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EFFECTS OF CLIMATE FACTORS ON DAYTIME CARBON EXCHANGE FROM AN OLD GROWTH FOREST IN COSTA RICA

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ABSTRACT. Eddy covariance measurements of CO_2, H_2O, and heat were conducted in tropical lowland wet forest at the La Selva Biological Station in Costa Rica. The system was based on a closed-path infrared gas analyzer with the sample inlets and sonic anemometer mounted on a 42-m tower. Prevailing winds were easterly from the Caribbean with little anthropogenic influence. The tower footprint was primary upland forest. Concurrent measurements included standard micrometeorological sensors for energy balance and six levels of continuous canopy profile sampling for CO_2, H_2O, and air temperatures. Canopy roughness at the site is very high and may contribute to mixing at low wind speeds. Data are presented for 39 days of daytime CO_2 fluxes. Carbon dioxide fluxes at high irradiances ranged from -10 to -20 μmol m^2 s^{-1}. The response of CO_2 fluxes to solar radiation was curvilinear and did not saturate under ambient irradiance regimes. No effects of vapor pressure deficit on ecosystem carbon exchange were detected during the study period. Temperature, however, appeared to affect daytime carbon exchange slightly. The results suggest that solar radiation input is the primary limiting climatic factor for carbon uptake.

INTRODUCTION

Although they cover a relatively small proportion of the earth's terrestrial surface, tropical forest canopies are estimated to account for 32–43% (Field et al. 1998, Melillo et al. 1993) of potential terrestrial net primary production (NPP). Furthermore, the amount of carbon sequestered in tropical forests is large, perhaps as much as 53% of carbon in terrestrial biomass (Solomon et al. 1993). Despite the prominence of tropical forests in the global carbon cycle, relatively few studies of factors controlling carbon exchange in these forests have been made until recently. Field studies of tree growth have revealed substantial annual variation in diameter increment, apparently the result of climate variation (Clark & Clark 1994). Modeling analyses suggest that cloud cover, soil moisture, and temperature may play key roles in the carbon exchange of tropical forest (McKane et al. 1995, Kindermann et al. 1996, Tian et al. 1998, Williams et al. 1998).

The information available to address this issue recently has been increased by eddy covariance measurements of forest level carbon exchange (Fan et al. 1990, Grace et al. 1995a, Malhi et al. 1998). The eddy covariance technique provides a passive measure integrating carbon exchange over a large, ever-moving footprint (Baldocchi et al. 1988). The technique holds great promise for evaluating the climatic controls on tropical forest carbon exchange. It has been applied, however, at only three tropical forests, all in Amazonia, and for relatively short periods. Because of the high diversity of forest types in the tropics (Tuomisto et al. 1995, Prince & Steininger 1999), additional sites need sampling to understand the carbon exchange of these ecosystems.

Since early 1998, we have conducted eddy covariance measurements in old-growth forest in Costa Rica, where we are monitoring CO_2, H_2O, and heat exchange. The objective of this study was to examine the effects of climate factors on daytime carbon exchange of old-growth tropical forest. This study is the first of its kind for Central American forests.

METHODS

Study Site

This study was conducted at the La Selva Biological Station of the Organization for Tropical Studies (OTS) in the Atlantic lowlands of Costa

