Energy dynamics and modeled evapotranspiration from a wet tropical forest in Costa Rica

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Abstract

The effects of albedo, net radiation ($R_n$), vapor pressure deficit (VPD), and surface conductances on energy fluxes and evapotranspiration (ET) were determined for a wet tropical forest in NE Costa Rica from 1997 to 2000. Sensible heat fluxes ($H$) were estimated by the combination of eddy-covariance and the change in below-canopy heat profiles. Above-canopy latent heat fluxes ($\lambda E$) were estimated by the residuals from $R_n$ and $H$, and below canopy $\lambda E$ fluxes. Surface reflectance (albedo) was \(\sim 12\%\) of incident solar radiation and did not differ seasonally. $R_n$ was significantly different among years and explained \(\sim 79\%\) of the variation in $H$ and $\lambda E$ fluxes. The effects of VPD did not explain any additional variation in heat fluxes. $\lambda E$ fluxes were always greater than $H$ fluxes when $R_n > 40$ W m\(^{-2}\). Understory heat fluxes were small and contributed little towards daily energy exchange, but may be significant when $R_n$ is small. A dimensionless coefficient ($\Omega$) was used to determine the relative importance of aerodynamic conductance ($g_a$) and bulk canopy conductance ($g_b$) on $\lambda E$ flux. During the day, $\Omega$ was \(> 0.6\) and peaked at 0.85 suggesting that the forest was decoupled from physiological controls, $\lambda E$ fluxes are more dependent on $R_n$ than water availability, and $g_a$ exerts more control on $\lambda E$ fluxes than $g_b$. Because of these results, both the Priestly–Taylor and the Penman–Monteith models performed well using only $R_n$. Because the canopy is wet \(\sim 32\%\) of the time, there was better precision in estimating $\lambda E$ fluxes using the Priestly–Taylor model (with an empirically estimated $\alpha = 1.24$), when the canopy was wet. Annual ET were 1892, 2292 and 2230 mm for 1998, 1999 and 2000, respectively. Annual ET ranged from 54 to 66\% of bulk precipitation. Using a Rutter-type model, interception losses were 17–18\% of bulk precipitation. The overall amount of energy needed for annual ET accounted for \(\sim 88\) to 97\% of total $R_n$.

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1. Introduction

The energy balance of tropical forests is complex due to feedback mechanisms among radiation, cloud formation and precipitation (Wielicki et al., 2002; Hartmann et al., 2001; Sohn and Smith, 1992). This complexity extends to the potential role of the tropical energy balance in affecting tropical and global climates and general and anomalous circulations (Kelly and Randall, 2001; Timmermann et al., 1999; Chen and van den Dool, 1999; Fasullo and Webster, 1999; Larson et al., 1999). Much of our understanding of these dynamics has relied on model results, which have shown large spatial and temporal variability in both sensible and latent energy budgets (Kelly and Randall, 2001; Raman et al., 1998; Hulme and Viner, 1998; Shuttleworth, 1988). In situ studies have either scaled leaf level measurements to whole canopies (Bigelow, 2001; Avissar, 1993; Roberts et al., 1993), or have estimated the energy balance components using eddy covariance over short periods (cf. 8 d, Shuttleworth et al., 1984; 1 yr, Malhi et al., 2002; 1 yr, da Rocha et al., 2004). Quantifying the variation of energy balance parameters and their biophysical controls over longer periods (e.g. years) should allow for better predictions of runoff and improved models of regional and global climate.

Both physical and physiological factors influence forest energy fluxes, including incident radiation, surface albedo, rain, interception, canopy capacity, and aerodynamic ($g_a$) and bulk surface ($g_b$) conductances. Incident radiation in the tropics varies less seasonally than that at higher latitudes, and values at the surface are more related to cloudiness than changes in solar zenith angle. General circulation models tend to underestimate net radiation in the tropics because of uncertainties in estimating surface albedo and cloud cover (Cramer et al., 1999; Ruimy et al., 1995). Forest surface albedos range from 0.1 to 0.2 (Monteith and Unsworth, 1990), with annual and seasonal differences affecting the available energy. Large variability in annual rainfall totals have been observed in the tropics and are thought to be influenced by El Niño-Southern Oscillation (ENSO) and other anomalous circulations (e.g. McKinley et al., 2004; Malhi and Wright, 2004; Bousquet et al., 2000). This in turn affects the amounts of water available for evapotranspiration. A general observation is that 50–60% of annual rainfall is re-circulated to the atmosphere through transpiration and evaporation of intercepted water, with the other 50% as runoff from neotropical humid forests that receive 2400–3000 mm yr$^{-1}$ (da Rocha et al., 2004; Malhi et al., 2002; Shuttleworth, 1989). The results from these studies imply that local hydrology is strongly affected by how energy is partitioned at the surface.

Canopy conductances for tropical forests are typically determined by estimating bulk surface conductance ($g_b$) by scaling leaf-level or sap-flow measurements to the canopy (Whitehead, 1998; Dolman et al., 1991) or by deducing $g_b$ in relation to meteorological parameters and measured fluxes (Wright and Gash, 1996; Stewart, 1988). Aerodynamic conductance is generally calculated as a function of horizontal windspeed, zero-plane displacement, and roughness length (Denmead and Bradley, 1985). Unlike agronomic communities in which evapotranspiration is dominated by transpiration and controlled by the plant’s canopy conductance, evapotranspiration from tropical forests is generally thought to be strongly dependent on aerodynamic conductance, because of the high rainfall and the significant proportion of the time when the canopy is wet, reducing the importance of $g_b$ in evapotranspiration (Shuttleworth, 1989).

Our research objective was to define the surface controls on the energy fluxes from a wet tropical forest in Costa Rica, which included the temporal partitioning of $R_n$, below-canopy energy fluxes, conductances and overall surface energy fluxes, and to use these controls to model annual evapotranspiration.

