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Are tropical forests near a high temperature threshold?

Christopher E. Doughty¹ and Michael L. Goulden¹

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[1] We used leaf gas exchange, sap flow, and eddy covariance measurements to investigate whether high temperature substantially limits CO₂ uptake at the LBA-ECO (Large-scale Biosphere-Atmosphere) km-83 tropical forest site in Brazil. Leaf-level temperature-photosynthesis curves, and comparisons of whole-canopy net ecosystem CO₂ exchange (NEE) with air temperature, showed that CO₂ uptake declined sharply during warm periods. Observations of ambient leaf microclimate showed that leaves oscillate between two states: a cool, dimly lit stage and a hot, brightly illuminated stage where leaf temperatures are often greater than 35°C. The leaf-level rates of photosynthesis decreased when shaded leaves (\sim ambient air temperature and $< 500 \mu\text{mol m}^{-2} \text{s}^{-1}$) were transferred into a prewarmed, brightly illuminated chamber (35° to 38°C and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$), coincident with increased leaf temperature, increased evaporative demand, and stomatal closure. The rates of whole-canopy CO₂ uptake calculated at 5-min intervals increased initially at the onset of sunny periods that followed extended cloudy periods, but then decreased as the sunlight continued, leaf temperature and evaporative demand increased, and canopy conductance decreased. The forest at km-83 appears to be close to a high temperature threshold, above which CO₂ uptake drops sharply. This sensitivity results in part from the covariance between leaf temperature and leaf illumination; the brightly illuminated leaves that contribute disproportionately to canopy photosynthesis are warmed to the point that leaf gas exchange is curtailed.

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1. Introduction

[2] Researchers have hypothesized that increasing temperatures will have a negative impact on tropical forest production [Clark, 2004], resulting in a positive feedback that amplifies global climate change [Cox *et al.*, 2000]. High temperatures reduce CO₂ uptake by C3 plants through reversible, short-term increases in photorespiration, respiration and stomatal closure, and, in extreme cases, irreversible damage to biochemical machinery [Berry and Björkman, 1980]. Increases in temperature that increase photorespiration, total ecosystem respiration, or the incidence of stomatal closure would be expected to decrease tropical forest primary production. The Amazon Forest contains 93 (\pm 23) PgC (10^{15} g) of live biomass aboveground, and tropical forest accounts for at least 30% of global terrestrial primary production [Malhi *et al.*, 2006; Field *et al.*, 1998], underscoring the need to understand the sign and magnitude of this climate change feedback.

[3] Field observations have drawn attention to the possibility that tropical forest production is highly sensitive to temperature [Clark *et al.*, 2003; Feeley *et al.*, 2007]. Studies

of leaf gas exchange using chambers have found that photosynthesis by tropical leaves declines above 26 to 34°C [Koch *et al.*, 1994; Ishida *et al.*, 1999; Keller and Lerdau, 1999; Lerdau and Throop, 1999; Graham *et al.*, 2003; Tribuzy, 2005]. Sunlit canopy leaves in tropical forests may be several °C above air temperature [Ishida *et al.*, 1999; Leakey *et al.*, 2003; Tribuzy, 2005], implying that photosynthesis is sometimes constrained by high temperatures. Field measurements of whole-ecosystem CO₂ exchange in tropical forests made using the eddy covariance technique indicate that CO₂ uptake decreases markedly during warmer than average periods [Loescher *et al.*, 2003; Goulden *et al.*, 2004]. Field measurements using diameter tapes in tropical forest show a strong negative correlation between interannual temperature variability and wood increment [Clark *et al.*, 2003]. Taken together, these observations support the idea that tropical forests currently operate near a high temperature threshold, and that future increases in temperature will have a negative impact on primary production. However, field data are still inadequate to reach a strong conclusion and several uncertainties remain [Clark, 2004].

[4] One of the major questions involves the strength of the warming effects described by Loescher *et al.* [2003] and Goulden *et al.* [2004]. Goulden *et al.* reported that CO₂ uptake by an Amazonian forest decreased by $12 \mu\text{mol m}^{-2} \text{s}^{-1}$ during periods that were only 3°C warmer

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Table 1. Summary of Measured and Derived Variables

Variable	Definition	Method
PPFD _{leaf}	Photosynthetically active Photon Flux Density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	GaAsP sensors affixed to leaves
PPFD _{tower}	Photosynthetically active Photon Flux Density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	PPFD sensor at 64 m
R _{net}	Net radiation (W m^{-2})	Net radiometer at 64 m
T _{leaf}	Leaf temperature ($^{\circ}\text{C}$)	Thermocouples affixed to leaves
T _{air-gap}	Air temperature in a gap ($^{\circ}\text{C}$)	Thermistor with radiation shield
T _{air-40m}	Air temperature at 40 m ($^{\circ}\text{C}$)	Ventilated thermistors
T _{air-64m}	Air temperature at 64 m ($^{\circ}\text{C}$)	Ventilated thermistors
T _{canopy}	Aerodynamic canopy temperature ($^{\circ}\text{C}$)	Inverted Penman-Monteith equation
E _{t-leaf}	Leaf transpiration ($\text{mol m}^{-2} \text{s}^{-1}$)	Leaf gas exchange system
E _{t-branch}	Branch transpiration ($\text{mol m}^{-2} \text{s}^{-1}$)	Heat balance sap flow sensors
$\lambda E_{5\text{min}}$	Latent heat flux (W m^{-2})	Eddy covariance; 5 min averaging
$\lambda E_{30\text{min}}$	Latent heat flux (W m^{-2})	Eddy covariance; 30 min averaging
H _{5min}	Sensible heat flux (W m^{-2})	Eddy covariance; 5 min averaging
H _{30min}	Sensible heat flux (W m^{-2})	Eddy covariance; 30 min averaging
A _n	Net CO ₂ assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Leaf gas exchange system
F _{CO2-5min}	Net CO ₂ exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Eddy covariance; 5 min averaging
F _{CO2-30min}	Net CO ₂ exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Eddy covariance; 30 min averaging
NEE _{30min}	Net Ecosystem Exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	F _{CO2} plus change in profile CO ₂ storage
g _{s-leaf}	Leaf stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Measured by gas exchange system
g _{s-branch}	Branch stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Calculated from sap flow and T _{leaf}
G _c	Canopy conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Calculated from inverted Penman-Monteith equation
U	Horizontal wind speed (m s^{-1})	Measured with a 3-axis sonic anemometer at 64 m or in a gap

than average. The strength of this sensitivity is unexpected, since observations of gas exchange in temperate climates show that photosynthesis is generally well adapted and acclimated to average temperature [Berry and Björkman, 1980], and that the rates of photosynthesis are largely insensitive to typical diel and day-to-day temperature variation. Moreover, the maximum growing-season air temperatures imposed on many tropical forests are no higher than the maximum growing-season air temperatures imposed on many temperate forests [Breckle, 2002]. Loescher *et al.*'s [2003], Goulden *et al.*'s [2004], and Clark *et al.*'s [2003] findings imply that tropical forest CO₂ exchange is strongly sensitive to warming. Several studies show that tropical forest leaf photosynthesis decreases above 26 to 34°C [Koch *et al.*, 1994; Ishida *et al.*, 1999; Keller and Lerdau, 1999; Lerdau and Throop, 1999; Graham *et al.*, 2003; Tribuzy, 2005]. But it is unclear whether the leaf- and canopy-level observations are quantitatively compatible. More work is needed to mechanistically understand why tropical forest gas exchange declines markedly during warm periods.

[5] The goal of this paper is to relate whole-forest observations of tropical forest gas exchange to measurements of leaf and branch physiology and microclimate. We worked at the km-83 site in the Tapajos National Forest, Para, Brazil, an evergreen tropical forest that was a focus of the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA-ECO [Keller *et al.*, 2004]). We compare the effects of temperature and light on CO₂ exchange and stomatal conductance measured using eddy covariance, sap flow and leaf-level gas exchange (Table 1).