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Rica (83°59′W, 10°26′N). Elevation ranges 30–130 m above sea level (asl), and mean annual precipitation is 4100 ± 700 mm (mean ±SD), with a short January–April dry period (Sanford et al. 1994). The forest has been classified as a tropical wet forest (Hartshorn 1983). Mean forest height is 20–25 m with occasional emergents exceeding 55 m (Clark et al. 1996). The forest is dominated by one species, *Pentaclethra macroloba* (Willd.) Kuntz (Mimosaceae), which accounts for ca. 40% of the basal area. Leaf area index (LAI) at La Selva is uncertain, because no direct measurements of LAI have been taken in old-growth forest. Randomly sampled photographic estimates of LAI using Winphot (ter Steege 1996) ranged from 3.8 for dry season to 4.9 for wet season in 1998. These values seem somewhat lower than expected, but the forest at La Selva is dynamic (Denslow & Hartshorn 1994) with tree and branch falls extremely common. Mean daily solar radiation (1993–1998) input is 14.9 MJ m^{-2} (with an extreme range of 0.7 to 31.3 MJ m^{-2}). Daily temperatures averaged 25.0°C for 1993–1998 (OTS unpubl. data). Soils range from relatively fertile inceptisols to low pH, low phosphorus ultisols (Sollins et al. 1994). The site has been described in detail by McDade et al. (1994).

The eddy flux tower is located within old-growth forest more than 1.5 km downwind of second growth or human disturbance. The tower was sited such that, with the prevailing easterly winds, air sampled comes primarily from upland forest rather than the less diverse swamp forest that covers only about 9% of La Selva old-growth forest (Clark et al. 1999).

Eddy Covariance

In eddy covariance measurements, the mean vertical turbulent flux of an atmospheric scalar such as CO_2 is determined by measuring the covariance of the vertical wind velocity and a measure of the scalar concentration. The measurements are made at a single height within the vegetative boundary-layer (VBL). The eddy covariance technique primarily estimates the flux of a scalar when turbulent exchange (either convectional or mechanical) is occurring in the VBL. The eddy flux is calculated as follows:

$$F = \overline{w'\rho'_c} \qquad (1)$$

F = the measured flux (g C m^{-2} s^{-1}), ρ'_c = the gas density in dry air (g C m^{-3}), and w' = the vertical component of wind velocity (m s^{-1}). The overbar represents the covariance time-averaged over a specified period (30 minutes), and the primes indicate the deviation of instantaneous (10 Hz signal) from a 300 s digital filter (a mathematical procedure to remove linear trends). In practice, wind velocities are measured by sonic anemometer, and concentration is determined with a fast-response sensor. The data are post-processed to include spectral corrections. Because the flux is based on molar fractions, density corrections are not necessary (Webb et al. 1980). The assumptions of eddy covariance include zero net vertical air flow and a turbulent coupling between the canopy and the atmosphere developed by horizontal air movement.

Operating an eddy covariance system in rain forest presents unique challenges. High humidity and frequent lightning are continuous concerns. Over the course of a day, the mean vertical wind is typically nonzero. Still air leads to frequent large storage of CO_2 within the canopy. The forest canopy roughness length (a measure of the effect of the canopy on drag) is very high, approximately 2 m. Power spectra are plots of the variance in velocity or other scalars such as CO_2 against frequency to characterize the size and speed of eddies. These plots for wind statistics and atmospheric components during conditions of laminar flow show a dissipation of energy in the inertial sub-range indicating a transfer of mass and energy at relatively low values (ca. $<$ 0.14 m s^{-1}) of frictional velocity, u^* (a term that quantifies the turbulent velocity fluctuations). Calculation of total daily net ecosystem exchange (NEE) requires adding the following terms to the basic Equation 1: a term for the nonzero vertical air movement, a term for canopy storage, and a term for horizontal advection not accounted for by the digital filter. Detailed descriptions of eddy flux measurements and theory can be found elsewhere (Baldocchi et al. 1988, Hollinger et al. 1994, Goulden et al. 1996, Grelle & Lindroth 1996).

