



Effect of smoke on subcanopy shaded light, canopy temperature, and carbon dioxide uptake in an Amazon rainforest

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[1] Daytime Net Ecosystem CO₂ uptake (NEE) in an Amazon forest has been shown to increase significantly during smoky periods associated with biomass burning. We investigated whether the increase in CO₂ uptake is caused by increased irradiance in the lower canopy, which results from increased above-canopy diffuse light, or by decreased canopy temperature, which results from decreased above-canopy net radiation. We used Sun photometers measuring aerosol optical depth to find nonsmoky (Aerosol Optical Depth (AOT) < 0.35), smoky (AOT > 0.5) and very smoky (AOT > 0.7) periods for the Tapajós region in the Amazon. Using a network of subcanopy photosynthetic photon flux density (PPFD) sensors, we detected a $\sim 4 \mu\text{mol m}^{-2} \text{s}^{-1}$ increase in subcanopy diffuse light during smoky periods relative to nonsmoky periods. Using a pyrgeometer to measure upwelling longwave radiation and, hence, canopy surface temperature, we found a $\sim 0.5^\circ\text{C}$ cooling relative to air temperature during smoky periods. We modeled subcanopy irradiance based on the subcanopy PPFD sensors and combined this with subcanopy leaf photosynthesis measurements to determine how the increased lower canopy light affected NEE. We used the relationship between temperature and NEE measured by eddy covariance to determine the effect of decreased canopy temperature on canopy CO₂ uptake. We found that the increase in CO₂ uptake at high aerosol optical depths is primarily a result of increased shaded light in the subcanopy (accounting for $\sim 80\%$) and to a lesser extent the effect of decreased canopy temperature (accounting for $\sim 20\%$).

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1. Introduction

[2] Extensive biomass burning in the Amazon rainforest creates atmospheric aerosols that can affect the region in multiple ways. Aerosols from tropical forest fires can reduce surface solar radiation by as much as 375 W m^{-2} and reduce surface temperatures by 2°C – 3°C [Schafer *et al.*, 2002]. Aerosols may cool the surface while warming the lower atmosphere (2–4 km) [Eck *et al.*, 1998; Satheesh and Ramanathan, 2000]. Aerosols may indirectly warm the surface by reducing shallow cumulus clouds during periods of heavy smoke, thereby, causing an increase in solar radiation absorbed by the surface [Koren *et al.*, 2004]. Aerosols can

influence precipitation by changing the height at which clouds form [Andreae *et al.*, 2004].

[3] Atmospheric aerosols from biomass burning may influence ecosystems directly by scattering light, which decreases overall irradiance but increases the diffuse component. Clouds and volcanic ash, in addition to biomass burning, can increase diffuse light, and their effect on ecosystems has been studied previously. Studies comparing Sun photometers measuring optical depth [Holben *et al.*, 1998] to eddy covariance towers measuring CO₂ exchange [Baldochi *et al.*, 2001] concluded that diffuse light increased CO₂ uptake in crops and forests and decreased CO₂ uptake in grasslands [Niyogi *et al.*, 2004]. Other studies have shown an increase in canopy light use efficiency by forests during periods of increased diffuse light [Misson *et al.*, 2005; Baldochi, 1997; Knohl and Baldochi, 2008]. Large volcanic eruptions increase diffuse light and provide a global test of the effect of diffuse light on gross production. An increase in aerosols from the Mount Pinatubo eruption coincided with a global increase in net CO₂ uptake [Gu *et al.*, 2003], possibly because of reduced respiration [Lucht *et al.*, 2002]. However, in northern ecosystems, Net Primary Production (NPP)

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decreased in response to volcanic events, based on an analysis of tree rings [Krakauer and Randerson, 2003].

[4] Most of these studies attribute the positive correlation between CO₂ uptake and aerosol optical depth to increased subcanopy diffuse light [Roderick *et al.*, 2001]. Canopy top leaves are generally light saturated during midday conditions, and a marginal reduction in total irradiance does not decrease photosynthesis by these leaves. Subcanopy leaves, on the other hand, are often strongly light limited, and an increase in incoming diffuse light, which penetrates more deeply into the subcanopy, may increase the light levels in the subcanopy and the rates of photosynthesis by lower leaves. Others have suggested that increased radiation sharing because of varied leaf orientation within the canopy instead of increased beam penetration is the main cause of the increase in light use efficiency [Alton *et al.*, 2007].

[5] Atmospheric aerosols may also influence ecosystems by reducing leaf temperature, which decreases respiration and heat stress on leaves. Field observations have drawn attention to the possibility that tropical forests are highly sensitive to temperature [Clark *et al.*, 2003; Doughty and Goulden, 2008a; Feeley *et al.*, 2007]. 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]. These observations raise the possibility that aerosol induced cooling increases CO₂ uptake by tropical forests. Some recent studies have suggested that temperature may be as important as diffuse radiation in increasing CO₂ uptake during periods of increased optical depth [Min, 2005; Steiner and Chameides, 2005].

[6] The effect of biomass burning on surface radiation balances can be quantified using AERONET monitoring stations, which measure the increase in column light extinction relative to pure Rayleigh scattering [Holben *et al.*, 1998]. Aerosol concentrations in the Amazon reached 30,000 particles per cubic centimeter in the dry season and an aerosol optical thickness of 3 at 500 nm [Andreae *et al.*, 2004; Procopio *et al.*, 2004], although the Tapajos region rarely exceeded AOT > 1.

[7] A previous study quantified the effects of biomass burning on the Amazon by comparing CO₂ fluxes from eddy covariance towers with aerosol optical depth in two regions of the Amazon forest [Oliveira *et al.*, 2007]. Net ecosystem exchange (NEE) increased during periods of high optical depth associated with biomass burning. The authors could not determine if increased NEE was caused by an increase in subcanopy light or a decrease in canopy temperature.

[8] In this paper we investigated whether increased aerosol optical depth in an Amazonian forest increased NEE because of increased diffuse light or decreased temperature. We used measurements of aerosol optical depth, eddy covariance CO₂ flux, subcanopy PPFD, emitted long-wave radiation for canopy skin temperature, and subcanopy leaf-level photosynthesis to test three hypotheses:

Hypothesis 1: For a given global irradiance, diffuse light in the subcanopy increases during smoky, noncloudy periods compared to nonsmoky, noncloudy periods.