2. Methods

2.1. Site

[6] This study was conducted at the Floresta National do Tapajos (FLONA) as part of LBA-ECO. The FLONA Tapajos is located on the eastern side of the Tapajos River,

extending from 50 to 150 km south of Santarem, Para, Brazil ($-3.020833^{\circ}\text{S}$, $54.972221^{\circ}\text{W}$). We worked at the km-83 [Goulden *et al.*, 2004] and km-67 [Saleska *et al.*, 2003] sites. The vegetation at both sites was closed tropical forest, with a canopy height of ~ 40 m and emergent trees with heights up to 55 m. An analysis of precipitation showed the FLONA Tapajos was in the 27th driest percentile ($\pm 3\%$) of Amazonian forests for both annual precipitation and length of the wet season [Saleska *et al.*, 2003]. The forest was on a broad, flat plateau. Soils were mainly yellow latosol clay (Haplic acrorrhox).

[7] An area extending 2- to 3-km east of the main km-83 eddy covariance tower was selectively logged in September 2001 as part of the larger LBA-ECO experiment. The logging was patchy, creating a mosaic of new gaps within patches of relatively intact forest. The logging removed $\sim 12\%$ of the large trees and increased the area of gaps from $\sim 4\%$ to $\sim 12\%$ [Miller *et al.*, 2007; Figueira *et al.*, 2008]. The rates and seasonality of CO₂ exchange and the stem increment by large trees were largely unchanged by the logging [Figueira *et al.*, 2008]. The stem increment by smaller, understory trees [Figueira *et al.*, 2008] and the ventilation of the subcanopy [Miller *et al.*, 2007] were increased following logging. The changes in subcanopy ventilation and small-tree growth imply that the logging opened the canopy and increased the amount of light reaching the understory, even in areas that were not immediately adjacent to gaps [Figueira *et al.*, 2008].

2.2. Leaf Microclimate

[8] We made leaf level measurements at both field sites, working off a 45-m tall scaffold tower at km-67 and a 30-m tall tower at km-83. The km-83 scaffold was located 300 m from the eddy covariance tower. We measured leaf temperature (T_{leaf}; Table 1) with fine wire thermocouples (copper-constantan 0.005" Omega, Stamford, CT) that were attached to the underside of leaves by threading the wire through the

leaf and inserting the end of the thermocouple into the abaxial surface. The thermocouples were wired into an AM25T multiplexer attached to a Campbell Scientific 23X data logger (Campbell Scientific, Logan, UT) and the data were recorded at 1 Hz. We measured wind speed with a 3-axis sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT); Photosynthetically active Photon Flux Density (PPFD) with silicon quantum sensors (LI190, Li-Cor Biosciences, Lincoln, NE); air temperature with thermistors mounted in radiation shields (model 107, Campbell Scientific, Logan, UT); and the irradiance at the leaf surfaces ($PPFD_{leaf}$) with Gallium-Arsenide-Phosphide (GaAsP) sensors. The voltage of the GaAsP sensors was linearly related to PPFD [Pontailier, 1990].

[9] We studied the leaf microclimate in three separate campaigns. In the first campaign, which occurred during July and August 2003, we rotated the instruments among several locations that were dominated by different plant functional types (gaps, understory, midcanopy, emergent), working for roughly a week at each site. The locations included two ground-level gaps that were located ~50 m northeast of the km-83 tower, an understory site that was located at the base of the km-83 platform tower, a midcanopy site that was roughly 20-m above ground level at km-83, a canopy-top site at 30-m above ground level at km-83, and a canopy level site at 45-m at km-67.

[10] In the second campaign, which lasted the dry season from July to December 2004, we focused on three canopy tree species that were accessible from the top of the km-83 platform tower. We placed 50 thermocouples on leaves of *Sextonia rubra*, *Micropholis sp.*, *Lecythis lurida*. In the third campaign, which lasted the dry season from July to December 2005 and focused on the same three species at km-83, we repeated the measurements made during the second campaign and added heat balance sap flow sensors [Sakuratani, 1981] on 6 branches. Observations of transpiration ($E_{t-branch}$) were recorded every 2 min, along with temperature (T_{leaf}) and light ($PPFD_{leaf}$). We measured the average area of a leaf for each branch on a subsample of leaves, and determined the total area of leaves by counting leaves. We then converted sap flow to leaf-area-based stomatal conductance ($g_{s-branch}$) as:

$$g_{s-branch} = \frac{E_{t-branch}P}{(e_i - e_a)} \quad (1)$$

where $E_{t-branch}$ is leaf-area based transpiration in $\text{mol m}^{-2} \text{s}^{-1}$, P is atmospheric pressure in (Pa), e_i is water vapor partial pressure in the leaf calculated from T_{leaf} , and e_a is water vapor partial pressure in the air.

2.3. Leaf Gas Exchange Measurements

[11] We visited the field at least once a week from August to December 2004 to make photosynthesis measurements on three focal species (*Sextonia rubra*, *Micropholis sp.*, *Lecythis lurida*) using a portable gas exchange system (LI 6400, Li-Cor Biosciences, Lincoln, NE). We made repeated measurements of the response of leaf gas exchange to irradiance holding leaf temperature constant at 30°C, and the response to leaf temperature holding flow, irradiance and CO₂ concentration constant. The temperature response curves were made by placing leaves in the chamber at 30°C

and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, allowing conditions to equilibrate for several minutes, and then raising the temperature in the chamber while recording the observations every 20 s. Each temperature response curve took 10 to 20 min, and the maximum achievable temperature was ~42°C. Observations immediately after the initial temperature increase were often out of calibration and were removed from subsequent analysis. Rising temperature increased evaporative demand and Vapor Pressure Deficit (VPD) and decreased relative humidity (RH). The changes in temperature, VPD and RH were tightly correlated, and we were unable to determine which factor was better correlated with the rates of gas exchange.

2.4. Transient Leaf Gas Exchange Measurements

[12] We used the leaf gas exchange system to investigate the transient effect of a sudden, concurrent increase in temperature and irradiance. We placed cool, shaded (~air temperature, < 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) leaves into a prewarmed (35° to 38°), brightly illuminated (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) chamber to replicate the coincident increase in irradiance and temperature that occurs when a sun-fleck hits a leaf. We recorded the observations every 20 s, and discarded the observations during the first 1 to 2 min.

2.5. Whole Canopy Gas Exchange

[13] The tower observations were made at the km-83 site as described by Miller *et al.* [2004], Goulden *et al.* [2004], and da Rocha *et al.* [2004]. The turbulent fluxes of CO₂ (F_{CO_2}), sensible heat (H), latent heat (λE), and momentum were determined at 64-m above ground level on a 67-m tall tower (Rohn 55G, Rohn, Peoria, IL, USA) using the eddy covariance technique [Baldocchi, 2003; Wofsy *et al.*, 1993]. The wind and temperature were measured at 4 Hz with a 3-axis sonic anemometer (Campbell Scientific, Logan, UT). The CO₂ and H₂O densities were measured with a Li-Cor 7500 open path infrared gas analyzer (IRGA; Li-Cor Biosciences, Lincoln, NE) at 4 Hz. We mathematically rotated the wind speed so that both the mean cross and vertical wind were zero over each half hour, and made density corrections to the open path IRGA following Miller *et al.* [2004].

[14] Measurements of the physical environment were recorded at 0.5 Hz, including: net radiation (R_n) with a ventilated net radiometer (Q*7.1; REBS, Seattle, WA, USA), Photosynthetically active Photon Flux Density ($PPFD_{tower}$) with silicon quantum sensors (Li-Cor LI190), and air temperature ($T_{air-40m}$, $T_{air-64m}$) with ventilated thermistors (model 076B; Met One, Grants Pass, OR; model 107, Campbell Scientific, Logan, UT).

