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Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest

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Abstract

Difficulty in balancing the global carbon budget has lead to increased attention on tropical forests, which have been estimated to account for up to one third of global gross primary production. Whether tropical forests are sources, sinks, or neutral with respect to their carbon balance with the atmosphere remains unclear. To address this issue, estimates of net ecosystem exchange of carbon (NEE) were made for 3 years (1998–2000) using the eddy-covariance technique in a tropical wet forest in Costa Rica. Measurements were made from a 42 m tower centred in an old-growth forest. Under unstable conditions, the measurement height was at least twice the estimated zeroplane height from the ground. The canopy at the site is extremely rough; under unstable conditions the median aerodynamic roughness length ranged from 2.4 to 3.6 m. No relationship between NEE and friction velocity (*u) was found using all of the 30-min averages. However, there was a linear relationship between the nighttime NEE and averaged *u** ($R^2 = 0.98$). The diurnal pattern of flux was similar to that found in other tropical forests, with mean daytime NEE ca. $-18\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ and mean nighttime NEE 4.6 μmol $CO_2\,m^{-2}\,s^{-1}$. However, because $\sim$80% of the nighttime data in this forest were collected during low *u** conditions ($< 0.2\,m\,s^{-1}$), nighttime NEE was likely underestimated. Using an alternative analysis, mean nighttime NEE increased to 7.05 μmol $CO_2\,m^{-2}\,s^{-1}$. There were interannual differences in NEE, but seasonal differences were not apparent. Irradiance accounted for $\sim$51% of the variation in the daytime fluxes, with temperature and vapour pressure deficit together accounting for another $\sim$20%. Light compensation points ranged from 100 to 207 μmol PPFD $m^{-2}\,s^{-1}$. No was relationship was found between 30-min nighttime NEE and tower-top air temperature. A weak relationship was found between hourly nighttime NEE and canopy air temperature using data averaged hourly over the entire sampling period ($Q_{10} = 1.79$, $R^2 = 0.17$). The contribution of below-sensor storage was fairly constant from day to day. Our data indicate that this forest was a slight carbon source in 1998 (0.05 to $-1.33\,t\,C\,ha^{-1}\,yr^{-1}$), a moderate sink in 1999 (-1.53 to $-3.14\,t\,C\,ha^{-1}\,yr^{-1}$), and a strong sink in 2000 (-5.97 to $-7.92\,t\,C\,ha^{-1}\,yr^{-1}$). This trend is interpreted as relating to the dissipation of warm-phase El Niño effects over the course of this study.**

Keywords: carbon, eddy covariance, La Selva, net ecosystem exchange, productivity, tropical wet forest

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Introduction

Inverse model calculations based on atmospheric CO_2 concentrations and $^{13}CO_2/^{12}CO_2$ and O_2/N_2 ratios indicate that the terrestrial biosphere is currently a net carbon

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sink, partially offsetting the additions of CO_2 from fossil fuel combustion and deforestation (Schimel *et al*., 2001). Temporal variation in carbon uptake and emissions by terrestrial ecosystems has an effect on interannual variations in atmospheric CO_2 concentrations (Schimel *et al*., 2001), although the magnitude remains uncertain (IPCC, 1995; Houghton, 1996; Houghton *et al*., 1998). Recent attempts to measure net ecosystem CO_2 exchange (NEE) with the atmosphere have focused on temperate, boreal, and arctic ecosystems (Frolking *et al*., 1996; Goulden *et al*., 1996; Vourlitis & Oechel, 1997; Clark *et al*., 1999; Black *et al*., 2000; Valentini *et al*., 2000; Aubinet *et al*., 2001; Law *et al*., 2001), with only few studies occurring in tropical forests (Fan *et al*., 1990; Grace *et al*., 1996; Mahli *et al*., 1998). However, tropical forests account for $\sim 35\%$ of global net primary productivity, $> 50\%$ of the carbon in above-ground terrestrial biomass and $\sim 20\%$ of the soil carbon (Melillo *et al*., 1993; Dixon *et al*., 1994). Old-growth rainforests were historically thought to be carbon neutral (input = output, NEE = 0). This was challenged by Grace *et al*. (1995a) and Fan *et al*. (1990) based on eddy covariance, which suggested that apparently long undisturbed Amazon forests sequester carbon. If generally true, the implications for carbon science and policymaking are enormous.

The objective of this study was to define the patterns of diurnal and annual NEE and their climatic controls for a lowland tropical wet forest in north-eastern Costa Rica. At this forest, large interannual fluctuations in above-ground net primary productivity since 1984 closely paralleled fluctuations in atmospheric CO_2 concentrations and were negatively correlated with average nighttime minimum temperatures (Clark *et al*., in review). In this paper, we assess the effects of environmental variations on the diurnal, seasonal, and interannual patterns NEE for this forest from 1998 through 2000.

Materials and methods

Study site

This study was conducted as part of a long-term study of tropical forest carbon cycling, the CARBONO project, at the La Selva Biological Station, Puerto Viejo de Sarapiquí, Costa Rica (10°25′51″N, 84°00′59″W, elevation 80–150 m.a.s.l). La Selva is located in north-eastern Costa Rica in the Caribbean lowlands at the base of the central volcanic chain. The forest was classified as tropical wet forest in the Holdridge life zone system by Hartshorn & Peralta (1988). La Selva averages 100 trees $ha^{-1} > 10$ cm diameter ha^{-1} from ~ 100 species (Lieberman *et al*., 1985), dominated by the *mimosoid* legume canopy species, *Pentaclethra macroloba* (34% of the basal area, Clark & Clark, 2000). Mean tree height is 20–25 m, with emergents exceeding 60 m. Canopy gaps occupy ~ 0.01–0.04 ha ha^{-1} (Denslow & Hartshorn, 1994) making the overall canopy very aerodynamically rough. Incident mean (1993–1998) daily solar radiation was 14.9 MJ m^{-2} d^{-1}, with a range from 0.4 to 31.3 MJ m^{-2} d^{-1}. Mean annual temperature (1982–1998) was 24.6 °C (Organization for Tropical Studies (OTS), unpublished weather records). Mean annual precipitation was 4000 mm (1963–91), with a short drier period from December to the end of May, but with no month receiving less than 100 mm (Sanford *et al*., 1994). The La Selva landscape contains primarily two features, residual lava flows in upland areas, which drained north-east into riverine areas. This creates a rolling topography with ~ 20–30 m relief between stream bottoms and ridge-tops. Soils range from relatively fertile Inceptisols in riverine areas to low pH, low phosphorus Ultisols in upland areas (Sollins *et al*., 1994). There was no interannual variation of soil CO_2 emission rates from 1998 to 2000 (Schwendenman *et al*., in press). Temporal variations in soil CO_2 efflux from that study were primarily related to soil water content, not temperature. For both soil types at La Selva, CO_2 efflux decreased with higher soil water content, likely due to lower diffusion rates and lower CO_2 production rates (Schwendenman *et al*., in press).

Moisture-laden north-east trade winds originating over the Caribbean Sea dominate surface winds (Hastenrath, 1991). During most (85%) daytime hours, the annual mean surface wind direction is 90°. The wetter season (June through November) and drier season (mid-December through May) are controlled by the movement of the equatorial low-pressure trough (i.e. the eastern Pacific intertropical convergence zone, or ITCZ). During the drier season, the subtropical Hadley cell dominates general circulations, while the tropical cell dominates wet season circulations (Sanford *et al*., 1994). Other circulations may influence wet season climate, including *temporales,* polar air masses that move down the North American continent generating depressions and prolonged rain events chiefly occurring in November and December (Schultz *et al*., 1998). *Veranillos*, temporary and often irregular movement of the South Pacific anticyclone northward, create short dry periods typically lasting 7–10 days in September or October. Sanford *et al*. (1994) and Holdridge *et al*. (1971) provide further information for La Selva, and Waylen *et al*. (1996a) and Hastenrath, (1991) provide more details on its climatology.

Because La Selva is located at 10°N latitude, there is little diurnal change in sunlight over the course of the year, with only a 40-min difference in day length between solstices. For this study, sunrise and sunset were defined as 0600 and 1800, delineating daytime and nighttime periods.

A 42 m tower was used to access the canopy environment and to support meteorological instrumentation.

The site was a relatively flat upland area where ridgetops are ~450 m apart, with ~20–30 m relief between stream bottoms and ridgetops (OTS unpublished digital elevation model). After accounting for stability effects, a source area model (Schuepp *et al.*, 1990) was used to estimate that under stable conditions, 95% of the cumulative flux was derived from within 1.2 km of the tower (at a mean horizontal windspeed of 3 m s^{-1}). The tower was sited to minimize edge effects, below-canopy advection either to or from the site, and any major directional differences due to forest composition and structure.

Meteorological data

Microclimate data were collected continuously at the tower top. Measured variables included incident radiation (LI-190, LI-Cor Inc., Lincoln, NE), photosynthetic photon flux density (PPFD, LI-200X, LI-Cor Inc.), aspirated air temperature (T_a, 100 Ω platinum RTD, Omega Engineering, Stamford, CT), and bulk rainfall (TE525 metric, Texas Electronics, Dallas, TX). Atmospheric pressure (PB105, Vaisala, Helsinki, Finland) was monitored at ground level.

All of the above data were collected at an interval of 5 s and compiled as 30-min averages with dataloggers (CR10X and 21X, Campbell Scientific Inc., Logan, UT). Instruments were cleaned, leveled as necessary, and recalibrated according to manufacturers' instructions. At times when the PPFD sensor was not operational, PPFD was estimated by a linear regression equation relating PPFD to incident radiation ($R^2 > 0.99$). Likewise, when either power outages occurred or aspirated air temperature were not logged, air temperature was estimated from a regression against a CS500 air temperature sensor (Campbell Scientific) also mounted at 42 m in a radiation shield ($R^2 = 0.98$).

Long-term meteorological data from La Selva were used to examine decadal scale trends in microclimate (OTS, http://www.ots.duke.edu). PPFD and air temperature have been measured since 1982 and bulk precipitation since 1961.

To assess zero-plane displacement (d), or the mean level of momentum absorption, four 3-cup anemometers (Model 03103-L, R.M. Young, Traverse City, MI) were mounted vertically along the tower at 35.5, 31.6, 28.2, and 25 m above the ground. d was then estimated by determining the intercept (y_0) of Eqn (1):

$$\log d = \int_{Z_{25}}^{Z_{35.5}} \log(\bar{u}) + y_0 \tag{1}$$

where Z is measurement height above the ground (m), $\bar{u}$ is the 30-min time average of the instantaneous measurement of horizontal wind velocity (cm s^{-1}) at each height.

