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The effect of canopy gaps on subcanopy ventilation and scalar fluxes in a tropical forest

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Abstract

Forest gaps may provide conduits that preferentially vent moist, CO_2 -rich subcanopy air to the atmosphere. We measured the above-canopy fluxes of momentum, sensible heat (H), CO_2 , and water vapor (E_t), and the vertical profiles of CO_2 and water vapor, from two 67-m meteorological towers in a selectively logged Brazilian rainforest. The logging removed ~ 3.5 trees ha⁻¹, and increased the incidence of gaps by a factor of 3 over nearby undisturbed forest. One tower was located in an intact patch of forest within the selectively logged area; the other was 400 m upwind in a large gap created by the logging. During daytime the subcanopy air in the intact patch of forest had more CO_2 , more water vapor, and was cooler than the air at comparable altitudes in the gap. Meanwhile, the daytime CO_2 flux was less negative (reduced CO_2 uptake) above the gap than above the intact forest, the daytime E_t was greater above the gap than the intact forest, and the daytime H was lower above the gap than the intact forest. These patterns cannot be explained fully by the local loss of canopy gas exchange in the gap, but are consistent with the horizontal transport into the gap, and subsequent vertical transport out of the gap, of high- CO_2 , humid, cool air from the forest understory. The understory was drier and warmer during daytime after the logging, which would be expected to increase flammability. Further measurement and modeling efforts are needed to better understand the effect of canopy gaps on the local CO_2 and energy exchange, as well as the flux footprint.

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Keywords: Canopy gaps; Carbon dioxide exchange; Eddy covariance; Tropical forest; Microclimate; Ventilation; Tropical logging; LBA-ECO

1. Introduction

Forest gaps, caused by the death of canopy trees due to disease, stress, age, strong winds, lightning, or selective logging, may provide conduits that preferentially vent moist, CO_2 -rich subcanopy air to the atmosphere. Winds penetrate more easily into the lower forest near gaps, increasing subcanopy ventilation and drying (Laurance, 2004). Gaps alter the microclimate as more solar energy reaches the understory. The temperatures in gaps may be higher than those in intact forest areas (van Dam, 2001), creating the possibility of buoyant air motions and a "chimneyeffect". Venting has the potential to dry and warm the subcanopy air, with implications for forest flammability (Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997; Nepstad et al., 1999; Cochrane, 2003). Venting also has the potential to redistribute the flux of CO₂, with implications for the use of eddy covariance to determine ecosystem carbon balance (Acevedo, 2001). The tall

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trees, dense canopy, and common occurrence of an atmospherically stable subcanopy layer in tropical forest (Fitzjarrald et al., 1990; Goulden et al., 2006) may enhance the importance of gap venting in the tropics compared to other regions.

The micrometeorological technique eddy covariance is commonly used to measure the carbon dioxide and water vapor exchange by terrestrial ecosystems (Baldocchi et al., 1988; Wofsy et al., 1993). Eddy covariance provides a direct, high-precision flux measurement averaged over a relatively large footprint. For daytime measurements at $\sim 10 \text{ m}$ above a rough forest canopy, the upwind forest area that contributes to the flux is of order tens to hundreds of ha (e.g., Rannik et al., 2000). The forest-atmosphere exchange in a horizontally uniform (homogeneous) area is assumed to occur in the vertical direction only, and the net ecosystem exchange (NEE) of carbon dioxide is considered the sum of the vertical turbulent flux and the decline or accumulation of carbon dioxide in the air column beneath the flux sensors (storage). The formal expression for NEE over a heterogeneous surface includes additional terms in the mass conservation equation to account for horizontal gradients and advection. Simulations of turbulent flow over a forest gap predict spatial variations in scalar fluxes driven by local flow patterns, buoyant heating at the gap surface, and the entrainment of overlying air into the gap airspace (Acevedo, 2001). Key issues for the use of eddy covariance above forest are whether canopy gaps create local circulations that violate the assumption of horizontal homogeneity, and whether and how locating eddy covariance towers close to or within a gap effects turbulent fluxes (Sun et al., 1998).