2. Methods

2.1. 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 northeastern Costa Rica in the Caribbean lowlands at the base of the central volcanic chain and was classified as tropical wet forest in the Holdridge
life zone system by Hartshorn and Peralta (1988). This forest has an average 400 trees ha\textsuperscript{−1} > 100 mm diameter ha\textsuperscript{−1} from ~100 species (Lieberman et al., 1985), and is dominated by the mimosoid legume canopy species, *Pentaclethra macroloba* (34% of the basal area, Clark and Clark, 2000). Mean tree height is 20–25 m, with emergents exceeding 60 m. Canopy gaps occupy ~0.01–0.04 ha ha\textsuperscript{−1} (Denslow and Hartshorn, 1994) making the overall canopy very aerodynamically rough. Incident mean (1993–1998) daily solar radiation was 14.9 MJ m\textsuperscript{−2} d\textsuperscript{−1}, with a range from 0.4 to 31.3 MJ m\textsuperscript{−2} d\textsuperscript{−1}. Mean annual temperatures were 24.6 °C (1982–1998, Organization for Tropical Studies, OTS, unpublished weather records). Mean annual precipitation was 4000 mm (from 1963 to 2000), 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). Soils range from relatively fertile Inceptisols in riverine areas to low pH, low phosphorus Ultisols in upland areas (Sollins et al., 1994).

Moisture-laden northeast 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 (ITCZ). During the drier season, the sub-tropical Hadley cell dominates general circulations, while the tropical cell dominates wet season circulations (Sanford et al., 1994). There are no data showing the exact passing of the ITCZ in Costa Rica. Hence, seasons are defined here as either wet season beginning on May 1 (DOY 121), or dry season, beginning December 20 (DOY 354). These dates are ~10 d after the average date that the ITCZ passes through Barro Colorado Island, Panama (Steve Paton, Smithsonian Tropical Research Institute, personal communication). 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 site information for La Selva, and Waylen et al. (1996a,b) 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 06:00 and 18:00 h, delineating daytime and nighttime periods.

A 42 m tower (Upright, Inc., Selma, CA) was used to access the canopy environment and to support meteorological instrumentation. The site was a relatively flat ridgetop in an area of generally rolling topography, 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) estimated 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\textsuperscript{−1}), indicating the source area is within the boundaries of this forest for both day- and night-time measured fluxes. By placing the tower away from treefall gaps and on a flat area, effects due to forest edges, below-canopy advection either to or from the site, and any major directional differences due to forest composition and structure were minimized.

2.2. Experimental data

All measurements were collected from September 1997 to December 2000. Instrumentation for measuring air temperature, relative humidity, bulk precipitation, and net radiation were mounted at the top of the tower (Upright, Inc., Selma, CA). Prior to March 1, 1999, air temperature (\( T_a \)) was measured with a CS500 probe (Campbell Scientific, Inc., Logan, UT) installed within a radiation shield, and linearly back-corrected to fit the response of the aspirated temperature sensor (\( R^2 = 0.98 \)). After March 1, 1999, \( T_a \) was measured with platinum resistance thermometers (100 Ω PRT, Omega Engineering, Stamford, CT) mounted in an aspirated shield. Rainfall was measured with a tipping bucket rain gauge (model TE525, metric, Texas Electronics, Dallas, TX).
From August 1, 1997 to March 1, 1999 \( R_n \) was measured with a Fritschen-type sensor (model Q*7.1, Radiation Energy Balance Systems, Seattle, WA). Net radiation, \( R_n \), was measured from March 1, 1999 to December 2000 with a closed-cell thermopile-style sensor (NR-lite, Kipp and Zonen, Delft, the Netherlands). All data collected with the Q*7.1 were linearly back-corrected to fit the response of the NR-lite (\( R^2 = 0.97 \)) and corrected for advected sensible heat across the sensor faces. Another radiometer was also used to measure upward and downward welling short-and longwave radiation (model CNR1, Kipp and Zonen, Delft, the Netherlands) to estimate albedo during February–April, July, and September 2000.

Specific humidity was sampled from six inlets at 0.50, 7.30, 11.95, 16.55, 21.20, and 27.60 m on the tower. Solenoids switched the flow (\( \sim 3.0 \) lpm) from each inlet through an infra-red gas analyzer (model Li-6262, Li-Cor, Lincoln, NE) for 5 min during each 30 min averaging period; data were only used for the final 4 min in the 5 min interval. A second Li-6262 sampled specific humidity continuously at 42 m and 30 min averages were used in the vertical integrations of \( Z_v \) (Eqs. (2a) and (2b)). The profile temperature, \( \theta_p \), was measured with PRTs housed in radiation shields and co-located with each inlet and when sampling occurred, the airflow acted to aspirate the PRTs. The temperature probe mounted at the top of the tower was used for \( \theta_p \) at 42 m.

Soil heat flux plates (model HFT-3, Radiation Energy Balance Systems) were installed at a depth of 5 cm, in each of three \( 1 \times 1 \) m plots > 20 m distance apart near the base of the tower. Atmospheric pressure was measured at \( \sim 3 \) m (PB105, Vaisala, Helsinki, Finland). All meteorological data were collected at 5 s intervals and compiled as 30 min averages with a datalogger (CR10X, Campbell Scientific, Inc., Logan, UT). Instruments were cleaned, leveled as necessary, and recalibrated according to manufacturers’ instructions.