Roughness length (z_0) was estimated using d

$$z_0 = (Z_m - d) \cdot \left(\exp \frac{u^*}{\bar{u}_m k}\right)^{-1} \tag{2}$$

where Z_m is the measurement height (42 m), u^* is friction velocity (m s^{-1}), $\bar{u}_m$ is the 30-min time average of the instantaneous measurement of horizontal wind velocity at measurement height (m s^{-1}), and k is the von Karmen constant (0.41, dimensionless).

The ratio of convective to mechanical production of turbulent kinetic energy (Monin-Obukov length, L) was used to determine atmospheric stability as in Eq. (3):

$$L = \frac{-\rho C_p T_a u^{*3}}{gkH} \tag{3}$$

where, r is the density of air (kg m^{-3}), C_p is the specific heat capacity of air (J kg^{-1} K^{-1}), T_a is in Kelvin (K), g is acceleration due to gravity (m s^{-2}), and H is the sensible heat flux density (J m^{-2} s^{-1}) (Rosenberg *et al.*, 1983; Montieth & Unsworth, 1990; Pahlow & Parlange, 2001).

Net ecosystem exchange (NEE) measurements

A closed-path eddy covariance system was used to estimate the portion of NEE contributed by turbulent exchange. Because the below-canopy environment was not always subject to turbulent transfer (i.e. well-mixed conditions), a profile system was used to estimate the rate of change of [CO$_2$] below the canopy. NEE was then estimated as:

$$\mathrm{NEE} = \overline{w'\mathrm{CO}_2'} + \int_{Z_{0.5}}^{Z_{27}} \frac{\partial[\mathrm{CO}_2]}{\partial t}\,\partial Z_{27} \tag{4}$$

where w' and $\mathrm{CO}_2{}'$ are the deviations of instantaneous values from a running mean of vertical windspeed (m s^{-1}) and molar fraction of CO$_2$ (μmol CO$_2$ mol^{-1}), respectively, and Z_x is measurement height (m). The first term of Eqn (4) is the 30-min time-averaged eddy covariance flux. The second term is the storage flux below 42 m. The convention used is that negative values of NEE correspond to uptake of CO$_2$ by the forest from the atmosphere.

A 3-D sonic anemometer (K-probe, Applied Technologies Inc., Boulder CO) was used to measure wind velocities in each polar coordinate (w, v, u) and sonic temperature (θ). The gas sampling inlet was mounted on the sonic anemometer, colocated with the top transducer in the w-axis, and sampled close to the sonic 3-D volume without disturbing the pathway between transducers. There was no significant effect on the frequency response of the wind statistics using the gas sampling inlet at this location, based on an examination of flow from the mean wind direction. Infrared gas analysers

(IRGA, model LI-6262, LI-Cor Inc.) were used to measure concentrations of CO_2 and H_2O vapour, controlled for pressure and temperature at ground level inside a climate-controlled structure. Flow rates were maintained by pumps (KNF Neuberger, Trenton, NJ) and mass flow controllers (Model series 200, 0–10 lpm, Teledyne Hastings Inc., Los Angeles CA). Sampled air flowed through ~60 m of tubing (4.8 mm ID Teflon tubing) at a rate of 8 lpm resulted in a lagtime of ~14.2 s.

The NOAA flux software program (McMillen, 1988), with a 400 second digital recursive running mean and a fixed lagtime, was used to collect raw eddy covariance data files. To address concerns that this averaging time would not fully account for the transfer of CO_2 at longer time scales, we compared flux estimates using 400, 600, and 800 s time constants and found no significant differences in either flux densities, or frequency attenuation. Additional analyses compared estimates based on the 400 s time constant to estimates derived using Reynolds detrending for 30-min periods and found only small differences during transitional periods (i.e. during rapidly building or decaying convective boundary layers). Relative differences were as large as 13%, but during these periods, absolute fluxes were generally small so effects on NEE slight. Over 60 min intervals, average differences between the two estimates were ± 3%. An intercomparison of NEE was conducted using the 'standard' AmeriFlux roving system and our eddy covariance system in the spring of 1999, which yielded a slope of a 1 : 1 regression and a $R^2 = 0.98$ (unpublished data).

A 12-bit analogue-to-digital board digitized IRGA voltage outputs. Covariances, wind and scalar statistics, and coordinate rotations were calculated in real time at 10 Hz. Protocols for accuracy, precision, quality control and assurance were used as defined by the AmeriFlux Science Plan (http://cdiac.esd.ornl.gov/programs/ameriflux/scif.htm).

For valid eddy covariance measurements, the response of all instruments must be as fast as, or faster than, the turbulence that is carrying the bulk of mass and energy. This process occurs between frequencies of 1–10 Hz, within the inertial subrange (Kaimal & Finnigan, 1994). While the sonic anemometer operates at 10 Hz, the frequency response for the IRGA is slower, at ~8–9 Hz. To account for this frequency loss on NEE, Fast Fournier Transfer (FFT) analyses were applied. Since temperature (θ) was measured by the sonic anemometer at 10 Hz, the cospectra for $w'\theta'$ was considered ideal (e.g. Goulden *et al.*, 1996; Hollinger *et al.*, 1999). The proportion of signal lost was determined by comparing the summed cospectral density in the inertial subrange to that of the total spectra for $w'\theta'$ and $w'CO_2{}'$ to estimate a spectral correction factor, SC_f:

$$\frac{SC_\mathrm{f} = \sum_{0.1}^{1} nS_{w'\mathrm{CO}_2'} * w'\mathrm{CO}_2'^{-1} \Big/ \sum_{0.001}^{10} nS_{w'\mathrm{CO}_2'} * w'\mathrm{CO}_2'^{-1}}{\sum_{0.1}^{1} nS_{w'\theta'} * w'\theta'^{-1} \Big/ \sum_{0.001}^{10} nS_{w'\theta'} * w'\theta'^{-1}} \tag{5}$$

where $S_{w'x'}$ is spectral density of w' and $CO_2{}'$ or θ', n is the natural frequency, and $w'x'$ is the mean covariance of w' and $CO_2{}'$ or θ' (Baldocchi & Meyers, 1989; Meyers & Baldocchi, 1991). Although we assumed that the dissipation of turbulent kinetic energy occurred in the inertial subrange for all the scalars, we did not expect that the Kaimal spectral relationship (a slope of $-2/3$ within the inertial subrange) would hold for every 30-min period because of roughness, differing stabilities, and possible density driven flows over time.

Profile measurements were used to calculate below-canopy CO_2 storage dynamics (Eqn 4). CO_2 was collected from 6 inlets at 0.5, 7.3, 11.95, 16.55, 21.2, and 27.6 m. A datalogger (model 21X, Campbell Scientific Inc.) was used to operate solenoids that switched the flow (~3 lpm) from each inlet through the IRGA (Li-Cor 6262) for 5 min during each 30-min period and to record the raw data. Platinum resistance thermometers (100 Ω PRT, m68, Omega Engineering) housed in radiation shields were colocated with each inlet. When sampling occurred, the airflow acted to aspirate the PRTs. Temperature and humidity profiles were used to account for changes in mass flow due to changes in density (Webb *et al.*, 1980). Below-canopy storage was calculated from line-averaged profile measurements using Eqn (4); it was assumed that this profile was similar across the flux source area.

Both eddy covariance and profile measurements began in April 1998 and continued through the end of December 2000. Gaps in measurements occurred for periods of 2–14 days when either power failure or instrumentation malfunctions occurred. IRGAs were calibrated every 2–3 days. Improved precision in calibration was achieved starting in February 1999 by plumbing nitrogen through the IRGA reference cell as a zero reference.

A model was used to relate daytime NEE to PPFD (Ruimy *et al.*, 1995):

$$\mathrm{NEE_{day}} = R_E + \frac{\phi\alpha P_\mathrm{max}}{\phi\alpha + P_\mathrm{max}} \tag{6}$$

where $\mathrm{NEE_{day}}$ was calculated using Eqn (4), P_max is maximum ecosystem CO_2 uptake rate (μmol CO_2 m^{-2} s^{-1}), R_E is ecosystem respiration (mmol CO_2 m^{-2} s^{-1}), ϕ is PPFD (μmol m^{-2} s^{-1}), and α is apparent quantum efficiency ($\partial CO_2/\partial\phi$).

To describe the effects of temperature on nighttime NEE, a second model was used

$$\mathrm{NEE_{night}} = R_0 \exp^{(b*T)} \qquad (7)$$

where R_0 is the base ecosystem respiration rate (μmol $\mathrm{CO_2\,m^{-2}\,s^{-1}}$) when air temperature is 0 °C, T is temperature (°C), and b is an empirical coefficient.

A general linear model (SAS ver. 8.01, Cary, NC) was used to test first and second order effects of other variables on NEE, including PPFD, temperature, VPD, season and year. Sigmaplot ver. 5.0 (SPSS Inc., Richmond, CA) was used to describe these relationships.

Data screening and gap filling for annual NEE estimation

To determine the response of NEE to PPFD, VPD and temperature, eddy covariance data were screened for validity and removed when either (i) the standard deviation of w', $\mathrm{CO_2}'$, or θ' was >1.74 SD from the mean (Gaussian distribution), (ii) rain occurred, (iii) 30-min data collection periods were incomplete, or (iv) signals from either the sonic anemometer or the IRGA were out-of-range (Hollinger *et al.*, 1995; Anthoni *et al.*, 1999). Profile data were removed when either (i) data were beyond 3 SD from the mean, (ii) 30-min data collection periods were incomplete, or (iii) signals from the IRGA were out-of-range.

To estimate annual NEE, from collected eddy covariance and profile data were similarly screened with the exception that no variance criterion was applied. This was to better account for exchanges of carbon during large ejections and ventilations through the canopy profile.