Hypothesis 2: For a given global irradiance, NEE increases during noncloudy, high AOT periods, because of increased irradiance of subcanopy shade leaves.

Hypothesis 3: Applying current understanding of factors governing NEE, the elevated NEE rates that are observed under smoky conditions cannot be explained solely by enhanced photosynthesis because of increased diffuse light.

2. Methods

2.1. Site

[9] This study was conducted at the Large-scale Biosphere-Atmosphere project (LBA-ECO) km-83 site (3.020833 S, 54.972221W) in the Floresta Nacional do Tapajos (FLONA). The FLONA Tapajos extends from 50 to 150 km south of Santarem, Para, Brazil, on the eastern side of the Tapajos River. The vegetation was closed tropical forest, with a canopy height of ~40 m and scattered emergent trees up to 55 m. The FLONA was in the 27th percentile ($\pm 2\%$ to 3%) of Amazonian forests with respect to both annual precipitation and wet season length [Saleska *et al.*, 2003]. The forest was on a broad, flat plateau [Goulden *et al.*, 2004]. Soils were mainly yellow latosol clay (Haplic acrorthox). 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 Large-scale Biosphere-Atmosphere project (LBA-ECO) experiment, and its effect is described in previous papers [Miller *et al.*, 2007; Figueira *et al.*, 2008].

2.2. Tower Measurements

[10] We used the eddy covariance method [Wofsy *et al.*, 1993; Baldocchi, 2003a] to measure the turbulent fluxes of CO₂ at 64 m above ground level. Tower equipment and data processing are explained in previous papers [da Rocha *et al.*, 2004; Goulden *et al.*, 2004; Miller *et al.*, 2004]. Tower top meteorological measurements were recorded at 0.5 Hz. Incoming photosynthetically active photon flux density (PPFD) at 64 m was measured with silicon quantum sensors (LI-COR LI190; Lincoln, Neb). We measured air temperature with ventilated thermistors (model 076B; Met One, Grants Pass, Ore; model 107, Campbell Scientific, Logan, Utah) and long-wave radiation emitted by the forest (CG2 net pyrometer; Kipp and Zonen, Delft, Holland). Below-canopy PPFD was measured with 8 quantum sensors (Apogee Instruments, Logan, Utah) that were horizontally mounted at ~30 cm above the forest floor. The sensors were arrayed at 5 m intervals along two 15 m transects in a forest patch that was ~20 to ~40 m from the nearest logging-created gap and that was ~40 m from the tower. This is an adequate sample size to get a representative sample of indirect shaded light [Reifsnyder *et al.*, 1971].

2.3. Analysis of Half Hour Averaged Tower Data

[11] We calculated forest light curves using half hourly averaged eddy flux data from October–December 2002 and October–December 2003. We compared light curves on smoky days (at aerosol optical depths >0.5, >0.7, >1) versus nonsmoky days (AOT < 0.35). We compared half hour averaged gross ecosystem exchange (GEE), which was cal-

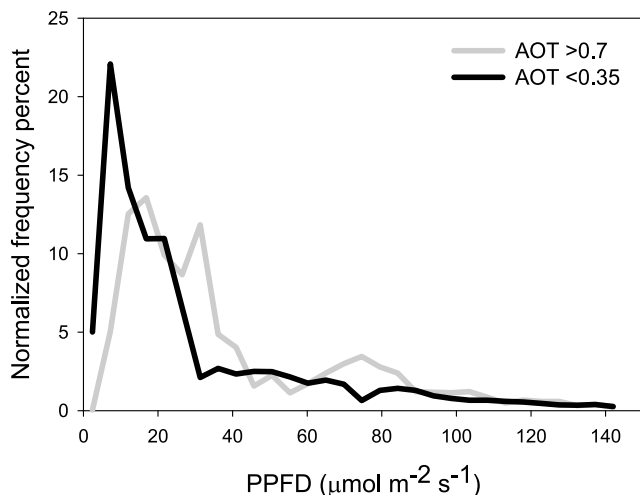


Figure 1. Seven ground level PPFD sensors averaged together during midday (1100–1300) noncloudy (PPFD > 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) smoky (AOT > 0.7) (gray line) ($n = 13,395$) and noncloudy (PPFD > 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) non-smoky periods (AOT < 0.35) (black line) ($n = 34,651$). Data are normalized histograms with bin widths of 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

culated by subtracting respiration from NEE, to half hourly incoming PPFD at the tower top. To calculate respiration during the daytime, we used a simple Arrhenius type model shown below [Lloyd and Taylor, 1994]

$$R_{\text{eco}} = rb \exp\left(E_0 \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{air}} - T_0} \right)\right), \quad (1)$$

where rb ($\mu\text{mol C m}^{-2} \text{s}^{-1}$) is the average nighttime forest respiration for 3 days prior at the reference temperature (T_{ref}), E_0 ($^{\circ}\text{C}$) is the temperature sensitivity, T_{air} is the air temperature, and T_0 ($^{\circ}\text{C}$) is kept constant at -46.02°C following the study of Lloyd and Taylor [1994].

2.4. Analysis of 5 Min Averaged Tower Data

[12] To increase our sample size and separate noncloudy and cloudy periods, we screened the data to find 5 min periods that were consistently noncloudy or cloudy and used these periods to calculate the eddy covariance fluxes. 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, 2003b]. There are few continuously noncloudy or cloudy half-hour periods in the tropics. By calculating fluxes at 5 min intervals, we increased our sample size and reduced random sampling error [Doughty and Goulden, 2008a]. We screened the tower top PPFD data to identify intervals with either 10 cloudy minutes (PPFD < 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or 10 noncloudy minutes (PPFD > 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$). We calculated the turbulent fluxes of CO_2 for the second 5 min interval to avoid transient effects that may be present in the first 5 min interval.

