6. Hourly changes in ecosystem leaf respiration estimated from scaled chamber data using an allometric leaf area model (Fig. 5). The daytime fluxes were reduced by 40% to account for light inhibition of mitochondrial respiration. There were no hour 7 measurements.

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for F_{eco} , and 8.4 (7.5 – 9.4) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for F_{ac} . Because F_{ac} and F_{eco} under SHT conditions were highly variable (large SD) and log-normally distributed, use of Eq. 1 was important. The simple arithmetic means of F_{ac} and F_{eco} under SHT conditions were 7.4 and 7.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (respectively), and a difference of ~ 1.0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ is quite large when calculating carbon balance. F_{ac} was not statistically different from F_{eco} during SHT conditions because F_{bc} approaches zero.

Both F_{ac} and F_{eco} were dependent on turbulent conditions during most nighttime hours. However, F_{eco} is a composite variable (the sum of F_{ac} and F_{bc}) with a complex error structure, and after accounting for variability associated with u^* terms, no biologically meaningful correlations were found. The F_{ac} data had a simpler error structure that allowed a more sensitive exploration for ecologically important information. F_{ac} was offset by a constant (4) so that negative fluxes could be included in the analysis, and F_{ac} was inverse square-root transformed ($1/\sqrt{F_{\text{ac}} + 4}$). There was a highly significant relationship between transformed F_{ac} and $\log(u^*)$ (above 0.01 m/s) (Table 1, no. 1). The third-order term was important because F_{ac} at low and high values of u^* were relatively stable, and there was a steep increase in F_{ac} at intermediate values of u^* . The change in u^* from one (half hourly) observation to next (Δu^*) was also an important variable (Table 1, no. 2), demonstrating that variation in F_{ac} was not only dependent on the value of u^* , but also on whether or not u^* had changed from the previous observation. For example, the predicted F_{ac} for a u^* of 0.4 with Δu^* of 0.3 (i.e., large increase in u^* from the previous hour) was about twice that predicted for a u^* of 0.4 with Δu^* of 0.0 (i.e., no change in u^* from the previous observation). In addition, the average u^* for a number of hours preceding the present observation was a signif-

icant explanatory variable. Using averaging times ranging from four to eight hours demonstrated that the eight-hour average (u^*_8) was the most significant term (Table 1, no. 3). This “final” u^* model accounted for physical variability in F_{ac} associated with u^* , the change in u^* (Δu^*), and the long-term average u^* preceding the present observation (u^*_8).

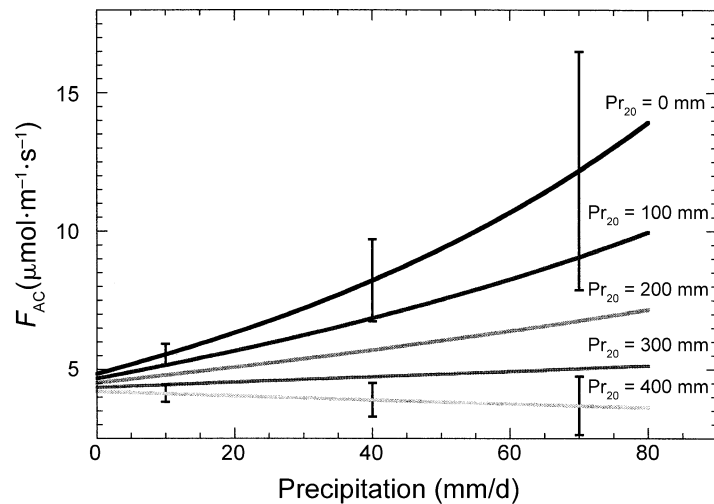
When precipitation variables were added to the final u^* model, both seasonal and daily changes in precipitation were important (Table 1, no. 4). Although there was only a small increase in the amount of unexplained variability, this was expected because variability in F_{ac} due to turbulence is much greater than variability due to physiological changes in respiratory processes. The low P value for the precipitation variables is more pertinent than the correlation coefficient, and demonstrates that mean F_{ac} response to changes in precipitation was significantly different than zero. Predictions from this model indicate how F_{ac} varied with precipitation when using SHT conditions for u^* variables (presumably where $F_{\text{ac}} = R_{\text{eco}}$) (Fig. 7). First, F_{ac} decreased as the preceding 20-d average precipitation (Pr_{20}) increased. This is similar to the finding of Araújo et al. (2002) using the same EC data that F_{eco} was depressed in the wet season and elevated in the dry season. The effect of Pr_{day} on F_{ac} depended on the value of Pr_{20} , as demonstrated by the significant interaction term (Table 1, no. 4). When a rainy day occurred after a number of dry days, F_{ac} was elevated, whereas when a rainy day occurred after a number of rainy days, F_{ac} was slightly depressed (Fig. 7).