2.6. Canopy Conductance and Temperature

[15] We used the inverted Penman-Monteith equation to calculate canopy conductance (G_c), which is analogous to stomatal conductance on a ground area basis [Monteith and Unsworth, 1990]:

$$G_c = \left[R_a \left(\frac{\Delta}{\gamma} (\beta - 1) - 1 \right) + \frac{\rho_a c_p}{\gamma} \frac{\delta e}{\lambda E} \right]^{-1} \quad (2)$$

where Δ is the slope of the saturation vapor pressure deficit curve (Pa K^{-1}), γ is the psychrometer constant (Pa

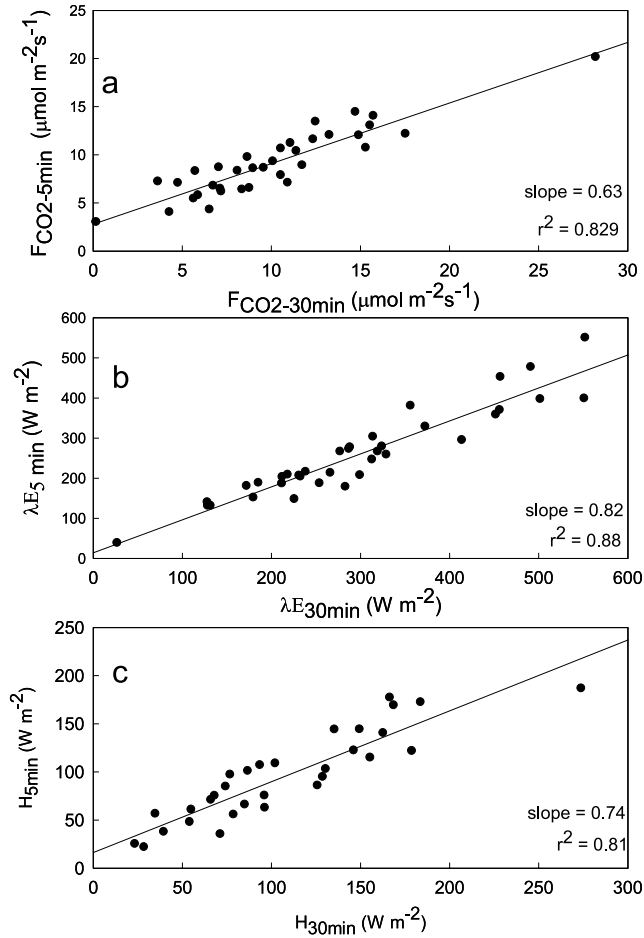


Figure 1. (a) Comparison between eddy-covariance CO_2 fluxes at the LBA-ECO km-83 tower calculated with a 30-min averaging time (F_{CO_2-30} in $\mu\text{mol m}^{-2}\text{s}^{-1}$; a positive flux indicates CO_2 uptake) and simultaneous average CO_2 fluxes calculated with 5-min averaging times (F_{CO_2-5} in $\mu\text{mol m}^{-2}\text{s}^{-1}$). (b) Comparison of latent heat fluxes (λE in W m^{-2}) calculated with 30- and 5-min averaging times. (c) Comparison of sensible heat fluxes (H in W m^{-2}) calculated with 30- and 5-min averaging times.

K^{-1}), ρ_a is the air density (kg m^{-3}), δe is the air saturation deficit pressure (Pa), λE is the latent heat exchange (W m^{-2}), c_p is the specific heat of air at constant pressure ($\text{J kg}^{-1}\text{K}^{-1}$), β is the Bowen ratio, and R_a is the aerodynamic resistance (s m^{-1}). Aerodynamic resistance (R_a) was calculated as [Monteith and Unsworth, 1990]:

$$R_a = \frac{U}{u^*2} + 6.2u^* - 2/3 \quad (3)$$

where U is the mean horizontal wind speed (m s^{-1}) and u^* is the friction velocity (m s^{-1}).

[16] We calculated the aerodynamic canopy temperature (T_{canopy}) as [Monteith and Unsworth, 1990]:

$$T_{\text{canopy}} = R_a \left(\frac{H}{c_p \rho_a} \right) + T_{\text{air-64}} \quad (4)$$

where $T_{\text{air-64}}$ is air temperature at 64-m and H is the sensible heat flux (W m^{-2}).

2.7. Transient Whole Canopy Gas Exchange

[17] Eddy covariance fluxes are usually calculated using a half-hour averaging time to ensure that the low frequency contributions to the flux are captured [Baldocchi, 2003]. This averaging period is longer than the dynamics we are interested in, such as stomatal closure and cloud movement, and half hour averages mask important transition states of the forest. We therefore recalculated the eddy covariance observations at km-83 using 5-min averages for flux analysis to investigate the transient response of whole forest CO_2 exchange to changes in irradiance associated with cloud passage. We focused on naturally occurring intervals during the 2000 to 2002 dry seasons (July to December), when cloudy periods were followed by extended sunny conditions. We screened the tower top PPFD data ($\text{PPFD}_{\text{tower}}$) to identify intervals with 10 cloudy minutes ($\text{PPFD}_{\text{tower}} < 600 \mu\text{mol m}^{-2}\text{s}^{-1}$) followed by 20 sunny minutes ($\text{PPFD}_{\text{tower}} > 900 \mu\text{mol m}^{-2}\text{s}^{-1}$). We divided these half hour intervals into six 5-min intervals and calculated the turbulent fluxes of sensible heat, latent heat, CO_2 , and momentum for each 5-min interval.

[18] We selected a 5-min averaging time as a compromise that would be short enough to resolve the expected physiological dynamics, and long enough to avoid markedly underestimating the flux carried by low frequency eddies. We tested the validity of the 5-min fluxes by regressing the covariance calculated for 30-min intervals using 30-min averaging times ($F_{\text{CO}_2-30min}$) against the average of the six fluxes calculated for that same period using 5-min averaging times (F_{CO_2-5min}) (Figure 1). We filtered the data to remove outliers, which were associated with nonstationary periods. The r^2 between the two CO_2 fluxes was 0.83 and the slope was 0.63. The slope indicates the 5-min fluxes systematically underestimated the 30-min fluxes by 37%, presumably due to the underestimation of transport by low frequency eddies. An analysis of the frequency-weighted cospectra confirmed that 5-min averaging underestimated the CO_2 flux due to low frequency transport (Figure 2). The 5-min fluxes showed similar shapes among themselves and in comparison to the half-hour fluxes, with periods 4 to 6 (20 to 30 min) showing greater power associated with increased flux during sunny periods. Cospectra for latent heat, sensible heat, and momentum showed comparable patterns (figure not shown). These analyses confirm that F_{CO_2-5min} systematically underestimates the flux, while providing a reliable measure of the relative change from one 5-min interval to the next.

3. Results

3.1. Whole Canopy CO_2 Exchange

[19] Previous analyses of the relationship between irradiance and CO_2 exchange at the km-83 site indicate that whole canopy photosynthesis saturates at a $\text{PPFD}_{\text{tower}}$ of $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ [Goulden et al., 2004]. We therefore analyzed the rates of NEE_{30min} during periods with $\text{PPFD}_{\text{tower}}$ above $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ to determine the sensitivity of light-saturated CO_2 exchange to air temperature

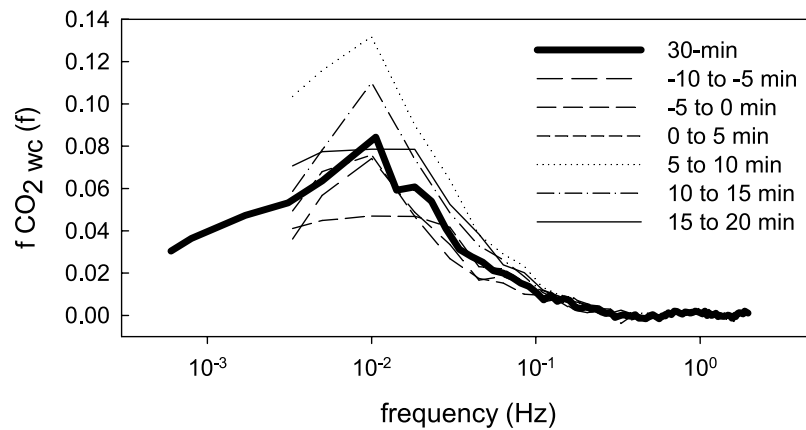


Figure 2. Frequency weighted cospectra ($f\text{CO}_2_{wc}$ in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ Hz}^{-1}$; a positive flux indicates CO_2 uptake) between vertical velocity and CO_2 mixing ratio. Cospectra for half hour periods with 10 cloudy minutes followed by 20 sunny minutes were calculated for the entire half-hour period and averaged (thick black line; $n = 42$) and for each separate 5-min interval (thin black lines; $n = 42$). The 5-min intervals are labeled by time, with -10 min to -5 min and -5 min to 0 min corresponding to the cloudy interval. The intervals from 0 min to 20 min were sunny and have correspondingly higher fluxes.