2.5. AERONET Data

[13] We used optical depth data from an AERONET station ~ 40 km away from our eddy covariance tower. In

remote regions, aerosol optical depths at this distance are well correlated [Andreae et al., 2004; Procopio et al., 2004]. AERONET has an algorithm to exclude cloud contamination of the AOT measurements [Holben et al., 1998]. We screened the km-83 eddy flux data with three daily averaged optical depths thresholds: nonsmoky (AOT < 0.35), smoky (AOT > 0.5), and very smoky (AOT > 0.7). We used AERONET level 2.0 (cloud screened and recalibration of the CIMEL Sun photometer) daily averaged 500 nm aerosol optical depth from the nearby Belterra site ($02^{\circ}39'S$ and $54^{\circ}58'W$) (~ 40 km from our tower site) to determine AOT above our eddy covariance tower. We used data from October to December because these months had both high aerosol optical depth, relatively steady leaf area index (LAI), net ecosystem exchange (NEE) [Doughty and Goulden, 2008a], and soil moisture [Bruno et al., 2006]. We compared the measured decrease in downwelling shortwave irradiance to the predicted decrease in downwelling irradiance at different aerosol optical depths. The predicted decrease, calculated using a radiative transfer model modified for the Amazon, was based on digitized data from the study of Oliveira et al. [2007].

2.6. Analysis of Radiation Data

[14] We used the tower top PPFD sensor to find 10 min, midday (~ 1100 – 1300 local time), noncloudy (PPFD > 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$), or cloudy intervals (PPFD < 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for nonsmoky (AOT < 0.35) days, smoky (AOT > 0.5) and very smoky days (AOT > 0.7). We compared irradiance between the tower top and subcanopy PPFD sensors to determine the effect of aerosol optical depth on subcanopy light. We removed all observations with a subcanopy PPFD greater than 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to eliminate sunflecks and isolate the subcanopy shaded irradiance. We selected a threshold of 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ -based analyses of the distribution of subcanopy light which show a substantial decrease between light levels above 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and much higher light levels (Figure 1). We tried several different thresholds to screen for light flecks, and all resulted in similar results. The PPFD sensors have the capability to measure changes of 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in irradiance (Apogee Instruments, Logan Utah, personal communication), and we programmed our data storage systems (Campbell CR23X) with sufficient bit size to record such a change. The light sensors are truly linear to complete darkness (Apogee Instruments, Logan, Utah, personal communication), and the observed sensor signals at night sensors were zero. We used midday periods (~ 1100 – 1300 local time) to avoid confounding zenith angle effects.

[15] We confirmed that the tower top and subcanopy sensors were synchronized by maximizing the covariance between the two data sets. We consider each 10 min period as a single sample for statistical analysis, in order to avoid pseudo replication.

[16] We calculated canopy temperature using a pyrgeometer to measure long-wave emission (L) (W m^{-2}). We calculated canopy skin temperature as

$$T = \left(\frac{L}{\varepsilon\sigma} \right)^{.25}, \quad (2)$$

Table 1. AERONET Aerosol Optical Depth at 500 nm for the Belterra Site Between October–December 2002 and October–December 2003^a

Data Classification for Oct–Dec 2002 to Oct–Dec 2003	Average AOT 500	Days AOT 500 That Met the Requirements	Expected Relative Irradiance [<i>Oliveira et al.</i> , 2007]	% Expected Decrease in Solar Radiation	% Measured Decrease in Solar Radiation
AOT < 0.35	0.23	68	0.94		
AOT > 0.5	0.71	32	0.84	11%	8%
AOT > 0.7	0.91	12	0.81	14%	13%

^aWe found averaged AOT and the number of days where AOT < 0.35, > 0.5 and > 0.7. We calculated expected relative irradiance for AOT < 0.35, > 0.5 and > 0.7 for the Belterra site following [*Oliveira et al.*, 2007]. We compared the expected relative irradiance due to aerosols to the actual decrease in shortwave downwelling irradiance at our site.

where ε is emissivity (0.98 for canopies) [*Monteith and Unsworth*, 1990] and σ is the Boltzmann constant ($5.670 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$).

2.7. Leaf Gas Exchange

[17] We measured leaf gas exchange from scaffold towers [*Doughty and Goulden*, 2008b; *Doughty et al.*, 2006] at the LBA-ECO km-83 [*Goulden et al.*, 2004] and km-67 [*Saleska et al.*, 2003] field sites. Both sites were in closed-canopy evergreen forest in the FLONA Tapajós. The km-83 scaffold tower was located within 300 m of the main eddy flux tower. We measured the following subcanopy and understory species: *Eschweilera amazonica*, *Lecythis* sp., *Chimarrhis turbinata*, *Faramea platyneura*, *Sclerolobium paraense*.

[18] We used a portable gas exchange system (LI 6400; Li-Cor Biosciences, Lincoln, Neb) in April and May 2002 to measure the rates of gas exchange at a range of light levels (PPFD 0, 50, 100, 200, 500, 1000, 1500, 1800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), with constant temperature (30°C) and ambient CO_2 . We grouped the data into understory (0–10 m) and subcanopy (10–25 m) leaves.

2.8. Canopy Radiation Transfer Model

[19] To model the partitioning of diffuse and direct radiation beneath the canopy top, we applied an adapted version of the shortwave narrowband model [*Zender et al.*, 1997], which computes multistream fluxes using DISORT [*Stamnes et al.*, 1988]. We used 10 canopy layers. We assumed a spherical leaf angle distribution, such that optical depth within each layer was $0.5 \times (\text{leaf} + \text{stem area index})$. We assumed leaves were the fundamental scattering element, and single-scatter albedo equaled leaf albedo. We applied the suggested aerosol optical properties for tropical forest from the study of *Reid et al.* [2005], extending 550 nm values to the full spectrum using a Mie solver.

[20] The model predictions of forest floor light did not match the observations: the model predicted a larger change between smoky and nonsmoky periods than was observed. Our PPFD sensors originally had a median value of $1.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ during low AOT periods. This is lower than previous measured wet tropical forest subcanopy light which averaged between 5 and 50 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ [*Chazdon and Percy*, 1991]. Our sensors darkened over several years because of downward drift in the signals associated with aging or the accumulation of dirt on the instrument surfaces [*Doughty and Goulden*, 2008b]. We calculated the average downward linear trend for all sensors and used these regressions to correct

for the downward drift in the understory sensors. This increased median peak diffuse understory irradiance to $7.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at low AOTs (Figure 1) which is within the range found by others [*Chazdon and Percy*, 1991]. With these corrections, the model estimation of increased diffuse light because of smoke was close to our subcanopy sensors but still almost double our measurements. Therefore, to calculate the increase in diffuse light at each LAI, we divided the vertical profile model output by the model at each LAI by the ratio of the bottom of canopy light observed versus modeled, which was ~ 2 .

