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Foliar and ecosystem respiration in an old-growth tropical rain forest

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ABSTRACT

Foliar respiration is a major component of ecosystem respiration, yet extrapolations are often uncertain in tropical forests because of indirect estimates of leaf area index (LAI). A portable tower was used to directly measure LAI and night-time foliar respiration from 52 vertical transects throughout an old-growth tropical rain forest in Costa Rica. In this study, we (1) explored the effects of structural, functional and environmental variables on foliar respiration; (2) extrapolated foliar respiration to the ecosystem; and (3) estimated ecosystem respiration. Foliar respiration temperature response was constant within plant functional group, and foliar morphology drove much of the within-canopy variability in respiration and foliar nutrients. Foliar respiration per unit ground area was 3.5 ± 0.2 μmol CO_2 m^{-2} s^{-1}, and ecosystem respiration was 9.4 ± 0.5 μmol CO_2 m^{-2} s^{-1} [soil = 41%; foliage = 37%; woody = 14%; coarse woody debris (CWD) = 7%]. When modelled with El Niño Southern Oscillation (ENSO) year temperatures, foliar respiration was 9% greater than when modelled with temperatures from a normal year, which is in the range of carbon sink versus source behaviour for this forest. Our ecosystem respiration estimate from component fluxes was 33% greater than night-time net ecosystem exchange for the same forest, suggesting that studies reporting a large carbon sink for tropical rain forests based solely on eddy flux measurements may be in error.

Key-words: autotrophic respiration; canopy structure; carbon balance; foliar N; foliar P; LMA; photosynthesis; plant functional group; Q_{10}; tropical wet forest.

INTRODUCTION

Tropical forests account for more than one-third of global plant productivity (Saugier, Roy & Mooney 2001), and at least half of this carbon is released back into the atmosphere as autotrophic respiration (Edwards *et al.* 1981; Chambers *et al.* 2004). Results vary widely about whether tropical forests are presently acting as carbon sources or sinks, or how this may be affected by global warming. Several eddy flux studies have concluded that tropical rain forests are primarily acting as carbon sinks (Fan *et al.* 1990; Grace *et al.* 1995; Malhi *et al.* 1998; Loescher *et al.* 2003, but see Saleska *et al.* 2003). Many atmosphere–biosphere modelling studies, on the other hand, predict that tropical forests will be an increased carbon source with global warming (Kindermann, Würth & Kohlmaier 1996; Braswell *et al.* 1997; Tian *et al.* 1998; Cox *et al.* 2000; Ito & Oikawa 2000; White, Cannell & Friend 2000; Cramer *et al.* 2001; Clark *et al.* 2003). A better understanding of autotrophic respiration at the landscape scale is a crucial first step in predicting how tropical rain forest ecosystem carbon balance may change with climate change.

Foliage can account for 18–40% of total ecosystem respiration (Chambers *et al.* 2004; Curtis *et al.* 2005), yet extrapolations are uncertain in tropical rain forests because of access difficulties and the lack of unbiased leaf area index (LAI) estimates. This study presents results from an intensive 2-year field campaign where we measured LAI and foliar respiration across gradients of soil fertility in an old-growth tropical rain forest in Costa Rica. We used a portable scaffolding tower to access canopy foliage for respiration measurements and to harvest foliage from forest floor to canopy top to estimate LAI. To our knowledge, this is the first foliar respiration estimate for a tropical rain forest where the ecosystem extrapolation is based on detailed information of within-canopy variation in foliar respiration and LAI.

Foliar respiration standardized to a common temperature is influenced by many variables, including canopy height, foliar or soil nutrients, foliar morphology and species (Bolstad, Mitchell & Vose 1999; Mitchell, Bolstad & Vose 1999; Turnbull *et al.* 2003). To complicate matters further, the temperature response of foliar respiration can also change with any of the mentioned variables (Atkin *et al.* 2005). Standardizing respiration measurements to a common temperature according to within-canopy and across-landscape variability in temperature response will

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greatly reduce uncertainty involved in extrapolating foliar respiration to the ecosystem.

Foliar dark respiration is a primary trait in the 'leaf economics spectrum' (Wright *et al.* 2004). Respiration, leaf lifespan, photosynthetic capacity (A_{max}), leaf mass per area (LMA), nitrogen (N) and phosphorus (P) have been found to correlate with each other across plant functional groups and ecosystem types, revealing convergent evolution on a global scale (Reich, Walters & Ellsworth 1997). We expected night-time foliar respiration to be linearly related to LMA, foliar N, P and A_{max}, in accordance with the leaf economics spectrum.

Some studies suggest that the more limiting the nutrient is, the tighter it will correlate with foliar respiration (Ryan 1995; Meir, Grace & Miranda 2001). We expected foliar respiratory rates to be better correlated with soil P than soil N, because phosphorus, rather than nitrogen, is likely limiting in this rain forest (McDade *et al.* 1994). The ratio of photosynthetic capacity to respiration (A_{max}/R) may also vary in relation to nutrient limitation (Turnbull *et al.* 2005), and the ability of plants to maintain constant A_{max}/R may be related to thermal acclimation (Dewar, Medlyn & McMurtrie 1999). To characterize these sources of variation and compare them to variation in respiration per unit leaf area (R_A) and leaf mass (R_M), we analysed the responses of R_A, R_M, R/N, R/P and A_{max}/R to changes in soil N and P stocks, plant functional group and canopy height.

We devised six different estimates of night-time foliar respiration per unit ground area (R_{foliar}), including two complex and four simple methods. The more complex estimates used detailed information of within-canopy variability and temperature data, while the four simpler methods used overall means to see if we could provide realistic extrapolations of foliar respiration for this forest with less investment.

This study had five objectives. Firstly, we sought to characterize the variation in foliar respiration with temperature. Secondly, we asked if respiration corrected to a common temperature of 25 °C varied with foliar nutrients, LMA, plant functional group, height or soil nutrients. Thirdly, we examined the relationship between foliar respiration and photosynthetic capacity (A_{max}). Fourthly, we used relationships identified in (1) and (2) to compare several methods of extrapolating foliar respiration to a ground-unit basis. Finally, we estimated ecosystem respiration by combining our detailed estimate of foliar respiration per unit ground area with previously published values of woody, soil and coarse woody debris (CWD) respiration, and compared the total to an estimate of eddy flux night-time net ecosystem exchange (NEE_{night}) for the same location (Loescher *et al.* 2003). The eddy flux technique has several possible sources of error, including complex canopies, non-flat topography, still night-time air and biased air movement, which all can result in a systematic underestimation of night-time respiration (Baldocchi 2003). Consequently, independent estimates of ecosystem respiration that help constrain estimates of night-time effluxes should be extremely useful.

