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Soil respiration and aboveground litter dynamics of a tropical transitional forest in northwest Mato Grosso, Brazil

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[1]   Measurements of soil CO_2 efflux, litter production, and the surface litter pool biomass were made over a 1 year period in a tropical transitional forest near Sinop, Mato Grosso, Brazil with the aim of quantifying the seasonal variation in soil respiration and litter decomposition and the annual contribution of litter decomposition to soil CO_2 efflux. Average annual soil CO_2 efflux (±95% confidence interval (CI)) was 7.91 ± 1.16 g C m^{-2} d^{-1}. Soil CO_2 efflux was highest during the November–February wet season (9.15 ± 0.90 g C m^{-2} d^{-1}) and lowest during the May–September dry season (6.19 ± 1.40 g C m^{-2} d^{-1}), and over 60% of the variation in seasonal soil CO_2 efflux was explained by seasonal variations in soil temperature and moisture. Mass balance estimates of mean (±95% CI) decomposition rates were statistically different between the wet and dry seasons (0.66 ± 0.08 and 1.65 ± 0.10 g C m^{-2} d^{-1}, respectively), and overall, decomposition of leaf litter comprised 16% of the average annual soil respiration. Leaf litter production was higher during the dry season, and mean (±95% CI) leaf litter fall (5.6 ± 1.7 Mg ha^{-1}) comprised 73% of the total litter fall (7.8 ± 2.3 Mg ha^{-1}). Average (±95% CI) annual litter pool biomass was estimated to be 5.5 ± 0.3 Mg ha^{-1}, which was similar to the measured pool size (5.7 ± 2.2 Mg ha^{-1}). Overall, seasonal variations in environmental variables, specifically water availability (soil moisture and rainfall), had a profound influence on litter production, soil respiration, and surface litter decomposition.

1.   Introduction

[2]   Tropical ecosystems, including rain forests, seasonally dry forests, and savanna, are thought to play a key role in global carbon (C) storage and cycling; however, the CO_2 balance of the Amazon Basin remains highly uncertain [*Keller et al.*, 2004]. For example, results from eddy covariance studies of net ecosystem CO_2 exchange (NEE) suggest that Brazilian tropical ecosystems may be large sinks for atmospheric CO_2 [*Araújo et al.*, 2002; *Carswell et al.*, 2002; *Kruijt et al.*, 2004; *Malhi et al.*, 1998; *Miranda et al.*, 1996], approximately in balance [*Priante-Filho et al.*, 2004; *Rocha et al.*, 2002; *Vourlitis et al.*, 2004], or net sources of CO_2 to the atmosphere [*Saleska et al.*, 2003].

[3]   NEE is the balance between total (gross) ecosystem photosynthesis (GEP) and whole ecosystem respiration, and of these large CO_2 fluxes, soil (root + microbial) respiration can make up 50–76% of the total ecosystem respiration and may be more responsible for the magnitude and direction of NEE than GEP [*Saleska et al.*, 2003; *Valentini et al.*, 2000; *Vourlitis et al.*, 2005]. Soil respiration has been shown to vary substantially over space and time as a result of many factors including temperature [*Lloyd and Taylor*, 1994], soil moisture [*Sotta et al.*, 2004], soil C quality and/or availability [*Giardina and Ryan*, 2000], and root biomass [*Ohashi et al.*, 2000]. Furthermore, soil respiration is composed of several component processes, including respiration from roots and decomposition of aboveground litter, soil organic matter, and root exudates; however, there is still considerable uncertainty on the relative contribution of these processes to soil respiration [*Hanson et al.*, 2000; *Raich and Tufekcioglu*, 2000; *Sulzman et al.*, 2005]. For example, the contribution of root respiration to total soil respiration in broadleaf forests reportedly ranges between 5 and 90% [*Hanson et al.*, 2000], while aboveground litter decomposition has been estimated to comprise 19–34% of soil respiration in temperate coniferous and tropical broadleaf forests, respectively [*Chambers et al.*, 2004; *Li et al.*, 2004;

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Sulzman et al., 2005]. The considerable uncertainty in these estimates highlights the need for studies that assess the relative contribution of these processes to overall soil respiration. These studies are needed to understand the mechanisms controlling soil CO$_2$ efflux and provide a means to understand how global change processes, including climate, land cover, and atmospheric change, may potentially alter soil and ecosystem C sequestration. In light of this pressing research need, the aim of this work was to quantify the seasonal variation in soil respiration, litter production, and aboveground litter decomposition in a tropical transitional (ecotonal) forest over an annual cycle and to determine the possible environmental controls over these processes.