Leaf area estimation

Although the La Selva forest is largely evergreen, seasonal differences in leaf area index (LAI) occur, because 8% of the tree species are deciduous in the dry season and 28% of tree species produce annual leaf flushes, many at the onset of the wet season (Frankie *et al.*, 1974). Furthermore, many of the tree species are facultatively deciduous, losing up to half of their leaves during prolonged dry periods (Richards, 1996). Photographic estimates of eLAI (estimated LAI) were derived using the WINPHOT program (Ter Steege, 1996) each year during the wet and dry seasons across 18 randomly stratified 0.5 ha plots (for description of statistical design for plot layout see Clark & Clark, 2000). Within each plot, 6 photographs were made at each sampling date under diffuse light conditions at the same randomly chosen points. Because these estimates were derived optically with no means of direct calibration, they should be viewed relatively.

Results

Characterizing canopy level turbulence

There were $-2/3$ slopes for the normalized spectra of wind velocities in the inertial subrange during periods of both stable and unstable atmospheric conditions, confirming a transfer of energy to the canopy with shear forces dominating (Fig. 1). The spectral density decreased during stable conditions (Fig. 1b), as did the eddy covariance flux estimates, but the general relationships still held. Buoyancy forces produced measurable vertical wind movement at night, as indicated by the positive 1 : 1 slopes at frequency 1 Hz. The observed shift in the spectral peak between stable and unstable conditions was similar to that reported in other studies (Anderson *et al.*, 1986; Kaimal & Finnigan, 1994). The spectral correction factor based on these data ranged from 1.18 to 1.08 and varied with u^* (Fig. 2).

Zero-plane displacement (d) and z_0 for momentum also varied with stability (Table 1). During unstable periods ($L < -50$ m), z_0 increased to ~ 2.4 m, a long roughness length even for a forest (Hansen, 1993), with a mean level of drag (d) of ~ 22 m. Aerodynamic roughness lengths

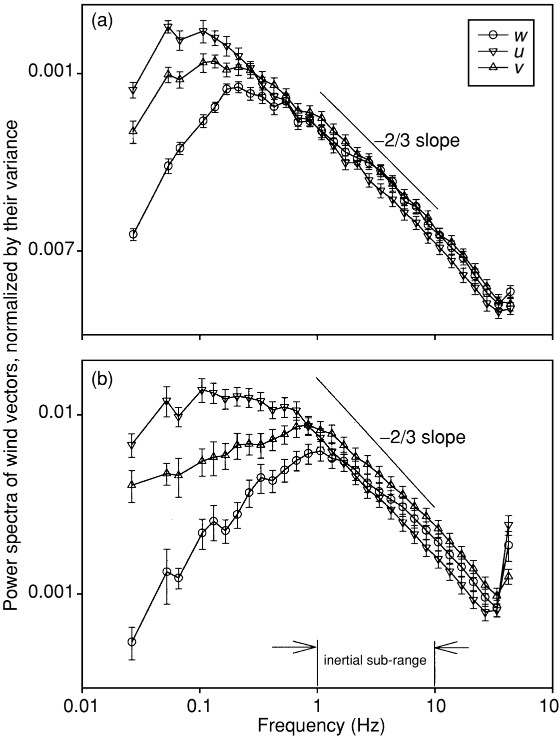

Fig. 1 The relationship between the normalized power spectra for the three wind vectors against frequency. Data are averages from 73, 30-min periods from January 10 to Februray 28th, 1999, (a) Mid-day, unstable conditions, beginning at 12:00–12:30 pm, and (b) Mid-night, stable conditions, beginning at 23:00–23:30 pm. Graph is plotted in a log–log scale. Error bars are ± 1 SE.

sharply decreased from slightly unstable conditions ($-50 < L < -10$) to neutral conditions ($-10 < L < 10$), indicating the quick formation of stratified laminar flow and the decoupling of the below-canopy environment.

The relationship between NEE_{day} and u^* was linear (Fig. 3a). There was an increase in the nighttime eddy covariance data with u^*, although no obvious threshold was observed (Fig. 3b). When nighttime eddy covariance data were averaged across u^* intervals of $0.025\,m\,s^{-1}$, the relationship was strongly linear below a u^* of $0.45\,m\,s^{-1}$ (Fig. 3b). No relationship, was found between the residuals from the energy budget and u^* under any stability conditions, so that no u^* threshold could be determined and used to filter data, as has been done in most other studies (e.g. Goulden *et al.*, 1996; Clark *et al.*, 1999). Because nighttime eddy covariance increased linearly with u^*, we assumed the air column was never fully purged and that the most accurate estimate of nighttime NEE was the combination of eddy covariance and storage fluxes which occurred at larger values of u^* (i.e. $> 0.4\,m\,s^{-1}$). The consequences of these assumptions are discussed below.

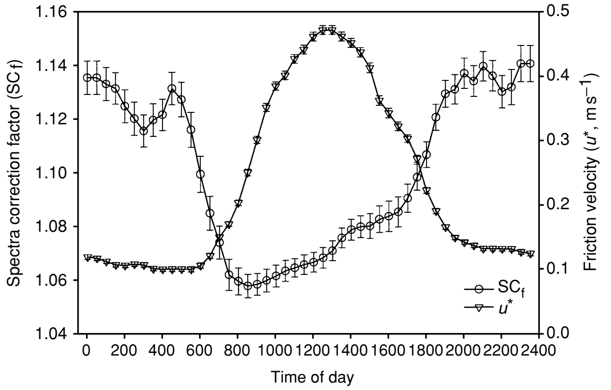

Fig. 2 Diurnal time series of the spectra-based correction factor for CO_2 fluxes from La Selva as calculated from Eqn (5). Data are 90-min running means centred on the 30-min interval. Data are from 1998 to 2000. Error bars are ±1 SE.

Diurnal patterns in NEE

The diurnal pattern of the CO_2 storage flux was very consistent throughout the year (Fig. 4a). The greatest fluxes were observed in early morning hours, when

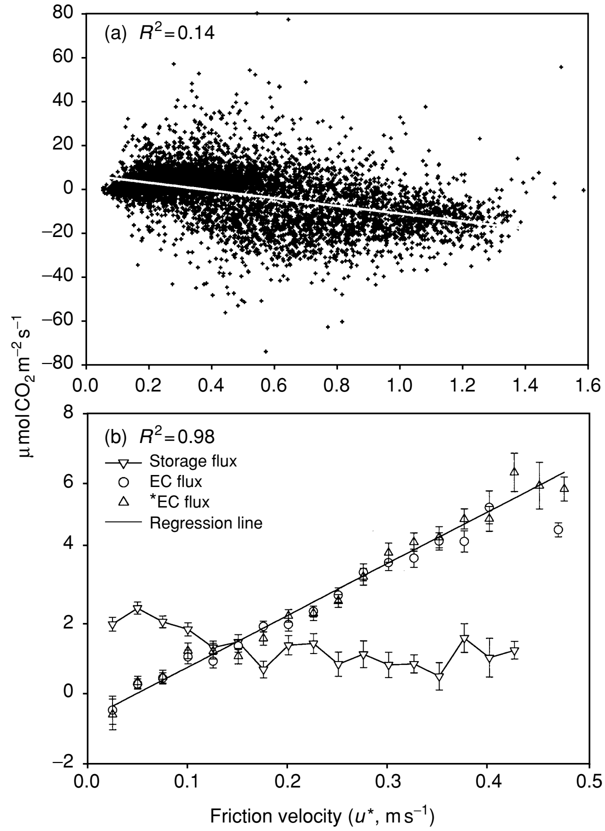

Fig. 3 The relationship between u^* and 30 min daytime NEE (a), and nighttime eddy covariance and storage flux (b). Values of the both fluxes were averaged across intervals of $0.025\,m\,s^{-1}$, except for the righthand most eddy covariance point, in which were averaged for all data $u^* > 0.4\,m\,s^{-1}$. All screens were applied to EC flux data with the exception to *EC flux data, where a variance criterion was ignored to better estimate the contributions from ventilations. Error bars are ±1 SE.

Table 1 Estimates of zero-plane displacement (*d* from Eqn (1)), aerodynamic roughness length (z_0, Eqn (2)), according to stability class (*L*, Eqn (3), from La Selva Biological Station. Because estimates of *d* made using cup anemometers under neutral and stable conditions can be uncertain, u^* values are also reported. zero-plane displacement (*d*) and u^* estimates are median values ± 95% CI, *L*-values are means ± 1 SE, and *n* is number of 30-min periods

Stability class	z_0 (m)	*d* (m)	u^* (m s^{-1})	*L* (m)	*n*
Unstable	2.41 ± 1.04	21.5 ± 1.80	0.37 ± 0.46	−716 ± 428	57
Slightly unstable	3.62 ± 0.95	19.4 ± 1.91	0.34 ± 0.13	−22 ± 1.5	51
Neutral	0.45 ± 0.01	22.1 ± 6.73	0.11 ± 0.05	1 ± 0.6	84
Stable	0.44 ± 0.21	23.0 ± 1.00	0.22 ± 0.05	814 ± 553	186

below-canopy CO_2 that was respired during the night and stored in the air column below the sonic anemometer was vented or re-fixed through photosynthesis. The magnitude of morning ejections may be underestimated, because venting may skew the distribution of wind statistics in the 30-min dataset, and so other valid data could have been inadvertently removed during the screening process.

The maximum average storage flux was $-5.6\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$, which occurred at ~0800 when the convective boundary layer was developing, as shown by the increasing vertical windspeed in Fig. 4b. Storage fluxes decreased until ~1400, after which only net effluxes from below the canopy were observed. This also coincided with peaks in below-canopy temperature (Fig. 4b) and vertical windspeed. Storage efflux increased to a peak just after sunset. The maximum nighttime (before 0600) storage efflux was $2.97\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$, with an average of $1.6 \pm 0.13\,\mu$mol $CO^2\,m^{-2}\,s^{-1}$. Storage generally decreased throughout the night, along with temperature and vertical windspeed. Vertical windspeed and below-canopy temperatures diverged between 1630 and 0130, which indicates that horizontal advection of below-canopy CO_2 off the site may have occurred and that a portion of the flux may have been missed (Mahrt *et al.*, 2000).