We investigated the possibility that a large gap created by selective logging in an Amazonian tropical forest was a preferential vent for the evacuation of subcanopy air during the daytime. Our study took advantage of a selective logging operation within the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA-ECO; Keller et al., 2004). The logging created a mosaic of gaps and intact forest. We measured the carbon dioxide and water vapor exchange simultaneously from two nearby towers. The first tower operated for 3 years beginning 1 year before logging in an intact patch of forest that was within the selectively logged area. The second tower operated for 2 years beginning after logging, and was located in a large gap approximately 400 m upwind of the first tower. Our analysis focused on comparing the daytime fluxes of momentum, heat, carbon dioxide and water vapor, and the vertical profiles of carbon dioxide and water vapor between the towers.

2. Methods

2.1. Site

The measurements were made in the Floresta Nacional do Tapajos, near the 83 km marker on the Santarem-Cuiaba highway (BR 163), \sim 70 km south of Santarem in the state of Para, Brazil (3.010308°S, 54.581508°W). The vegetation was tropical humid forest on a broad, flat plateau, with a canopy height of \sim 20–40 m. The soil was yellow latosol clay (Haplic acrorthox). Additional details of the landscape and local topography are reported by Hernandez Filho et al. (1993) and Goulden et al. (2006). Details of the experimental design and the pre-logging meteorology and fluxes are described in Goulden et al. (2004), Rocha et al. (2004), and Miller et al. (2004).

A 700-ha area was selectively logged during 3 months beginning in September 2001 (Fig. 1). The logging included reduced-impact techniques such as pre-selection of the trees to be harvested, and the planning of felling directions, skid trails and log landings (Pereira et al., 2002). Six months before logging, vines of selected trees were cut to reduce canopy damage during felling. After the logging, gap location, size, and shape were mapped in a $600 \text{ m} \times 300 \text{ m}$ intensively studied area that extended 500 m to the northeast of the intact tower and that encompassed the area around the gap tower. We also calculated the incidence of gaps upwind of the two towers and also in larger tracts of logged and unlogged forest using a classified IKONOS image (Fig. 1). We calculated the Normalized Difference Vegetation Index (NDVI) from the Red and near Infrared IKONOS bands. We then created a classified image of the occurrence of gaps using a NDVI threshold, where gaps had an NDVI < 0.4 and intact crowns had an NDVI \ge 0.4.

2.2. Micrometeorological measurements

The meteorological measurements were made from two 67-m-tall, 46-cm-triangular-cross-section towers (Rohn 55G, Peoria IL) located within the selectively logged area (Fig. 1). The logging extended several kilometers to the east (the climatological upwind direction) of the towers. The first tower was installed and operating in June 2000, 15 months before the logging (Goulden et al., 2004; Miller et al., 2004; Rocha et al., 2004). The nearest gap created by the logging in the upwind direction was 50–75 m from the tower, and we refer to this tower as the 'intact' tower (Fig. 1). The second tower (the 'gap' tower) was installed and



Fig. 1. (a) False color IKONOS image for November 14, 2001 at 14:15 Universal Time showing the locations of the intact tower, the gap tower, and the approximate boundary between selectively logged areas to the south and unlogged forest to the north. The image was pan sharpened to 1 m resolution using the HSV algorithm and stretched using a 2 standard deviation setting. Red corresponds to the IKONOS red band: Green is the near IR band: Blue is the blue band. Vegetation shows up as green due to the reflectance of foliage in the near IR; bare soil, litter and slash show up as pink, shadows are dark. The sun was to the southeast during the image (Sun Azimuth: 133.4°, Sun Elevation: 67.2°), and the northwestern sides of gaps are mostly pink (illuminated soil) and the southeastern sides of gaps are mostly dark (shadow). The 2.5-m \times 3.5-m instrument hut at the base of the gap tower is visible, as are many individual tree crowns. (b) Same as Fig. 1a, except gaps, which were identified as areas with a Normalized Difference Vegetation Index (NDVI) of less than 0.4 are shown as blue.

operating in June 2002, 400 m east of the intact tower. The gap tower was installed in the middle of a $50 \text{ m} \times 50 \text{ m} \log \text{ landing (Fig. 1)}$.