The eddy covariance system was comprised of a sonic anemometer (K-probe, Applied Technologies, Inc., Boulder, CO) and a laptop computer. The sonic anemometer measured the wind velocities in three dimensions at 10 Hz, where \( w \) is vertical windspeed, and \( u \) and \( v \) are the two horizontal windspeed components, as well as the sonic potential temperature, \( \theta_s \). Covariance fluxes were calculated in real time at 10 Hz using a software program (McMillen, 1988), which also collected raw eddy covariance data files. To determine the turbulent fluctuations, instantaneous measurements of \( \theta \) and \( w \) were subtracted from a 600 s recursive mean. Contributions by low frequency (i.e. longer, 30 min averaging operators) only caused additional variability in 30 min averages of sensible heat (\( H \)) flux (Loescher et al., 2003). However, these data were observed only during early morning hours and were filtered out because of non-stationarity (cf. Foken and Wichura, 1996). Data were also removed when rain occurred, the 30 min data collection periods were incomplete, or when signals from either the sonic anemometer were out-of-range (Hollinger et al., 1995; Anthoni et al., 1999). Protocols for accuracy, precision, and quality control and assurance were used as defined by the AmeriFlux Science Plan (http://cdiac.esd.ornl.gov/programs/ameriflux/scif.htm).

Leaf area estimates were made monthly by a plant canopy analyzer (Li-2000, Li-Cor, Inc., Lincoln, NE) and constrained by litterfall estimates, hemispherical photography and destructive sampling after harvest.

### 2.3. Energy flux estimates

The energy equation uses a control volume approach where the top of the control volume is the tower top (42 m) and the bottom is the ground surface. Here, we account for energy fluxes in and out of the control volume and the change in energy stored in the control volume. The storage fluxes were estimated by the changes of heat through the forest profile in the air column and through the leaf area (Aubinet et al., 1995; Anthoni et al., 1999). Protocols for accuracy, precision, and quality control and assurance were used as defined by the AmeriFlux Science Plan.

Ecosystem-level energy balance was estimated by

\[
R_n - \lambda E - H - G = \int_{Z_0}^{\infty} \frac{\partial \theta_p}{\partial t} dz + S_{\text{net}} C_{\text{pm}} L_{\text{area}} \int_{Z_0}^{\infty} \frac{\partial \theta_p}{\partial t} dz + \lambda E_{\text{BC}}
\]

(1)

assuming horizontal homogeneity in source area, \( R_n \) is net radiation, \( \lambda E \) is the latent heat flux, \( H \) is the sensible heat flux, and \( G \) is the soil heat flux (all units are \( \text{W m}^{-2} \)). The right-hand terms are the non-turbulent heat fluxes (\( \text{W m}^{-2} \), i.e. change in below-canopy heat profiles), where the first term is the change in sensible heat in the air column (\( H_{\text{BC}} \).
the second term is the change in sensible heat in the leaf biomass \((H_{\text{leaf}})\), the third term is the change in latent heat stored in the air column \((\lambda E_{\text{BC}})\), such that \(C_p\) is specific heat capacity of air \((\text{J kg}^{-1} \text{K}^{-1})\), \(\rho_a\) is the density of air \((\text{kg m}^{-3})\), \(\theta_p\) is the potential temperature from profile measurements \(\text{(C)}\), \(S_{\text{at}}\) is the specific weight of leaf water \((\text{kg m}^{-3} \text{ leaf area})\), \(C_{pw}\) is the heat capacity of water \((\text{J g}^{-1} \text{H}_2\text{O} \text{K}^{-1})\), and \(L_{\text{area}}\) is the one-sided leaf area based on LAI from polyculture plantations at La Selva \((\text{i.e. 4.5 m}^2 \text{ m}^{-2}, \text{S. Bigelow and J. Ewel, pers. comm.})\). Changes of sensible heat in the leaf biomass were included in Eq. (1) because leaves have small thermal inertia but significant amounts of water. It was assumed that the temperature profiles were similar throughout the flux source area.

Net ecosystem exchange of sensible heat was estimated by the combination of turbulent and storage fluxes \((\text{Eq. (2a)})\), and the turbulent latent energy exchange was calculated as a residual flux \((\text{Eq. (2b)})\), such that

\[
H_{\text{NEE}} = C_p \rho_a \frac{w' \theta_p'}{\theta_p} + C_p \rho \int_{z_0}^{z} \frac{\partial \theta_p}{\partial t} \, dz
+ S_{\text{at}} C_{pw} L_{\text{area}} \int_{z_0}^{z} \frac{\partial \theta_p}{\partial t} \, dz
\]

\[
\lambda E = R_a - G - H_{\text{NEE}} - f \rho_w \lambda \int_{z_0}^{z} \frac{\partial q}{\partial t} \, dz
\]

where \(w'\) and \(\theta_p'\) are the deviations of instantaneous values from a running mean of vertical windspeed \((\text{m s}^{-1})\) and \(\theta_p\) as a function of the speed of sound and changes in air density (excluding water vapor, i.e. potential temperature), \(w'/\theta_p'\) is the turbulent exchange of sensible heat flux as estimated by eddy covariance method, \(f\) is molar volume of air \((\text{mol m}^{-3})\), \(\rho_w\) is the molar weight of water \((18.015 \text{ g mol}^{-1})\), and \(q\) is the specific humidity \((\text{mol H}_2\text{O mol}^{-1} \text{ air})\). Hence, \(\lambda E\) is calculated by residual and, in practice, forces energy balance closure \((\text{e.g. Twine et al., 2000; van der Tol et al., 2003})\). Errors associated with this technique are discussed later.

Storage flux through stem biomass was not estimated here. Moore and Fisch (1986) modeled heat flux in stem biomass from an Amazonian forest. Using their relationships based on air temperature profiles, heat flux in stem biomass from La Selva was likely \(~ 7 \text{ W m}^{-2}\) \((30 \text{ min average, cf. Fig. 3})\). Moore and Fisch (1986) also report that their model error is \(\pm 7 \text{ W m}^{-2}\) and estimates should not exceed \(15 \text{ W m}^{-2}\) averaged over a 30 min period. Moreover, their model was developed in a more structurally complex forest that had twice the amount of the above-ground biomass with a greater proportion of radiation penetrating the canopy than the La Selva forest. Hence, the modeled estimate of \(7 \text{ W m}^{-2}\) (similarly, averaged over a 30 min period) is likely an overestimate and considered inconsequential in light of other uncertainties.