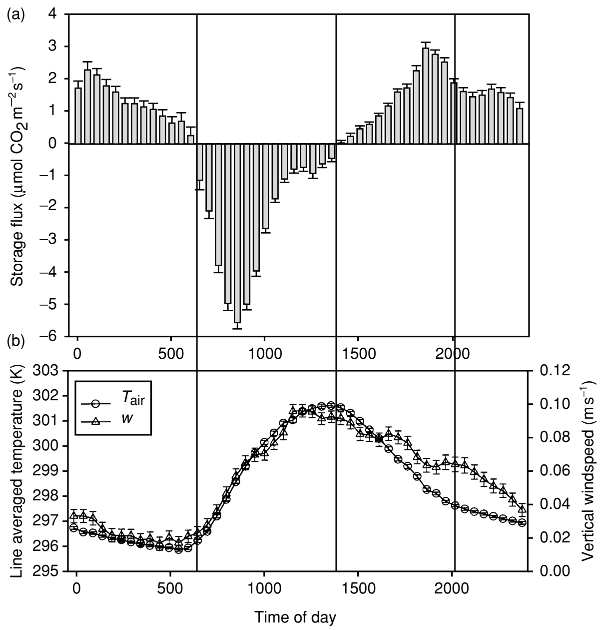

Fig. 4 Diurnal characteristics of (a) storage fluxes, and (b) line-averaged temperature and nonrotated vertical windspeed from La Selva (1998, 1999, 2000). A 90-min running average was used, with each estimate centred on the 30-min interval as indicated. Sample size for storage and line-averaged temperature were 5566 and for vertical windspeed 16333. Error bars are ±1 SE.

The maximum NEE_{day} based on the 3-year mean for each half-hour occurred at ~1130, and closely followed the inverse pattern of PPFD (Fig. 5). Night-time eddy covariance flux was positive and fairly constant throughout the night. At dawn, this flux sharply decreased (uptake into the forest) for ~30 min with decreases in L (Eqn (3)).

Environmental controls on NEE

NEE_{day} NEE_{day} was negatively correlated with PPFD and had an estimated mean maximum of $-18 \pm 9\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ (Fig. 6a). PPFD alone accounted for 51% of the variation, with no significant effect of season. Residuals from this function were weakly related to temperature and VPD (Fig. 6b, c). A linear model that included second-order effects of year, PPFD, and VPD explained ~72% of the total variation in $NEE_{day.}$

Since VPD includes temperature as a component, VPD and temperature are correlated, and since VPD directly affects stomatal conductance (Landsberg & Gower, 1997; Law *et al.*, 2001), we examined the influence of VPD on NEE_{day} further by separating NEE_{day} into three VPD classes (0–0.5, 0.51–1.00, and >1.0 kPa) and refitting Eqn (6) for each year. The results (Fig. 7, Table 2) show that the response function is more linear within a VPD class. P_{max} and R_E in 1998 were significantly lower than those found in 1999, while a in 2000 was greater than in the other two years (Table 2). Light compensation points ranged from 110 to 207 μmol $CO_2\,m^{-2}\,s^{-1}$.

NEE_{night} The absolute mean NEE_{night} was $4.82 \pm 0.6\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ (mean ± 1 SD). This however,

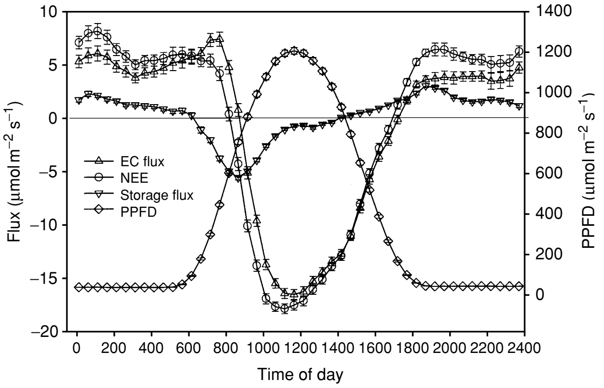

Fig. 5 The mean diurnal pattern of eddy covariance (above-canopy) and storage (below-canopy) fluxes, NEE and PPFD from La Selva (1998, 1999, 2000). All screens were applied towards the carbon flux data with the exception of the variance criteria. This was done to better estimate the contributions of ventilations in the overall flux. Error bars are ±1 SE.

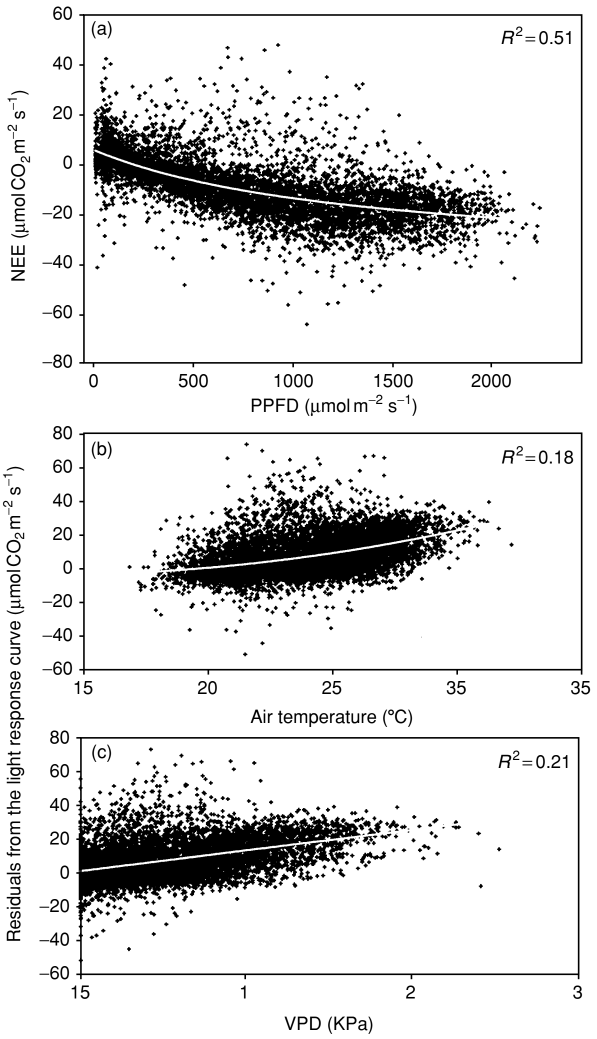

Fig. 6 Main effects of environmental variables on daytime NEE, where (a) is the light response of NEE for all data (1998–2000), (b) and (c) show the residuals from the light response function in relation to temperature and VPD, respectively.

may be an underestimate because $>80\%$ of the nighttime turbulent exchange measurements were made with $u^* < 0.4\,m\,s^{-1}$. Using only data with $u^* > 0.4\,m\,s^{-1}$, the estimate becomes considerablely larger, 7.05 μmol $CO_2\,m^{-2}\,s^{-1}$, with 5.97 ± 0.28 and 1.08 ± 0.41 μmol $CO_2\,m^{-2}\,s^{-1}$ (mean ± 1 SE) the contributions from eddy covariance and storage fluxes, respectively. The averaged daytime R_E values (from Eqn (6), Table 2) ranged from 5.07 to 6.42 μmol $CO_2\,m^{-2}\,s^{-1}$, which supports the greater validity of these higher NEE_{night} values.

NEE_{night} was weakly related to temperature over the entire sampling period (Fig. 8), with a Q_{10} of 1.79 ($P < 0.053$).

Estimating annual NEE

We estimated annual NEE in two ways. In the first case, half-hourly meteorological data were used to drive Eqn (6) for each year and VPD class to derive an annual NEE_{day}. Then a fixed NEE_{night} of 7.05 μmol $CO_2\,m^{-2}\,s^{-1}$ was subtracted (see above). We refer to these results as $NEE_{modeled}$. In the second case, measured NEE_{day} and NEE_{night} (with $u^* > 0.4\,m\,s^{-1}$) were used, and only the gaps were filled using the procedure above; results are referred to as NEE_{gap}. There were marked differences in the cumulative NEE among years depending upon the method of estimation (Fig. 9). Annual NEE was estimated to be higher in 1999 and 2000 than in 1998, with 2000 the strongest sink year.

Discussion

Characteristics of the La Selva canopy

We assume that the eddy covariance measurements from La Selva were robust and represent the nature of CO_2 exchange between the canopy and the atmosphere on the basis of two requirements generally prescribed for this method: (1) a consistent energy cascade in the inertial subrange in the power spectra under both stable and unstable conditions (Kaimal & Finnigan, 1994), and (2) a measurement height was at least 1.8 times d (it was in fact at least 8 times z_0 above d in unstable conditions and 6 z_0 above d under all other stability classes, Montieth & Unsworth, 1990; Schmid *et al.*, 2000). We found a well-developed energy cascade during nighttime conditions, likely due to roughness induced turbulence in the nighttime flows.

It is unclear why no u^* threshold in the eddy covariance data was observed. Turbulence structures above a fixed plane (e.g. a vegetated canopy) from other studies have generally been described using Monin-Obukov theory (Leclerc *et al.*, 2003) and measured over uniform canopies with short aerodynamic roughness. As roughness lengths become greater (>1 m), the effect on turbulence in the well-mixed layer and applicability of Monin-Obukov theory become questionable (Raupach & Finnigan, 1997; Ayotte *et al.*, 1999; Nakamura & Mahrt, 2001). Under these conditions, u^* becomes homogenized over a broader range of turbulence lengths and potentially has less explanatory power (Nakamura & Mahrt, 2001). At La Selva, the uniformly linear relationship between NEE_{night} and u^* was likely due to the lack of well-mixed conditions at night. There were insufficient data to see if this relationship held for values $>0.45\,m\,s^{-1}$, or if it ultimately reached some asymptote. Some data that would have contributed toward developing a u^* filter may also have been screened out by other criteria.