MATERIALS AND METHODS

Study site

La Selva Biological Station is located in the Caribbean lowlands of northern Costa Rica (elevation 37–150 m, 10°20′ N, 83°50′ W). La Selva, classified as tropical wet forest in the Holdridge life-zone system (Hartshorn 1983), has a mean annual rainfall of ~4000 mm, and a mean annual temperature of 26 °C. This study includes sampling from within La Selva's 515 ha of old-growth forest. Further information about the soils and plant communities of La Selva is found in McDade *et al.* (1994).

Tower construction and sampling scheme

The tower sampling design and construction were part of a larger project where we sought to characterize canopy structure and function across environmental gradients in a tropical rain forest. We constructed an aluminium walk-up scaffolding tower (Upright, Inc., Dublin, Ireland) to the top of the canopy at each of 55 sites in the old-growth forest of La Selva Biological Station. See Cavaleri, Oberbauer & Ryan (2006) for site selection details. Towers were constructed one $1.30 \times 1.86 \times 1.86$ m ($L \times W \times H$) section at a time, harvesting all foliage within each section. A cantilever balcony installed on the top of the tower during harvesting increased the sample area to a total of 4.56 m^2. Tower heights varied from 1.86 m (one section) to 44.64 m (24 sections). All harvested foliage was separated by height and plant functional group and measured with a leaf area meter (Li-3100; Li-Cor, Inc., Lincoln, NE, USA). Plant functional groups for this study were trees, palms, lianas (woody vines) and herbaceous plants (including herbs, epiphytes, vines and ferns). All foliar physiology sampling occurred on undamaged foliage accessible from the side of the tower after each tower was constructed. We dismantled the tower after all measurements were taken 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. Photosynthesis and foliar respiration were sampled from 52 of the 55 towers constructed.

Foliar gas exchange, morphology and nutrients

We measured photosynthetic capacity (A_{max}), foliar respiration, foliar nitrogen (N), foliar phosphorus (P) and LMA for every species accessible from the tower, at every tower section in which the species was found. For each unique species at each unique tower section, A_{max} was measured *in situ*, and adjacent foliage segments were flagged for respiration sampling. Each flagged foliage segment (two to six small leaves or one large leaf) was cut under water in the afternoon and placed in a water-filled floral tube so that cut surfaces were never exposed to air. Detached foliage samples were transported back to the lab for night-time respiration measurements. Three replicates of A_{max} and two

replicates of respiration were measured for each unique species at each unique height, and replicates were averaged prior to statistical analyses. These data represent 990 foliar respiration measurements: two replicate measurements each of 495 plant samples, representing over 162 species and 53 families.

We measured A_{max} with an open-system portable infrared gas analyser with an integrated blue–red light source inside the leaf chamber (Li-6400, Li-Cor, Inc.). Measurements were taken at a constant reference CO_2 concentration of 390 μmol mol^{-1} and an air flow of 500 μmol s^{-1}. The photosynthetic photon flux densities (PPFDs) were determined as the saturating PPFD values from a photosynthesis/light curve on the same species at the same height. Saturating PPFD values ranged from 500 to 1500 μmol m^{-2} s^{-1} at heights <10 m, and from 1000 to 2000 μmol m^{-2} s^{-1} for heights >10 m.

Prior to the construction of the first tower, we conducted a pilot study to ensure the validity of measuring respiration on detached foliage. We measured foliar respiration *in situ* on 42 attached samples at night, detached the same samples the next afternoon and measured them again on the second night. Samples represented three functional groups and 13 species: trees (seven species; $n = 25$), herbaceous (one species of vine; $n = 4$) and palms (five species; $n = 13$). A repeated measures analysis of variance (ANOVA) with functional group as a factor and attached–detached as the within-subjects factor showed no effect of detachment (d.f. = 39; $P = 0.24$). Several additional studies have also found no difference between respiration rates on attached versus detached foliage (Bolstad *et al.* 1999; Mitchell *et al.* 1999; Turnbull *et al.* 2005).

We measured night-time foliar respiration with LCA-3 and LCA-4 open-system infrared gas analysers (Analytical Development Company, Hoddesdon, UK). We clamped foliage into a clear polycarbonate custom-made chamber with a neoprene gasket (internal volume = 1750 mL; 12.5 × 28 × 5 cm), with only the stem or petiole protruding during measurement. A 9 V battery-operated fan was installed to stir the air inside the chamber. Air flow rates through the chamber ranged from 330 to 340 μmol s^{-1}, and chamber seals were checked with a flowmeter. Intake air was drawn through a 19 L mixing chamber to maintain stable reference CO_2 concentrations. We recorded the difference in CO_2 concentration between the reference and the chamber after it had been stable for at least 2 min. Respiration measurements were taken in the dark between 1900 and 0500 h at ambient temperature. Foliage temperature was measured with a thermocouple thermometer. All foliage that was inside the chamber was measured with a leaf area meter (Li-3100; Li-Cor, Inc.) to determine respiration rates per unit leaf area. Foliage was dried to constant weight at 60 °C to calculate LMA (g m^{-2}).

For a subsample of nine towers, we measured foliar respiration–temperature response curves on all accessible species × height combinations, excluding understory species. Respiration–temperature response data included two replications each of 31 tree samples (19 species), 13 liana samples (six species), eight palm samples (four species) and one species from each of the herbaceous groups: fern, epiphyte and vine. A temperature-controlled cuvette with a peltier cell was attached to the LCA-3 infrared gas analyser to measure response curves (Hubbard, Ryan & Lukens 1995). A datalogger- (Campbell 21X; Campbell Scientific, Logan, UT, USA) controlled temperature and logged foliar respiration rates over the temperatures 15, 25, 30 and 35 °C. The intake air passed through a tube of $CaSO_4$ desiccant (Drierite, Xenia, OH, USA) to minimize condensation at the lower temperatures. To correct for the desiccant effect on CO_2 flow, we took a reading with no leaf in the chamber before and after each temperature curve and linearly interpolated between these two 'zero' points to calculate a zero for each measurement of the temperature curve.

Replicates of foliage samples measured for respiration and respiration–temperature response were bulked for nutrient analyses and ground in a Wiley mill with 20-mesh sieve. We analysed foliar samples for N concentration with a LECO TruSpec CN Determinator, (LECO, Inc., St. Joseph, MI, USA). Foliar P concentrations were determined with nitric acid/hydrogen peroxide digests and an inductively coupled plasma spectrometer (PerkinElmer 4300 Optima Dual View, Norwalk, CT, USA) by MDS Harris Laboratories, Lincoln, NE, USA.