[21] We calculated the percentage LAI shaded at each LAI and multiplied this by the increase in diffuse light with the quantum yield (carbon fixed per quanta light) of photosynthesis from 0 to 50 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. We determined the change in net canopy photosynthesis due to increased shaded light as

$$\sum_{i=1}^5 \Delta D(\text{LAI}_i) \times S(\text{LAI}_i) \times Q(\text{LAI}_i), \quad (3)$$

where ΔD is the increase in subcanopy light at each LAI, S is percentage LAI shaded at each LAI, and Q is the quantum yield for leaves at each LAI. We assumed an LAI of 6 [*Doughty and Goulden*, 2008b].

3. Results

3.1. Effect of Aerosol Optical Depth on Irradiance

[22] There were 68 days at Belterra when the daily averaged 500 nm AERONET aerosol optical depth was below 0.35, 32 days when it was above 0.5, and 12 days when it was above 0.7, during October–December 2002 and October–December 2003. The average AOT was 0.23 at AOT < 0.35, 0.71 for AOT > 0.5, and 0.91 for AOT > 0.7. We compared measured decreases in irradiance due to smoke for the Tapajós region to modeled decreases [*Oliveira et al.*, 2007] to ensure that the decrease in irradiance during smoky periods was due to the smoke. Modeled irradiance predicted a 11% decline between AOT 0.23 and AOT 0.72 and a 14% decline between AOT 0.23 and AOT 0.91 at zenith angles between 20° and 30° [*Oliveira et al.*, 2007]. Averaged downwelling shortwave irradiance at the km-83 field site decreased during noncloudy periods (defined as $>1200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance) between 1100 and 1300 local time by 8% between averaged AOT = 0.23 and averaged AOT 0.72 and decreased by 13% between averaged AOT = 0.23 and averaged AOT =

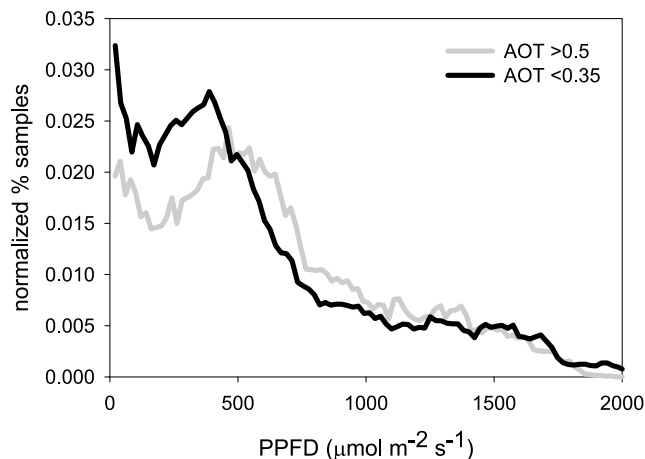


Figure 2. Two second tower top PPFD for smoky days (gray line) ($AOT > 0.5$) and nonsmoky days ($AOT < 0.35$) (black line) for October–December 2002 and October–December 2003.

0.91 (Table 1). Measured changes in irradiance, due to smoke, closely matched modeled changes in irradiance.

[23] The occurrence of periods with irradiance above $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ decreased substantially during smoky times ($AOT > 0.5$) compared with nonsmoky intervals ($AOT < 0.35$) (Figure 2). However, contrary to our expectations, irradiance increased slightly during cloudy periods (irradiance between $600\text{--}800 \mu\text{mol m}^{-2} \text{s}^{-1}$) that were also smoky ($AOT > 0.5$) relative to nonsmoky intervals ($AOT < 0.35$).

3.2. Effect of Aerosol Optical Depth on Half-Hour Averaged Canopy Fluxes

[24] We compared half-hour averaged gross ecosystem exchange (GEE) between October to December at various optical depths ($AOT > 0.5$, $AOT > 0.7$, and $AOT > 1$) (Figure 3). There were no significant differences between light-saturated GEE ($PPFD > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) during nonsmoky periods ($AOT < 0.35$) and smoky periods ($AOT > 0.5$). However, there was a significant increase in light-saturated GEE at $AOT > 1$ ($P < 0.05$) and the increase in GEE at $AOT > 0.7$ was large and nearly significant ($P = 0.08$). The mean light-saturated GEE ($PPFD > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) \pm standard deviation at $AOT < 0.35$ was -19.8 ± 7.1 , -19.8 ± 8.0 at $AOT > 0.5$, -22 ± 6.5 at $AOT > 0.7$, and -25.8 ± 5.1 at $AOT > 1$.

3.3. Effect of Aerosol Optical Depth on 5 Min Averaged Canopy Fluxes

[25] We calculated 5 min averaged NEE for smoky and nonsmoky periods. CO_2 uptake increased significantly ($P > 0.05$) during smoky, noncloudy periods ($AOT > 0.5$) and during ($P > 0.001$) very smoky, noncloudy periods ($AOT > 0.7$) compared to nonsmoky ($AOT < 0.35$), noncloudy periods (Figure 4). CO_2 uptake at $AOT > 0.7$ was significantly greater ($P > 0.05$) than CO_2 uptake at $AOT > 0.5$. There were no significant differences between smoky, cloudy, and

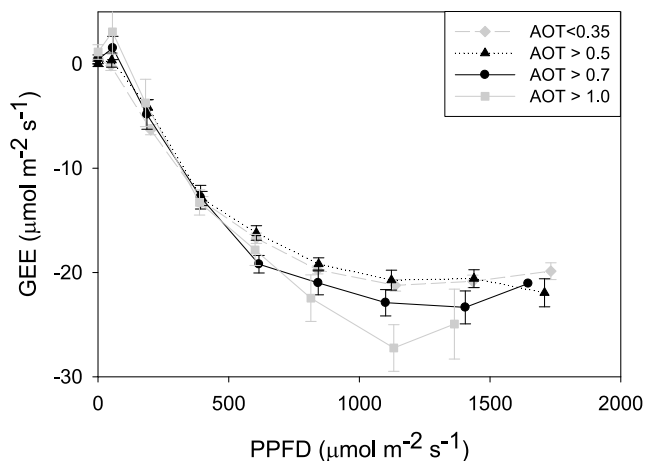


Figure 3. Light curves using half-hour averaged PPFD and GEE for $AOT > 0.5$ (dotted black line), > 0.7 (solid black line), > 1 (solid gray line) and $AOT < 0.35$ (dashed gray line) for October–December 2002 and October–December 2003. GEE is calculated as NEE minus averaged nighttime respiration over a 3 day period adjusted for daytime temperatures using an Arrhenius-type model [Lloyd and Taylor, 1994].

nonsmoky, cloudy periods, although there was a slight decrease in mean CO_2 uptake during smoky, cloudy periods.