2.4. Modeled conductance and evapotranspiration

Evapotranspiration estimates were partitioned into whole forest transpiration and the evaporation of intercepted precipitation. \(\lambda E\) was modeled using the Penman–Monteith equation \((\text{Monteith and Unsworth, 1990})\)

\[
\lambda E_{\text{pm}} = \frac{\Delta R_n + \rho_s C_p [e_s(T_a) - e_a(T_a)] g_a}{\Delta + \gamma \left(1 + \frac{g_a}{g_b}\right) f}
\]

where \(\lambda E_{\text{pm}}\) is latent energy flux \((\text{W m}^{-2})\), \(\Delta\) is the is the rate of increase in saturated water vapor pressure with temperature \((\text{kPa K}^{-1})\), \(e_s\) is the saturated water vapor pressure at \(T_a\), \(e_a\) is the actual ambient water vapor pressure \((\text{kPa})\), \(g_a\) is the aerodynamic conductance \((\text{mol m}^{-2} \text{ s}^{-1})\), \(\lambda\) is the latent heat of vaporization \((\text{J kg}^{-1})\), \(\gamma\) is the psychrometric constant at \(25 \degree C\) \((0.0665 \text{ kPa K}^{-1})\), \(g_b\) is the bulk canopy conductance \((\text{mol m}^{-2} \text{ s}^{-1})\). To change units of energy to depth, \(\lambda E_{\text{pm}}\) was multiplied by a conversion factor that included molar volume \((f, \text{mol m}^{-3})\) and weight \((\text{kg mol}^{-1})\). The use of the notation \(\lambda E\) denotes energy flux \((\text{W m}^{-2})\), and ET, water depth \((\text{mm per unit time})\), hence evapotranspiration depth estimated by Eq. (3) is noted in the text as \(\text{ET}_{\text{pm}}\). Based on Monin–Obukov similarity theory, a negative exponential wind profile was assumed.
and aerodynamic conductance estimated by

$$g_a = \frac{k^2 u}{\left[ \ln \left( \frac{z_w}{z_m} \right) \right]^2 + \ln \left( \frac{z_h}{z_m} \right) \left[ \ln \left( \frac{z_w}{z_m} \right) + \Psi_m - \Psi_h \right]}$$

(4)

where $k$ is von Karman’s constant (0.40), $d$ is the zero-plane displacement (m), $z_m$ is the aerodynamic roughness length (m), and $\Psi_m$ and $\Psi_h$ are the diabatic correction factors (dimensionless) for momentum and sensible heat, respectively (Yasuda, 1988; Arya, 1988). Zero-plane displacement and aerodynamic roughness changed with stability and were empirically estimated for this study period (Loescher et al., 2003). Diabatic correction factors are a function of stability (i.e. Monin–Obukov length) and are explained in Denmead and Bradley (1985), Kaimal and Finnigan (1994), and Panofsky and Dutton (1984).

Bulk canopy conductance, $g_b$, was estimated by

$$g_b = \frac{g_a}{C_r \rho E} - 1 + \frac{\lambda E}{\rho_a D_{42}}$$

(5)

where $D_{42}$ is the specific humidity deficit at the measurement height (kg kg$^{-1}$).

Annual ET was modeled because gaps in long-term datasets were inevitable due to sensor calibrations, and sensor and power failures. Consequently, empirical relationships were developed for $g_a$ with horizontal windspeed, and for $g_b$, relationships with $R_n$ and the vapor pressure deficit (VPD) for use in Eq. (3). $g_b$ was normalized by the maximum value of $g_b$, i.e. to unity, and the upper limit to $R_n$ determined (cf. Jarvis, 1976; Livingston and Black, 1987). This limit function was used to estimate a theoretical maximum, $g_{max}$, by increasing $g_b$ as though $R_n$ was not limiting. Then $g_{max}$, in turn, was related to VPD, assuming that maximum conductance would take place with 0 VPD and high $R_n$. This technique has been tested and rigorously applied by Martin et al. (1997), but differs slightly from Wright and Gash (1996), which involved a multi-variate optimization and a hypothetical $g_{max}$ that was never reached in practice.

A dimensionless decoupling coefficient, $\Omega$, was used to determine the relative effects of $g_a$ and $g_b$ on evapotranspiration (Jarvis and McNaughton, 1986):

$$\Omega = \frac{\Delta}{\gamma + 1} + \frac{\Delta}{\gamma + \frac{\Delta}{g_b}}$$

(6)

A second method of modeling $\lambda E$, the Priestly–Taylor equation, was used to compare with the Penman–Monteith results. The Priestly–Taylor equation (Eq. (7)) simplifies the transfer process that is explicit in Eq. (3), and in doing so, is thought to be appropriate for large-scale, well-watered vegetative canopies, like those typically found in the wet tropics (Priestly and Taylor, 1972), and is defined as

$$\lambda E_{PT} = \alpha R_n \left[ \frac{\Delta}{\Delta + \gamma} \right]$$

(7)

where $\alpha$ is a coefficient estimated by fitting the model results to measures of $\lambda E$ from Eq. (2b). Monteith (1981) estimated an average $\alpha$ on a theoretical basis as 1.26, but values observed over rough canopies have varied greatly (Jones, 1992).

To determine annual ET, evaporation of intercepted water by the canopy was modeled using a Rutter-type model (Calder et al., 1986). Canopy water storage increased exponentially with precipitation to a maximum capacity ($C_{max}$). The rate by which the canopy filled with water was estimated by a unitless fill constant (a value of 0.28 was used from a broadleaf plantation forest at La Selva, Bigelow, 2001). An empirical estimate of 1.53 mm was used for $C_{max}$ (Loescher et al., 2002). The stemflow component of interception was ignored because it was assumed to be a small volumetric flux, i.e. <2% of rain (Schroth et al., 1999; Neal et al., 1993). The canopy conditions were modeled as either completely wet or completely dry for any 30 min period (Calder et al., 1986). If the amount of ‘free’ canopy water was less than the amount of modeled ET, then the remainder of canopy free water was modeled as transpiration ($g_h > 0$) not evaporation (i.e. setting $g_a / g_h$ in the denominator of Eq. (3) to zero, cf. Bigelow, 2001; Ubarana, 1996).