($T_{\text{air-40m}}$). $\text{NEE}_{30\text{min}}$ was relatively insensitive to changes in air temperature below 28.5°C and highly sensitive to changes in air temperature above 28.5°C (Figure 3). The 3°C rise from 28.5°C to 31.5°C resulted in a $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ reduction in CO_2 uptake, which corresponds to a 55 to 60% reduction in net ecosystem exchange and a 35 to 40% reduction in gross exchange, assuming a respiration rate of $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ [Goulden *et al.*, 2004]. The level of temperature sensitivity is similar to that previously described for km-83 by

Goulden *et al.* [2004]. This sensitivity is unlikely to result from increasing soil respiration, since automated chamber measurements at the site indicate soil respiration changes by only $\sim 1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from morning to afternoon [Goulden *et al.*, 2004]. The response is strong (the rates of CO_2 exchange changed markedly with just a few degree rise in air temperature) and occurs at a relatively modest temperature (many temperate ecosystems are exposed to air temperatures above 28.5°C during the growing season). The

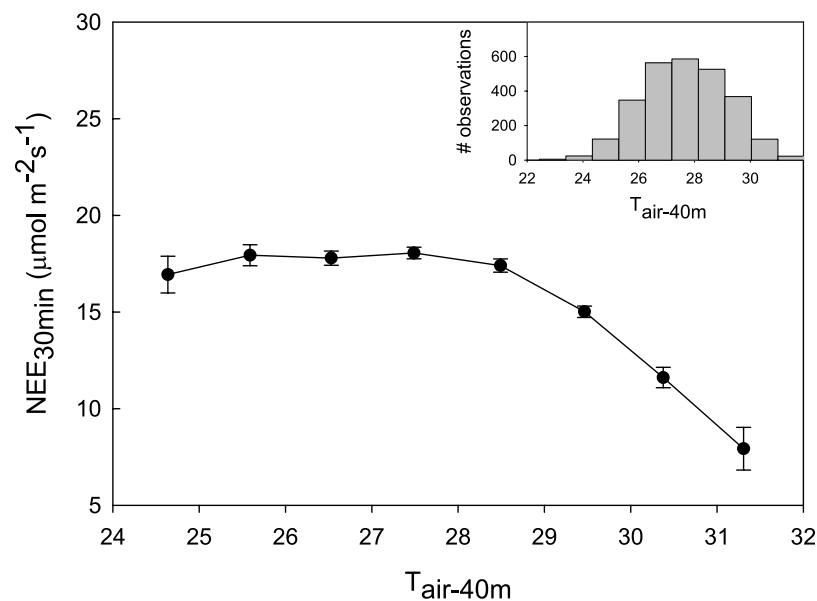


Figure 3. Net ecosystem exchange ($\text{NEE}_{30\text{min}}$) for periods with $\text{PPFD}_{\text{tower}}$ above $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from 1 July 2000 to 1 July 2001. Points show the mean for 1°C wide bins \pm se ($n = 82, 287, 543, 637, 562, 398, 134, 23$). $\text{NEE}_{30\text{min}}$ was calculated as $F_{\text{CO}_2-30\text{min}}$ plus CO_2 storage, and is plotted with CO_2 uptake as a positive flux. The decrease in NEE above 28°C indicates a reduction in photosynthesis or an increase in respiration. In the upper right corner there is a histogram of 40 m air temperature when $\text{PPFD}_{\text{tower}}$ is above $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from 1 July 2000 to 1 July 2001.

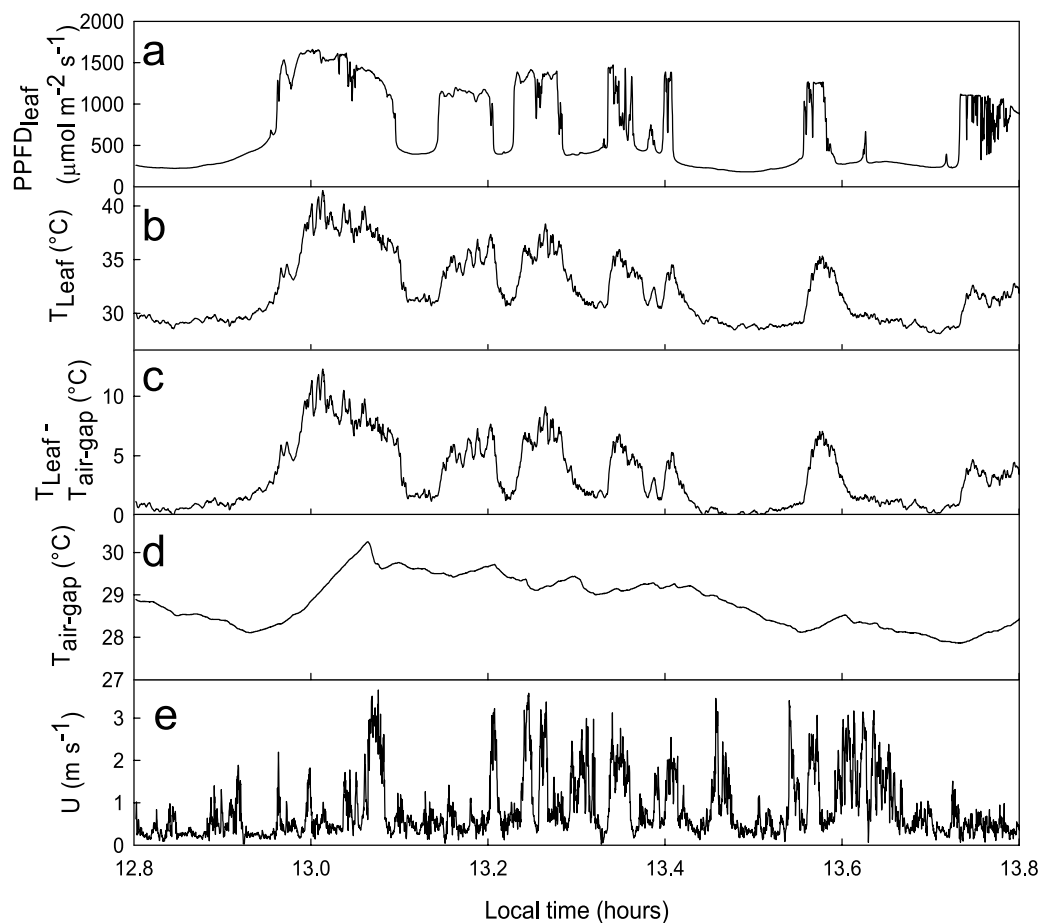


Figure 4. Environmental conditions of a gap leaf (*Distachya huber*; a horizontally oriented leaf that was ~ 15 -cm across) over an hour on 14 September 2003. Lines connect 1 Hz observations of (a) Photosynthetically active Photon Flux Density ($\text{PPFD}_{\text{leaf}}$ in $\mu\text{mol m}^{-2}\text{s}^{-1}$), (b) leaf temperature (T_{leaf} in $^{\circ}\text{C}$), (c) leaf minus air temperature ($T_{\text{leaf}} - T_{\text{air-gap}}$ in $^{\circ}\text{C}$), (d) air temperature ($T_{\text{air-gap}}$ in $^{\circ}\text{C}$), and (e) wind speed (U in m s^{-1}).

sensitivity of the forest to temperature was similar both before and after the logging. CO_2 uptake declined at air temperatures above 29°C versus below 29°C in saturated light conditions ($\text{PPFD}_{\text{tower}} > 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$) in a similar, statistically significant ($P < 0.001$) manner before ($3.85 \mu\text{mol m}^{-2}\text{s}^{-1}$) and after ($3.92 \mu\text{mol m}^{-2}\text{s}^{-1}$) the logging.