Soil nutrient sampling

At each site, we sampled soil to a depth of 1 m with a 0.03-m-diameter half-core auger. Two subsamples were taken at a distance of 1 m from the tower base centre and at a 180° angle from each other. Six to eight additional subsamples were taken at a distance of 2 m from the tower base centre at regularly spaced angles. Each subsample was separated into four layers by depth: 0–0.1, 0.1–0.3, 0.3–0.5 and 0.5–1 m. All subsamples for each tower were mixed by layer and organic material, and stones removed. Samples were air-dried, sieved through a 2 mm screen, ground in a coffee mill and stored until nutrient analysis. Samples were oven-dried at 40 °C for 2–3 d, and 20 g of each sample was finely ground in an agate mill (Fritsch, Idar-Oberstein, Germany). Total N (mg g^{-1}) was analysed by combustion with a C/N-Analyzer (CHN-O-RAPID, Heraeus, Hanau, Germany), and total P (mg g^{-1}) was analysed with a HNO_3-pressure extraction and inductively coupled plasma spectrometry (ICP Spectro, Kleve, Germany). Stocks of N and P (mg ha^{-1}) for each soil layer were calculated using the mean bulk density of each layer (0.67, 0.79, 0.85 and 0.89 g cm^{-3}, respectively, at depths 0–0.1, 0.1–0.3, 0.3–0.5 and 0.5–1 m), measured from six permanent plots within the old-growth forest of La Selva Biological Station (Clark, unpublished data). N and P stocks for each layer were summed for cumulative soil N and P stocks by tower.

Data analysis

We used the following equation to model each respiration temperature response curve:

$$R_{\mathrm{Tleaf}} = \beta_0 \times \exp(T_{\mathrm{leaf}} \times \beta_1) \quad (1)$$

where β_0 and β_1 are model parameters, and R_{Tleaf} is respiration rate (μmol CO_2 m^{-2} s^{-1}) at the measured foliage temperature, T_{leaf} (°C). Q_{10}, the change in respiration rate with 10 °C change in temperature, is defined as $\exp(10 \times \beta_1)$. We also modelled each respiration temperature response curve with a modified Arrhenius function described by Lloyd & Taylor (1994), shown as follows for a base temperature of 25 °C or 298K:

$$R_{\mathrm{Tleaf}} = R_A \times \left\{ \exp\left[\left(\frac{E_0}{R_{\mathrm{g}}} \right) \left(\frac{1}{298} - \frac{1}{T_{\mathrm{leaf}}} \right) \right] \right\} \quad (2)$$

where R_{g} is the gas constant (0.008314 kJ mol^{-1} K^{-1}), and E_0 (kJ mol^{-1} K^{-1}) is a parameter which describes the magnitude of temperature response, described as the energy of activation. We examined variation in Q_{10} and E_0 with simple linear regression (R_{A}, LMA, foliar N, foliar P, soil N, soil P and height), analysis of covariance (ANCOVA) (functional group + height) and ANOVA (functional group) procedures. Based on the results of these analyses, we used functional group-specific Q_{10} values to standardize respiration rates to a base temperature of 25 °C. For all further statistical analyses, we corrected respiration rates to 25 °C using:

$$R_{\mathrm{A}} = \frac{R_{\mathrm{Tleaf}}}{Q_{10}^{(T_{\mathrm{leaf}}-25)/10}} \quad (3)$$

Mass-based respiration rates at 25 °C (R_{M}: nmol g^{-1} s^{-1}) were calculated with LMA (g m^{-2}) for each leaf. For both area- and mass-based measurements, we used simple linear regressions to analyse variation in foliar respiration with LMA and foliar nutrients. In further analyses, we did not use slopes of these regressions to determine respiration per unit nitrogen (R/N: μmol g^{-1} N s^{-1}) or respiration per unit phosphorus (R/P: μmol g^{-1} P s^{-1}), because the area- and mass-based slopes differed. Instead, we calculated R/N and R/P for each individual sample, which is the same value whether using mass- or area-based measurements (LMA cancels out). The A_{max} versus R_{A} relationship was modelled with a non-linear rectangular hyperbola.

We used ANCOVA procedures to model R_{A}, R_{M}, R/N, R/P and $A_{\mathrm{max}}/R_{\mathrm{A}}$ (Table 1) with the following predictor variables: canopy height (m), soil N (mg ha^{-1}), soil P (mg ha^{-1}) and functional group (trees, lianas, palms and herbaceous groups). All statistical analyses were performed with SAS version 9.1 (SAS Institute, Inc., Cary, NC, USA), with $\alpha = 0.05$.

Estimating foliar respiration per unit ground area and ecosystem respiration

We compared six estimates of foliar respiration per unit ground area (R_{foliar}) using two complex and four simpler methods of extrapolation (Table 2). For estimates 1 and 2, we used half-hourly temperature data (Loescher *et al.* 2003) from 1999, a 'normal' year, and 1998, a strong El Niño Southern Oscillation (ENSO) year (Table 2). Using functional-group-specific Q_{10} values, we calculated mean deviations from respiration rates at 25 °C ($R_{\mathrm{Tair}}/R_{\mathrm{A}}$) for each plant functional group in each year. We multiplied these mean deviations by mean R_{A} values and LAI stratified by the corresponding height and functional group (data not shown), and summed over categories to obtain a value per unit ground area (R_{foliar}; μmol CO_2 m^{-2}_{ground} s^{-1}).

R_{foliar} estimates 3–6 were simpler because they were neither extrapolated using within-canopy variability of respiration, nor modelled with actual temperature data