3.4. Effect of Aerosol Optical Depth on Subcanopy Shaded Light

[26] Subcanopy shaded light increased slightly during smoky, noncloudy periods versus nonsmoky, noncloudy

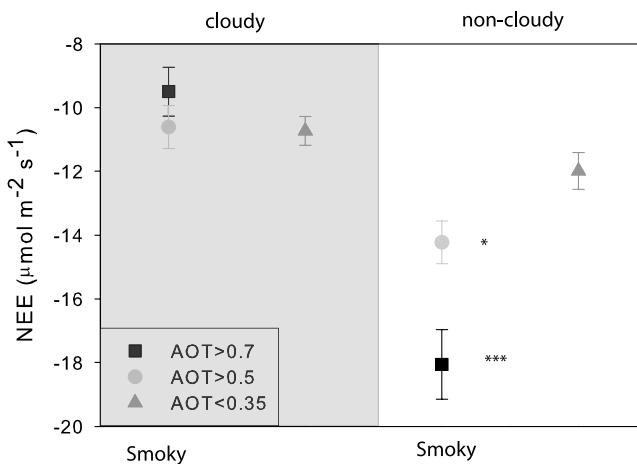


Figure 4. Midday NEE data (1000–1400) calculated using 5 min eddy flux intervals during cloudy ($PPFD < 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) smoky ($AOT > 0.5$ and $AOT > 0.7$), cloudy ($PPFD < 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) nonsmoky ($AOT < 0.35$), noncloudy ($PPFD > 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) smoky ($AOT > 0.5$ and $AOT > 0.7$), and noncloudy ($PPFD > 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) nonsmoky periods ($AOT < 0.35$). All 5 min flux calculations were preceded by a 5 min period with identical conditions to avoid edge effects. The errorbars are \pm SE. *** indicates significance at the $P < 0.001$. * indicates significance at the $P < 0.05$.

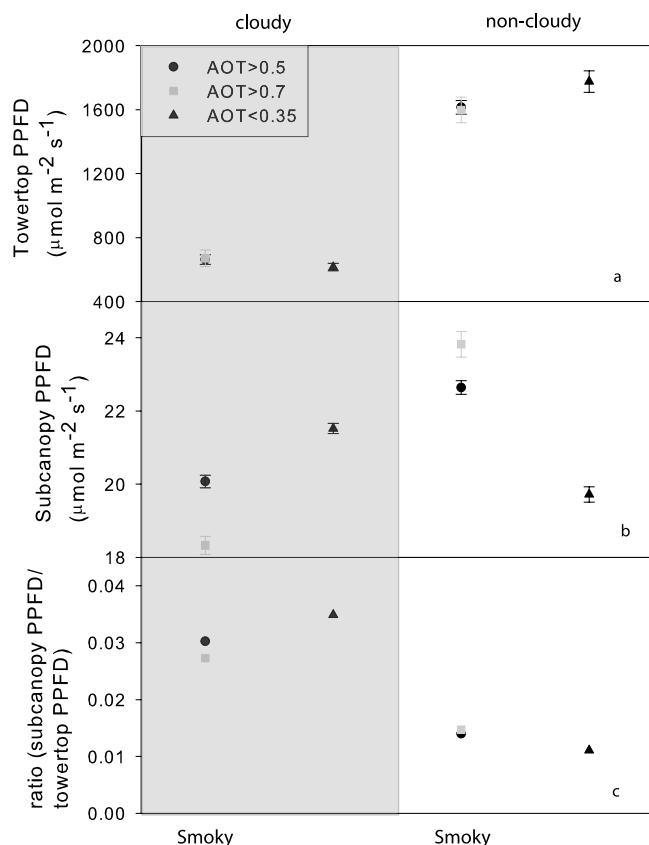


Figure 5. Noontime data (1100–1300) for (a) tower top PPFD during periods of cloudy (PPFD < $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) smoky (AOT > 0.5 and AOT > 0.7), cloudy (PPFD < $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) nonsmoky (AOT < 0.35), noncloudy (PPFD > $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) smoky (AOT > 0.5 and AOT > 0.7), and noncloudy (PPFD > $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) nonsmoky periods (AOT < 0.35). (b) The amount of PPFD reaching the subcanopy during these periods. The errorbars are 95% confidence intervals. (c) The ratio between PPFD at the top of the canopy and diffuse light (nonsunflecks) intercepted by seven ground level subcanopy PPFD sensors during the same intervals.

periods (Figure 1). Light levels were significantly greater ($P < 0.05$) during smoky and very smoky periods (AOT > 0.5, > 0.7) than nonsmoky periods (AOT < 0.35) during midday (1100–1300 local time) noncloudy periods (PPFD > $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 5). There were no significant differences in subcanopy shaded light between midday (1100–1300 local time), cloudy (PPFD > 400 and PPFD < $800 \mu\text{mol m}^{-2} \text{s}^{-1}$), nonsmoky (AOT < 0.35), and midday, cloudy, smoky (AOT > 0.5) periods. There was a significant decrease in subcanopy shaded light during cloudy, very smoky AOT > 0.7 periods versus cloudy, nonsmoky AOT < 0.35 periods.

[27] The ratio of irradiance reaching the subcanopy is significantly higher during cloudy intervals than noncloudy intervals (0.035 cloudy at AOT < 0.35 versus 0.01 noncloudy at AOT < 0.35). However, the actual subcanopy PPFD levels (after removing sunflecks) are only slightly higher during

cloudy versus noncloudy intervals ($21.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ cloudy at AOT < 0.35 versus $19.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ noncloudy at AOT < 0.35).