3.2. Leaf Microclimate

[20] Leaves are exposed to a rapidly fluctuating micro-environment associated with the passage of sun-flecks ($\text{PPFD}_{\text{leaf}}$; Figure 4). Sun-flecks result from the movement of shadows cast by clouds or higher branches. Rapid changes in leaf temperature (T_{leaf}) were associated with the changes in $\text{PPFD}_{\text{leaf}}$; T_{leaf} was linearly related to $\text{PPFD}_{\text{leaf}}$ at an r^2 of 0.84 (figure not shown). Changes in T_{leaf} were damped and lagged by 1 to 2 min relative to changes in $\text{PPFD}_{\text{leaf}}$, presumably as a result of thermal inertia.

[21] T_{leaf} varied moderately even during periods when $\text{PPFD}_{\text{leaf}}$ was constant, as a result of changing wind speed (U) and gap air temperature ($T_{\text{air-gap}}$). Extended periods of

sunlight resulted in moderate increases in $T_{\text{air-gap}}$. $T_{\text{air-gap}}$ varied by 1 to 2° between cloudy and sunny conditions and changed more slowly in response to changes in sunlight than did T_{leaf} . Increases in $T_{\text{air-gap}}$ depended on the length of the sunny period; a relatively long sunny period that began at 12.95 Local Time (LT) caused air temperature to warm by $\sim 1.5^{\circ}$ (Figures 4a and 4d). The rise and fall in $T_{\text{air-gap}}$ caused a similar rise and fall in T_{leaf} . Wind speed also affected $T_{\text{air-gap}}$, with wind gusts at 13.05 LT ventilating the gap and reducing air temperature by $\sim 0.5^{\circ}$ (Figures 4d and 4e).

[22] The above canopy light environment ($\text{PPFD}_{\text{tower}}$) during midday (11–12 AM local time) was bimodal, with a near normal distribution around a sunny peak at $\sim 1450 \mu\text{mol m}^{-2}\text{s}^{-1}$ and a second near normal distribution around a cloudy peak at $\sim 450 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Figure 5a). The central irradiance of each peak, and the relative occurrence of sunny periods compared to cloudy periods, varied with both time of day and season. The intensity of light at the leaf surfaces ($\text{PPFD}_{\text{leaf}}$; Figure 5b), and the temperature difference between the leaf and the air (T_{leaf} ; Figure 5c), were also bimodal. The bimodal patterns

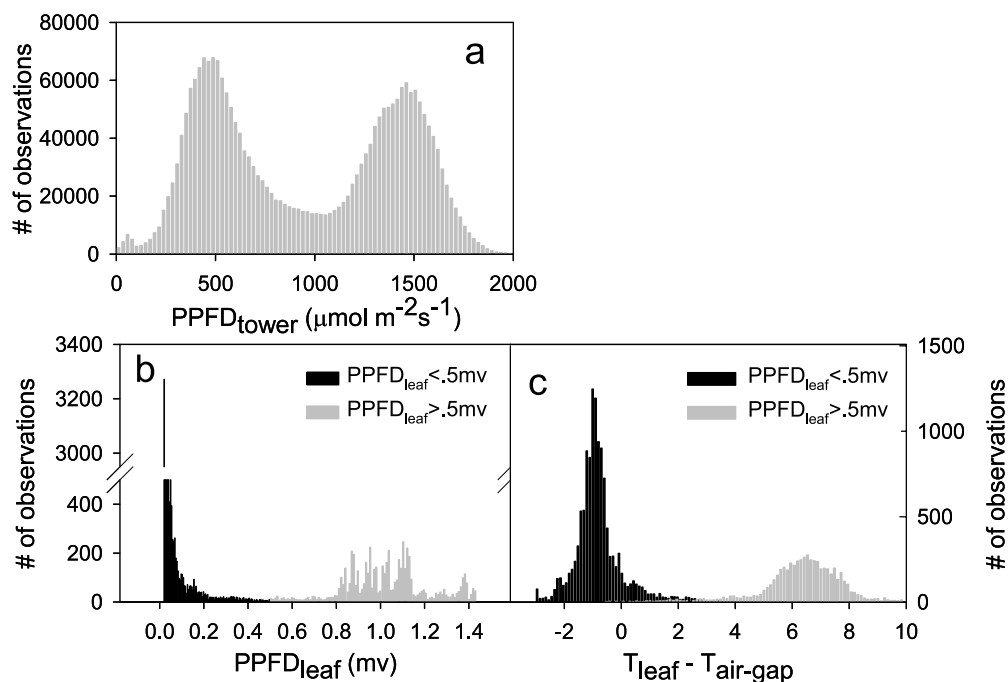


Figure 5. (a) Frequency distribution of instantaneous, incident, midday (1100 to 1200 Local Time (LT)) irradiance ($\text{PPFD}_{\text{tower}}$ in $\mu\text{moles m}^{-2} \text{s}^{-1}$) from July to December 2001. (b) Frequency distribution of leaf-level irradiance ($\text{PPFD}_{\text{leaf}}$ in mV), and (c) leaf minus air temperature ($T_{\text{leaf}} - T_{\text{air-gap}}$ in $^{\circ}\text{C}$) in a gap on 21 August 2003 from 1030 LT to 1530 LT. The observations in Figures 5b and 5c were separated into brightly illuminated ($\text{PPFD}_{\text{leaf}} > 0.5$ mV, which corresponds to $\sim 500 \mu\text{mol m}^{-2} \text{s}^{-1}$; gray bars) and shaded ($\text{PPFD}_{\text{leaf}} < 0.5$ mV; black bars) intervals to illustrate the effect of irradiance on leaf temperature.

of both $\text{PPFD}_{\text{leaf}}$ and T_{leaf} were the result of sun-flecks. Strong and sustained sun-flecks invariably resulted in elevated leaf temperatures as a result of increased solar load. Leaves alternated between two states: a dimly lit state with leaf temperatures that were close to ambient air temperature and a brightly illuminated state with leaf temperatures that were elevated by several degrees.

3.3. Canopy Temperature

[23] We calculated canopy temperature two ways: (1) the average temperature of canopy-top leaves measured with thermocouples (T_{leaf}) and (2) the aerodynamic canopy temperature calculated from the momentum and sensible heat fluxes (T_{canopy}). Both measures increased following increased sunlight (Figure 6). The average T_{leaf} reached a new value within 2 min of increased illumination, whereas T_{canopy} required 7.5 min to reach a new value. This lag is likely a measurement artifact. T_{leaf} provides a direct measure of leaf temperature, and responds rapidly to increased illumination, whereas T_{canopy} will not record an increase until any change in canopy temperature results in a change in the 5-min-averaged sensible heat flux past the tower top. Both T_{leaf} and T_{canopy} indicated an increased leaf temperature of 2.5 to 3 $^{\circ}\text{C}$. The individual measurements of T_{leaf} indicated marked heterogeneity in the amount that canopy leaves warmed. T_{canopy} provides a measure of the temperature of the leaves that contribute to aerodynamic drag. Both T_{leaf} and T_{canopy} indicate the aggregate increase in leaf temperature, which reflects the combined effect of well-illuminated

leaves that were warmed more than 2.5 to 3 $^{\circ}\text{C}$ and poorly illuminated leaves that remained near air temperature.