Table 1. Abbreviations used and their description

Variable	Description	Units
A_{max}	Photosynthetic capacity	μmol CO_2 m^{-2} s^{-1}
$A_{\mathrm{max}}/R_{\mathrm{A}}$	The ratio of A_{max} to R_{A}	Unitless
E_0	Energy of activation	kJ mol^{-1} K^{-1}
CWD	Coarse woody debris	–
LAI	Leaf area index, leaf area per unit ground area	m^2 m^{-2}_{ground}
LMA	Leaf mass per unit leaf area	g m^{-2}
$\mathrm{NEE}_{\mathrm{night}}$	Night-time net ecosystem exchange from eddy flux*	μmol CO_2 m^{-2}_{ground} s^{-1}
N_{A}	Foliar N per unit leaf area	g m^{-2}
N_{M}	Foliar N per unit leaf mass	mg g^{-1}
N_{tot}	Total mass of foliar N per unit ground area	g m^{-2}_{ground}
P_{A}	Foliar P per unit leaf area	g m^{-2}
P_{M}	Foliar P per unit leaf mass	mg g^{-1}
Q_{10}	Change in respiration with 10 °C change in temperature	Unitless
R_{Tleaf}	Foliar respiration rate at T_{leaf}	μmol CO_2 m^{-2} s^{-1}
R_{Ta}	Foliar respiration rate at T_{a}	μmol CO_2 m^{-2} s^{-1}
R_{A}	Foliar respiration per unit leaf area at 25 °C	μmol CO_2 m^{-2} s^{-1}
R_{M}	Foliar respiration per unit leaf mass at 25 °C	nmol CO_2 g^{-1} s^{-1}
R/N	Foliar respiration at 25 °C per unit mass of foliar N	μmol CO_2 g^{-1} N s^{-1}
R/P	Foliar respiration at 25 °C per unit mass of foliar P	μmol CO_2 g^{-1} P s^{-1}
R_{eco}	Ecosystem respiration per unit ground area	μmol CO_2 m^{-2}_{ground} s^{-1}
R_{foliar}	Foliar respiration per unit ground area	μmol CO_2 m^{-2}_{ground} s^{-1}
R_{soil}	Soil respiration per unit ground area†	μmol CO_2 m^{-2}_{ground} s^{-1}
R_{woody}	Woody respiration per unit ground area‡	μmol CO_2 m^{-2}_{ground} s^{-1}
R_{CWD}	Coarse woody debris respiration per unit ground area§	μmol CO_2 m^{-2}_{ground} s^{-1}
T_{a}	Above-canopy temperature at night	°C or K
T_{leaf}	Leaf temperature at time of measurement	°C or K

*Data from Loescher *et al.* (2003).
†Data from Schwendenmann *et al.* (2003).
‡Data from Cavaleri *et al.* (2006).
§Data from Clark *et al.* (2002).

Table 2. Six estimates of foliar respiration extrapolated to the ecosystem (R_{foliar}; μmol CO_2 m^{-2}_{ground} s^{-1}), representing two complex (1 and 2) and four simpler (3–6) methods

Estimate code	Temperatures used to model respiration (mean ± 1 standard error)	Method of calculating estimate	R_{foliar}
1. LAI–normal	1999 Temperatures, a normal year (mean half-hourly night-time temperature: 23.14 ± 0.02 °C)	Sum of [(LAI mean) × (R_A mean)] by group and height	3.5 ± 0.2
2. LAI–ENSO	1998 Temperatures, an ENSO year (mean half-hourly night-time temperature: 24.18 ± 0.02 °C)	Sum of [(LAI mean) × (R_A mean)] by group and height	3.8 ± 0.2
3. LAI–mean	Standardized to 25 °C	(LAI overall mean) × (R_A overall mean)	3.6 ± 0.5
4. *R*/N–mean	Standardized to 25 °C	(N_{tot} overall mean) × (*R*/N overall mean)	3.7 ± 0.7
5. R_A/N_A–slope	Standardized to 25 °C	(N_{tot} overall mean) × (slope of R_A/N_A)	3.9 ± 0.8
6. R_M/N_M–slope	Standardized to 25 °C	(N_{tot} overall mean) × (slope of R_M/N_M)	1.2 ± 0.3

See text for details about estimate and error calculations.
LAI, leaf area index.

(all respiration measurements were corrected to 25 °C; Table 2). Estimate 3 was calculated by multiplying the overall tower mean and standard error of LAI (6.03 ± 0.32 m^2 m^{-2}_{ground}; $n = 45$) by the overall sample mean and standard error of R_A (0.59 ± 0.02 μmol CO^2 m^{-2} s^{-1}; $n = 495$). Estimates 4–6 were each calculated by multiplying the overall tower mean and standard error of total N per unit ground area (N_{tot} = 11.62 ± 0.65 g N m^{-2}_{ground}; $n = 45$), by three different estimates of *R*/N and their corresponding standard errors. For estimate 4, we used the overall sample mean of *R*/N (0.32 ± 0.01 μmol CO^2 g^{-1} N s^{-1}; $n = 495$). For estimate 5, we used the slope of the regression between R_A and N_A (0.34 ± 0.02 μmol CO^2 g^{-1} N s^{-1}; Fig. 2a), and for estimate 6, we used the slope of the regression between R_M and N_M (0.10 ± 0.03 μmol CO^2 g^{-1} N s^{-1}; Fig. 2d). For estimates 4–6, N_{tot} was calculated for each tower by summing: [total LAI (m^2 m^{-2}_{ground}) × mean LMA (g m^{-2}) × mean N_M (g g^{-1})] for each functional group in each tower section. All additive and multiplicative errors in this study were calculated as per Mood, Greybill & Boes (1974). For example, when two or more means (*X* and *Y*) with standard errors of the mean (SE*Mx* and SE*My*) were added yielding the value *Z*; the standard error of *Z* was calculated as follows:

$$SEM_Z = \sqrt{(SEM_X)^2 + (SEM_Y)^2} \quad (4)$$

and if *X* and *Y* were multiplied, the resulting standard error of *Z* was calculated as follows:

$$SEM_Z = Z \times \sqrt{\frac{(SEM_X)^2}{X} + \frac{(SEM_Y)^2}{Y}} \quad (5)$$

We estimated ecosystem respiration for the forest (R_{eco}) by adding our best estimate of R_{foliar} to published estimates of woody respiration (R_{woody}), soil respiration (R_{soil}) and CWD respiration (R_{CWD}) from the old-growth rain forest of La Selva Biological Station. Cavaleri *et al.* (2006) reported R_{woody} as 1.34 ± 0.36 μmol CO_2 m^{-2}_{ground} s^{-1}, based on extrapolated chamber measurements. To estimate R_{CWD}, we divided published values of downed CWD total carbon biomass (22.3 ± 2.7 mg C ha^{-1}), by turnover time (9 years) (Clark *et al.* 2002), and converted units to yield 0.66 ± 0.05 μmol CO_2 m^{-2}_{ground} s^{-1}. For R_{soil}, we used soil CO_2 efflux data from plots located in the same soil type as the eddy flux tower (Schwendenmann *et al.* 2003). We calculated the mean ± 1 standard error of six soil chamber measurement plot averages (3 plots × 2 years) and converted units for a value of 3.88 ± 0.22 μmol CO_2 m^{-2}_{ground} s^{-1} (Schwendenmann *et al.* 2003).

We compared the summed value of ecosystem respiration to eddy flux night-time net ecosystem exchange (NEE_{night}) for the same forest: 7.05 ± 0.69 μmol CO_2 m^{-2} s^{-1} (Loescher *et al.* 2003). This NEE_{night} estimate was based on data for turbulent nights only, when friction velocity (u^*) was greater than 0.4 m s^{-1} (Loescher *et al.* 2003).