To characterize the stability within at the tower top, $Z_x$, a stability parameter ($\zeta$) was used, such that

$$\zeta = \frac{Z_x - d}{L}$$

$$L = \frac{u^3 \rho_a C_p T_a}{kgH}$$

(8)
$d$ is the zero plane displacement (m) which is the height at which the wind profile extrapolates to $\sim 0 \text{ m s}^{-1}$ within the canopy, $L$ is the Monin–Obukov length (m), ratio of convective to mechanical turbulent production, with $u_*$ defined as friction velocity ($\text{m s}^{-1}$) and determined by the covariance of $\overline{w'u'}$ as measured by the sonic anemometer, and $g$ the acceleration due to gravity ($\text{m s}^{-2}$).

3. Results

3.1. Energy fluxes

Here, the measured atmospheric stability, the energy balance components, and below canopy energy exchanges are analyzed. Subsequently, the modeled net ecosystem energy fluxes are examined.

The stability index, $\zeta$, differed only with incident radiation, and did not differ with year or season. On a diurnal basis, $\zeta$ was neutral ($\sim 0$ m) during the night, and decreased during the day time until 14:00 when the boundary layer became weakly unstable ($\zeta \sim -125$ m, Fig. 1). After 14:00 h, $\zeta$ sharply increased, and the boundary-layer became weakly stable ($\sim 100$ m) at 16:00 h, but then returned to neutral conditions by nightfall.

Total daily $R_n$ ranged from 1.47 to 27.54 $\text{MJ d}^{-1}$ during the measurement period, and differed among years (using a general linear model with an alpha = 0.05, $p < 0.0001$, Fig. 2) with mean daily totals for 1998–2000 of $13.31 \pm 0.028$, $17.48 \pm 0.050$, and $15.33 \pm 0.040$ $\text{MJ d}^{-1}$ (mean $\pm 1\text{SE}$), respectively. $R_n$ also varied significantly with season ($p < 0.0001$). Mid-day albedo did not change seasonally, and ranged from 0.118 to 0.135.

Diurnal temperature and water vapor profiles in the canopy (Fig. 3) followed trends similar to those of other forests (Shaw et al., 1988). Heating of the canopy air column during the day increased with height, i.e. there was a positive temperature gradient. However, negative temperature (counter) gradients were often observed between 21 and 27 m, where the leaf area was concentrated. Cooling during the night often produced neutral or slightly negative gradients, often with warmer temperatures at ground levels.

Fig. 1. Diurnal patterns of the stability parameter over an old growth wet tropical forest. Data are averages using all data from 1998 to 2000. Intervals A, B, C, and D indicate neutral, unstable, weakly unstable, and weakly stable boundary conditions, respectively. Error bars are $\pm 1\text{SE}$.
Negative or neutral water vapor gradients were observed all times, with negative gradients present during non-rain days between 11 and 21 m height.

Soil heat fluxes followed very similar diurnal patterns throughout the year, and ranged $G \leq 16$ W m$^{-2}$ at any point in time, with negative flux into the system during the daytime (Fig. 4A). On a day-to-day basis, the contribution of $G$ varied little, and though the soil thermal properties for these soils were not known, the change in annual $G$ was expected to be negligible. At night, $\lambda E_{BC}$ was $\sim 3$ to $5$ W m$^{-2}$, larger $\lambda E_{BC}$ occurred in the early morning hours, presumably from convective winds mixing the below-canopy airspace and evaporating free water. $\lambda E_{BC}$ flux continued to be positive throughout the afternoon, but was more variable, with mean daytime values ranging from $\sim 6$ to $7$ W m$^{-2}$. This flux remained positive throughout the day across all years. Mean nighttime storage of sensible heat ($H_{BC} + H_{leaf}$) ranged from ca. $-7$ to $-14$ W m$^{-2}$, and became negative in the early hours as the air space increased in temperature. The maximum average $H_{BC} + H_{leaf}$ was $\sim 18$ W m$^{-2}$, which occurred at $\sim 08:00$ h when the convective boundary layer was developing. $H_{BC} + H_{leaf}$ decreased and became negative at $\sim 14:00$ h, which coincided with a late afternoon weakly stable/unstable boundary layer (Fig. 1). The below-canopy environment continued to lose sensible heat until $\sim 19:00$ h, when neutral canopy conditions prevailed. The maximum daytime soil flux lagged peak fluxes of $\lambda E_{BC}$ and $H_{BC} + H_{leaf}$ by $\sim 7.5$ h. The total storage flux (Fig. 4B) became negative (out of the ecosystem) at $\sim 16:00$ corresponding to the decrease in $H_{BC} + H_{leaf}$. During nighttime neutral conditions, the flux was $\sim 8$ to $10$ W m$^{-2}$. The daytime minima were ca. $-5$ W m$^{-2}$ and the peak efflux was $30$ W m$^{-2}$, which occurred during weakly stable conditions (Fig. 4B).

The average 30-min $\lambda E$ was greater than $H_{NEE}$ for all daytime hours and across seasons and years (i.e. $H/\lambda E = \beta < 1.0$, Fig. 5). The largest relative contribution of $H_{NEE}$ occurred between 09:00 and 12:00 h (Fig. 5), coinciding closely with the observed diurnal pattern of $T_a$. A statistical (linear) model that included second-order effects of year, season, VPD and $R_n$ explained 79% of the total variation in $H_{NEE} + \lambda E$. 

![Cumulative net radiation for 1998–2000 over an old-growth forest in La Selva, Costa Rica. Daily means were derived using first-order regression. Each year was significantly different at the $a = 0.05$ level, $p < 0.001$, and $R^2 = 0.99$.](Fig. 2)
Because \( R_n \) and VPD are auto-correlated and VPD did not explain any additional variation, it was removed from the linear model. \( R_n \) alone accounted for 69 and 68\% of the variation in \( H_{\text{NEE}} \) and \( \lambda E \), respectively.