Our flux system consists of a 3-dimensional sonic anemometer (K-probe, Applied Technology, Inc., Boulder, Colorado) mounted on a 42-m aluminum walk-up tower (Upright Scaffolding, Selma, California). A high flow gas stream is sampled adjacent to the anemometer and routed through Teflon tubing to an adjacent air-conditioned shed, where CO_2 and water vapor concentrations are determined under constant flow, temperature, and pressure with a Li-6262 infrared gas analyzer (IRGA, LI-COR Inc., Lincoln, Nebraska). The data stream from the sonic anemometer and analyzer channels is fed at 10 Hz into the serial port of a notebook computer. To evaluate canopy storage of CO_2, a second pump and IRGA continuously sample CO_2 and H_2O vapor concentrations at six heights up the forest profile using an automated solenoid and manifold system. Canopy profile data are logged and compiled with a Campbell 21X micrologger (Campbell Scientific, Logan, Utah) and laptop computer. Periodic CO_2 calibrations follow the AmeriFlux science plan (Wofsy & Hollinger 1997), using span gases traceable to NIST standards and scrubbed N_2. Similarly, H_2O calibration is based on water vapor generated at a known dewpoint using a LI-COR Li-610 dewpoint generator. Raw data, calculated flux, and non-coordinate rotated files are archived on recordable CD-ROM. Incident solar radiation is measured with a LI-COR LI200X pyranometer. Atmospheric moisture and temperature are measured by thin layer capacitance sensor and thermister (Vaisala Inc., Woburn, Massachusetts) in a Gill radiation shield.

The study resulted in daytime data with strong turbulent coupling between the forest and canopy (the frictional velocity is > 0.2 m s^{-1}). Additional correction terms, such as for canopy storage, are not required in the flux equation (Equation 1). We use atmospheric conventions for terminology that treats release to atmosphere as positive flux; and uptake by the canopy is negative. Data are presented as half-hour averages for the period 9 January–17 February 1999, which corresponds to early dry season. Volumetric soil moisture ranged from 0.39 to 0.77 V^3 V^{-3}, and bulk precipitation totaled 203 and 122 mm for January and February, respectively. From a long-term record, 1963–to date, mean (SE) bulk precipitation readings for those months were 263.2 (22.9) and 191 (19.4) mm.

Data Analysis

To analyze effects of the vapor pressure deficit (VPD) and temperature, we fit a photosynthesis model (Thornley 1976) to the response of net ecosystem exchange and solar radiation using nonlinear regression:

$$\mathrm{NEE} = \frac{\phi\alpha\mathrm{NEEmax}}{\phi\alpha + \mathrm{NEEmax}} - \mathrm{R} \qquad (2)$$

NEE = the net ecosystem CO_2 exchange, NEEmax = maximum ecosystem CO_2 uptake rate, $\varnothing$ = incident solar radiation, α = quantum efficiency, and R = ecosystem respiration rate. We estimated the parameters NEEmax, R, and α by the regression analysis. The residuals from that modeled relationship were plotted against VPD and temperature and examined for significance. This form of model, which assumes a constant ecosystem respiration rate based on the intercept of NEE at irradiance of 0, thus fails to account for temperature effects on soil and aboveground biomass respiration. Some of the scatter around the NEE versus irradiance relationship may be the result of temperature responses of leaf, bole, and soil respiration. To account for these respiration components, we replaced the constant respiration R in Equation 2 with an Ahrrenius function for temperature:

$$\mathrm{R} = \beta e^{(-E_a/RT)} \qquad (3)$$

β = a constant, E_a = the activation energy in Joules per mol, R = the gas constant, and T = air temperature in °K (Hollinger et al. 1994). The nonlinear regression procedure, however, was unable to reach a solution for the combined model, suggesting a weak respiratory temperature effect on the data. Consequently, data are presented using the fixed model (Equation 2) only. At the Reserva do Cuieiras in Amazonas, where diurnal variation in soil temperature was low, Malhi et al. (1998) were unable to detect a daily or seasonal temperature effect on respiration. Estimates of a fixed R obtained by Hollinger et al. (1994) were similar to night-time respiration rates.

RESULTS

Net ecosystem uptake measured by eddy covariance increased with solar radiation (FIGURE 1). Maximum CO_2 uptake reached approximately -20 μmol m^{-2} s^{-1} at 500 W m^{-2}. The forest uptake shows an asymptotic response that did not saturate within the range of measured solar radiation.