RESULTS

Temperature response

Regression, ANOVA and ANCOVA results showed that neither Q_{10} nor E_0 showed any relationships with soil nutrients, LMA, respiration at 25 °C or foliar nutrients per unit leaf mass or area. Both Q_{10} and E_0 varied with height ($P < 0.01$), but the differences were caused by the distribution of functional groups with height. Functional group explained 56% of the variability in both Q_{10} and E_0, and the addition of height to the models improved the r^2 by less than 1% in both cases. Although liana respiration rates were highest, trees showed the largest response with temperature (Fig. 1a), and both Q_{10} and E_0 varied similarly among functional groups (Fig. 1b,c). For all further analyses, respiration rates per unit area (R_A) and mass (R_M) were standardized to 25 °C using a different Q_{10} value for each plant functional group. Mean Q_{10} values were: herbaceous = 1.7, palm = 1.8, liana = 2.1 and tree = 2.3 (Fig. 1c) Mean E_0 values for each group were: herbaceous = 35.5, palm = 44.4, liana = 55.6 and tree = 57.7 kJ mol^{-1} (Fig. 1b).

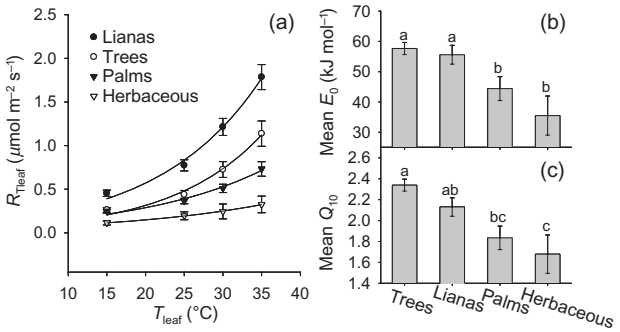

Figure 1. Foliar respiration temperature response curves (plot a), and least square mean E_0 (plot b) and Q_{10} (plot c) values by functional group. Both temperature response metrics were higher for trees and lianas, compared to palms and herbaceous groups. Means with the same letter are not significantly different, based on Fisher's least significant difference (LSD). Error bars are standard errors of the mean. Equations for each temperature response curve are as follows: lianas: $R_{Tleaf} = 0.13 \times \exp(0.76 \times T_{leaf})$; trees: $R_{Tleaf} = 0.057 \times \exp(0.85 \times T_{leaf})$; palms: $R_{Tleaf} = 0.086 \times \exp(0.61 \times T_{leaf})$; and herbaceous groups: $R_{Tleaf} = 0.053 \times \exp(0.52 \times T_{leaf})$.

Response to foliar nutrients, LMA, height, functional group and soil nutrients

R_A was linearly related to N_A, P_A and LMA (Fig. 2a–c). R_M had weak relationships with both N_M and P_M, and the regression with LMA was not significant (Fig. 2d–f). Respiration rates at 25 °C per area, mass, N and P varied with height and soil N, but not with soil P stocks (Table 3). The height × group interaction was significant for both R_A and R/N (Table 3). No three-way interactions were significant, and were therefore pooled into error for all models. The ANCOVA predicting R_A had the highest r^2 (0.39; Table 3). Model-predicted least square means were plotted for each respiration variable for the height × soil N and height × group interactions (Fig. 3). R_A varied almost sixfold, while R_M, R/N and R/P were much less variable, at around two- to threefold from the understory to the upper canopy. Respiration rates on any basis increased with height and decreased with soil N (Fig. 3a–d). The effects of soil N were more pronounced higher in the canopy, and respiration increased more steeply with height at the lowest soil N levels (Fig. 3a–d). Trees and lianas generally had higher respiration rates than palms and herbaceous groups, and liana rates increased more steeply with height than the other groups (Fig. 3e–h). The group difference was also more pronounced higher in the canopy (Fig. 3e–h).

Relationship between respiration and photosynthetic capacity

The relationship between area-based respiration at 25 °C (R_A) and photosynthetic capacity (A_{max}) was non-linear, with A_{max} levelling off at high R_A (Fig. 4a). The curve was described by a rectangular hyperbola ($P < 0.0001$; $r^2 = 0.24$), where $A_{max} = (10.9 \times R_A)/(0.52 + R_A)$. Photosynthetic capacity reached a maximum of about 10 μmol CO_2 m^{-2} s^{-1} as respiration increased from 1 to 2.5 μmol CO_2 m^{-2} s^{-1} (Fig. 4a). A_{max}/R_A varied with height and soil N, and all interactions were pooled into error (Table 3). Figure 4b shows the height effect at mean soil N (13.9 mg ha^{-1}) and averaged overall functional groups, while Fig. 4c shows the soil N effect at mean height (11.9 m) and averaged overall functional groups. The ratio A_{max}/R_A varied twofold from ~7 to 14, decreased with height and increased with soil N stocks (Fig. 4).

Foliar respiration per unit ground area and ecosystem respiration

Estimated R_{foliar} was ~9% higher for the ENSO year (estimate 2) compared with a normal year (estimate 1; Table 2). Estimate 6 of R_{foliar}, which used the slope of the $R_M - N_M$ regression to estimate R/M, was about one-third that of estimates 1–5 (Table 2). Three of the R_{foliar} estimates calculated using the simpler methods of extrapolation (estimates 3–5) were similar to those estimated with the more complex methods (estimates 1 and 2; Table 2). Trees contributed the most to R_{foliar} (66%), with 15% from lianas, 12% from palms and 7% from herbaceous groups.

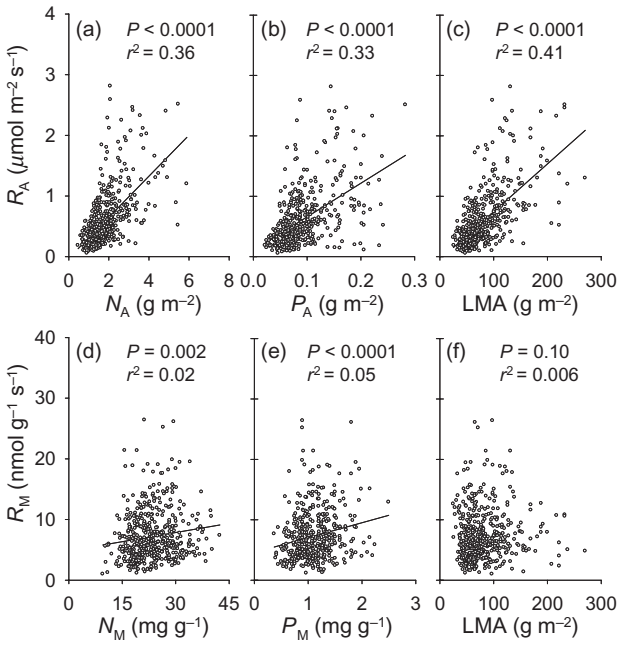

Figure 2. Regression plots between area- (plots a–c) and mass-based (plots d–f) foliar respiration, nitrogen, phosphorus and leaf mass per area (LMA). Leaf-area-based correlations between respiration and foliar nutrients (plots a & b) were stronger than mass-based correlations (plots d & e). Equations for each significant ($P < 0.05$) regression were: $R_A = -0.03 + 0.34 \times N_A$; $R_A = 0.04 + 6.5 \times P_A$; $R_A = -0.05 + 0.008 \times$ LMA; $R_M = 4.77 + 0.10 \times N_M$; and $R_M = 4.3 + 2.5 \times P_M$.