The towers were equipped with similar instrumentation to measure heat, water vapor, and carbon dioxide exchange between the forest and the atmosphere. The core measurements included the turbulent fluxes at the top of the tower, and CO_2 and H_2O profiles between the surface and 64 m. At each tower, the wind vector and speed of sound were measured at 64 m with a 3-axis sonic anemometer pointed east (Campbell Scientific, Logan UT). Fast response CO_2 and H_2O at 64 m were measured by open-path InfraRed Gas Analyzers (IRGA, LI-COR LI7500, Lincoln NE) mounted at 64 and 0.5 m from the sonic anemometer. Turbulent fluxes were calculated each half hour using methodology described in Goulden et al. (2004) and Miller et al. (2004).

The CO_2 and H_2O molar density profiles at each tower were measured using LI7000 closed-path IRGAs that sequentially sampled 12 levels between 0.1 and 64 m for 4 min, resulting in a complete cycle every 48 min. The average CO_2 and H_2O mixing ratios at each level were calculated during the last minute of each 4-min interval, and observations were then interpolated to each half-hour to synchronize with the eddy flux measurements.

The closed-path IRGA at the intact tower used to measure the profile was calibrated automatically twice daily for CO_2 and once daily for water vapor. To facilitate comparison, we used this IRGA's 30-min averaged CO_2 and H_2O signals to calibrate the closedpath profile IRGA CO_2 and H_2O signals at the gap tower by linear regression on 7-day segments of 30-minaveraged CO_2 mixing ratio at 64 m.

Subcanopy winds were measured using 2-dimensional ultrasonic anemometers at 30, 20 and 1.4 m (Met One 35A, Grants Pass, OR). Radiation and temperature were measured at the intact tower. Incoming and reflected shortwave and long wave radiation at 64 m were measured with thermopile pyranometers and pyrgeometers (Kipp & Zonen CM6B and CG2, Delft, The Netherlands). Air temperatures at 64, 40, 30, 20, and 10 m height were measured with ventilated thermistors (Met One 076B, Grants Pass OR; Campbell Scientific 107, Logan UT). A tripod tower was installed 20 m east of the intact tower to measure air temperature at 2 m in an intact area. After the logging, we installed additional 2-m air temperature sensors in a relatively small gap (~ 20 m diameter) approximately 50 m east of the intact tower. All temperatures (T) were converted to potential temperature (θ) according to $\theta = T + (g/C_p)z$, where g is gravity, $C_{\rm p}$ the specific heat capacity of air, and z is height above ground-level (Stull, 1988). Virtual potential temperature (θ_{v}) was then calculated using the measured water vapor mixing ratio (r), $\theta_{\rm v} = \theta (1 + 0.61 r M_{\rm v} / M_{\rm a})$, where $M_{\rm v}$ and $M_{\rm a}$ are the molecular weights of water vapor and air (Stull, 1988).

Temperature is reported as virtual potential temperature.

3. Results

3.1. Effect of logging on forest structure

The logging created a mosaic, with gaps embedded in a matrix of largely intact forest (Fig. 1). A groundbased 18-ha survey immediately upwind of the original tower indicated the logging removed 3.5 trees ha^{-1} , or $\sim 10\%$ of the upper canopy. The logging created an average of 2.5 new gaps ha^{-1} , which ranged in size from single tree fells that were ~ 10 m across to log landings used to temporarily store boles that were \sim 50 m across. The intact tower was located in a small, relatively undisturbed patch of forest, and the gap tower was centered in a log landing, which can be thought of as a large and persistent gap. The area of the log landing was several times larger than the average gap, and a 50-cm thick layer of red, iron-rich clay soil (laterite) was compacted on the surface, which prevented vegetation regrowth. The vegetation regrew quickly in the smaller gaps, whereas the log landing was largely free of vegetation even 3 years after logging.