To test the effect of VPD on ecosystem exchange, we separated the data set into classes of VPD in 0.5 kPa intervals (0.0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, and 2.0–2.5 kPa). Within these classes of VPD, we fit the simple radiation-based photosynthesis model (Equation 2) to the flux and solar radiation data. The models derived from this procedure were similar and suggest that VPD was not influencing NEE strongly at this time of season (FIGURE 2A). In one instance where VPD = 2.0–2.5 kPa, the model deviated from the other four models at low solar radiation as a result of lack of data in the low solar radiation-high VPD range. To further examine the effects of VPD, we fit the radiation-photosynthesis model to all the data regardless of VPD class and plotted the deviation of the flux data from the irradiance model versus VPD (FIGURE 2B). The residuals revealed no VPD effect on NEE.

The relationship between NEE and air temperature showed increased canopy uptake with increased temperature (FIGURE 3A). Because the air temperature and solar radiation were positively correlated ($r^2 = 0.30$), this increase in uptake is partially the result of increased solar radiation. As with the VPD relationship, we fit the

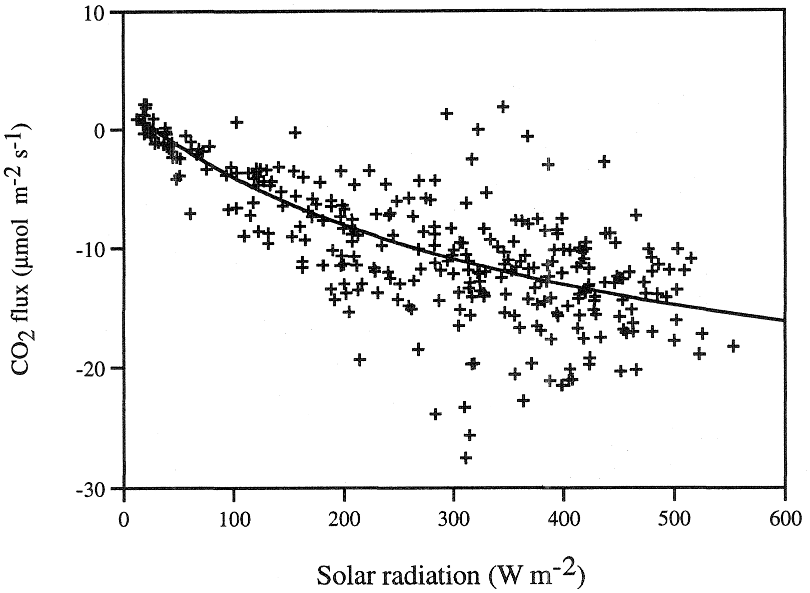

FIGURE 1. Relationship between net ecosystem exchange measured by eddy covariance and solar radiation. The solid line is nonlinear fit of simple photosynthesis model (Equation 2, $r^2 = 0.36$). NEE values include points with frictional velocity (u^*) > 0.2 m s^{-1}.

irradiance-photosynthesis model to the flux data and tested the residuals against air temperature (FIGURE 3B). The best fit of the residuals with temperature suggested a slight parabolic response ($r^2 = 0.17$) with optimal temperature in the range of 26–27°C.