TABLE 1. Summary of regression equations used to estimate the above-canopy flux (F_{ac}) as a function of u^* and precipitation variables (Pr_{day} , Pr_{20}).

No.	Regression equation	r^2_{adj}
1	$F_{\text{ac}} = (0.342 + 0.365 \log[u^*] + 0.654 \log[u^*]^2 + 0.230 \log[u^*]^3)^{-2} - 4$	0.474
2	$F_{\text{ac}} = (0.418 + 0.263 \log[u^*]^3 + 0.798 \log[u^*]^2 - 0.477 \Delta u^* - 0.504 \log[u^*] \Delta u^* + 0.553 \log[u^*]^{-2} - 4$	0.489
3	$F_{\text{ac}} = (0.510 + 0.245 \log[u^*]^3 + 0.692 \log[u^*]^2 + 0.254 \log[u^*_8] - 0.440 \log[u^*] \Delta u^* + 0.110 \log[u^*] \log[u^*_8] - 0.350 \Delta u^* + 0.465 \log[u^*] + 0.0410 \log[u^*_8]^2)^{-2} - 4$	0.517
4	$F_{\text{ac}} = (0.511 + 0.245 \log[u^*]^3 + 0.691 \log[u^*]^2 + 0.250 \log[u^*_8] - 0.431 \log[u^*] \Delta u^* + 0.113 \log[u^*] \log[u^*_8] + 0.468 \log[u^*] - 0.347 \Delta u^* - 0.030 \text{Pr}_{\text{day}} + 0.0408 \text{Pr}_{20} \text{Pr}_{\text{day}} + 0.0367 \log[u^*_8]^2 + 0.0155 \text{Pr}_{20})^{-2} - 4$	0.523

Note: The variables are listed in order of significance as ranked by the F statistic. Both Pr_{day} and Pr_{20} are in units of mm/h so that regression coefficients would fall within the same order of magnitude. Pr_{day} and the interaction term $\text{Pr}_{\text{day}} \text{Pr}_{20}$ were significant at $P < 0.0001$, and Pr_{20} was significant at $P = 0.02$.

FIG. 7. Predicted variability in the above-canopy eddy covariance flux (F_{ac}) using regression equation no. 4 from Table 1 and variability in seasonal (Pr_{20}) and daily (Pr_{day}) precipitation. The predictions are based on SHT (sustained high turbulence) conditions (atmospheric turbulence $u^* = 0.20$ m/s, $u_g^* = 0.20$ m/s at 8 h, and $\Delta u^* = 0.0$) where F_{ac} is presumably a reliable measure of R_{eco} . The accuracy of these mean predictions is indicated by the 95% CI for high and low Pr_{20} , although the predictions also change with the exact values used for SHT conditions.