We used satellite imagery to compare the areas upwind of the two towers after selective logging (Fig. 1b). Gaps accounted for 4% of the area in a patch of unlogged forest that was north of the two towers and 12% of the area in the 110 ha block of forest that was selectively logged and that included the two towers. Logging increased the incidence of gaps by a factor of 3 over undisturbed forest. The areas upwind of the two towers had similar gap fractions after selective logging. Gaps accounted for 11% of the area in a 400 m east– west by 200 m north–south rectangle that began 25 m east of gap tower, and 13% of the area in a 400 m east– west by 200 m north–south rectangle that began 25 m east of the intact tower.

3.2. Temperature, H_2O and CO_2 profiles in the intact area

The daytime virtual potential temperature (temperature) profile was relatively warm between 10 and 40 m, presumably due to the absorbtion of radiation by the canopy (Figs. 2 and 3; Goulden et al., 2006). This resulted in an unstable temperature gradient above the canopy and a stable temperature gradient below about 10 m during daytime. The nighttime temperature profile was relatively cool at the canopy level, presumably due to net long-wave radiation loss from the canopy. This

Fig. 2. Average daily cycle of 30-min averaged virtual potential temperature at several heights on the intact tower: 64 m (thin, solid), 40 m (dashed), 10 m (dot-dash), and 2 m (thick, solid). The data were collected between November 25, 2002 and February 7, 2004 (440 days). For each 30-min interval and each level, reliable temperature and water vapor data were available for over 90% of the 440 days. Inset shows the average daily virtual potential temperature at 2 m in the intact area (solid) and in a gap created by the logging (dash). The intact area 2 m temperature sensor is the same in the main plot and the inset, but the inset data are averaged only during the period when the gap tower measurements were available.

resulted in neutral or slightly unstable conditions below about 30 m and a stable temperature gradient above 30 m. The local stable layer above 30 m would be expected to decrease vertical exchange across this layer at night. Similarly, the local stable layer below 10 m

Fig. 3. Mean virtual potential temperature profiles (solid) for daytime (10:00 and 16:00 h) and nighttime (22:00 and 04:00 h) between November 25, 2002 and February 7, 2004; wet season (January 1–June 30, dash), and dry season (July 1–December 31, dot-dash).

Fig. 4. Mean daytime and nighttime (a) water vapor (mmol mol⁻¹) and (b) CO_2 (µmol mol⁻¹) profiles at the intact and gap towers: intact tower nighttime (solid), gap tower nighttime (dash), intact tower daytime (dot-dash), and gap tower daytime (dotted). Data used to calculate the profiles were obtained between June 3, 2002 and January 19, 2004. Only periods where reliable profiles from both the intact and gap towers were available, and represented approximately 28% (169 days) of the 600-day interval.

would be expected to decrease vertical exchange across this layer during daytime.

The vertical profile of water vapor mixing ratio changed markedly from day to night (Fig. 4a). The water vapor mixing ratio was nearly constant with height at night, presumably as a result of the nocturnal reduction of transpiration and the occurrence of mixing below 30 m associated with local weakly unstable conditions (Fig. 3). The water vapor mixing ratio increased at all levels at the intact tower during daytime, reflecting the increase in evapotranspiration. The daytime water vapor mixing ratio was particularly high close to the ground, even though the greatest water vapor source was probably from the canopy (Rocha et al., 2004), presumably as a result of the combined effect of soil surface evaporation and the isolation of the subcanopy air parcel (Fig. 3).