Table 3. Predictor variable *P* values for analysis of covariance (ANCOVA) models of respiration per unit leaf area (R_A), mass (R_M), nitrogen (R/N), phosphorus (R/P) and the ratio of photosynthetic capacity to respiration (A_{max}/R_A)

Predictor variables	Response variables				
	R_A	R_M	R/N	R/P	A_{max}/R_A
Height	<0.001	<0.01	<0.001	<0.01	0.001
Group	ns	ns	ns	ns	ns
Soil N	ns	ns	ns	ns	< 0.001
Height × group	0.01	ns	0.05	ns	–
Height × soil N	0.05	<0.05	<0.05	<0.05	–
Group × soil N	ns	ns	ns	ns	–
Height × group × soil N	–	–	–	–	–
Overall model	<0.001	<0.001	<0.001	<0.001	<0.001
Model r^2	0.39	0.18	0.20	0.16	0.06

Soil P was not a significant predictor for any response variable, and was removed. Three-way interactions were pooled into error for all five response variables, and two-way interactions were pooled into error for A_{max}/R_A. See Figs 4 and 5 for model-predicted effects.
ns, not significant.

R_{eco}, summed from R_{foliar}, R_{soil}, R_{woody} and R_{CWD}, was 9.40 ± 0.47 μmol CO_2 m^{-2}_{ground} s^{-1} (Fig. 5). We used R_{foliar} from estimate 1 (Table 2) because this extrapolation method was based upon the most information, and it was modelled with temperature data from a normal year. The contributions of each component part to R_{eco} were: soil = 41%, foliage = 37%, woody = 14% and CWD = 7%.

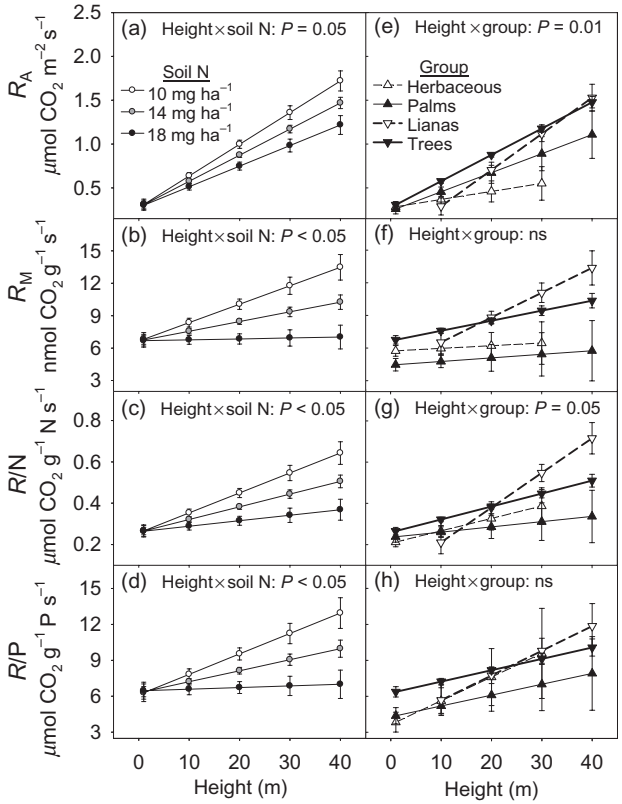

Figure 3. Model-predicted least square means and standard errors for the height × soil N (plots a–d) and height × group (plots e–h) interactions from analyses of covariance (ANCOVAS) predicting R_A, R_M, R/N and R/P (Table 3). Respiration increased with height and decreased with soil N. Trees and lianas generally had higher respiration rates than palms and herbaceous groups. Effects of soil N and functional group were more pronounced higher in the canopy.

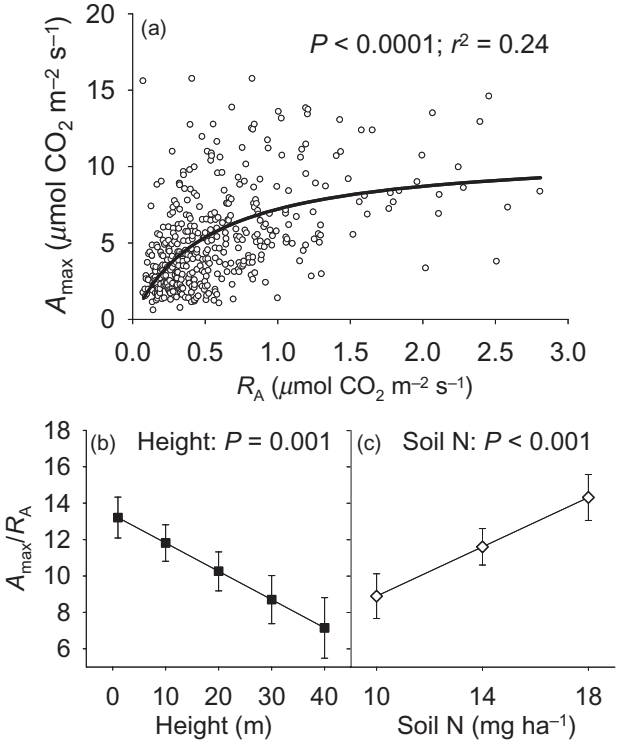

Figure 4. The relationship between area-based respiration at 25 °C (R_A) and photosynthetic capacity (A_{max}) (plot a), and the least square means and standard errors for height and soil N effects from the analysis of covariance (ANCOVA) predicting A_{max}/R_A (b & c; Table 3). The curve in plot (a) was described by a rectangular hyperbola, where $A_{max} = (10.9 \times R_A)/(0.52 + R_A)$. Plot (b) shows the height effect at mean soil N (13.9 mg ha^{-1}) and averaged overall functional groups. Plot (c) shows the soil N effect at mean height (11.9 m) and averaged overall functional groups.