DISCUSSION

Processes contributing to ecosystem respiration

Both R_s and R_w demonstrated significant seasonal variability, with the variation most pronounced in R_s . The soil flux consists of both heterotrophic and autotrophic respiratory sources, and heterotrophic respiration is probably more sensitive to moisture stress. For example, Chambers et al. (2001c) demonstrated that respiration from coarse surface litter (dead trunks and branches >10 cm diameter, R_{csl}), which amounted to an ecosystem flux of $\sim 0.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, declined sharply once moisture content fell below $0.5 \text{ g H}_2\text{O/g}$ dry wood. Also, Toledo (2002) found that respiration from fine surface litter (R_{fsl} ; leaves, small twigs, etc.) dropped appreciably when moisture content fell below

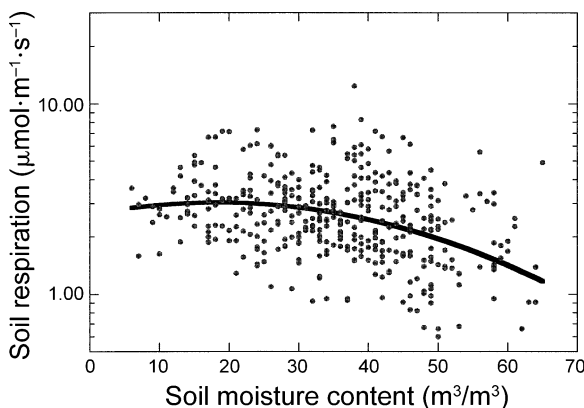


FIG. 8. Relationship between soil respiration (R_s) and soil volumetric water content (VWC) measured using a TDR probe. The relationship was curvilinear with R_s declining rapidly once VWC increased above about 0.30. Some very high VWC values were associated with saturated soils in the valleys, where dense roots helped to create soil gaps filled with water (i.e., a portion of the area integrated by the TDR probe had a VWC of 100%).

about $1.0 \text{ g H}_2\text{O/g}$ dry litter. Fungi are the primary decomposers of surface litter, and are sensitive to moisture stress (Dix and Webster 1995). The respiratory flux from fine and coarse surface litter is greatly reduced when moisture is limiting, and rapidly attains maximum rates soon after a rainfall event.

Contrary to our expectations, the highest R_s corresponded to lowest soil moisture content (VWC), although VWC was rarely less than about 0.20 (Fig. 8). The observed decline in mean R_s with an increase VWC may have been caused by inhibition of respiratory activity due to inadequate oxygen supply in saturated soils (Davidson 1993, Shuur 2003). There may also be seasonal variability in R_a (including soil R_a) associated with changes in phenology. A large increase in litterfall is associated with the onset of the dry season (Fig. 1) in the Central Amazon (Luizão and Schubart 1987, Luizão 1995), which probably reduces LAI, ecosystem photosynthetic capacity (Malhi et al. 1998), and root respiration (R_r). Wood production is also reduced throughout the dry season in the central Amazon (Silva et al. 2002), which may also be driven by seasonal changes in LAI, and there is presumably a similar belowground growth response. Thus the main contributors to R_s (R_r , R_{fsl} , R_{csl} , R_{SOM}) may often be responding in different ways to changing environmental conditions. For example, while respiration from surface litter may be declining due to moisture stress, respiration from soil organic matter may be increasing because soil dries more slowly.

Comparing our estimates with an earlier study, Yoda (1983) measured total autotrophic respiration (R_a) for a lowland tropical forest in Pasoh, Malaysia using a static chamber method (KOH titration) on harvested tissues, and aboveground R_a for trees >9.5 cm D_b was $7.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In comparison, aboveground R_a ($R_l + R_w$) from this study was $3.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Nay et al. (1994) found that static chamber methods tend to

overestimate low rates, and underestimate high rates, at least for soil respiration. This methodological bias may explain part of the difference between these estimates, although damage to tissues harvested by Yoda et al. (1983) may have also increased respiratory activity. Nevertheless, Yoda (1983) quantified R_a for trees <9.5 cm D_b , understory and undergrowth (R_u), which contributed an additional $1.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or 19% of the total R_a flux. Although 19% may be an overestimate because static chambers tend to overestimate low flux rates (presumably found in the understory), our R_{eco} estimate is entirely missing this source. If we assume that the difference between Yoda (1983) and this study are entirely methodological, our estimate of R_{eco} should be increased by at least $0.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to account for vegetation <10 cm D_b .