[28] Subcanopy shaded light during noncloudy periods increased $2.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ at AOT > 0.5 (average optical depth 0.72) and $4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ at AOT > 0.7 (average optical depth 0.91). When plotted with an increase of $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ at AOT < 0.35 (average optical depth 0.23), there was a slope of $6.1 \mu\text{mol m}^{-2} \text{s}^{-1} \text{AOT}^{-1}$, which means that for every increase in AOT of 1, subcanopy shaded PPFD increased $\sim 6.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 6), an increase of $\sim 30\%$ assuming a mean subcanopy noncloudy PPFD of $20 \mu\text{mol m}^{-2} \text{s}^{-1}$.

3.5. Effect of Aerosol Optical Depth on Canopy Temperature

[29] We quantified the decline in canopy temperature due to decreased irradiance from smoke. We subtracted air temperature from canopy temperature because air temperature, a controlling factor in canopy temperature, often shows variability not related to changing irradiance. During very smoky periods (AOT > 0.7), downwelling shortwave irradiance decreased by 123 W m^{-2} relative to nonsmoky periods (AOT < 0.35) (Table 1: $123 \text{ W m}^{-2} = 13\%$ measured decrease in solar downwelling radiation). Canopy skin temperatures cooled relative to air temperatures by 0.41°C during very smoky periods (AOT > 0.7) versus nonsmoky periods (AOT < 0.35). During smoky periods (AOT > 0.5), downwelling shortwave irradiance decreased by 79 W m^{-2} relative to nonsmoky periods (AOT < 0.35). Canopy skin temperatures cooled relative to air temperatures by 0.26°C in smoky periods (AOT > 0.5) versus nonsmoky periods (AOT < 0.35). A linear regression had a slope of $\sim 300 \text{ W m}^{-2} \text{C}^{-1}$, meaning that canopy temperature decreases 1°C relative to air temperature for every 300 W m^{-2} decrease in downwelling solar radiation (Figure 7).

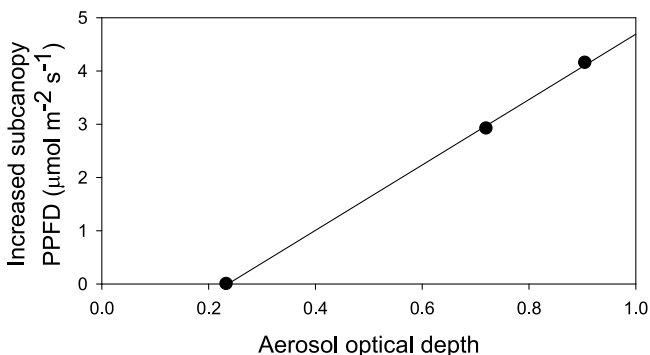


Figure 6. Increase in subcanopy PPFD measured by seven subcanopy PPFD sensors after removing all light flecks during noncloudy (tower top PPFD > $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) noontime (1100–1300 local time) periods where averaged daily averages of AOT > 0.5 and > 0.7 are subtracted from daily averages when AOT < 0.35. This was plotted against mean AOT for AOT > 0.5, > 0.7, and < 0.35. There are no error bars because we subtract means with different sample sizes.

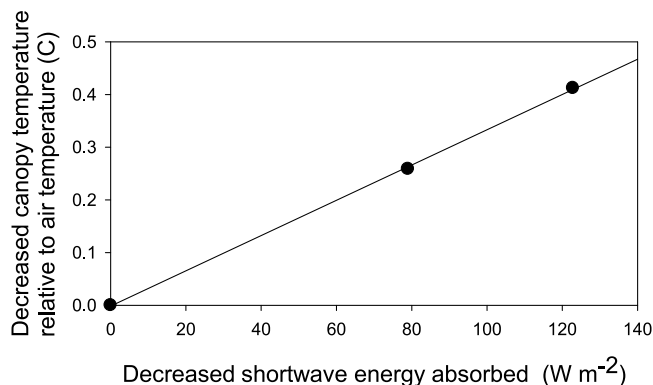


Figure 7. Mean downwelling shortwave irradiance during noontime (1100–1300 local time) and $AOT > 0.5$ and $AOT > 0.7$ subtracted against mean noontime downwelling shortwave irradiance at $AOT < 0.35$ from October–December 2002 and 2003. These data are plotted against average canopy temperature measured with a longwave pyrgeometer subtracted from average air temperature for the same periods of time. There are no error bars because we subtract means with different sample sizes. These data are plotted through the origin, which is the mean shortwave irradiance and mean canopy minus air temperature at $AOT < 0.35$.

[30] Air temperatures cooled slightly, by 0.15°C , between very smoky ($AOT > 0.7$) and nonsmoky ($AOT < 0.35$) periods. Surprisingly, air temperatures warmed slightly between smoky ($AOT > 0.5$) and nonsmoky ($AOT < 0.35$) periods. Even though the air was slightly warmer at smoky ($AOT > 0.5$) than nonsmoky ($AOT < 0.35$) periods, the overall canopy temperature still cooled because of decreased solar irradiance.

3.6. Whole Canopy CO_2 Exchange as a Function of Skin Temperature

[31] Previous analyses of the relationship between irradiance and CO_2 exchange at the km-83 site indicated that whole canopy photosynthesis saturates at a PPFD of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ [Goulden *et al.*, 2004]. We therefore analyzed the rates of GEE during periods with PPFD above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ to determine the sensitivity of light-saturated CO_2 exchange to canopy skin temperature (Figure 8). GEE was relatively insensitive to changes in canopy skin temperature below 28°C and highly sensitive to changes in canopy skin temperature above 28°C . We analyzed a subset of the data using 5 min averaged NEE and canopy temperature from midday (1000–1400 local time), October–December 2002 and October–December 2003, noncloudy (PPFD $> 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$), nonsmoky ($AOT < 0.35$) periods to ensure that the temperature effect was due to temperature and not clouds or aerosols (Figure 8). The forest had a similar response of CO_2 uptake to temperature in both data sets (a $\sim 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ decrease in canopy CO_2 uptake for every 1°C increase in temperature above 28°C , a $\sim 13\%$ decrease).