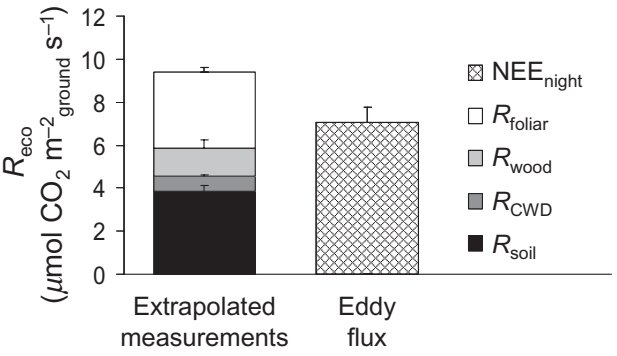

Figure 5. A comparison of ecosystem respiration (R_{eco}), as estimated by eddy flux night-time net ecosystem exchange (NEE_{night}) versus the summation of extrapolated measurements of component parts. R_{eco} from extrapolated measurements (9.40 ± 0.47 μmol CO_2 m^{-2} s^{-1}) was 33% higher than NEE_{night} (7.05 ± 0.69 μmol CO_2 m^{-2} s^{-1}; Loescher *et al.* 2003) for the same forest. NEE_{night} was based on data for turbulent nights only, when friction velocity (u^*) was greater than 0.4 m s^{-1} (Loescher *et al.* 2003). For the old-growth forest at La Selva, soil respiration was 3.88 ± 0.22 μmol CO_2 m^{-2} s^{-1} (Schwendenmann *et al.* 2003); woody respiration was 1.34 ± 0.36 μmol CO_2 m^{-2} s^{-1} (Cavaleri *et al.* 2006); coarse woody debris (CWD) respiration was estimated to be 0.66 ± 0.05 μmol CO_2 m^{-2} s^{-1}, from published total CWD carbon and turnover time (Clark *et al.* 2002); and foliage respiration was 3.5 ± 0.2 μmol CO_2 m^{-2} s^{-1} using estimate (1) of this study (Table 2).

DISCUSSION

Foliar respiration response to temperature, foliar nutrients, LMA, height, functional group and soil nutrients

We found no difference in Q_{10} or E_0 with either height or nutrients, indicating that the primary source of variation in temperature response was genetically controlled differences among species or functional groups, greatly simplifying our subsequent modelling and extrapolation procedures. Xu & Griffin (2006) also found consistency in E_0 with height which simplified further extrapolation.

As predicted by the leaf economics spectrum, respiration rates were correlated with foliar N, P and LMA. Respiration is linked to photosynthesis, and 90% of plant N is in proteins, with ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco) comprising up to half of all plant proteins (Lawlor 1993; Ryan *et al.* 1996). Phosphorus is necessary for protein synthesis, nucleic acids, plasma membranes, ADP phosphorylation and triose phosphate production (Amthor 1989; Stitt 1990). In the full vertical transect of forest canopies, foliar respiration tends to relate better to foliar N and P when expressed on a leaf area basis than a leaf mass basis (Mitchell *et al.* 1999; Meir *et al.* 2001; Xu & Griffin 2006), likely as a result of increasing LMA with height in forest canopies (Ford & Newbould 1971; Hutchison *et al.* 1986; Oberbauer & Strain 1986; Hollinger 1989; Niinemets & Kull 1995; Niinemets & Tenhunen 1997; Meir *et al.* 2001; Marshall & Monserud 2003; Koch *et al.* 2004). In our data set, LMA also had a strong linear relationship with height (data not shown), and we believe the changes in LMA within the canopy profile underlie the strong covariance between area-based respiration and leaf nutrients.

Even without the influence of LMA, R/N, R/P and R_M, all still increased with height, and were highest for trees and lianas (which dominate the upper canopy). Higher in the canopy where light is more abundant, more N and P may be allocated to respiratory and photosynthetic proteins, rather than other compounds such as those used in herbivory defence. Lianas showed the steepest increase in foliar respiration with height of all the groups (Fig. 3), likely because lianas rely on neighbouring trees for support. Lianas can allocate increasing resources into metabolic compounds as light increases, whereas trees still need to allocate energy and nutrients to woody growth (Putz 1983).

Our overall sample mean for R/N was 0.32 μmol CO_2 g^{-1} N s^{-1} (Fig. 3), which was quite similar to R/N reported for *Pinus radiata* (0.31 μmol CO_2 g^{-1} N s^{-1} when standardized to 25 °C with the reported Q_{10} of 2.5 (Ryan *et al.* 1996). A value reported for boreal and subalpine forests (0.53 μmol CO_2 g^{-1} N s^{-1} when standardized to 25 °C with the reported Q_{10} of 2.0) was 66% greater than our mean R/N, (Ryan 1995). Within forest canopies, respiration per unit nitrogen (R/N) is often less variable than R_M (Ryan 1995), and the variability of respiration per unit phosphorus (R/P) has not been well-studied. Fertilization increased the variability in R/N of *P. radiata*, either because of an increased variability of the proportion of N in protein, or an increase in the variability in Rubisco activation (Ryan *et al.* 1996). We found R/N, R/P and R_M all to be less variable than R_A, likely because of the influence of the LMA gradient with height on R_A.

Both N_A and P_A explained a similar amount of variation in R_A (Fig. 2); therefore, we did not find foliar phosphorus to constrain respiration more strongly than foliar nitrogen did, as Meir *et al.* (2001) reported in a tropical rain forest in Cameroon. Turnbull *et al.* (2005) found an increase in R_A with soil fertility along a soil chronosequence in New Zealand, but none of the respiratory variables in our study varied with soil P, contrary to expectation. In fact, respiration decreased with increasing soil N stocks, which is difficult to interpret because respiration and foliar N were positively correlated. In this forest, it seems that soil N and foliar N are decoupled; soil N stocks are not related to N_{tot}, N_M or N_A (data not shown), supporting the assumption that nitrogen is not limiting in this system (McDade *et al.* 1994).

Respiration and photosynthetic capacity

Values of A_{max}/R_A by height and soil N varied from ~7 to 14 (Fig. 4), with similar values found in temperate rain forests, deciduous and coniferous forests (Turnbull *et al.* 2001, 2005; Vose & Ryan 2002). At high values of A_{max}, leaf metabolism appears to increase at a faster rate than the plant's ability to assimilate CO_2, indicated by the non-linear relationship between R_A and A_{max} (Fig. 4). Reich *et al.* (1998) found the relationship between R_A and A_{max} to be linear within biomes (indicating a constant ratio of A_{max}/R_A), but

non-linear when several biomes and functional groups were plotted together. Our data were from one biome, however, and the non-linearity is still present when only trees are plotted (data not shown). In our study, A_{max}/R_A increased with increasing soil N content (Fig. 4c), primarily because of the decrease in R_A with increasing soil N; A_{max} did not change with soil N ($P = 0.59$; data not shown).