Our R_{eco} estimate is probably low due to a number of factors. First, a closed dynamic chamber (CDC) such as employed here for R_w and R_s tends to create a positive pressure with respect to the local atmosphere, which may inhibit gas flux (Lund et al. 1999). Although few studies have evaluated this effect directly, Nay et al. (1994) found that a CDC consistently underestimated a known flux by $\sim 15\%$. We employed an equilibration vent on our soil chambers to help equalize pressure (Trumbore et al. 1995), although our stem chambers had no vent. Second, Yoda (1983) found that R_w for a given stem diameter increased with canopy height, and if this phenomenon is general, our branch respiration estimate (a portion of R_w) is probably low. It is worth noting that Levy et al. (1999) found a small portion of the stem CO_2 efflux may have ultimately come from the soil, although this potential bias would not have significantly affected our R_w estimate. Third, we only measured R_l during the dry season months, and it is likely that R_l is higher in wet season months, similar to our R_w results, and also supported by seasonal variability in tree growth (Silva et al. 2002) and maximum carbon assimilation rate (Malhi et al. 1998). Finally, surface roots in the valley forests tend to aggregate on the surface in a root mat where respiration chambers could not be installed, so R_s for valley forest may be underestimated. There are few significant factors we can identify that would result in large systematic overestimation of R_{eco} components in this study, although more work on R_l during the day is needed to better quantify light inhibition of R_l .

Comparisons with other studies support the conclusion that our R_{eco} estimate is conservative. Sotta (1998) estimated R_s for a plateau forest ~ 10 km from our study site of $6.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas Wofsy et al. (1988) estimated R_s of $4.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for plateau forest at Ducke reserve ~ 50 km from our site. Similarly, Trumbore et al. (1995) working in a drier forest near Paragominas, Brazil, estimated a R_s of $6.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and Meir et al. (1996) measured a mean R_s of 5.5 for a forest in Rondônia, Brazil. Nepstad et al. (2002) es-

timated a mean R_w of $0.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{stem}\cdot\text{s}^{-1}$ for a forest near Santarem, Brazil; Ryan et al. (1994) estimated means of 1.2 and $0.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{stem}\cdot\text{s}^{-1}$ for two tree species at La Selva in Costa Rica; and Meir and Grace (2002) estimated an average of $\sim 0.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{stem}\cdot\text{s}^{-1}$ for 23 species in Rondônia, Brazil. Reich et al. (1991) found an average large tree R_l of $0.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{leaf}\cdot\text{s}^{-1}$ in a closed-canopy forest near San Carlos del Rio Negro, Venezuela. Estimates of LAI for Amazon forests range from 4.4 to 7.5 (Williams et al. 1972, Saldarriaga 1985, McWilliam et al. 1993, Roberts et al. 1996) including 5.7 for a forest near Manaus (McWilliam et al. 1993).

EC data

There were only a restricted set of conditions (SHT) where F_{eco} and F_{ac} were independent of turbulence as measured by u^* variables. This suggests that R_{eco} can only be directly estimated by the EC method during nighttime conditions that are infrequent. However, there is some question over whether or not high concentration soil CO_2 can be entrained in the eddy flux during SHT conditions, leading to overestimates of R_{eco} . If this was the case, we would expect F_{eco} and F_{ac} to always be dependent on u^* because CO_2 trapped in the soil would probably rarely if ever be fully flushed. If changes in the concentration of soil CO_2 driven by turbulence are minimal, F_{ac} during SHT conditions should provide a reliable estimate of R_{eco} .