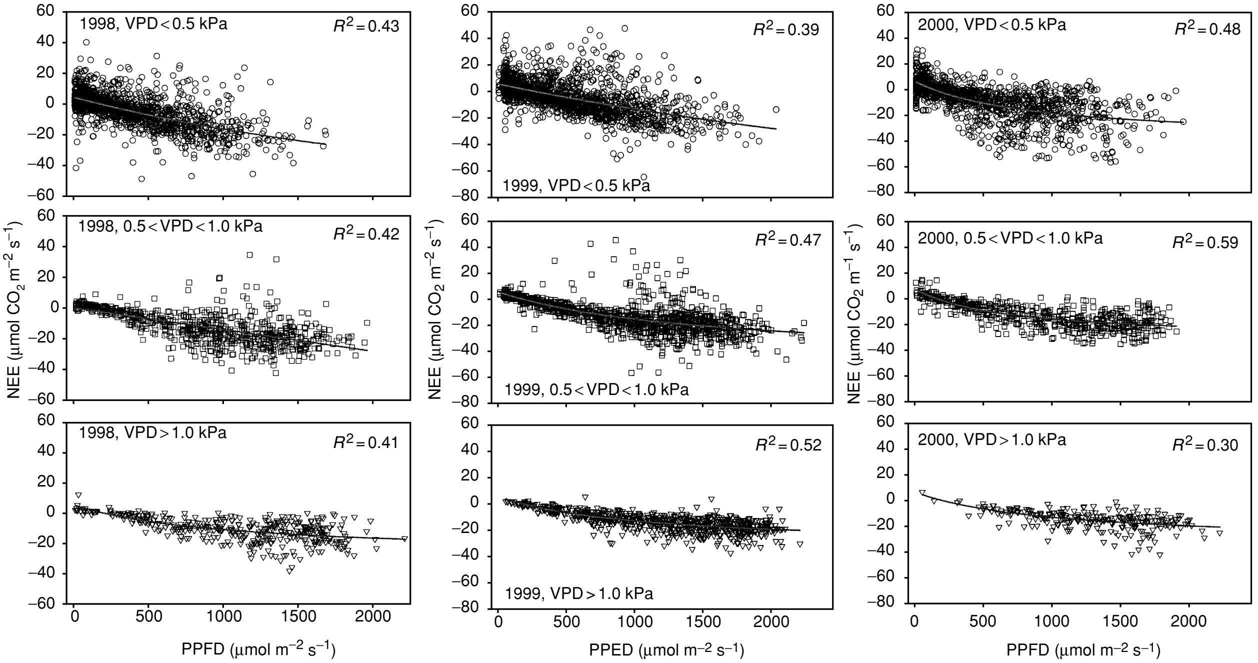

Fig. 7 NEE as a function of PPFD across a gradient of vapour pressure deficits for years 1998, 1999 and 2000 from La Selva, Costa Rica.

Table 2 Parameter estimates and statistics from the light response function Eqn (5) across VPD classes and year (mean ± 1 CI, [*]*P*-value). The P_{max} coefficients are presented at 2200 μmol m^{-2} s^{-1} in the VPD class 0–0.5 kPa, because the light response function has a close to linear relationship

VPD	Year	P_{max}	α	R_E	R^2	Light compensation point
0–0.50	1998	−32.72 na < 0.002	0.0260 ± 0.003	4.51 ± 0.35	0.44	
0.51–1.00		−43.60 ± 4.92	0.0356 ± 0.007	4.50 ± 1.13	0.45	
> 1.0		−32.40 ± 3.70	0.0317 ± 0.010 0.0019	5.33 ± 1.90 0.005	0.35	
Pooled		−40.80 ± 3.95[†]	0.0346 ± 0.005[‡]	5.07 ± 0.60[†]	0.49	146 ± 1.6
0–0.50	1999	−29.99 na < 0.03	0.0217 ± 0.0020	5.77 ± 0.44	0.39	
0.51–1.00		−52.40 ± 5.34	0.0344 ± 0.0052	5.52 ± 0.99	0.47	
> 1.0		−37.80 ± 1.79	0.0377 ± 0.0083	5.92 ± 1.73 0.0006	0.52	
Pooled		−55.01 ± 5.78[§]	0.0311 ± 0.0035[§]	6.42 ± 0.66	0.50	207 ± 2.2
0–0.50	2000	−26.52 na	0.054 ± 0.009	6.02 ± 0.94	0.48	
0.51–1.00		−39.00 ± 3.0	0.058 ± 0.016	7.85 ± 2.13	0.59	
> 1.0		−40.10 ± 7.2	0.039 ± 0.036 0.067	6.57 ± 8.80 0.22	0.30	
Pooled		−37.00 ± 2.07	0.058 ± 0.009	6.33 ± 0.83	0.51	110 ± 1.3

[*] All parameter estimates were at least significant to $P < 0.0001$ with an $\alpha = 0.05$, unless otherwise noted.

[†] Denotes a significant difference between 1998 and 1999.

[‡] Between 1998 and 2000.

[§] Between 1999 and 2000.

Environmental controls on NEE

The average diurnal pattern in NEE (Fig. 5) is strongly symmetrical around 1130. On average, the storage term contributed 33% to NEE$_{night}$. The power spectra for nighttime eddy covariance indicated a transfer of mass and energy, but the flux was relatively small and the source distance quite long (1.5–2.0 km). The nighttime

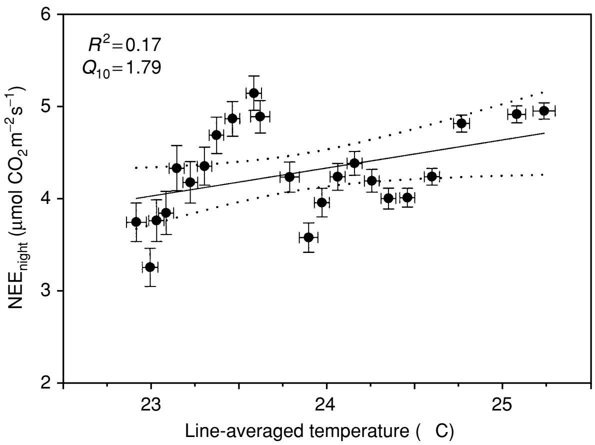

Fig. 8 The relationship between NEE$_{night}$ and line-averaged (below-canopy) temperature. NEE$_{night}$ estimates are the aggregated averages from each nighttime 30-min period from the whole study period (Fig. 4a). Temperature is an average from six measurements through the canopy profile from 27 to 0.5 m.

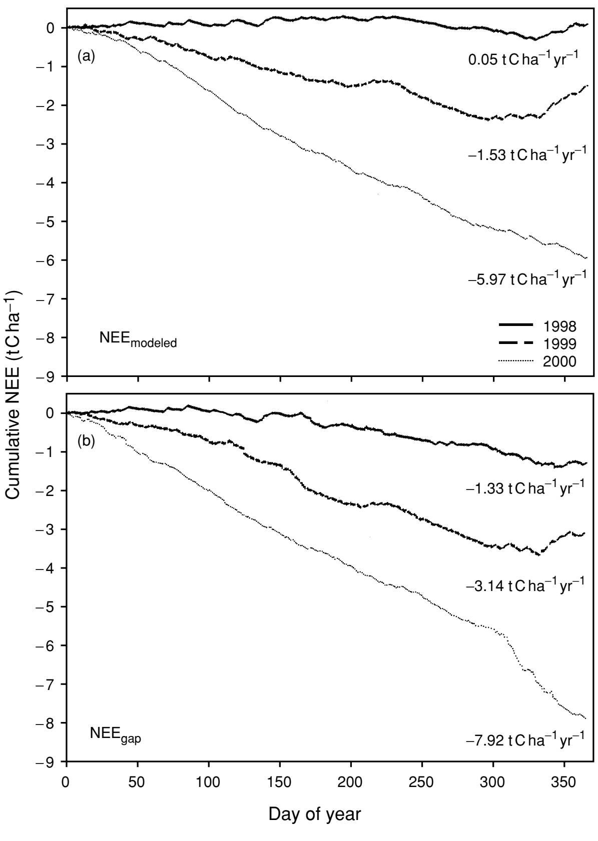

Fig. 9 Cumulative NEE from La Selva Costa Rica for 1998–2000. Estimates were calculated using (a) the results from the light response equations across VPD classes and a fixed estimate for nighttime respiration, and (b) direct estimates of daytime and nighttime NEE with gaps filled using data from NEE$_{modeled}$.

environment below the canopy is quite different from that at the tower top and subject to diabatic flows controlled by changes in air density and slope (Mahrt, 1992), making the source area for the storage flux more localized. The greatest variation in nighttime CO$_2$ profiles occurred during periods with the most rapid changes in T_a. The diurnal patterns in CO$_2$ profiles and respective storage fluxes, however, were relatively constant throughout our measurement period. After the morning vents re-assimilation of stored CO$_2$ dissipated, NEE$_{day}$ was clearly dominated by above-canopy fluxes. Increases in the observed below-canopy efflux from 1400 to 1930 were likely due to less mixing of the airspace (i.e. decreases in u* and mean vertical velocity, Figs 2 and 4b), and a larger fraction of respiration contributed by photosynthesis and growth.

A coarse estimate of the amount of recycled CO$_2$ can be obtained as the difference between integrated NEE$_{night}$ and the morning storage flux. This yields a value of 32% for the fraction of integrated NEE$_{night}$ that was recycled below 42 m, similar to isotopically derived estimates of re-synthesized CO$_2$ from the Ducke forest near Manaus, Brazil (39%, Sternberg *et al.*, 1997) and within the range from another neotropical forest in Panama (31–38%, Sternberg *et al.*, 1989).

The lack of a relationship between 30-min averages of NEE$_{night}$ and temperature was likely due to the combination of different factors. First, there are numerous sources of CO$_2$ for ecosystem respiration, each with their own controlling factors (Davidson *et al.*, 1998). Soil respiration can be influenced by soil type, water status and temperature (Schwendenmann *et al.*, in press), and foliar respiration may be influenced by nitrogen and/or photosynthate availability in the canopy at the time of leaf expansion. Second, there was only a small range annual nighttime temperature ($<9\,^{\circ}$C). Third, the above-canopy source area is much larger than below-canopy (Raupach *et al.*, 1992), so that the storage flux may be subjected to localized biotic effects or the possibility of below-canopy advection. Fourth, as mentioned above, 80% of flux estimates were made under conditions with low u* ($<0.4\,\mathrm{m\,s^{-1}}$), questionable conditions for eddy covariance. Finally, carbon may have been exported from the system as CO$_2$, as large ventilation events may not have been fully quantified, particularly during periods of rain (Mahrt, 1992; Wilson *et al.*, 1998). Using the variance of wind and scalars as screening criteria may have contributed to this error. The potential contribution of carbon lost by ventilations was $\sim 0.1\,\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ when this criteria was not applied.

Purging of soil CO$_2$ from the soil profile during rain was not thought to be a source of error. Schwendenmann *et al.* (in press) found a negative linear relationship between soil CO$_2$ flux and soil water content. They also found no seasonal changes in the storage of CO_2 in the soil profile at La Selva, and CO_2 in the upper soil profile (0–1 m) tended to increase in concentration during the wet season, likely due to decreased production and diffusion through the profile. Soils tended to be relatively wet all the time, with soil water content ranging from 35 to 70%.