The canopy was a net sink of carbon dioxide during daytime due to photosynthesis, and the forest floor was a source of carbon dioxide due to decomposition and autotrophic respiration (Goulden et al., 2004). The canopy photosynthesis resulted in a $\sim 5 \,\mu$ mol mol⁻¹ drawdown of carbon dioxide during daytime within the canopy layer relative to the background atmospheric mixing ratio (Figs. 4b and 6). The daytime profile of carbon dioxide above ~ 10 m in the intact area was close

to the background atmospheric value, presumably due to convective mixing of the canopy air with overlying atmospheric air. The air layer below ~ 10 m remained stably stratified throughout the day (Fig. 3), and the carbon dioxide respired by the soil and understory vegetation accumulated in this layer.

After selective logging, the subcanopy air in the intact forest was both warmer and drier during daytime (Fig. 5). The daytime temperature difference from 64 to 10 m at the intact tower was typically ~ 1 °C during the year before logging, except for January 2001 when frequent storms flushed the subcanopy airspace (c.f., Fitzjarrald et al., 1990). The daytime temperature difference after logging decreased to less than 0.5 °C, corresponding to a warming of the subcanopy air. Similarly, there was a marked decrease in the 64-10-m water vapor gradient following logging, corresponding to a drying of the subcanopy air (see also Uhl and Kauffman, 1990). These gradients reflect the degree to which the subcanopy air is decoupled from the above-canopy air, and imply that the daytime exchange of air out of the subcanopy became more efficient after logging. The trends in subcanopy CO₂ mixing ratios from before to after logging were confounded by the large amount of slash and detritus that was left after logging, and neither support nor counter a change in subcanopy ventilation (data not shown).

Fig. 5. Afternoon potential temperature, water vapor, and relative humidity gradients between subcanopy and above-canopy before, during, and after the selective logging operation. For each curve, a single point is obtained for each day as the 30-min average beginning at 2 p.m. local time. A running mean filter (10-day mean for temperature, and 6 day mean for water vapor) was applied to reduce day-to-day variations. (a) 64–10 m potential temperature gradient (dash), and 64–2 m potential temperature gradient (solid). (b) 64–10 m water vapor gradient (dots), and 64–3 m water vapor gradient (solid); (c) relative humidity gradient (percent relative humidity) calculated from temperature and humidity gradients, same line types as in (b). The 3-month logging interval occurred between September and December 2001.

3.3. Gap tower versus intact tower profiles and fluxes

The logging removed all of the vegetation from the gap (Fig. 1), and the 50 cm thick laterite cap on the soil surface, combined with the lack of litterfall and live roots, presumably reduced the rate of soil respiration. We therefore assume the sources and sinks of carbon dioxide and water vapor in the gap were markedly reduced relative to the intact forest.

The daytime air temperature near the surface of a nearby gap was warmer than the temperature at the same height below the understory (Fig. 2). The daytime water vapor mixing ratio in the canopy space and above (from 10 to 20 m upwards) was reduced in the gap relative to the intact area (Fig. 4a). This local drying

Fig. 6. Diel cycle of the difference in CO_2 mixing ratio between intact and gap areas at several heights (intact area minus gap area mixing ratio, µmol mol⁻¹): 64 m (solid), 35 m (dash), 20 m (dot-dash), 10 m (squares), 3 m (triangles). Data used to calculate the profiles were obtained between June 3, 2002 and January 19, 2004. Only periods where reliable profiles from both the intact and gap towers were available, and represented approximately 28% (169 days) of the 600day interval.

presumably reflects both the lack of local water vapor sources and the increased mixing of dry overlying air into the gap. The water vapor mixing ratios below 10 m were similar in both intact and gap areas (Fig. 4a).