Despite the paucity of SHT conditions at night, F_{ac} under SHT conditions was predicted with a reasonably small 95% CI. It appears that nighttime EC data under turbulent conditions are valuable, and additional years will allow more accurate estimates of nighttime R_{eco} . Moreover, additional data should also allow more precise analyses of ecological factors that control variability in respiratory processes, which are much more subtle than changes in F_{ac} driven by turbulence. Our analyses have demonstrated that despite turbulence (i.e., u^*) controlling a large amount of F_{ac} variability, there was still important ecological information contained in the EC data as demonstrated by the significance of seasonal and daily changes in precipitation.

Comparison of chamber and EC data

Given the many potential sources of error, our scaled-chamber R_{eco} estimate of $7.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ is probably not statistically different from our nighttime F_{ac} estimate under SHT conditions of $8.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (7.5 – $9.4 = 95\%$ CI). We did not attempt the difficult task of calculating a 95% CI for our scaled-chamber R_{eco} estimate, although most identified factors would tend to underestimate of the actual flux. If F_{ac} under SHT conditions is a reliable measure of R_{eco} , our R_{eco} estimated from F_{ac} is probably more accurate than the scaled-chamber data because F_{ac} integrates all respiratory activity, and may be a reasonably direct measure of R_{eco} .

Conversely, chamber measurements allow exploration of factors that control variability in individual sources, and provide valuable information for developing a process level understanding of respiratory variability.

Interestingly, both the scaled chamber and EC data showed a similar response to changes in precipitation. First, R_s declined with increasing soil moisture, with R_s being depressed during wet months and elevated during dry months, although dry months were relatively wet during this study. The EC data also demonstrated a decrease in F_{ac} with increasing 20-d average precipitation (Fig. 7), which may have been largely driven by a reduction in R_s under high VWC when low oxygen concentration can limit respiratory activity. Second, Chambers et al. (2001c) and Toledo (2002) demonstrated that respiration is very low from dry litter (coarse and fine), increases sharply with increasing moisture, and quickly saturates at maximum rates. Similarly, F_{ac} increased appreciably after a rainfall event when the 20-d average was low (i.e., wet-up of dry litter), whereas additional rainfall when the 20-d average was high resulted in a slight decrease in F_{ac} (Fig. 7).

More nighttime EC data under SHT conditions should provide additional information on the cumulative response of R_{eco} to changing environmental conditions. However, it is important to point out that an apparently insignificant difference of $0.26 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ corresponds to an annual flux of $1.0 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, which if simply scaled over the entire Amazon basin ($5 \times 10^{12} \text{ km}^2$) results in a globally significant 0.5 Pg yr^{-1} carbon sink or source. Thus, developing whole ecosystem carbon balance with an accuracy of greater than $\pm 1.0 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ may not be possible using flux measurements. Nevertheless, mechanistic studies into factors controlling carbon cycling variability at the cellular to ecosystem scale will aid considerably in the development of predictive models that can simulate ecosystem response to disturbance and atmospheric changes.

NPP, GPP, and CUE

We define carbon use efficiency (CUE) as the ratio of production (i.e., NPP) to total gross carbon fixation ($R_a + \text{NPP}$), and CUE is an important parameter for comparing carbon cycle variability among ecosystems (Ryan et al. 1996a, 1997, Amthor 2000). At the ecosystem scale, CUE is analogous to the NPP/GPP ratio, and provides a measure of what fraction of total carbon assimilation becomes incorporated into new tissues. Using R_w and R_l presented here, and production estimates for wood and leaves (Chambers et al. 2000, 2001b) we calculate a woody tissue CUE of 0.43 and a leaf CUE of 0.25. Weighting for the relative production of each component, total aboveground CUE was 0.32. Thus we estimate that only about 30% of carbon

allocated aboveground is used to construct new tissues, the remainder being R_a .