3.4. Leaf Gas Exchange

[24] Leaf photosynthesis (A_n) declined gradually at leaf temperatures from 30.5 $^{\circ}$ to 37.5 $^{\circ}\text{C}$ and more rapidly above 37.5 $^{\circ}\text{C}$ (Figure 7a). The decline in A_n above 37.5 $^{\circ}\text{C}$ coincided with stomatal closure ($g_{s\text{-leaf}}$, Figure 7b). Transpiration ($E_{t\text{-leaf}}$) increased with leaf temperature and evaporative demand to 37.5 $^{\circ}$, and declined at higher temperatures (Figure 7c). The leaf gas exchange measurements indicate that A_n and $g_{s\text{-leaf}}$ are modestly sensitive to leaf temperatures from 30.5 $^{\circ}$ to 37.5 $^{\circ}\text{C}$ and more strongly sensitive to leaf temperatures above 37.5 $^{\circ}\text{C}$. The immediate cause of this response was not determined. Higher temperatures could result in reduced rates of photosynthesis due to photorespiration or other biochemical effects, and subsequent reductions in conductance. Alternatively, a change in vapor pressure deficit or relative humidity could cause stomatal closure and subsequent reduction in CO_2 uptake. The reduction in $E_{t\text{-leaf}}$ above 37.5 $^{\circ}\text{C}$ cannot be explained solely by a tendency for leaves to prevent transpiration from rising above, or water potential from dropping below, a physiological set point.

3.5. Leaf Gas Exchange Transient Response to Increased Illumination

[25] We investigated the effect of a simultaneous increase in light and temperature by placing cool, shaded leaves ($T_{\text{leaf}} \sim$ air temperature, $\text{PPFD}_{\text{leaf}} < 500 \mu\text{mol m}^{-2} \text{s}^{-1}$)

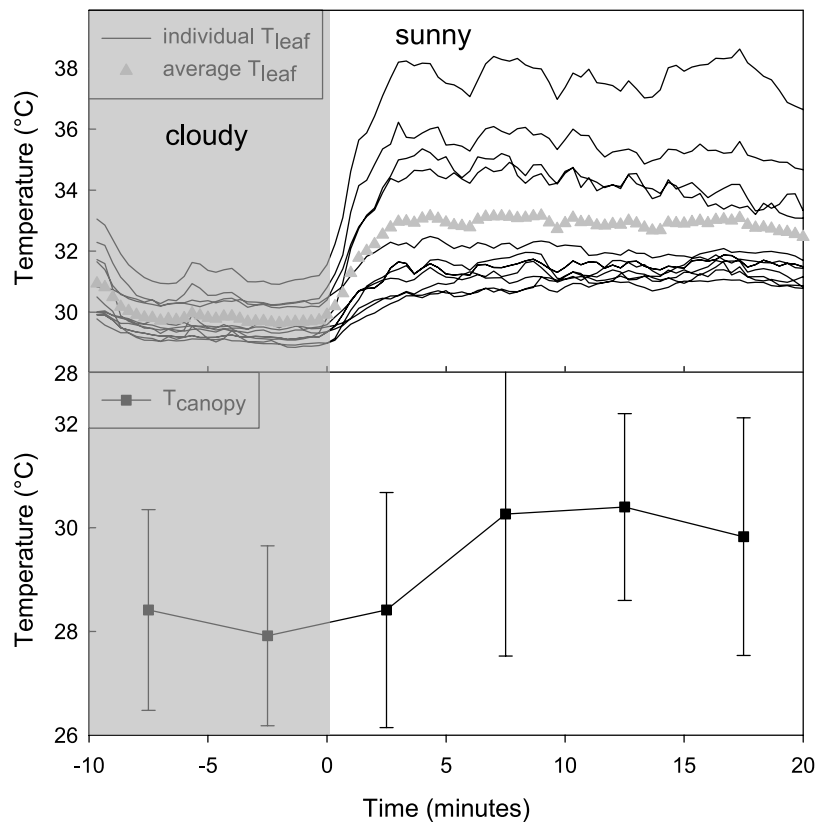


Figure 6. Time response of canopy temperature averaged for ensembles of half hour periods with 10 cloudy minutes followed by 20 sunny minutes. (a) Individual average time series for 11 leaf thermocouples (solid lines; T_{leaf} in °C, $n = 54$), and averaged for 11 leaf thermocouples (gray triangles). (b) Aerodynamic canopy temperature (T_{canopy} in °C, $n = 42$) \pm sd.

into a prewarmed, brightly illuminated leaf gas exchange chamber. These leaves rapidly equilibrated to the chamber temperature of 35 to 38°C, and began to show a decline in A_n , g_{s-leaf} , and E_{t-leaf} within 3 min of placement into the chamber (Figure 8). The rates of decline became more gradual after ~ 6.5 min. The changes in CO_2 uptake and conductance were tightly correlated, and it was not possible to determine whether the change in assimilation was causing the change in conductance or the change in conductance was causing the change in assimilation.

3.6. Whole Forest Transient Response to Increased Illumination

[26] We focused on forty-two 30-min intervals with 10 cloudy minutes followed by 20 sunny minutes. Most of these periods were in the afternoon. Cloudy periods (-10 to 0 min) had a mean $PPFD_{tower}$ of $\sim 300 \mu\text{moles m}^{-2} \text{s}^{-1}$ and a range of 150 to $500 \mu\text{moles m}^{-2} \text{s}^{-1}$. Sunny periods (0 to 20 min) had a mean $PPFD_{tower}$ of $1200 \mu\text{moles m}^{-2} \text{s}^{-1}$ and a range of 1000 to $1500 \mu\text{moles m}^{-2} \text{s}^{-1}$ (Figure 9a).

[27] Both latent (λE_{5min}) and sensible (H_{5min}) heat fluxes increased beginning 5 min after increased illumination, and remained relatively constant thereafter (Figure 9b). The 5-min lag was presumably a result of the time required for a change at the leaf surfaces to translate into a change in the 5-min-averaged turbulent flux past the tower top. The sum of λE_{5min} and H_{5min} was $\sim 23\%$ less than the coincident

net radiation (R_{net} ; Figure 9c). This imbalance is greater than the 13% reported for the site based on 30-min averaged fluxes [*da Rocha et al.*, 2004], a pattern that is consistent with the underestimation of flux caused by 5-min averaging (Figures 1 and 2). The sum of λE_{5min} and H_{5min} was a constant fraction of R_{net} from 5 to 20 min (Figure 9c). The sap-flow-based leaf conductance ($g_{s-branch}$) increased during the first 6 min of illumination, and then declined from 6 to 20 min (Figure 9d). The eddy-covariance-based canopy conductance (G_c) increased after a 5-min lag and then declined from 10 to 20 min (Figure 9e). The CO_2 flux (F_{CO_2-5min}) followed a trend that was similar to G_c , with an initial peak at 5 to 10 min followed by a decline at 10 to 20 min (Figure 9f).

4. Discussion

4.1. Does Warming Negatively Impact Tropical Forest Photosynthesis?

[28] The leaf and canopy measurements confirmed that gas exchange decreases with increased temperature. The leaf measurements showed a $\sim 25\%$ decrease in CO_2 uptake with a 5-to-8° rise in leaf temperature above 30°C (Figure 7). The decrease in leaf CO_2 exchange either resulted from or caused rapid stomatal closure. The 30-min whole-canopy observations indicated a 35-to-40% reduction in gross CO_2 exchange with a 3°C rise in air temperature above 28.5°C

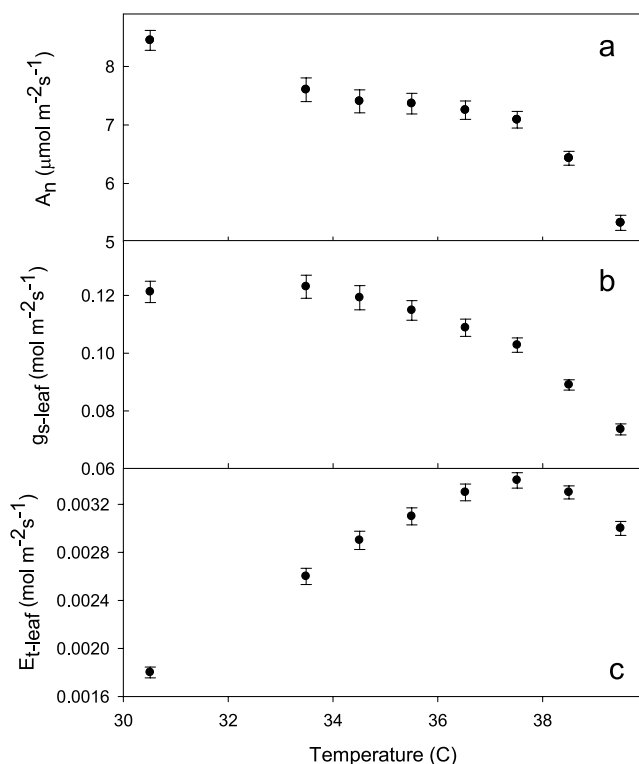


Figure 7. Average leaf temperature response (means \pm se; $n = 66$) for (a) net CO_2 assimilation (A_n ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), (b) stomatal conductance ($g_{s\text{-leaf}}$; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), and transpiration ($E_{t\text{-leaf}}$; $\text{mol m}^{-2} \text{s}^{-1}$) measured with a portable gas exchange system on three canopy-level species (*Sextonia rubra*, *Micropholis sp.*, and *Lecythis lurida*) at the LBA-ECO km-83 site from August to December 2004.