The mixing ratio of CO₂ at both towers increased markedly at night and declined markedly during daytime (Fig. 4b). The CO₂ profile in the gap had a similar shape to the intact area during both day and night. The gap profile CO₂ mixing ratio was lower than in the intact area during nighttime, presumably due to lack of canopy respiration. The gap profile CO₂ mixing ratio was also lower than in the intact area during daytime, presumably due to mixing of air in the gap with lower-CO₂ overlying air. The timing of the morning transition from high CO_2 to low CO_2 differed between towers, with the morning transition occurring earlier at the gap than the intact site. This timing difference was reflected in the large differences in CO₂ mixing ratio at equal measurement heights between the towers that developed from \sim 700 to 900 local time (Fig. 6). The earlier morning CO_2 decline in the gap occurred despite the lack of local vegetation and photosynthesis, indicating that it was caused by accelerated vertical mixing. The importance of vertical mixing in causing the morning CO₂ reduction at the gap was confirmed by direct measurements of the fluxes at the tower tops (Fig. 7d). The increase in CO₂ efflux at \sim 700 local time was noticeably higher at the gap than

Fig. 7. Diel cycle of fluxes measured at 64 m above the intact (solid) and gap (dashed) areas: (a) momentum flux, u^* (ms⁻¹); (b) sensible heat flux (W m⁻²); (c) latent heat flux (W m⁻²); and (d) CO₂ flux (µmol m⁻² s⁻¹). The mean flux for each half hour was calculated using data collected between June 3, 2002 and February 7, 2004 (615 days). Data were used only when both the intact and gap tower fluxes were available, resulting in a minimum of 29% (175 days) retained at 06:30 GMT and a maximum 54% (332 days) retained at 20:00 GMT for the CO₂ flux. 95% confidence intervals are shown for each 30-min interval.

the intact forest site. This difference implies that the CO_2 fluxes measured above the gap were influenced at least partially by efflux from the gap. This difference also implies that the air in the gap was better coupled to the above canopy air than was the air at comparable altitudes in the intact forest.

The daytime (09:00–15:00 local time) average sensible heat flux (H) measured above the gap was 16 W m^{-2} less than that measured above the intact area, with a daytime maximum difference of 20 W m⁻² (Fig. 7b). The daytime average latent heat flux (λ E) measured above the gap was 21 W m⁻² greater than that measured above the intact area, with a daytime maximum difference of 47 W m⁻². The sensible heat flux reduction measured above the gap was opposite that expected for the higher surface temperatures measured within a nearby gap (Fig. 2). Likewise, the latent heat flux

difference above the gap compared to the intact area was opposite the difference in the water vapor mixing ratio between gap and intact areas (Fig. 4). The average daytime CO₂ exchange above the gap was ~1.8 µmol m⁻² s⁻¹ less negative above the intact forest, with a maximum difference of 2.6 µmol m⁻² s⁻¹ (Fig. 7d). In principle, this CO₂ flux difference could have resulted from either a reduction in daytime carbon dioxide uptake above the gap due to canopy loss, or from venting of CO₂-rich subcanopy air from intact forest through the gap.

4. Discussion

The possible effects of gaps on the tower-top flux may be divided into two categories: (1) the local-gap effect caused by the presence of the large gap that is immediately under the tower, and (2) the effect of the many upwind gaps that are further upwind. Though the furthest upwind extent of forest that contributes to the turbulent flux measured by the tower is not precisely known, footprint models indicate it is likely several hundred meters (e.g., Rannik et al., 2000). The IKONOS satellite imagery showed a similar incidence of gaps in the areas 400 m upwind of the two towers (Fig. 1). Further, the aerodynamic 'roughness' upwind of the two towers was similar, as indicated by a comparison of the momentum fluxes measured at the tops of the intact and gap towers (Fig. 7a). The similarity in upwind gap area, and the similarity in aerodynamic properties, imply that the upwind-gap effect was similar between the two towers.