Raich and Nadelhoffer (1989) offered a means for estimating belowground productivity by constraining fluxes which assumes that net changes in carbon pools are much smaller in magnitude than gross inputs and outputs, and Amazon soil studies support this quasi-steady-state assumption (Telles et al. 2003). However, an important parameter in the Raich and Nadelhoffer (1989) method is the partitioning of belowground respiration which is difficult to measure directly. Thus, based on temperate forest (Waring et al. 1998) and modeling (Dewar et al. 1999) studies, belowground CUE is often assumed to be a constant (0.50). However, since our estimate varied significantly from this constant, we used our measured aboveground CUE to approximate belowground CUE. Using this approach, we estimate a belowground NPP of $2.6 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and combined with aboveground NPP, an ecosystem NPP of $9.0 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; (but see Clark et al. 2001a, b, and Chambers et al. 2001b for potential missing NPP components). Partitioning belowground respiration provides ecosystem estimates for R_a and R_h of 21.0 and $8.5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively (Fig. 9, Table 2). R_s was about equally divided between R_a (roots) and R_h ($R_{\text{SOM}} + R_{\text{fsl}}$) similar to results from Hogberg et al. (2001) that a large fraction of soil respiration was from recently assimilated carbon. If we assume that R_{eco} approximates GPP, gross photosynthetic assimilation (A_g) of carbon by this Central Amazon forest is $\sim 30 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$.

Amthor (2000) compiled data from other tropical forest studies (Müller and Nielsen 1965, Odum 1970, and Kira 1975) to calculate a related autotrophic respiration to gross photosynthesis ($R_a/A_g = 1 - \text{CUE}$) ratio, and including our estimate here, R_a/A_g averages 0.26 for tropical forests. In contrast, R_a/A_g ratios for temperate forests compiled from ~ 20 studies (Amthor 2000) ranged from 0.32 to 0.72 and averaged 0.54. Waring et al. (1998) found a conservative R_a/A_g ratio of 0.53 ± 0.04 ($\pm 1 \text{ SD}$) for 12 temperate forest sites which used comparable methods. Thus, it appears that many tropical forests are an exception to the presumably invariant R_a/A_g ratio found in temperate studies. Tropical forests often have a high capacity for capturing atmospheric carbon, but only a small fraction of that carbon becomes incorporated into new tissues.

One possible reason for this difference is that respiratory demands per unit photosynthate are simply greater in tropical forests. Some studies suggest that the R_a/A_g ratio should increase with mean annual temperature (Woodwell 1983, Ryan 1996b), whereas others suggest this ratio should be relatively constant with temperature (Gifford 1995, Dewar 1999), and in response to CO_2 fertilization (Cheng et al. 2000). Another possibility is that in nutrient-deficient forests such as central Amazon terra firme, more carbon is fixed via