3.7. Leaf Photosynthesis

[32] We made 25 light photosynthesis curves on leaves below 10 m and 42 light photosynthesis curves on leaves

between 10 and 25 m from the ground between April and May 2002 to quantify the effect of increased shaded light on subcanopy leaf photosynthesis. Leaves below 10 m became light saturated at $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a maximum photosynthetic capacity (A_{max}) of $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 9a). Leaves between 10 and 25 m became light saturated at $\sim 600 \mu\text{mol m}^{-2} \text{s}^{-1}$, with an A_{max} of $\sim 5 \mu\text{mol m}^{-2} \text{s}^{-1}$. We linearly regressed photosynthesis and irradiance at light levels of 0 and $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and found a quantum yield of 0.039 ± 0.57 at 0–10 m and a quantum yield of 0.039 ± 0.83 at 10–25 m (Figure 9b). These quantum yields are less than those typically reported for C_3 dicots ($0.052 \text{ mol CO}_2 \text{ E}^{-1}$; [Ehleringer and Pearcy, 1983]). This difference may be due in part to our calculation of quantum yield based on the incident light, as opposed to the true quantum yield, which is based on absorbed light.

4. Discussion

[33] We focused our study on the 3 months during the dry season, when AOT was highest (October to December), rather than the whole year, as done by Oliveira *et al.* [2006]. Our focus on this period reduced the confounding influence of seasonal changes in LAI [Doughty and Goulden, 2008a], soil moisture [Bruno *et al.*, 2006], and specific humidity [da Rocha *et al.*, 2004]. We found no significant differences between smoky and nonsmoky periods for soil moisture (volumetric soil moisture at 20 cm $AOT > 0.7 = 0.390 \text{ m}^3 \text{ m}^{-3}$

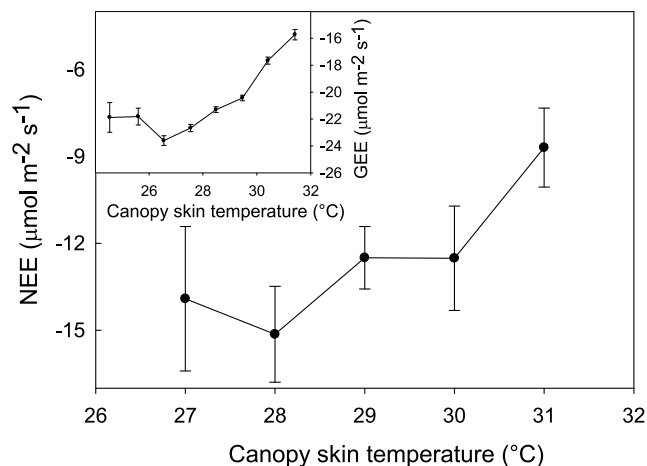


Figure 8. The bigger graph is canopy temperature and 5 min averaged $\text{NEE} \pm \text{SE}$ from midday (1000–1400 local time), October–December 2002 and October–December 2003, noncloudy (PPFD $> 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$), nonsmoky ($AOT < 0.35$) periods ($n = 21, 26, 31, 23$, and 15). The smaller graph is half-hour averaged gross ecosystem exchange (GEE) for periods with PPFD above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ from July 2000 to March 2004. Points show the mean for 1°C wide bins $\pm \text{SE}$ ($n = 73, 278, 653, 1029, 1111, 917, 439$, and 135). GEE was calculated as NEE (CO_2 flux plus CO_2 storage) minus 3 day averaged nighttime respiration adjusted for daytime temperatures using an Arrhenius-type model [Lloyd and Taylor, 1994]. The increase in GEE above 28°C indicates a reduction in photosynthesis or an increase in respiration.

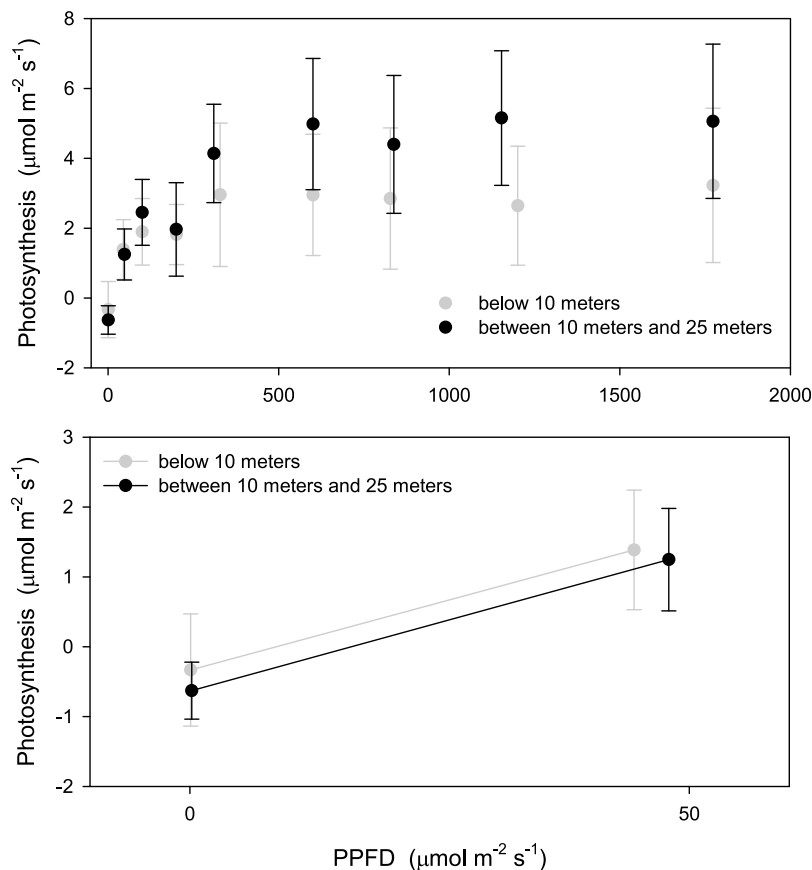


Figure 9. (a) Photosynthesis $\mu\text{mol m}^{-2} \text{s}^{-1} \pm \text{SD}$ at various light levels (30°C and ambient CO_2) for species at the km-83 and km-67 field sites below 10 m and between 10 and 25 m. Measurements were made on canopy platform towers between April and May 2002. (b) Quantum yield in the subcanopy as determined by the increase in photosynthesis from 0 to $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ for species below 10 m and species between 10 and 25 m.

versus $\text{AOT} < 0.35 = 0.394 \text{ m}^3 \text{ m}^{-3}$ for 1100–1300 local time, October–December 2002 and October–December 2003), LAI ($\text{AOT} > 0.7 = 6.26 \text{ m}^2 \text{ m}^{-2}$; $\text{AOT} < 0.35 = 6.23 \text{ m}^2 \text{ m}^{-2}$) [Doughty and Goulden, 2008b], or specific humidity ($\text{AOT} > 0.7 = 27.90 \text{ mmol mol}^{-1}$; $\text{AOT} < 0.35 = 27.63 \text{ mmol mol}^{-1}$).