The relationship between NEE_{night} and temperature (Fig. 8) based on longer averaging intervals is subject to the same potential sources of error as mentioned above and may also lead to underestimated annual NEE_{night}. Schwendenmann *et al*. (in press) reported that soil respiration rates at La Selva from upland soils ranged from 3.3 to 4.3 μmol $CO_2\,m^{-2}\,s^{-1}$. Given that soil respiration accounts for roughly 50% of R_E for a wide range of forests (Ryan, 1991; Amthor, 1994), this further suggests that our higher value (7.05 μmol $CO_2\,m^{-2}\,s^{-1}$) for NEE_{night} is more likely correct. Moreover, when we recalculated annual NEE_{night} using the nighttime respiration function in Fig. 8, it also resulted in a very low value (4.3 μmol $CO_2\,m^{-2}\,s^{-1}$), similar to that found using the NEE_{night} data across all u* values, and again a value completely out of step with measured soil respiration and our other estimation of NEE_{night}.

The potential exists that below-canopy nighttime advective flow contributes to error in NEE_{night}. However, for this to occur there must exist specific conditions, such as a strong upslope temperature gradient, a breakdown of below-canopy resistance to flow, and/or a net vertical movement of wind into the forest. At La Selva, however, there is only a small change in temperature over a large upslope area, there is considerable resistance presented by large below-canopy leaf area and tree stems, and nighttime above-canopy vertical and below-canopy horizontal windspeeds (data not shown) were not much different from the expected accuracy of the sonic anemometer (i.e. 0.05 m s^{-1}). This is an unresolved issue at La Selva, but one also shared by other tower flux sites (Massman & Lee, 2001).

In the face of increasing global temperatures (National Academy of Science, 2000), there is increased focus on the role of temperature in controlling the carbon dynamics in the tropics. Kindermann *et al*. (1996) modelled the effects of increased temperature on carbon stores and with even small increases in temperature (~0.5 °C), projected large effluxes of carbon to the atmosphere. It has been hypothesized that most released carbon will be from the tropics (Trumbore *et al*., 1996). At La Selva, large year-to-year fluctuations over the past 16 yr in above-ground biomass increments have been negatively correlated with both the mean nighttime temperature and variations in annual fluctuations in atmospheric CO_2 concentrations (Clark *et al*., in review). In this study, we found only a small temperature influence on NEE_{day} and $NEE_{night,\ and}$ only when all three years of data were pooled and hourly averages used. The effect of temperature on NEE_{day} may be entirely due to VPD, or partially due to photorespiration. Interestingly, Grace *et al*. (1996) and Mahli *et al*. (1998) did not report a nighttime temperature response for Amazonian forests using eddy covariance. It may well be that effects of temperature on ecosystem respiration from tropical forests will only become apparent after many years of observation.

There were large interannual differences in apparent forest-level quantum efficiency (α) estimated from the NEE_{day} data. This may indicate large adjustments in forest structure and physiology in response to the climatic variation among our study years. Waring *et al*. (1995) concluded that seasonal differences in both LAI and canopy-level a largely controlled productivity from a deciduous forest in the north-eastern US. In our study, the estimated α for 2000 was significantly higher than those from the preceding two years and approached the theoretical maximum for C_3 leaves (Farquhar *et al*., 1980; Lloyd *et al*., 1995). Interannual changes in α suggest a lagged physiological response to changing environmental conditions expressed in the photosynthetic ability of new leaves. However, eLAI did not follow this pattern and increased only 1999 and into the dry season of 2000 (Table 3). That neither changes in LAI nor α were related to annual NEE suggests that there are interactions between NEE, canopy leaf dynamics and climate for this complex tropical wet forest.

The effect of VPD on NEE_{day} could be a result of either physiological or physical factors. A physiological factor could be stomatal closure in response to a hydrologic limitation, either high VPDs or indirectly, through decreases in soil moisture availability. The location of the hydraulic limitation in the La Selva forest is not known. A physical factor could be through modification of canopy architecture due to premature leaf drop, leaf folding or changes in leaf orientation. Whole forest canopies do not fully light saturate with respect to NEE even at full insolation (Ruimy *et al*., 1995; Wang & Polglase, 1995). Changes in leaf angle or leaf closure in the upper

Table 3 Annual and seasonal differences in estimated leaf area index (eLAI) $m^2\,m^{-2}$ from La Selva, Costa Rica (S.F. Oberbauer unpublished data)

Season year	Mean (median) ± 1 SE
Dry 1998	3.85 (3.96) ± 0.19
Wet 1998	4.85 (4.79) ± 0.11
Dry 1999	2.71 (2.52) ± 0.13
Wet 1999	3.76 (3.84) ± 0.11
Dry 2000	3.48 (3.51) ± 0.07
Wet 2000	3.43 (3.30) ± 0.13

canopy allows penetration of light to deeper canopy layers, allowing for increased carbon gain in the lower canopy. This offsets the effect of leaf closure or changes in orientation at leaf scale in terms of light response at the ecosystem level. At La Selva, only 8% amount of the time, however, were VPD values $>1\,\mathrm{kPa}$ and during 97% of the daytime (when net radiation was $>40\,\mathrm{W\,m^{-2}}$), latent heat fluxes were greater than sensible heat fluxes ($\beta<1$, unpublished data). This strongly suggests that the La Selva canopy had access to abundant soil water. The only exception was in the 1998 dry season, when 30% of daytime VPDs were $>1\,\mathrm{kPa}$, precipitation was the lowest ever recorded (68, 38, 126 mm monthly total rainfall in January, February and March, respectively), and daily mean T_a was $>1\,^{\circ}\mathrm{C}$ above the long-term average.

The 1998 dry season was at the end of the 1997–1998 warm-phase El Niño Southern Oscillation (ENSO) event and was warmer and drier. During December 1998, a cold-phase (la Niña) ENSO event brought greater precipitation, cooler temperatures, and lower mean daily insolation (and PPFD), with several days receiving $<5\,\mathrm{MJ\,d^{-1}}$. Overall, 1998 was warmer and drier during the dry season, but had more precipitation, cooler temperatures and reduced light during the latter part of the year (compared to the other two years, Table 4). The greater eLAI in 1998 coupled with lower α, a greater portion of time with VPDs $>1\,\mathrm{kPa}$ in the dry season, and overall lower mean daily insolation ($13.3\,\mathrm{MJ\,d^{-1}}$, Table 4), likely contributed to the La Selva forest being close to carbon neutral in 1998.

During 1999, the daily insolation was well above the long-term trend, but in November and December the insolation was well below the long-term average due to a prolonged *temporal*, suggesting that the effects of increased annual incident radiation outweighed those of reduced eLAI and the *temporal*, making this forest a moderate sink of carbon.

Despite these seasonal variations in climate, we did not find any seasonal effects on NEE for any year. Even though seasonal displacements of the ITCZ alter Hadley cell circulations, changes in individual environmental factors do not necessarily occur in concert as a result. The initial passing of the ITCZ can be intermittent and there can be multiple 'false starts' (Hastenrath, 1991). Moreover, the most northern progression of the ITCZ is just north of Costa Rica and with erratic movement, prolonged periods of dry weather can occur during the otherwise 'wet season' (Sanford *et al*., 1994). Other regional anomalies can occur, as during 1998 and 1999, when heavy rains persisted from December into January, even after the ITCZ passed. In 1998, this was brought about by a cold-phase ENSO event, and in 1999 by a prolonged *temporal*.

The climatic trends observed during the 1997–98 ENSO were typical for this region (Cavazos & Hastenrath, 1990; Waylen *et al*., 1996b) as were the conditions observed during *temporales* (Sanford *et al*., 1994). The 1997–1998 ENSO, however, brought the highest temperatures in the 19-year La Selva record. The apparent increasing frequency and magnitude of ENSO events (Corti *et al*., 1999; Timmermann *et al*., 1999), may have implications for interpreting the effects of climate change on NEE, as 1998 had the lowest estimated NEE at La Selva. This supports the findings of Tian *et al*. (1998) who concluded in a modelling study that variations in NEE of tropical forests are controlled, in part, by macro-level changes in climate, which in turn are driven by the timing, frequency and magnitude of ENSO events.

Table 4 Meteorolgical data for years 1998–2000 from La Selva Biological Station, CR. Data are means ± 1 SE. To determine statistical significance among years, cumulative meteorological data were used with a general linear model, and differences in the slopes were tested. For each year the slopes did not differ not the means and were highly linear, $R^2=0.98$, $P<0.001$

Time period	Mean air temperature (°C)	Mean minimum temperature (°C)	Mean soil temperature (°C)	Mean daily insolation, $\mathrm{MJ\,d^{-1}}$	Total precipitation
1998	*24.23 ± 0.015	*24.03 ± 0.015	*23.43 ± 0.018	*13.3 ± 0.24	3495
1999	23.4 ± 0.014	23.19 ± 0.014	21.29 ± 0.023	†16.82 ± 0.28	3475
2000	23.66 ± 0.016	23.44 ± 0.016	21.24 ± 0.022	‡14.97 ± 0.26	4127
January 1998	25.09 ± 0.025	24.8 ± 0.026	23.84 ± 0.002	12.51 ± 0.12	68
February 1998	25.48 ± 0.047	25.23 ± 0.46	24.71 ± 0.002	12.7 ± 0.15	38
March 1998	25.44 ± 0.055	25.17 ± 0.053	24.79 ± 0.003	13.3 ± 0.17	126
June 1998	26.01 ± 0.031	25.73 ± 0.029	23.44 ± 0.043	12.44 ± 0.13	400
December 1998	23.7 ± 0.03	23.47 ± 0.03	21.22 ± 0.042	9.72 ± 0.15	909
November 1999	24.62 ± 0.048	24.31 ± 0.047	22.67 ± 0.003	13.78 ± 0.17	309
December 1999	22.03 ± 0.037	22.79 ± 0.05	20.85 ± 0.002	8.73 ± 0.13	524

Note: *† and ‡denote significant difference ($\alpha=0.5$, $P<0.0001$) for 1998, 1999 and 2000 from the other two years, respectively.