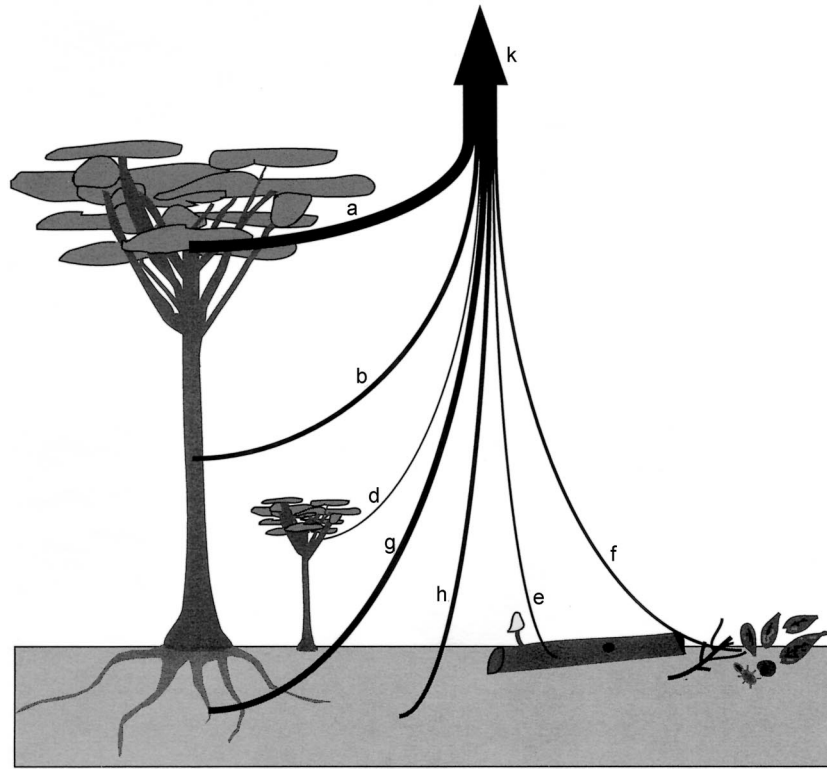


FIG. 9. Summary of estimates provided by this study and literature data used to calculate total ecosystem respiration (R_{eco}) and carbon use efficiency (CUE). The sizes of the flow lines in the figure are proportional to the flux, and the letters correspond to the identification in Table 2. Fluxes are given in $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ($1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1} = 0.264 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

photosynthesis than can be utilized by growth and functional respiration. In this scenario, a significant amount of carbon may be respired via the alternative pathway, and other futile cycles, as wastage respiration (R_{wa}) (Lambers 1982, 1997). Perhaps if growth (R_g), main-

tenance (R_m), and wastage (R_{wa}) respiration components were estimated independently, the $(R_g + R_m)/A_g$ ratio would be conservative across all ecosystems. It will be informative to investigate whether or not enhanced R_{wa} in tropical forests accounts for different R_g/A_g ratios.

TABLE 2. Descriptions, estimates, and sources of components in Fig. 9.

Identification	Symbol	Description	Estimate	Source
a	R'_l	leaf respiration	9.8	this study
b	R'_w	wood respiration	4.2	this study
c	R'_s	soil respiration	12.1	this study
d	R'_u	understory respiration	1.5	Yoda (1983)
e	R'_{csl}	respiration from coarse surface litter	1.9	Chambers et al. (2001a)
f	R'_{isl}	respiration from fine surface litter	2.6	Toledo (2002)
g	R'_r	root respiration (soil autotrophic)	5.5	$(c - r) \times (1 - w)$
h	R'_{SOM}	respiration from soil organic matter	4.0	$c - g - f$
i	R'_a	ecosystem autotrophic respiration	21.0	$a + b + d + g$
j	R'_h	ecosystem heterotrophic respiration	8.5	$e + f + h$
k	R'_{eco}	ecosystem respiration	29.5	$i + j$
n	NPP_l	leaf production	3.3	Chambers et al. (2001b)
o	NPP_w	wood production	3.2	Chambers et al. (2001b)
p	NPP_s	belowground production	2.6	$(c - r) \times w$
q	NPP_{eco}	total production	9.0	$n + o + p$
r	C_l	total fine litterfall	4.0	Chambers et al. (2001b: references)
s	LAI	leaf area index	4.7	this study
t	SAI	stem area index	1.7	this study
u	CUE_l	leaf carbon-use efficiency	0.25	$n/(n + a)$
v	CUE_w	wood carbon-use efficiency	0.43	$o/(o + b)$
w	CUE_{ag}	aboveground carbon-use efficiency	0.32	$(n + o)/(n + o + a + b)$

As opposed to ecosystems where most respiration is functional (i.e., $R_g + R_m$; Lloyd and Farquhar 1996), an ecosystem with a large fraction of respiration as R_{wa} may be relatively insensitive to increases in atmospheric CO_2 .