(Figure 3). The decrease in canopy CO_2 exchange either resulted from or caused the rapid reduction in canopy conductance.

[29] Both the leaf- and canopy-level observations indicate that these responses occurred within 5 min of increased temperature (Figures 6, 8, and 9), and that the negative response to temperature was stronger than the positive response to light, such that a simultaneous increase in both irradiance and temperature resulted in a decrease in photosynthesis. The sap-flow measurements indicated a rapid but transient increase in stomatal conductance following increased illumination (Figure 9d). The eddy covariance measurements indicated the response lagged increased illumination (Figure 9), but this lag was likely an artifact of delays in atmospheric transport, and the true rate of canopy gas exchange probably responded very rapidly to increased irradiance. The increase in canopy gas exchange was transient, and the rates of conductance and photosynthesis began to decline within 5 min of reaching a peak (Figure 9), and within a few minutes of the increases in leaf and canopy temperature (Figure 6).

4.2. Why is Whole Forest CO_2 Uptake Highly Sensitive to Increased Temperature?

[30] A key question involves the strength of the warming effects we observed and whether the leaf- and canopy-level observations are congruent. The sensitivity of canopy gas

exchange to an increase in aerodynamic temperature appears greater than the sensitivity of leaf gas exchange to an increase in leaf temperature. A 3°C rise in air temperature caused a 35 to 40% reduction in whole-canopy gross gas exchange (Figure 3), whereas a 5 to 8°C rise in leaf temperature caused a $\sim 25\%$ reduction in leaf gas exchange (Figure 7).

[31] The difference between canopy- and leaf-level sensitivity appears to result from leaf-to-leaf heterogeneity in warming. Observations of the leaf microclimate indicate that leaves exist in two states: a well-illuminated, warm state and a poorly illuminated, cool state (Figures 4 and 5). The aerodynamic and air temperatures reflect the bulk properties of the physical environment. A few degree rise in aerodynamic temperature with increased illumination (Figure 6b) does not indicate that all the leaves in the canopy have warmed by a few degrees, but rather that the sunlit leaves warmed considerably while the shaded leaves remained relatively cool (Figure 6a). The most brightly illuminated leaves approached or exceeded the leaf temperature where gas exchange is curtailed, while the shaded leaves remained well below this threshold (Figure 6a). The rates of photosynthesis by the well-illuminated, warm leaves are

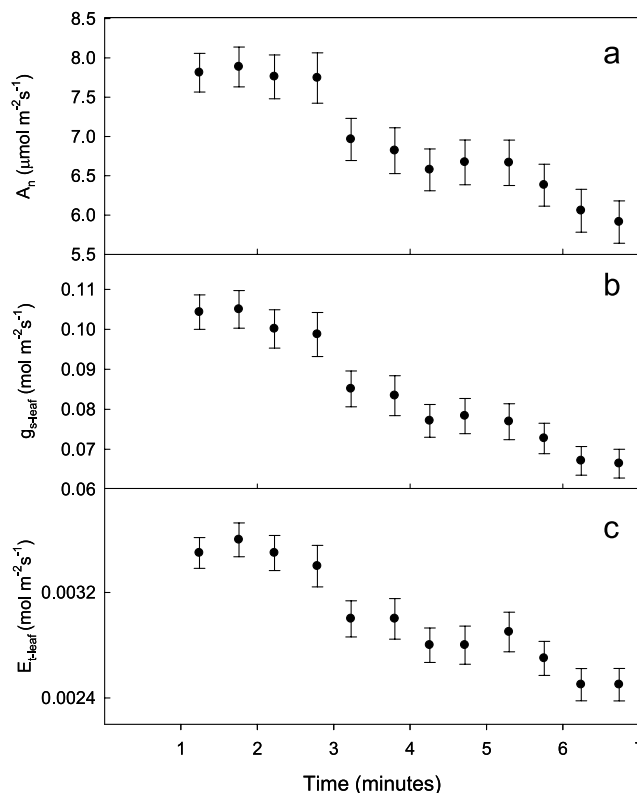


Figure 8. Transient response of leaf gas exchange when shaded (leaf surface PPFD $< 500 \mu\text{mol m}^{-2} \text{s}^{-1}$), relatively cool (leaf temperature \sim air temperature), canopy leaves were placed into a prewarmed (35 to 38°C), brightly illuminated ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) leaf gas exchange chamber ($n = 52$). Points show the average responses \pm se of (a) net CO_2 assimilation (A_n ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), (b) stomatal conductance ($g_{s\text{-leaf}}$; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), and transpiration ($E_{t\text{-leaf}}$; $\text{mol m}^{-2} \text{s}^{-1}$) for leaves of three species (*Sextonia rubra*, *Micropholis sp.*, and *Lecythis lurida*).