3.2. Modeled conductance and evapotranspiration

\( g_a \) was linearly correlated with horizontal wind-speed (Fig. 6A) and followed the diurnal patterns of convective activity throughout the day (Fig. 1). These diurnal patterns in \( g_a \) agree with observations over Amazonian forests (e.g. Grace et al., 1996; Wright and Gash, 1996). Values of \( \psi_M \) and \( \psi_M \) were small, contributed little, and all other parameters were relatively constant. The upper boundary of normalized \( g_b \) was a square hyperbolic function to \( R_n \) (Fig. 6B). \( g_{\text{max}} \) was expected to be negatively related to VPD because of the negative physiological
response of canopies to VPD (Martin et al., 1997). This relationship was not found, so an upper limit for \( g_{\text{max}} \) as a function of VPD could not be determined (Fig. 6C). \( g_b \) was modeled only as a function of \( R_n \), in concurrence with statistical results from a first-order regression. The minimum \( g_a \) was 1.0 mol m\(^{-2}\) s\(^{-1}\), which increased to > 2.0 mol m\(^{-2}\) s\(^{-1}\) during midday (10:00–15:00 h, Fig. 7A). Estimated values of \( g_b \) followed a similar diurnal pattern as \( R_n \), and at dawn, \( g_b \) was \( \sim 1 \) mol m\(^{-2}\) s\(^{-1}\) until 08:00 h, then steadily increased till noon, decreased during the later afternoon, and approached 0.1 mol m\(^{-2}\) s\(^{-1}\) at dusk (Fig. 7B). Modeled values of \( g_a \) and \( g_b \) behaved similarly to those derived using Eqs. (4) and (5) (Fig. 7). \( \Omega \) ranged from \( \sim 0.6 \) during the night to \( \sim 0.85 \) by 08:30 h. For the majority of daytime hours (06:00–16:00), \( \Omega \) was > 0.75 (Fig. 7C).

Both the Penman–Monteith and Priestly–Taylor equations performed well in estimating \( \lambda E \) (Fig. 8A). The slopes of all the regression lines were \( \sim 1.0 \). The Penman–Monteith equation explained 95% of the observed variation in \( \lambda E \), with the variation being

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**Fig. 4.** Diurnal patterns of below-canopy storage energy fluxes from an old-growth wet tropical forest in Costa Rica where (A) includes each of the components of the energy flux, and (B) the sum of the components contrasted with \( R_n \). Data are mean values from 1998 to 2000 with error bars \( \pm 1 \)SE.
equally distributed and increasing with increasing energy (Fig. 8A). There was no significant difference between using the Penman–Monteith equation for wet and dry canopy conditions. In contrast, the simpler Priestly–Taylor relationship accounted for R² of 98% of the observed variation (Fig. 8B). While there was also no significant difference in the use of the Priestly–Taylor equation to estimate LE for wet and dry canopy conditions, it did seem to overestimate LE when Rn was >500 W m⁻² under dry canopy conditions (Fig. 8C). Annual ETPT ranged from 1892 mm in 1998 to 2294 mm in 1999, and from 54 to 66% of bulk precipitation (Table 1). Mean daily ETPT rates were also lower in 1998 and greatest in 1999 (5.2–6.3 mm d⁻¹, respectively). Results using the Penman–Monteith model were not significantly different than the Priestly–Taylor model. Interception loss was greatest in 2000, with an annual total of 708 mm, accounting for 18% of bulk precipitation.

3.3. Uncertainty in modeled estimates

All 3 years of measured data were used to estimate the conductances, which in turn, were used to model ET. A traditional approach to assess uncertainty in modeled estimates would be to divide the data, use one set to derive parameters and test the results against the other set. For our data, this technique would only assess the uncertainty at ~1 yr. Alternatively, a statistical bootstrap technique (S-plus, v. 6.1, Lucent Technologies, Inc., Seattle, WA) resampled observations from the total dataset, mimicked the process of sampling each 30 min period observation (Shao and Tu, 1995; Bradley and Tibshirani, 1993). To assess uncertainty in our modeled conductance, estimates were compared to measured values at different timescales, resampling at 3, 7, 30, 165 d, 1 yr intervals (cf. Spencer et al., 2004; Magnussen and Burgess, 1997). Ten replications were used for the 3, 7 and 30 d intervals, and two replications for 165 d and 1 yr intervals. Differences between modeled and measured mean ga were <6% (of measured ga) with SE, <0.08 mmol m⁻² s⁻¹ for 30, 165 d, and 1 yr intervals. For intervals ≤7 d, modeled ga overestimated the measured ga by ~50% during the night, and underestimated measured ga by 25%.
Fig. 6. Empirical relationships of both aerodynamic and bulk conductance used to model ET_{pm}. Independent variables were averaged at different intervals, i.e. 0.25 m s\(^{-1}\), 50 W m\(^{-2}\), and 0.025 kPa, for A, B, and C, respectively. All data were median values with \( \pm 1SE \).
during the day (Fig. 9A). Measured $g_a$ also showed higher daytime SE among 3- and 7 d intervals, ranging 0.05–0.25 mmol m$^{-2}$ s$^{-1}$ (Fig. 9B). The observed variability in modeled $g_a$ was consistent among all resampling intervals with SE $\sim 0.01$ and $< 0.08$ mmol m$^{-2}$ s$^{-1}$ during night and daytime, respectively (Fig. 9C). Similar trends were observed for $g_b$. These results suggest that this modeling
approach cannot fully capture the short-term variability observed in the measured data (i.e. <7 d), but is robust for monthly, seasonal and annual estimates of conductance and $\lambda E$. Other systematic and random errors in determining the below canopy fluxes are discussed in Moore and Fisch (1986) and for the eddy-covariance approach by Kruijt et al. (2004).
4. Discussion