DISCUSSION

Maximum net ecosystem exchange from La Selva was similar to the range reported for the Amazonian sites, -10 to -20 µmol m^{-2} s^{-1} (Fan et al. 1990, Grace et al. 1995a, Malhi et al. 1998). The shape of the NEE response to irradiance at La Selva was curvilinear as has been reported for most ecosystems (Ruimy et al. 1995). Both the response curve and compensation point were similar to those of the Amazonian sites, 70, 120, 130, 80 Wm^{-2} (Fan et al. 1990, Grace et al. 1995a, Malhi et al. 1998, respectively). Responses from the sites differ, however, in the degree of saturation. At the Cuieiras site, where a full year of data exists, canopy uptake was nearly saturated at irradiances near 800 W m^{-2}. Irradiances in our data set did not exceed 600 W m^{-2}, and the response did not saturate up to that level. Daily solar radiation averages about 15 MJ m^{-2} (an average of 298 W m^{-2} during daylight hours) at La Selva; but it can total less than 1.0 MJ m^{-2} (15 W m^{-2} daylight average) during the wet season. In contrast, at the Cuieiras site, the lowest daily solar radiation was approximately 3 MJ m^{-2} (60 W m^{-2} daylight average, Malhi et al. 1998). The Rondônia site (Grace et al. 1995b) also did not saturate with irradiances up to 800 W m^{-2}. Given the radiation regime at La Selva, frequent limitation of uptake by irradiance at that site is a certainty. Wright and van Schaik (1994), using leaf level ecophysiological measurements, argue that tropical trees are adapted to maximize light capture and that tropical moist forests are radiation limited.

Our residual analysis of the temperature response suggests that temperature weakly influences daytime NEE. We found optimal temperatures for NEE to be near 26°–27°C. Other studies did not report explicit temperature responses of NEE. The temperature range at our tropical study site was relatively small compared to temperate sites, where stronger temperature responses are observed (Hollinger et al. 1994). Discerning potential temperature responses within our observed range and variance remains a challenge.

Unlike irradiance and temperature, VPD did not appear to be a significant control on ecosystem exchange at La Selva during the study period. Studies of both xylem sap flow of the dominant trees at La Selva and the Bowen ratio support this conclusion (J.J. O'Brien et al. unpubl. data; H.W. Loescher et al. unpubl. data). Leaf-level measurements of several canopy species (including *Pentaclethra macroloba*) and sub-