The intact tower was located in a patch of intact forest, whereas the gap tower was in a gap that extended 25 m in the upwind direction. The contribution of the area in the immediate vicinity of a tower to the flux is poorly known (e.g., Leclerc et al., 2003). If the entire flux footprint lies beyond 25 m, the gap tower would not be able to even "see" the gap in which it is located. However, model results indicate that the contribution of source areas within 25 m of a tower can be substantial. For a homogeneous canopy, Rannik et al. (2000) found that the area of forest within 25 m of a tower contributed as much as 20% of the total flux, and that downwind sources may contribute to the footprint as a result of horizontal mixing. For an inhomogeneous canopy, Acevedo (2001) used a turbulence model to simulate the effect of a canopy gap on the profiles and fluxes measured in a tall forest. He found that the scalar fluxes measured by a virtual tower located within or near a gap could be as much as three times as large as the areaaveraged flux.

The modeling results on local contributions to the footprint (Rannik et al., 2000), and the effect of a canopy gap on fluxes measured above a tall forest (Acevedo, 2001), indicate that the fluxes measured at the top of the gap tower were likely influenced by the local gap. The satellite imagery showed that the upwind gap effects were likely similar at the two towers. We therefore attribute the observed differences in vertical profiles and turbulent fluxes between the two towers to the large, local-gap in which the gap tower was located.

4.1. Do gaps vent the subcanopy?

The shifts in daytime water vapor mixing ratio and temperature that coincided with logging (Fig. 5) imply that gaps facilitate subcanopy ventilation, but provide only scant evidence of the actual physical process. We therefore compared the fluxes and vertical profiles at the two towers to better understand whether and how gaps act as preferential conduits.

The daytime fluxes of carbon dioxide, latent heat, and sensible heat differed between the towers in ways that were only partially consistent with the differences expected for a local loss of foliage (Fig. 7b-d). The removal of canopy in the gap would be expected to reduce the local rates of CO2 uptake and evapotranspiration, while increasing the sensible heat flux. In fact, evapotranspiration was increased and sensible heat flux was decreased above the gap relative to the intact forest. The observed flux differences can be best explained by the venting of subcanopy air from the intact forest through the gap. Relative to the above-canopy airspace, subcanopy air during daytime was higher in CO₂, higher in water vapor, and cooler (Figs. 2-4). The differences in scalar properties between the intact subcanopy and atmospheric air are consistent with the flux differences at the two towers. Venting of high-CO₂ subcanopy air would result in a more positive CO₂ flux; venting of humid subcanopy air would result in a higher latent heat flux; venting of cool subcanopy air would result in a lower sensible heat flux.

The ratio of the CO₂ flux difference between towers to the CO₂ mixing ratio gradient from the intact subcanopy to the gap tower top was similar to the ratio of the H₂O flux difference to the H₂O mixing ratio gradient. The difference in daytime CO₂ flux between the intact tower and the gap towers was ~1.8 µmol m⁻² s⁻¹ (Fig. 7c), and the difference in λE between the towers was ~21 W m⁻², which is equivalent to 0.47 mmol m⁻² s⁻¹. The daytime differences in scalar mixing ratios between the top of the gap tower and the lower levels in the intact forest were ~8.1 µmol CO₂ mol air⁻¹ and ~2.4 mmol H₂O mol air⁻¹ (Fig. 4). The ratio of the CO₂ flux difference to the CO₂ mixing ratio gradient was 0.006 ms⁻¹ (the result was divided by air molar density to obtain units of ms⁻¹) which is similar to the ratio of the H₂O flux difference to the H₂O mixing ratio gradient, which was 0.005 ms⁻¹. This similarity supports the hypothesis that the reduction in CO₂ flux and increase in water vapor flux at the gap tower was caused by the venting of subcanopy air from the intact forest subcanopy. Taken together, the measured fluxes and mixing ratio differences point to an increased contribution of subcanopy air to the flux above the gap.

4.2. What drives venting?

We believe daytime gap venting occurs in two steps: (1) the horizontal mixing of relatively cool, humid, CO_2 -rich subcanopy air into a gap, and (2) the vertical mixing of air from the gap into the atmosphere. The activity of both of these steps can be illustrated by considering the mixing ratio profiles that would be expected in the absence of either step.