The higher Q_{10} values in the functional groups of the upper canopy where temperatures are highest may lead to exponential losses of carbon with increasing global temperatures, depending upon the ability of canopy foliage to acclimate. According to Dewar *et al.* (1999), the metabolic adjustment of non-structural carbohydrates that allows plants to acclimate to higher temperatures can also result in a linear relationship between A_{max} and R_A (constant A_{max}/R_A). Because our data show A_{max}/R_A steadily decreasing with canopy height (Fig. 4b), perhaps these tropical plants are not able to metabolically adjust to the higher temperatures in the upper canopy, indicating a limited ability to thermally acclimate.

An alternate interpretation for the decrease in A_{max}/R_A with height is that R_A may be a closer approximation to actual assimilation rate than A_{max}, which is potential assimilation. Declining light levels may affect actual assimilation rate more than potential assimilation rate, thus the ratio between actual assimilation rate and R_A may indeed be constant with height.

Foliar respiration per unit ground area

Our estimation of R_{foliar} (3.5–4.0 μmol CO_2 m^{-2}_{ground} s^{-1}) was 35–50% higher than an estimate from the Amazon (Chambers *et al.* 2004). Estimates 1–3 of R_{foliar} (Table 2) were quite similar because the mean night-time temperature in 1998 was 24.18 °C, and the mean temperature in 1999 was 23.14 °C, which are both close to the standard temperature correction (25 °C) used in estimate 3. Three of the simpler extrapolations of R_{foliar} (estimates 3–5; Table 2) were very similar to results of the more complex extrapolations (estimates 1 and 2; Table 2), likely because our overall means for respiration, LAI and N_{tot} were based on good representations of the functional group and height distributions for the forest. Estimate 6, however, was quite low compared to the rest of the estimates because the correlation between R_M and N_M was poor, resulting in an underestimation of R/N (Fig. 2). We recommend not using the slope of R_M versus N_M as an estimation of R/N for ecosystem extrapolation within forest canopies.

While the difference between an ENSO and a normal year in R_{foliar} only represented a 9% increase in foliar respiration (0.3 μmol CO_2 m^{-2} s^{-1}), this is within the range of the difference between carbon sink versus source behaviour for this forest. In the ENSO year of 1998, the old-growth forest at La Selva was reported to range from a 0.01 μmol m^{-2} s^{-1} carbon source to a 0.35 μmol m^{-2} s^{-1} carbon sink (Loescher *et al.* 2003).

One source of uncertainty in R_{foliar} is the lack of a seasonality assessment. Foliar respiration rates have been found to change with season in temperate forests because of active growth early in the growing season or translocation later in the growing season (Vose & Ryan 2002; Atkin *et al.* 2005; Xu & Griffin 2006). In the old-growth forest of La Selva, studies have found seasonality in soil respiration (Schwendenmann *et al.* 2003), but not in woody respiration (Cavaleri *et al.* 2006). In our extrapolations, we measured only fully expanded leaves to minimize the effects of growth respiration, and we assumed rates were otherwise seasonally constant because this forest does not have a distinct dormant season. We did take into account the effects of seasonal temperature changes on foliar respiration in R_{foliar} estimates 1 and 2 (Table 2). Uncertainties in either the seasonality or the absolute value of LAI are also important because of the multiplicative effects when extrapolating. Studies in both temperate and tropical forests have found LAI of evergreen species to change seasonally (Curran, Dungan & Gholz 1992; de Wasseige, Bastin & Defourny 2003), and LAI (measured indirectly) has been reported to vary seasonally in the old-growth forest of La Selva (Loescher *et al.* 2003). We did not resample specific sites over time, but our tower sampling was continuous for 2 years, so we likely captured much of the variability in seasonal LAI even though we cannot formally test for it. Despite the possible sources of error, we are confident that our methods of extrapolating chamber respiration measurements represent the best available data for assessing ecosystem respiration of the old-growth forest of La Selva.

Ecosystem respiration

Our estimate of R_{eco} (9.40 $\pm$ 0.47 μmol CO_2 m^{-2}_{ground} s^{-1}) was 45% greater than an estimate for a tropical rain forest in Manaus, Brazil (Malhi, Baldocchi & Jarvis 1999), and about 20% greater than an estimate for an Amazonian tropical rain forest (Chambers *et al.* 2004). Although our total ecosystem respiration was greater, the percentages of respiration from component ecosystem parts were quite similar at La Selva (canopy and understory foliage = 37%, soil = 41%, woody = 14%, CWD = 7%) and the Amazonian forest [foliage (including 'understory') = 38%, soil = 41%, woody = 14%, CWD = 6%; Chambers *et al.* 2004].

R_{eco} from extrapolated measurements was 33% greater than the eddy flux NEE_{night} at La Selva (7.05 $\pm$ 0.69 μmol CO_2 m^{-2} s^{-1}; Loescher *et al.* 2003), even though NEE_{night} was based on turbulent nights only (Fig. 5). Loescher *et al.* (2003) noted that the greatest uncertainty of their study was associated with NEE_{night}, and this uncertainty was an impetus for the present study. If our independent estimates of ecosystem respiration approximate the true value of NEE_{night}, the old-growth forest at La Selva was likely a strong carbon source during the 1998 ENSO. The perception of tropical rain forests as strong sinks may need to be reconsidered if eddy covariance studies reporting a large sink for tropical rain forests (Fan *et al.* 1990; Grace *et al.* 1995; Malhi *et al.* 1998) have similarly underestimated NEE_{night}. These results emphasize the need for and value of

independent estimates of NEE_{night} for constraining estimates of ecosystem carbon balance.

CONCLUSIONS

- Q_{10} and E_0 were constant across height, foliar and soil nutrients, LMA and respiration at 25 °C, but functional groups dominating the upper canopy had higher Q_{10} and E_0 values than groups found lower in the canopy.
- As predicted by the leaf economics spectrum, foliar respiration, N, P and LMA were correlated.
- The influence of the LMA–height gradient resulted in both tighter correlations between area-based respiration versus leaf nutrients, and greater variation in R_A than R_M, R/N or R/P.
- Foliar respiration per unit ground area (R_{foliar}), estimated with ENSO year temperatures, was 9% greater than R_{foliar} estimated with temperatures from a normal year, which could be the difference between carbon sink versus source behaviour for this forest.
- We estimated total ecosystem respiration as 9.40 ± 0.47 μmol CO_2 m^{-2}_{ground} s^{-1}, which was 33% greater than eddy flux night-time net ecosystem exchange for the same forest, suggesting that studies reporting a large sink for tropical rain forests based on eddy flux measurements may be in error.

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