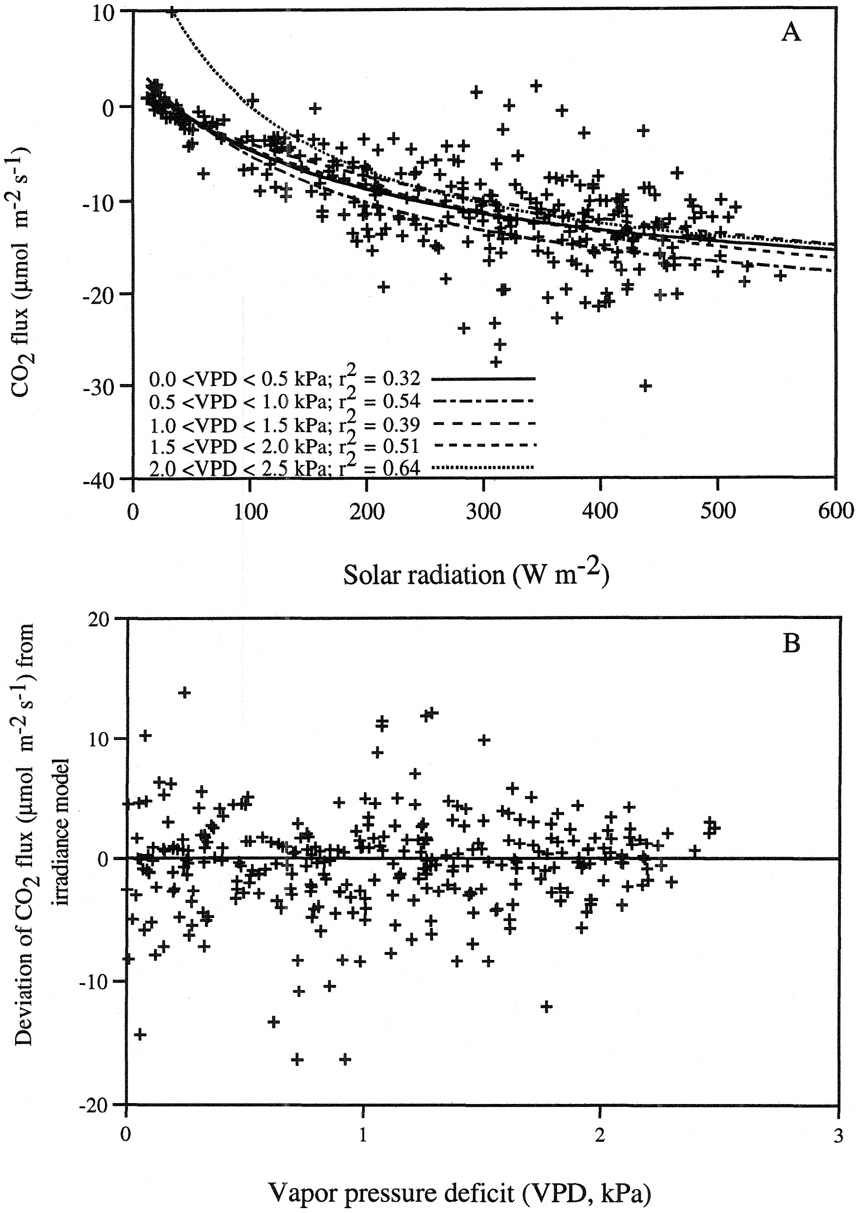

FIGURE 2. (A) Relationship between net ecosystem exchange measured by eddy covariance and solar radiation at different vapor pressure deficits (VPD). Lines are nonlinear fits of simple photosynthesis model (Equation 2) for data in ranges of VPD. Values of r^2 are from logarithmic fits to data. Values only include points with frictional velocity (u^*) > 0.2 m s^{-1}. (B) Relationship between deviation of measured eddy flux from solar radiation model (FIGURE 1) and vapor pressure deficit. Solid line indicates zero line.

canopy species also support this finding; Oberbauer (1985) found stomatal closure only at relatively high VPD values. In contrast, at both the Cuieiras and the Rondônia sites, VPD was a limit on canopy carbon uptake. The measurements reported here span a period of normal soil moisture and rainfall. The possibility, however, that VPD effects on net fluxes may increase as soil water becomes more limiting during extreme events, such as El Niño Southern Oscillation (ENSO) can not be discounted.

Williams et al. (1998) parameterized a gross primary productivity (GPP) model (Williams et al. 1997) for the Cuieiras flux site. Sensitivity