A possible alternative explanation for the large interannual variation in NEE at La Selva is that a substantial fraction of forest is in an early successional stage. There is a high frequency of treefall gaps in this forest, even though La Selva is below most hurricane pathlines. If we assume that the forest is aggrading carbon during its stand half-life, which was estimated as 77.3 year by Lieberman *et al.* (1990), and has gap formation rate of 0.96% area year^{-1} (Denslow & Hartshorn, 1994), then 74% of the land area is under recovery at any time. Moreover, the mortality rate for 1969–1982 was 2.03% (Lieberman *et al.*, 1990), but increased to 4.77% in 1997–98 (Clark *et al.*, unpublished data) in upland plots associated with gaps, suggesting that the gap formation rate also increased under climatic conditions imposed by both ENSO phases.

Comparisons with other tropical sites

The pattern and magnitude of NEE at La Selva were similar to those estimated by eddy covariance at three tropical moist forest sites in the Brazilian Amazon (Reserva Ducke, north central Amazon, Fan *et al.*, 1990; Jarú, south central Amazon, Grace *et al.*, 1995b; Cuieiras, north central Amazon, Mahli *et al.*, 1998). Mean maximum daytime NEE estimated for these three forests was 18 to 20 μmol $CO_2\,m^{-2}\,s^{-1}$ and mean nighttime NEE ~5–7 μmol $CO_2\,m^{-2}\,s^{-1}$ (Table 5). This suggests that these ecosystems may have similar controlling factors on NEE, even though there are marked differences in stand characteristics. Mahli *et al.* (1998) hypothesized that effects of cloudiness on insolation were the strong determinate of NEE_{day}, which may explain the low NEE in 1998 at La Selva. One difference is that VPD was found to play a stronger role in regulating carbon gain at the other sites than at La Selva (e.g. Mahli *et al.*, 1998). These other sites all receive $<2500\,mm\,yr^{-1}$ of annual precipitation and have lower soil water availability (Hodnett *et al.*, 1996; Tomasella & Hodnett, 1996), so that there are likely to be greater hydrologic constraints on daytime NEE (Mahli *et al.*, 1998; Williams *et al.*, 1998). The range in annual α at all these sites overlaps.

Reduction in leaf carbon gain can occur when leaves are wet, lowering rates of CO_2 diffusion into the leaf by a factor of 10^4 (Jones, 1992), thus reducing photosynthesis (Ishibashi & Terashima, 1995). Smith & McClean (1989) also found that photosynthesis was significantly reduced in wet leaves that had a wettable cuticle, but increased on leaves that had nonwettable cuticles. The ratio of species with wettable:non-wettable leaves at La Selva is not known. However, because eddy covariance data collected during rain events at La Selva were eliminated, NEE_{day} may have been over-estimated as a result. La Selva experiences rain for 18% of the time annually, as compared to only 13 and 8% at Jarú and Ducke, respectively (data from 1994 to 1996, http://www.abracos.com). For this reason, the likelihood of a sampling bias is potentially greater at La Selva due to the larger fraction of data removed in screening.

The range in our estimates of annual gross ecosystem production (GEP, Table 6) overlaps the estimate at Cuieiras. High ratios of NEE:GEP are thought to exist only with forests rapidly accumulating carbon (e.g. 0.02

Table 5 Comparison of stand attributes from four neotropical eddy covariance studies

Site		La Selva	Ducke	Jarú	Cuieiras
Location	Lat.	10°26′N	2°57′S	10°04′S	2°35′S
	Long.	83°59′W	59°57′W	61°56′W	60°06′W
Length of study period	(days)	1006	12	55	365
Mean annual temperature	(°C)	25	26†	25†	27.8
Annual rainfall	(mm)	4000	2400‡	1450†	2400‡
Holdridge life zone type		Tropical wet	Tropical moist	Tropical moist	Tropical moist
Above ground biomass	($t\,C\,ha^{-1}$)	160.5 (±18)	300–350	140–180	300–350
*Estimated LAI		2.7–4.9	5–6	4	5–6
Estimated quantum yield	(μmol CO_2 mmol photon^{-1})	0.022–0.058	0.051	0.025	0.048
Mean nighttime NEE	(μmol $CO_2\,m^{-2}\,s^{-1}$)	7.05	6.0	6.4	6.5
Peak daytime NEE	(μmol $CO_2\,m^{-2}\,s^{-1)}$	−18	−19	− 15	−17 to −21
Light compensation point	(μmol $m^{-2}\,s^{-1)}$	147–208	120	130	80
Annual NEE	($t\,C\,ha^{-1}\,yr^{-1)}$	§0.5 to −6.1	−2.2	−1.0	−5.9
Source		This study	Fan *et al.* (1990)	Grace *et al.* (1995b)	Mahli *et al.* (1998)

*Note, there are no estimates of LAI from tropical forests that have been measured directly through destructive sampling.

†Data obtained from ABRACOS webpage, http://yabae.cptec.inpe.br/abracos/available.html.

‡Hodnett *et al.* (1996).

§Data from $NEE_{modeled}$.

Table 6 Between year measures of productivity and ecosystem efficiency from La Selva, Costa Rica and Cuieiras, Brazil. Data from La Selva are computed from Eqn (5) using a fixed NEE_{night}, as noted in the text. Units of GEP and NEE are expressed as $t\,C\,ha^{-1}\,yr^{-1}$

Site	La Selva, Costa Rica			Cuieiras, Brazil
Year	1998	1999	2000	1995
GEP	28.41	30.6	33.9	30.4
NEE	0.05	−1.53	−5.97	−5.9
NEE:GEP	< 0.002 >	0.050	0.176	0.194

Note: The Cuieriras dataset is from Mahli *et al*. (1998), and Mahli & Grace, 2000.

for an old-growth *Pseudotsuga menziesii* forest, compared to 0.29 for rapidly a growing pine stand, Waring & Schlesinger, 1985). The NEE:GEP ratios were 0.176 and 0.194 for La Selva and Cuieiras, respectively, during 2000 and 1995, indicating that these systems can be very productive compared to other forests. All of the tropical sites cited here are considered 'old-growth', and assumed in the past to be near steady state with respect to carbon. However, eddy flux data from none of them support this view and suggest instead that tropical forests may be net sinks from around 0 to much as $-6\,t\,C\,ha^{-1}\,yr^{-1}$ (averaging c. $-2\,t\,C\,ha^{-1}\,yr^{-1}$). However, the systematic errors discussed earlier would collectively tend to increase NEE (reduce the apparent sink strength) into the forest, since the carbon would be measured when it enters the system at the tower top but not when it leaves the forest (e.g. as downslope drainage of CO_2, loss of C as unmeasured volatile organic compounds, etc.). Specifically where within the La Selva ecosystem carbon maybe accumulating remains unkown.

From this study, we learned that diurnal patterns of NEE at La Selva followed trends similar to those observed elsewhere, with turbulent fluxes dominating in the daytime, and storage fluxes contributing largely in the early morning. Daytime NEE was largely controlled by PPFD, and to a much lesser extent VPD. Hence, macro-climatic events such as el Niño and *temporales* that affect the light regime can greatly influence annual NEE even without large ranges in temperature. This is significant for productivity models that wish to assess the interannual NEE in the tropics, as well as for global climate change models to describe feedback mechanisms with terrestrial systems and to assess the controls on interannual variation of the rise of CO_2 in the atmosphere.

Our largest uncertainties were associated with estimates of nighttime flux. High variability in NEE_{night}, coupled with a small temperature range, low u^* conditions and the potential for CO_2 drainage, all contributed towards error in measurement. There was a large difference in the values of annual NEE between our two alternative estimates, but regardless of the calculation method used, the results indicate that there is a large interannual variation at La Selva related to large-scale regional climate dynamics. This finding supports other shorter term studies that have estimated a wide range in annual NEE, suggesting that tropical forests are not in steady state and furthermore may respond quickly to changes in climate.

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References

Amthor JS (1994) Plant respiration. In: *Plant–Environment Interactions* (ed. Wilkinson RE), pp. 501–554. M. Dekker Publisher, New York.

Anderson DE, Verma SB, Clement RJ *et al.* (1986) Turbulence spectra of CO_2, water vapor, temperature and velocity over a deciduous forest. *Agricultural and Forest Meteorology*, **38**, 81–99.

Anthoni PM, Law BE, Unsworth MH (1999) Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agricultural and Forest Meteorology*, **95**, 151–168.

Aubinet M, Chermanne B, Vandenhaute M *et al.* (2001) Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agricultural and Forest Meteorology*, **108**, 293–315.

Ayotte KW, Finnigan JJ, Raupach MR (1999) A second-order closure for neutrally stratified vegetative canopy flows. *Boundary-Layer Meteorology*, **90**, 189–216.

Baldocchi DD, Meyers TP (1989) The effects of extreme turbulent events on the estimation of aerodynamic variables in a deciduous forest canopy. *Agricultural and Forest Meteorology*, **48**, 117–134.

Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.

Cavazos T & Hastenrath SL (1990) Convection and rainfall over Mexico and their modulation by the Southern Oscillation. *Journal of Climatology*, **10**, 377–386.

Clark DB, Clark DA (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, **137**, 185–198.

Clark KL, Gholz HL, Moncreiff JB *et al.* (1999) Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems. *Ecological Applications*, **9**, 936–948.

Clark DA, Piper SC, Keeling CD *et al.* (in review) Tropical forest growth and atmospheric carbon dynamics linked to annual temperature variation. In: *Proceedings of the National Academy of Sciences.*

Corti S, Molteni F, Palmer TN (1999) Signature of recent climate change in frequencies of natural atmospheric circulation regimes. *Nature*, **398**, 799–802.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.

Denslow JS, Hartshorn GS (1994) Tree-fall gap environments and forest dynamic processes. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS), pp. 120–127. University of Chicago Press, Chicago, IL.

Dixon RK, Brown S, Houghton RA *et al.* (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.

Fan S-M, Wofsy SC, Bakwin PS *et al.* (1990) Atmosphere-biosphere exchange of CO_2 and O_3 in the Central Amazon forest. *Journal of Geophsical Research*, **95**, 12851–16864.

Farquhar GD, Caemmerer SV, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C-3 Species. *Planta*, **149**, 78–90.

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa-Rica. *Journal of Ecology*, **62**, 881–919.

Frolking S, Goulden ML, Wofsy SC *et al.* (1996) Modeling temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biology*, **2**, 343–366.

Goulden ML, Munge JW, Fan S-M *et al.* (1996) Measurements of carbon sequestration by long-term eddy-covariance: methods and critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.

Grace J, Lloyd J, McIntyre J *et al.* (1995a) Carbon dioxide uptake by an undisturbed tropical rainforest in southwest Amazonia, 1992 to 1993. *Science*, **270**, 779–780.