4.1. Ecosystem energy dynamics

Daytime profiles of temperature and water vapor in the upper canopy were often counter to the above-canopy gradients as a result of winds that did not fully penetrate the canopy. The top of the canopy, between 21 and 27 m, acted as a physical barrier to the removal of transpired moisture from below. As a result, the negative $\Delta E_{BC}$ at night was due to adiabatic cooling and consequent condensation. Storage fluxes can contribute substantially to the overall ecosystem energy flux when $R_n$ is small or during the night. On a diurnal basis, this was a very small component ($\approx 2\%$). Malhi et al. (2002) did not find this to be the case from a seasonally humid forest in Amazonia, where storage fluxes calculated by the residual from the energy balance accounted for as much as 30% of overall flux on an hourly basis. This suggests a strong contrast between tropical wet ($\geq 3200$ mm yr$^{-1}$) and seasonally humid forests (2200–3100 mm yr$^{-1}$).

Bowen ratios ($\beta$) were consistently $< 1$ indicated that water was not limiting $\lambda E$ at any time during the year (cf. de Rocha et al., 2004). Soils in the wet tropics generally do not exert hydraulic limitations on $\lambda E$ (De Bruin, 1983). This is likely also the case at La Selva, where soils have high water-holding capacity and high hydraulic conductivity (Wietz et al., 1997; Sollins et al., 1994).

The negligible response of $\lambda E$ and $g_b$ to VPD, further suggests that water was not limiting in this forest. *Pentaclethra macroloba*, the dominant tree species (42% of the basal area) is known to close its stomata and leaves in the late afternoon ($\approx 1530$ h). However, changes in either $H_{NEE}$ or $\lambda E$ due to associated changes in $P. macroloba$ physiology were not detected. This result suggests that either single species do not control energy partitioning, their controls cannot be detected at the ecosystem-level in heterogenous tropical wet forests with the eddy-covariance technique, or that the time of day when $P. macroloba$ closes its leaves and stomata is inconsequential to the above-canopy energy fluxes.

4.2. Conductances and other limits to annual energy fluxes

The general diurnal patterns found for $g_a$ and $g_b$ are similar to those reported for other tropical forests

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**Table 1**

<table>
<thead>
<tr>
<th>Site</th>
<th>Forest</th>
<th>Period</th>
<th>Annual $E_T$</th>
<th>Annual $E_i$</th>
<th>$E_T/E_i$</th>
<th>$E_i/E_T$</th>
<th>$E_i/R_n$</th>
</tr>
</thead>
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<tr>
<td>This study</td>
<td>Old-growth</td>
<td>Aug 98–Jan 99</td>
<td>3405</td>
<td>1892</td>
<td>0.95</td>
<td>0.55</td>
<td>0.95</td>
</tr>
<tr>
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<td>Aug 99–Jan 00</td>
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<td>2294</td>
<td>0.98</td>
<td>0.66</td>
<td>0.88</td>
</tr>
<tr>
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<td>Old-growth</td>
<td>Aug 98–Mar 83</td>
<td>4127</td>
<td>2220</td>
<td>0.97</td>
<td>0.68</td>
<td>0.88</td>
</tr>
<tr>
<td>La Selva, Costa Rica</td>
<td>Secondary</td>
<td>Aug 99–Nov 99</td>
<td>3156</td>
<td>1710</td>
<td>0.89</td>
<td>0.76-0.90</td>
<td>0.77-0.89</td>
</tr>
<tr>
<td>Janlappa, Java</td>
<td>Old-growth</td>
<td>July 98–July 99</td>
<td>2609</td>
<td>1224</td>
<td>1.06</td>
<td>0.62</td>
<td>0.88</td>
</tr>
<tr>
<td>Tapajos, Brazil</td>
<td>Old-growth</td>
<td>July 00–July 01</td>
<td>1300</td>
<td>600</td>
<td>1.06</td>
<td>0.48</td>
<td>0.88</td>
</tr>
<tr>
<td>Deque, Brazil</td>
<td>Old-growth</td>
<td>8 d in Sep 83</td>
<td>2000</td>
<td>1000</td>
<td>1.02</td>
<td>0.50</td>
<td>0.75</td>
</tr>
</tbody>
</table>

$E_T$ fluxes calculated using the Priestly–Taylor equation unless otherwise noted. Units for total $R_n$ are J yr$^{-1}$, and $E_T/E_i$ is the fraction of the total annual energy needed to evaporate $E_T$ of intercepted water is noted as $E_i$. Units for rain, $E_T$, $E_i$ are mm yr$^{-1}$, and daily $E_T$ are mm mm$^{-2}$ SE. nd. denotes no data.

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* Calder et al. (1986).
* Malhi et al. (2002).
* da Rocha et al. (2004).
* da Rocha et al. (2004).
* da Rocha et al. (2004).
* Shuttleworth et al. (1988).
We found however, higher late afternoon \( g_b \) rates for the old-growth forest than those found for three monocultural plantations at La Selva (\( \sim 0.5–0.8 \text{ mol m}^{-2} \text{ s}^{-1} \), Bigelow, 2001). Our higher observed afternoon \( g_b \) was likely an integrated response of all species, suggesting that the gas exchange measurement acquired with cuvettes from

Fig. 9. Statistics from resampling the measured- and modeled aerodynamic conductance (\( g_a \)) datasets at 3 and 30 d intervals with 10 replications across time of day. (A) represents the difference between the resampled measured- and modeled \( g_a \) as a fraction of the measured \( g_a \), and (B) and (C) represent the standard error after resampling for measured and modeled \( g_a \) data, respectively. Note different scales for (B) and (C).