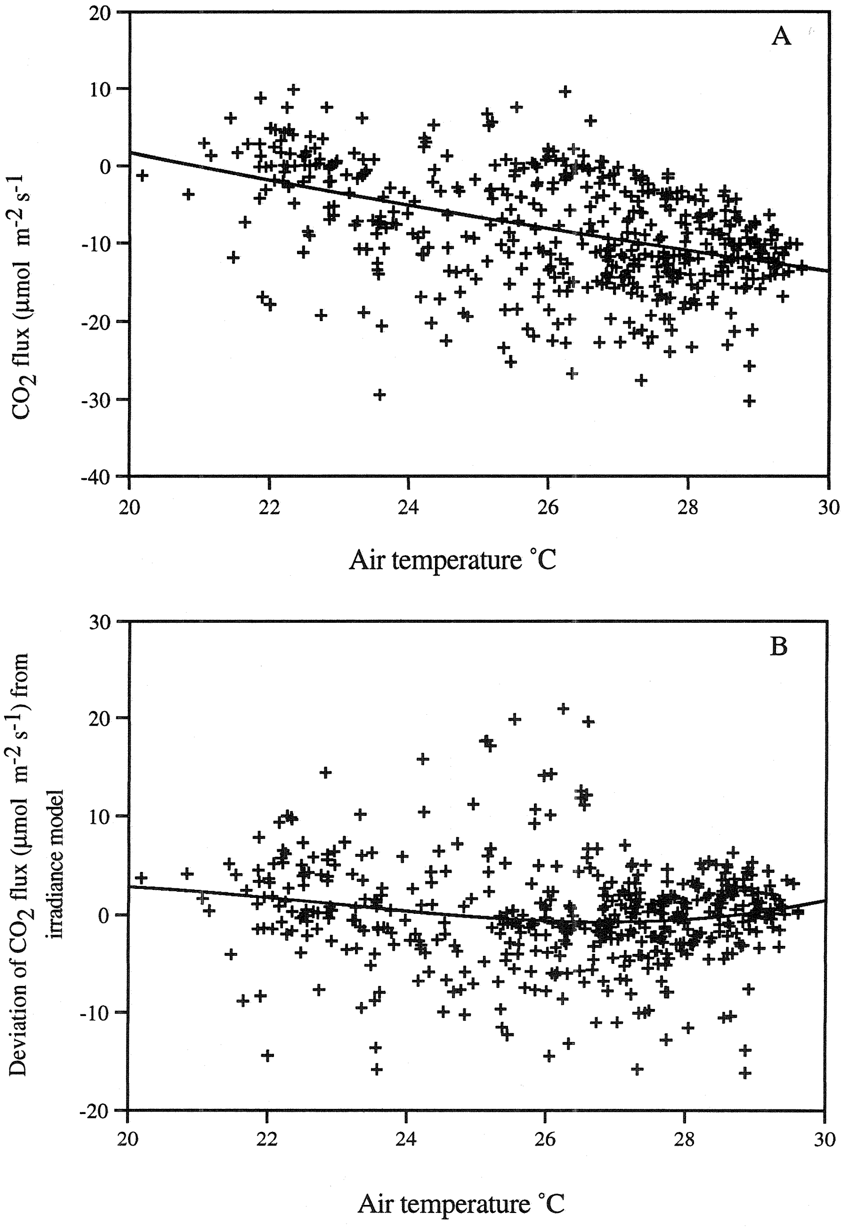

FIGURE 3. (A) Relationship between net ecosystem exchange measured by eddy covariance and air temperature. The solid line represents logarithmic fit to the data ($r^2 = 0.20$). (B) Relationship between deviation of measured eddy flux from solar radiation model (FIGURE 1) and air temperature. Solid line represents 2nd order polynomial fit to the data.

analysis identified irradiance, soil moisture, and soil/root hydraulic resistance as the primary climatic controls on GPP. The model closely estimated GPP during the wet season but overestimated uptake during the dry season, apparently because of increases in soil and/or root resistances. Malhi et al. (1998) suggest that the reported VPD effect at the Cuieiras site may be a result of soil moisture and that the VPD effect arises from a correlation between VPD and soil moisture. The model was relatively insensitive to air temperature.

Our results, which include only the daytime net ecosystem exchange, thus only represent the uptake potential of the ecosystem. The overall carbon balance of the forests also depends on the night-time respiration from soil and aboveground biomass. This data set thus does not provide evidence for the overall controls of the net carbon balance of the forest. Overall controls on the carbon balance of tropical forests have been investigated in several modeling analyses. Kindermann et al. (1996) suggest that, for tropical evergreen forests, increasing temperatures decrease net primary production via increased respiration. Grace et al. (1995a, 1995b) parameterized a process-based model of net ecosystem carbon balance, using the Rondônia flux data. They suggested that irradiance and temperature strongly affected the net carbon balance of the forest. Tian et al. (1998) concluded that Amazonian forests may be sources for carbon during extreme events such as ENSO because of decreases in soil moisture. Fan et al. (1990), Raich et al. (1991), and Melillo et al. (1993) suggested that the carbon balance of tropical evergreen forest is strongly affected by changes in irradiance. Presumably, frequency of cloud cover (and indirectly rainfall) control net irradiance. Our study site receives almost twice as much precipitation as do the Amazonian sites, suggesting that at La Selva the effects of irradiance overshadow those of temperature and VPD.

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