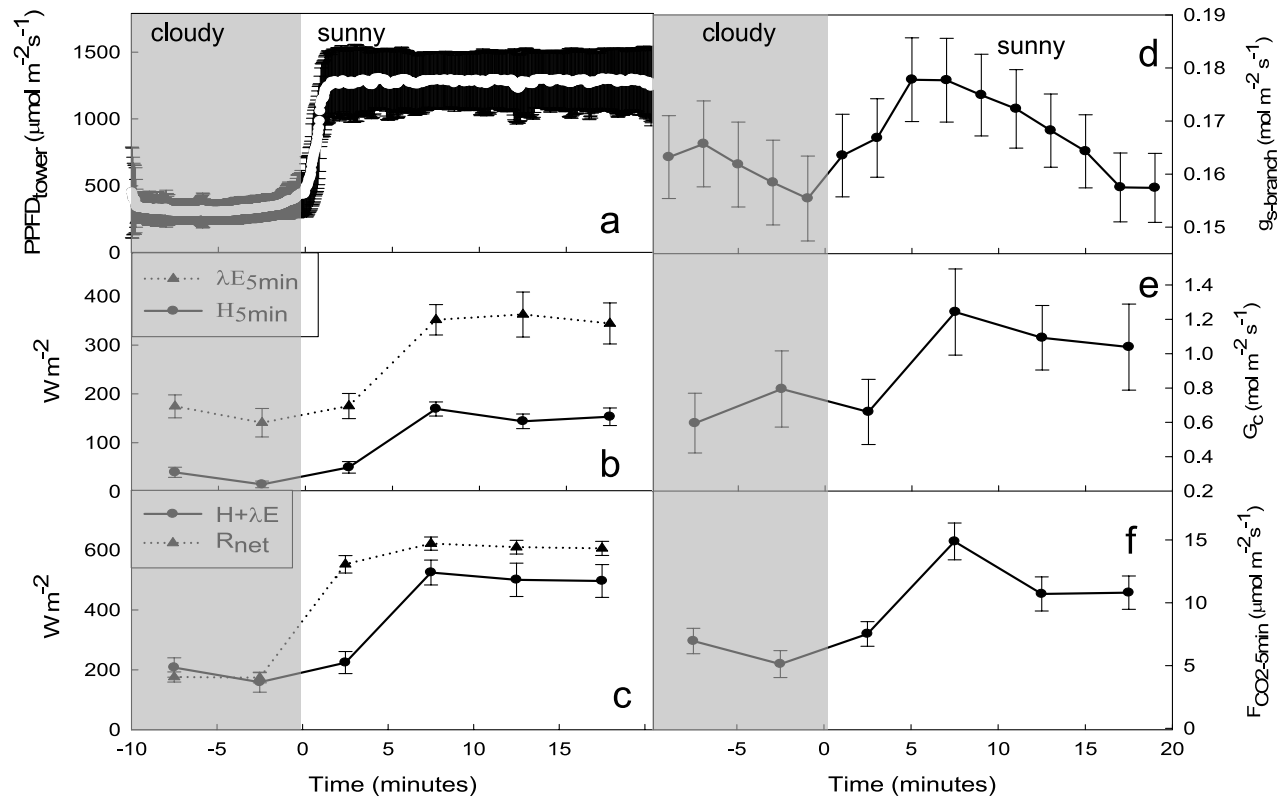


Figure 9. Transient response of canopy gas exchange to abrupt increases in illumination. All plots show ensemble averages ($n = 42$ for Figures 9a, 9b, 9c, 9e, and 9f; $n = 54$ for Figure 9d) for half hour periods with 10 cloudy minutes (time = -10 to 0 min) followed by 20 sunny minutes (time = 0 to 20 min). Individual panels show (a) tower top irradiance ($\text{PPFD}_{\text{tower}}$ in $\mu\text{mol m}^{-2}\text{s}^{-1}$) $\pm\text{sd}$, (b) latent heat flux ($\lambda E_{5\text{min}}$ in W m^{-2}) $\pm\text{se}$ and sensible heat ($H_{5\text{min}}$ in W m^{-2}) $\pm\text{se}$, (c) the sum of latent and sensible heat $\pm\text{se}$ and the net radiation (R_{net} in W m^{-2}) $\pm\text{se}$, (d) averages for 6 sap flow sensors ($g_{\text{s-branch}}$ in $\text{mol m}^{-2}\text{s}^{-1}$) $\pm\text{se}$, (e) canopy conductance (G_c in $\text{mol m}^{-2}\text{s}^{-1}$) $\pm\text{se}$, and (f) CO_2 uptake ($F_{\text{CO}_2-5\text{min}}$ in $\mu\text{mol m}^{-2}\text{s}^{-1}$) $\pm\text{se}$. Sensible heat, latent heat, and CO_2 uptake were calculated from the eddy covariance observations using 5-min averaging. CO_2 uptake is shown as a positive flux.

presumably limited by temperature; the rates of photosynthesis by the poorly illuminated, cool leaves are limited by light. The rate of whole canopy gas exchange is heavily dependent on the fluxes by sunlit leaves; shaded leaves contribute disproportionately less to whole ecosystem gas exchange. Whole ecosystem gas exchange is therefore strongly sensitive to modest increases in bulk temperature.

4.3. What Are the Implications for Modeling Tropical Forest Gas Exchange?

[32] Our observations explain the strong sensitivity of canopy gas exchange to temperature, and the apparent discrepancy between leaf and canopy observations. The finding provides a mechanism that potentially increases the sensitivity of tropical forest to warming. The finding also has implications for modeling canopy gas exchange. The relationship between leaf gas exchange and leaf temperature is nonlinear (Figure 7). The combination of a nonlinear leaf-level response and large, correlated heterogeneity in leaf irradiance and temperature (Figures 4 and 5) creates a nonlinear averaging problem for models of tropical forest gas exchange. The average response of leaves to their local environments differs from the response of leaves to the

average environment. A similar pattern may occur across the landscape at any given moment associated with the movement of clouds and correlated changes in temperature and irradiance. Photosynthesis by cloud-covered forest patches may be limited by light; photosynthesis by brightly illuminated patches may be limited by temperature. The average response of canopies in a grid cell to their local physical conditions may differ from the response of canopies to the grid cell's average physical conditions.

4.4. Does Decreased Cloud Cover Increase or Decrease Tropical Forest CO_2 Uptake?

[33] The light environment above many tropical forests is highly dynamic, with the rapid passage of small, shallow cumulus clouds that punctuate sunny intervals (Figure 4). Over 60% of the light at km-83 during the dry season arrives in intervals with less than 10-min duration (data not shown). The occurrence of frequent, brief cloudy intervals cools the canopy, and reduces the likelihood that leaf temperatures will reach the point of markedly diminished CO_2 uptake (Figures 4 and 6). The frequency of cloud cover in the tropics has declined in the last decade, with a reduction in low-level clouds in the spring and fall [Wielicki

et al., 2002]. *Nemani et al.* [2003] suggested that tropical forest production is light limited, and that the observed reduction in cloud cover in the Amazon Basin has markedly increased NPP. However, the decrease in Amazonian cloud cover would also be expected to lead to longer sunny intervals and greater canopy heating. This increased heating might have amplified the high temperature stress on tropical leaves, resulting in a much smaller effect on tropical production than *Nemani et al.* [2003] suggested. High aerosol optical depth due to smoke from biomass burning can also cool the canopy, reducing temperature stress and contributing to the observed increase in CO₂ uptake during smoky periods [*Oliveira et al.*, 2007] (*C. E. Doughty et al.*, Effect of smoke on subcanopy diffuse light, canopy temperature, and CO₂ uptake in an Amazon rainforest, submitted to *Global Biogeochemical Cycles*, 2008).

4.5. Will Climatic Warming Harm Tropical Forests?

[34] We have identified a mechanism that increases the sensitivity of tropical forest photosynthesis to warming; the brightly illuminated leaves that contribute disproportionately to canopy photosynthesis are warmed to the point that leaf gas exchange is curtailed. Tropical air temperatures are forecast to rise 2 to 5°C with global warming [*Cramer et al.*, 2004; *Zhang et al.*, 2001]. The air temperature in the tropics is expected to rise less than that in temperate or arctic regions. But the plants that grow in the tropics may be more sensitive to warming than the plants in temperate or arctic regions, and the impact of warming on the tropical biota may exceed that on the temperate or arctic biota. Will warming harm tropical forests? At least three unknowns will determine the answer to this question: Can tropical plants acclimate to warming? Are tropical plants carbon limited? Will elevated CO₂ offset the deleterious effects of warming on photosynthetic physiology and stomatal conductance?

[35] Most temperate plant species can acclimate to changing temperature conditions [*Berry and Björkman*, 1980], and it is possible that the plants at km-83 would simply acclimate to higher temperatures with a warmer climate. However, it remains uncertain whether most tropical species have the ability to acclimate to higher temperatures. The tropics are a thermally stable environment, and most tropical plants are not forced to acclimate to the wide seasonal fluctuations in temperature experienced by temperate ecosystems [*Janzen*, 1967]. There is evidence that tropical species are less likely than temperate species to acclimate to changing temperatures [*Cunningham and Read*, 2003a]. Tropical trees have a lower temperature optimum for carbon assimilation than for growth, which could cause increasing growth even as photosynthesis declines [*Cunningham and Read*, 2003b; *Raich et al.*, 2006]. Biochemical analyses indicate that tropical trees possess large carbohydrate pools and that plant growth is not limited by the availability of carbon [*Wurth et al.*, 2005]. A decrease in GPP associated with warming might not impact tropical forest NPP, if forest NPP is limited by something other than GPP such nutrients or water. Finally, an increase in atmospheric CO₂ concentration might offset the impact of warming, either by providing increased substrates for carboxylation or by reducing the limitation on photosynthesis imposed by stomatal closure.

[36] Large changes in tropical forests primary production have the potential to amplify global climate change [*Clark*,

2004; *Cox et al.*, 2000]. Further research is needed to determine whether the rapid, deleterious effects of warming on gas exchange that we have described will translate into a sustained reduction in primary production. Tropical forests currently appear close to a high temperature threshold, but whether they cross such a threshold in a warmer world will depend in a large measure on their ability to acclimate to high temperatures.

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