Grace J, Lloyd J, McIntyre J *et al.* (1995b) Fluxes of carbon dioxide and water vapor over an undisturbed tropical rainforest in south-west Amazonia. *Global Change Biology*, **1**, 1–12.

Grace J, Mahli Y, Lloyd J *et al.* (1996) The use of eddy covariance to infer net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology*, **2**, 209–217.

Hansen FV (1993) Surface roughness lengths. ARL technical Report, US Army, White Sands Missile Range, NM 88002–5501.

Hartshorn GS, Peralta R (1988) Preliminary description of primary forests along the La Selva-Volcan Barva altitudinal transect, Costa Rica. In: *Tropical Rainforests: Diversity and Conservation* (eds Alemda F, Pringle C), pp. 281–295. California Academy of Science, San Fransisco.

Hastenrath SL (1991) *Climate Dynamics of the Tropics*. Kluwer Academic, Boston, MA.

Hodnett MG, Tomasella J, Marques Filho AO *et al.* (1996) Deep water uptake by forest and pasture in central Amazonia: Predictions from long-term rainfall data using simple water balance model. In: *Amazonian Deforestation and Climate* (eds Gash JHC, Nobre CA, Roberts JM, Victoria RL), pp. 79–99. John Wiley, New York.

Holdridge LR, Grenke WC, Hatheway WH *et al.* (1971) *Forest Environments in Tropical Life Zones: a Pilot Study*. Pergamon Press, Oxford.

Hollinger DY, Goltz SM, Davidson EA *et al.* (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.

Hollinger DY, Kelliher FM, Schulze E-D *et al.* (1995) Initial assessment of multi-scale measures of CO_2 and H_2O flux in the Siberian taiga. *Journal of Biogeography*, **22**, 425–431.

Houghton RA (1996) Terrestrial sources and sinks of carbon inferred from terrestrial data. *Tellus Series B-Chemical and Physical Meteorology*, **48**, 420–432.

Houghton RA, Davidson EA, Woodwell GM (1998) Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Global Biogeochemical Cycles*, **12**, 25–34.

IPCC (1995) IPCC Second Assessment Report: Climate Change. Geneva, Switzerland, p. 64.

Ishibashi M, Terashima I (1995) Effects of continuous leaf wetness on photosynthesis: adverse aspects of rainfall. *Plant, Cell and Environment*, **18**, 431–438.

Jones H (1992) *Plants and Microclimate*. Cambridge University Press, New York.

Kaimal JC, Finnigan JS (1994) *Atmospheric Boundary-Layer Flows; Their Structure and Measurement*. Oxford University Press, UK.

Kindermann J, Wurth G, Kohlmaier GH *et al.* (1996) Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Global Biogeochemical Cycles*, **10**, 737–755.

Landsberg JJ, Gower ST (1997) *Applications of Physiological Ecology to Forest Management*. Academic Press, New York.

Law BE, Goldstein AH, Anthoni PM (2001) Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology*, **21**, 299–308.

Leclerc MY, Karipot A, Prabha T *et al.* (2003) Impact of a non-local advection on flux footprints over a tall forest canopy: a tracer flux experiment. *Agricultural and Forest Meteorology*, **115**.

Lieberman D, Hartshorn GS, Lieberman M *et al.* (1990) Forest dynamics at La Selva Biological Station, 1969–1985. In: *Four Neotropical Rainforests* (ed. Gentry AH), pp. 509–521. Yale University Press, New Haven.

Lieberman M, Lieberman D, Hartshorn GS *et al.* (1985) Small-scale altitudinal variation in lowland wet tropical forest vegetation. *Journal of Ecology*, **73**, 505–516.

Lloyd J, Grace J, Miranda AC *et al.* (1995) A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant, Cell and Environment*, **18**, 1129–1145.

Mahli Y, Nobre AD, Grace J *et al.* (1998) Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research*, **103**, 31, 593–31, 531, 612.

Mahrt L (1992) Momentum balance of gravity flows. *Journal of Atmospheric Sciences*, **39**, 2701–2711.

Mahrt L, Lee XH, Black A *et al.* (2000) Nocturnal mixing in a forest subcanopy. *Agricultural and Forest Meteorology*, **101**, 67–78.

Mahli Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution*, **15**, 332–333.

Massman WJ, Lee X (2001) Eddy covariance flux corrections and uncertainties in long term studies of carbon and energy exchanges. In: *Proceedings from the Workshop for Unaccounted Flux in Long Term Studies of Carbon and Energy Exchanges Boulder CO.*

McMillen RT (1988) An eddy-correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorology*, **43**, 231–245.

Melillo JM, McGuire AD, Kicklighter DW *et al.* (1993) Global climate change and terrestrial net primary productivity. *Nature*, **363**, 234–240.

Meyers TP, Baldocchi DD (1991) The budgets of turbulent kinetic-energy and Reynolds stress within and above a deciduous forest. *Agricultural and Forest Meteorology*, **53**, 207–222.

Montieth JL, Unsworth MH (1990) *Principles of Environmental Physics*. Edward Arnold Publishers, New York.

Nakamura R, Mahrt L (2001) Similarity theory for local and spatially averaged momentum fluxes. *Agricultural and Forest Meteorology*, **101**, 265–279.

National Academy of Science (2000) *Reconciling Observations of Global Temperature Change*. National Academy Press, Washington, DC.

Pahlow M, Parlange MB (2001) On Monin-Obukhov similarity in the stable atmospheric boundary layer. *Boundary-Layer Meteorology*, **99**, 225–248.

Raupach MR, Finnigan JJ (1997) The influence of topography on meteorological variables and surface–atmosphere interactions. *Journal of Hydrology*, **190**, 182–213.

Raupach MR, Weng WS, Carruthers DJ *et al.* (1992) Temperature and humidity fields and fluxes over low hills. *Quarterly Journal of Royal Meteorological Society*, **118**, 191–225.

Richards PW (1996) *The Tropical Rain Forest: an Ecological Study*. Cambridge University Press, Cambridge UK.

Rosenberg NJ, Blad BL, Verma SB (1983) *Microclimate: the Biological Environment*. Wiley, New York.

Ruimy A, Jarvis PG, Baldocchi DD *et al.* (1995) CO_2 fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–81.

Ryan MG (1991) A simple method for estimating gross carbon budgets for vegetation in forested ecosystems. *Tree Physiology*, **9**, 255–266.

Sanford R, Paaby P, Luvall JC *et al.* (1994) Climate, geomorphology and aquatic systems. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS), pp. 19–33. University of Chicago Press, Chicago, IL.

Schimel DS, House JI, Hibbard KA *et al.* (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–172.

Schmid HP, Grimmond SB, Cropley F *et al.* (2000) Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agricultural and Forest Meteorology*, **103**, 357–374.

Schuepp PH, Leclerc MY, Macpherson JI *et al.* (1990) Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. *Boundary-Layer Meteorology*, **50**, 355–373.

Schultz DM, Bracken WE, Bosart L (1998) Planetary- and synoptic-scale signatures associated with central American cold surges. *Monthly Weather Review*, **126**, 5–27.

Schwendenmann L, Veldkamp E, Brenes T *et al.* (in press) Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica. *Biogeochemistry*.

Smith WK, McClean TM (1989) Adaptive relationship between leaf water repellency, stomatal distribution, and gas exchange. *American Journal of Botany*, **76**, 456–469.

Sollins P, Sancho FM, Mata RC *et al.* (1994) Soils and soil process research. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS), pp. 34–53. University of Chicago Press, Chicago, IL.

Sternberg LSL, Moreira MZ, Martinelli LA *et al.* (1997) Carbon dioxide recycling in two Amazonian tropical forests. *Agricultural and Forest Meteorology*, **88**, 259–268.

Sternberg LSL, Mulkey SS, Wright SJ (1989) Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology*, **70**, 1317–1324.

Ter Steege H (1996) Winphot 5: a programme to analyze vegetation indices, light, and light quality from hemispherical photographs. *Tropenbos Guyana Report 95–2*, Tropenbos Guyana Programme, Georgetown, Guyana.

Tian H, Melillo JM, Kicklighter DW *et al.* (1998) Effect of interannual climate variability on carbon storage n Amazonian ecosystems. *Nature*, **396**, 664–667.

Timmermann A, Oberhuber J, Bacher A *et al.* (1999) Increasing El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–694.

Tomasella J, Hodnett MG (1996) Soil properties and van Genuchten parameters for an oxisol under pasture in central Amazonia. In: *Amazonian Deforestation and Climate* (eds Gash, JHC, Nobre CA, Roberts JM, Victoria RL), pp. 101–124. John Wiley, New York.

Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, **272**, 393–396.

Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Vourlitis GL, Oechel WC (1997) Landscape-scale CO_2, H_2O vapour and energy flux of moist-wet coastal tundra ecosystems over two growing seasons. *Journal of Ecology*, **85**, 575–590.

Wang YP, Polglase PJ (1995) Carbon balance in the Tundra, Boreal Forest and Humid Tropical Forest during climate-change–scaling-up from leaf physiology and soil carbon dynamics. *Plant Cell and Environment*, **18**, 1226–1244.

Waring RH, Law BE, Goulden ML *et al.* (1995) Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant, Cell, and Environment*, **18**, 1201–1213.

Waring RH, Schlesinger WH (1985) *Forest Ecosystems*. Academic Press, New York.

Waylen PR, Caviedes CN, Quesada ME (1996a) Interannual variability of monthly precipitation in Costa Rica. *Journal of Climate*, **9**, 2606–2612.

Waylen PR, Quesada ME, Caviedes CN (1996b) Temporal and spatial variability of annual precipitation in Costa Rica and the Southern Oscillation. *International Journal of Climatology*, **16**, 173–193.

Webb EK, Perman GI, Luening R (1980) Correction of flux measurements for density effects due to heat and water vapor transfer. *Quarterly Journal of the Royal Meteorological Society*, **106**, 85–100.

Williams M, Mahli Y, Nobre AD *et al.* (1998) Seasonal variation in net carbon exchange and evaporation in a Brazilian rain forest: a modelling analysis. *Plant, Cell and Environment*, **21**, 953–968.

Wilson JD, Finnigan JJ, Raupach MR (1998) A first order closure for disturbed plant canopy flows and its application to winds in a canopy on a ridge. *Quarterly Journal of Royal Meteorological Society*, **124**, 705–732.