(Bigelow, 2001; Wright and Gash, 1996; Shuttleworth et al., 1984).
these plantations do not fully capture the response from old-growth forests. Moreover, our $g_b$ estimates were also higher than Wright and Gash (1996) values from a tropical humid forest in Brazil. The lower $g_b$ estimates found by Wright and Gash (1996) were due to VPD constraints on $g_b$ that were not found in this study. For the most part, VPDs at La Selva were relatively low, <1.5 kPa. VPDs may, however, affect energy flux at the leaf-level in the upper canopy, but were not detected by the methods used here, suggesting that the lack of ecosystem-level response to the observed VPDs may be due to increased transpiration in the lower canopy, thereby offsetting any leaf-level effects in the upper canopy. We found significant differences in observed $g_b$ among years and seasons that followed the same trends as $R_n$. Between year differences in $R_n$ explained much of the interannual variability observed in measured and modeled $\lambda E$ from La Selva. Increased rainfall in 2000 increased the absolute amount of interception, but not the fraction of rainfall intercepted.

The direct effects of $g_b$ on $\lambda E$ could not be determined because these variables were not be independently measured. However, increasing values of $\Lambda$ (from 0.6 to $\sim 0.85$) during the early morning indicate that hours before 09:00 h were only times when strong physiological control on $\lambda E$ occurs, likely due to the opening and closing of stomata and leaves. Values of $\Lambda > 0.75$ suggest that mid-day $\lambda E$ is controlled more by $R_n$ and $g_a$, than $g_b$. $g_a$ explained 44% of the variation in $\lambda E$ during times when both conductances were used to calculate $ET_{PM}$ (i.e. dry canopy conditions). The importance of $g_a$ in controlling $ET_{PM}$ increased further because of the very high precipitation at La Selva, where 32% of the time the upper canopy was wet.

The Priestly–Taylor relationship for well-watered conditions described the $\lambda E$ dynamics of this tropical forest quite well, in particular for wet canopy conditions (Fig. 8C). However, the Priestly–Taylor relationship tended to overestimate the observed $\lambda E$ flux for dry canopy conditions with $R_n < 500$ W m$^{-2}$. Because the assumption that the $\alpha$ coefficient applies for optimal conditions (free water and maximum $R_n$) but not for hyperbolic change in $g_b$ with increasing $R_n$ (e.g. Fig. 6B), the fraction of available energy used for $ET_{PT}$ was similar year-to-year, suggesting a thermodynamic constraint on $H$ that limits maximum daily temperature (Calder, 1986). Wright and Gash (1996) and Calder et al. (1986) also found that potential evapotranspiration accounted for a large fraction of $R_n (>0.80)$ from a humid Amazonian and Javanese forest, respectively, as did Bigelow (2001) for monocultural plantations at La Selva (0.79–0.90).

In a previous study in the old-growth forest at La Selva, Luvall (1984) determined that the energy required for evapotranspiration exceeded $R_n$ by 25%. Although this seems counterintuitive, it may very well be true. This phenomenon has been observed over crops (Ham and Heilman, 1991) as well as other tropical forests (Jones, 1992; Shuttleworth, 1989; Calder, 1986). The likely explanation is that additional energy is locally advected into the flux field from surrounding and contrasting land use types, or from rapid movement of frontal systems (Newson and Calder, 1989). This is certainly possible at La Selva, where mean daytime wind direction is $\sim 90^\circ$ and the fetch is $\sim 2$ km, beyond which the landscape is dominated by pastures, crops and patches of secondary forests extending for $\sim 60$ km to the Caribbean shore. Advection of drier air masses with greater evaporative demand is possible, particularly during Luvall’s study in the early 1980s when much of the land in the Costa Rican coastal plain was being converted from forests to agriculture (Table 1). $ET_{PT}$ estimates reported here did not exceed available $R_n$, suggesting advection was not significant. But, we cannot rule out the possibility however, that advection contributed additional energy.

The magnitude of canopy capacity is in large part a function of physical surface area of a canopy (Waring and Schlesinger, 1985). At La Selva, high epiphytic loads, bromeliad tanks and arboreal soil mats can contribute towards additional capacity and may not have been fully accounted for in our estimates. We used a fixed estimate of capacity of 1.53 mm (Loescher et al., 2002). The fraction of intercepted rainfall was consistent from 1998 to 2000, as was Luvall’s study. This suggests that the canopy surface area at La Selva is often saturated, that the relative annual amount of interception is constant, and that changes in leaf surface area were not detectable over our measurement period.

This old-growth wet tropical forest fairly consistently retained and recycled $\sim 50\%$ of the annual bulk
precipitation. For a given amount of $R_n$, limited water losses to the atmosphere appears to be imposed by forest structure and function. It remains unknown if the 50% limit on bulk precipitation holds true for other tropical wet forests with differing age and structure. Annual $R_n$ and bulk precipitation are likely correlated to some degree. Data presented here suggest that 88–97% of $R_n$ is an upper bound on the partition of bulk precipitation from tropical forests having rainfall $>2800$ mm yr$^{-1}$ (Table 1). How this fraction may change with changes in climate is not known. For example, if changes in climate increased $R_n$ relative to precipitation, there would likely be ample water available for ET. In contrast, the amount of available energy would likely limit annual ET if annual precipitation increased relative to $R_n$, with a resultant increase in runoff.

The relatively constant understory temperatures with a modest diurnal range led to storage fluxes that contributed very little ($\sim 2\%$) to the overall daily energy fluxes. Daytime $\lambda E$ was always greater than sensible heat, suggesting that the trees in this forest have sufficient ground-water reserves to minimize hydraulic stress among seasons and years. Conductances followed similar trends reported from other tropical forests, but were higher in magnitude. $R_n$ was the largest determinant for the annual energy flux for this wet tropical forest, as demonstrated by both models. This was primarily because $\Omega$ was high and $g_b$ exerted little control during daytime hours when fluxes were at their greatest. Both the Penman–Monteith and Priestly–Taylor models performed well. The Priestly–Taylor model is more appropriate for wet canopy conditions that prevail for much of the time. This tropical wet forest behaved more like a classical well-watered agronomic crop rather than like many other forests that respond to hydraulic limitations.

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