If the subcanopy air in the gap were isolated and decoupled from the air at the same level in intact forest, we would expect the vertical profile throughout the gap would equilibrate with the air above the canopy. However, the mixing ratios of water vapor and CO₂ in the lower gap profile were higher than the abovecanopy (background) mixing ratios during daytime and nighttime (Fig. 4), implying the horizontal transport of air from intact forest into the gap. Mean horizontal winds at 1.4 and 20 m height are common at the site during both day and night (Goulden et al., 2006), providing a mechanism for the movement of air from intact forest into gaps. These winds are generally light $(0.05-0.1 \text{ ms}^{-1} \text{ at night and } 0.1-0.25 \text{ ms}^{-1} \text{ during}$ daytime), but sufficient to fully flush a 50-m wide gap once every 10-15 min at night and every 5-10 min during davtime.

If the air in the gap were isolated and decoupled from the air above the forest, we would expect the air in the gap would equilibrate with the air in the intact forest, and the profiles measured at the two towers would be identical. However, the daytime and nighttime mixing ratios of water vapor and CO_2 in the lower gap profile were less than those observed in the intact forest (Fig. 4), implying the subsequent upward transport out of the gap. The vertical exchange of subcanopy air from the gap was likely facilitated by the lack of canopy obstruction to airflow, so that eddies penetrated into the gap to sweep away air close to the ground level (Acevedo, 2001), a pattern that is consistent with the earlier morning venting observed in the gap (Figs. 6 and 7d).

The process of gap venting may be quite simple, requiring only that subcanopy air exchanges horizontally with the air at comparable altitudes in gaps, and that the vertical exchange of air through a gap is greater than the vertical exchange of air through intact forest canopy. Given this situation, gaps may effectively trap and remove subcanopy air from the intact area, and serve as preferential conduits to the overlying atmosphere. The effectiveness of a gap as a venting conduit might be accelerated if surface heating in the gap leads to buoyancy and further accelerates vertical and horizontal exchange, though this process is not necessary for preferential venting.

4.3. Implications for the subcanopy microenvironment

The analysis of data collected at the two towers shows that gaps can act as conduits that preferentially vent moist, CO₂-rich subcanopy air to the atmosphere. The long-term records of subcanopy temperature and humidity indicate selective logging increased ventilation. The increasing subcanopy temperature and decreasing subcanopy specific humidity reinforced each other, causing a 10-15% reduction in midday relative humidity after logging (Fig. 5). Relative humidity is a good measure of the flammability of fine fuels, and the subcanopy drying following logging would be expected to increase the likelihood of ground fire (Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997). The rates of soil respiration in tropical forest are tightly related to the moisture content of the surface litter, with a marked decline in respiration when litter becomes desiccated (Goulden et al., 2004). The venting of moist, cool air through gaps therefore has the potential to influence both the likelihood of fire and the rates of soil respiration in tropical forest.

4.4. Implications for eddy covariance estimates of ecosystem carbon balance

While the profile and turbulent flux measurements support the hypothesis of venting, quantifying the venting is difficult. The venting represents a spatial redistribution of ecosystem respiration, with more respired CO_2 exchanged through the gaps, and therefore less exchanged through the intact areas. Gap venting has the potential to decouple the annual CO_2 exchange integral determined by eddy covariance from the ecosystem's actual carbon budget. Integrated flux

measurements made close to a gap might underestimate annual carbon storage. If the contribution of the local gap area to the flux footprint were more quantitatively known, the daytime CO₂ venting flux per unit gap area could be estimated from the measured CO₂ flux difference between the two towers. However, the contribution of the local gap to the gap tower's footprint is difficult to assess (Schmid, 2002). The possibility of CO₂ venting underscores the need to better understand the local contributions to fluxes, and the effects of canopy heterogeneities caused by gaps. Observations of horizontal (and vertical) advective fluxes (e.g., Staebler and Fitzjarrald, 2004), combined with high-resolution tubulence simulations (e.g., Acevedo, 2001) may help improve our understanding of the effect of canopy gaps on fluxes measured over tall forest.

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