Forest carbon balance

There is some controversy over whether or not old-growth Amazon forests are acting as carbon sinks. A recent summary of results from eddy covariance (EC) and field studies suggests that old-growth Amazon forests are accumulating $\sim 1.4 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Grace and Malhi 2002, Malhi et al. 1999). However the magnitude and even the sign of NEP estimates from EC data are dependent on how the data are analyzed. Carbon balance, or even a small carbon source, cannot be ruled out from EC data (Miller et al. 2004), although Araújo et al. (2002) suggest that simply removing data during low turbulence conditions leads to overestimates of nocturnal R_{eco} . Analyses of Amazon forest permanent plot data indicate that trees are accumulating $\sim 0.7 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in aboveground biomass (Phillips et al. 1998, 2002). However, Clark (2002) finds that methodological artifacts inherent in the same permanent plot data lead to a 95% CI that includes carbon balance. Conversely, Phillips et al. (2002) find that systematic errors in permanent plot data are small and quantifiable, and that strong evidence supports biomass accumulation. Separately, empirical modeling of Central Amazon forest biomass dynamics demonstrated that although Amazon forests have a long-term capacity to sequester carbon in response to an increase in productivity, the annual aboveground sink potential was only $\sim 0.5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Chambers et al. 2001a). Thus, the carbon balance of old-growth Amazon forests remains an open question, although even under a strong CO_2 fertilization response, a sink greater than $\sim 1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ appears implausible.

The underlying rationale to support a tropical forest carbon sink is that trees are responding to increased atmospheric CO_2 with an increase in growth and biomass production (Lloyd and Farquhar 1996), which is more than enough to compensate for any increase in mortality or forest turnover rates (Phillips and Gentry 1994). Lloyd et al. (2001) propose that much of the additional carbon would eventually accumulate in the soil, although the potential annual sequestration rate of Amazon terra firme soils is quite low (Telles et al. 2003), and the lag time would probably be centuries to millennia. Also, the magnitude of a CO_2 fertilization response will likely be moderated by carbon and nutrient cycle linkages and feedbacks, and competitive interactions among individual trees. Lloyd and Farquhar (1996) found that if elevated carbohydrate supply ultimately results in increased nutrient acquisition from the soil, production in tropical forests is expected to respond strongly to higher concentrations of atmo-

spheric CO_2 . However, interactions of above- and belowground carbon and nutrient cycles are complex (e.g., Vitousek 1984, Herbert and Fownes 1995, Lloyd et al. 2001), and much additional research is needed to better understand tropical forests response to elevated atmospheric CO_2 .

We show here that aboveground R_a for trees in a Central Amazon forest is considerably greater than aboveground NPP, similar to the findings of earlier studies that employed less-accurate static-chamber and destructive-harvest methods (Odum 1970, Kira 1975, Müller and Nielsen 1965, Yoda 1983). Does this flux represent true respiratory costs, or are many Amazon trees sink limited, respiring a substantial fraction of carbon via the alternative oxidase, or other futile cycles? If carbon is already being supplied in excess of demand, it seems unlikely that plant production would increase in response to elevated atmospheric CO_2 . However, if the CO_2 flux largely represents true respiratory costs, an increase in photosynthesis from elevated atmospheric CO_2 may result in a larger than average increase in growth (Lloyd and Farquhar 2000). Quantifying the flow of carbon through the alternative respiratory pathway should help shed light on whether or not tropical forests are carbon limited.

ACKNOWLEDGMENTS

We would like to thank Jeff Amthor, Mike Goulden, Mike Ryan, and an anonymous reviewer for comments on this manuscript. INPAs Tropical Forestry department (CPST) provided invaluable support during all phases of this study. This work was made possible by support from NASA's LBA-ECO project, the Piculus project (Pilot Programs of the G-7 Nations), the Jacaranda project (Japanese International Cooperation Agency), and EC data was provided by the LBA-Eustach project with funding from European Commission DG Research's 5th Framework Program.

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