[34] We found a significant difference in light-saturated half-hour GEE between $\text{AOT} > 1$ and $\text{AOT} < 0.35$, and a large, nearly significant ($P = 0.08$), difference between $\text{AOT} > 0.7$ and $\text{AOT} < 0.35$ (Figure 3). There was no difference in mean light-saturated GEE between $\text{AOT} > 0.5$ and $\text{AOT} < 0.35$. Half-hour averaged GEE often blend noncloudy and cloudy periods which reduce the measured effect of smoky periods because cloudy, smoky periods do not increase GEE like non-cloudy, smoky periods.

[35] Five minute averaged NEE increased significantly ($P < 0.001$) between very smoky, non-cloudy and non-smoky, non-cloudy periods. NEE at $\text{AOT} > 0.7$ was substantially greater than NEE at $\text{AOT} > 0.5$, and both were greater than $\text{AOT} < 0.35$ (Figure 4). There were no significant changes in NEE between cloudy, smoky periods ($\text{AOT} > 0.7$) and cloudy, non-smoky periods ($\text{AOT} < 0.35$). However, despite having higher tower top light levels during smoky, cloudy periods, NEE was slightly lower in smoky periods than

non-smoky periods, possibly due to decreased subcanopy shaded light at $\text{AOT} < 0.35$ versus at $\text{AOT} > 0.7$.

[36] There were small but significant increases in subcanopy diffuse irradiance during noncloudy, smoky ($\text{AOT} > 0.5$) and noncloudy, very smoky periods ($\text{AOT} > 0.7$) compared to noncloudy, non-smoky periods ($\text{AOT} < 0.35$) (Figure 5). We multiplied the modeled increase in diffuse light (scaled to match the bottom of canopy PPFD measurements) with increased AOT at each LAI by the quantum yield at each LAI to get a net canopy scale noncloudy midday estimated increase in CO_2 uptake of $3.8 \mu\text{mol m}^{-2} \text{s}^{-1}$.

[37] Decreased irradiance with smoke cooled canopy skin temperature by 0.4°C relative to air temperature (Figure 7), which could impact NEE during peak midday temperatures. The total cooling (Δ air temperature + Δ canopy temperature) between canopy temperature at $\text{AOT} > 0.7$ and $\text{AOT} < 0.35$ was $\sim 0.55^\circ\text{C}$. There was a linear drop ($r^2 = 0.88$) in CO_2 uptake at canopy skin temperatures above 28°C with a slope of $\sim 1.93 \mu\text{mol m}^{-2} \text{s}^{-1} \text{C}^{-1}$ (Figure 8). A decrease in temperature of 0.55°C would increase CO_2 uptake by $\sim 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ at air temperatures above 28°C . The combined effects of temperature and diffuse light should result in an increase in CO_2 uptake of $\sim 4.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, with decreased tem-

perature accounting for 22% of the effect and increased diffuse radiation to the subcanopy accounting for 78% of the effect.

[38] Our site has an average noontime noncloudy NEE of $-12.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (which is an underestimate of real NEE due to the 5 min averaging period) at $\text{AOT} < 0.35$, $-14.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ at $\text{AOT} > 0.5$, and $-17.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ at $\text{AOT} > 0.7$. The combined effects of temperature and diffuse light are $\sim 4.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the difference in CO_2 fluxes between $\text{AOT} < 0.35$ and $\text{AOT} > 0.7$ is $\sim 5.1 \mu\text{mol m}^{-2} \text{s}^{-1}$. CO_2 uptake could also be affected through increased relative humidity that increased with decreased air temperature during smoky periods. A model based on the Ball Berry stomatal conductance equation showed that the effect of increased humidity on CO_2 uptake is quite small ($\Delta < 1\%$) under small changes in relative humidity (a 0.15°C decrease in air temperature will increase humidity by 0.73% which will change CO_2 uptake $< 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) [Collatz et al., 1991].

[39] In this study, changes in seasonal LAI, soil moisture, and specific humidity were not significantly different between periods of high and low AOT, and the effect of changing relative humidity between these periods on CO_2 uptake is likely small. The predicted combined effect of temperature and diffuse light closely matches experimental observations. We therefore feel confident in our prediction that the increase in CO_2 uptake during smoky periods is real and about 20% due to a reduction of temperatures and about 80% due to increased subcanopy diffuse radiation. We calculate that during the period of study, aerosols may have increased average noontime noncloudy NEE at our site by $\sim 2.7\%$ over an entire year ($(321 \text{ days } \text{AOT} < 0.35 \times 12.5 \mu\text{mol m}^{-2} \text{s}^{-1} + 32 \text{ days } \text{AOT} > 0.5 \times 14.4 \mu\text{mol m}^{-2} \text{s}^{-1} + 12 \text{ days } \text{AOT} > 0.7 \times 17.6 \mu\text{mol m}^{-2} \text{s}^{-1}) - 365 \text{ days } \text{AOT} < 0.35 \times 12.5 \mu\text{mol m}^{-2} \text{s}^{-1}$).

[40] It is difficult to know whether this proportion between temperature and diffuse light is applicable to forests worldwide or limited to tropical forests. Current evidence suggests small perturbations in temperatures have a large effect on tropical forests [Doughty and Goulden, 2008a; Clark et al., 2003] possibly because annual and seasonal temperatures changes in tropical forests are small. Temperate forests, with their larger variations in seasonal and annual temperatures, are likely to have smaller increases in NPP due to decreased temperatures during periods of high AOT than tropical forests. The effect of AOT on surface air temperatures at our site was much smaller than in previous studies [Schafer et al., 2002], and temperature effects may have a larger effect on NPP during other high aerosol events that more strongly affect surface air temperatures.

[41] Overall, aerosols increased CO_2 uptake at our site mainly due to increased subcanopy light (80%) and partially due to lower canopy temperatures (20%). Future studies are necessary to determine whether this increased CO_2 uptake would lead to increased tropical forest tree growth or increased respiration.

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