2. Material and Methods

2.1. Site Description

[4] This study was conducted in the southern portion of the Legal Amazon Basin [*Skole and Tucker*, 1993] in an upland (*terra firme*) forest located approximately 50 km northwest of Sinop, Mato Grosso, Brazil (11°24.75′S; 55°19.50′W). The forest is located 423 m above sea level in a climatic transition between Amazonian rain forest and savanna that spans 5° of latitude between 9°S and 14°S in northern Mato Grosso [*Ackerly et al.*, 1989]. Vegetation within this transition consists of savanna (cerrado), transitional vegetation (cerradão), and Amazonian forest, which on the southern fringes of the Amazon Basin near Sinop is recognized as dry (mata seca) or semideciduous mesophytic forest [*Ackerly et al.*, 1989; *Eiten*, 1972; *Ratter et al.*, 1978].

[5] Tree species at our study site are typical of semideciduous Amazonian forest [*Ackerly et al.* 1989; *Lorenzi*, 2000, 2002] and include *Protium sagotianum* Marchland, *Dialium guianense* (Aubl.) Sandwith, *Hevea brasiliensis* Müll. Arg., *Brosimum lactescens* (S. Moore) C.C. Berg, *Cordia alliodora* (Ruiz and Pav.) Oken, *Tovomita schomburgkii* Planch and Triana, and *Qualea paraensis* Ducke. There are approximately 80 species and 35 families of trees with a diameter ≥10 cm; however, nearly 50% of all individuals are within the Burseraceae (*P. sagotianum*), Clusiaceae (*T. schomburgkii*), and Moraceae (*B. lactescens*) families. The maximum canopy height is 25–28 m [*Vourlitis et al.*, 2001] and the density and basal area of trees ≥10 cm diameter is 483 ha^{-1} and 22.5 m^2 ha^{-1}, respectively. Leaf area index varies between 5 m^2 m^{-2} in the wet season and 2.5 m^2 m^{-2} in the dry season reflecting the semideciduous nature of the forest [*Vourlitis et al.*, 2004]. Soils are acidic (pH = 4.2), sandy (94% sand), well-drained nutrient-poor quartzarenic neosols with low organic matter content (2%). Concentrations of available phosphorus (P) (5.2 μg g^{-1}) and exchangeable cations (Ca and Mg) in the surface (0–20 cm) soil are similar to other Amazonian forests with comparable substrate [*Thompson et al.*, 1992].

[6] Being within a major climatic transition, the climate of this region is intermediate to Amazonian rain forest and savanna [*Vourlitis et al.*, 2002]. For example, average annual temperature in Sinop is 24°C while average annual temperature for cerrado (Brasília, Districto Federal) and rain forest (Porto Velho, Rondônia) is 21° and 26°C, respectively. Rainfall near Sinop is approximately 2 m a^{-1}, while rainfall for cerrado and rain forest is 1.5 and 2.2 m a^{-1}, respectively,

and Sinop experiences a 3–5-month dry season, which is longer than rain forest (0–3 months) but comparable to cerrado [*Vourlitis et al.*, 2002].

2.2. Field Measurements

[7] Soil respiration measurements were made monthly from February 2003 to January 2004 between 1000 and 1400 h local time at 20 randomly located points near an eddy covariance tower. Soil CO$_2$ efflux was measured using an infrared gas analyzer (IRGA) equipped with a closed chamber (LI-6400, LI-COR, Lincoln, Nebraska, and EGM-1/WMA-2, ADC Bioscientific Inc., Hoddesdon Herts, UK). The chamber was installed 2 cm into the soil and CO$_2$ efflux measurements were initiated when the chamber CO$_2$ concentration was equal to the ambient CO$_2$ concentration and the rate of change in CO$_2$ concentration was constant (approximately 2–3 min following chamber installation). Soil temperature was measured simultaneously in the upper 5 cm of soil with a temperature sensor and a digital thermometer (LI-6000-09TC, LI-COR, Lincoln, Nebraska). Instantaneous measurements of surface (0–30 cm) soil moisture were made adjacent to the tower ($n = 1$) using time domain reflectometry (TDR). Soil respiration measurements made during the midday periods are assumed to reflect the average daily rate of soil respiration because previous field research indicates that diurnal variations in soil respiration and temperature are negligible in this forest [*Borges et al.*, 2006].

[8] Aboveground litter production (>1 mm) was measured in 20 randomly located 1 m^2 collectors adjacent to the CO$_2$ efflux measurement points. Litter accumulated in each collector was collected monthly, washed with distilled water, separated in leaves, twigs, flowers and fruits, dried at 65–70°C for 72 h, and weighed on a digital balance. The litter biomass of the surface litter pool was measured adjacent to each litter fall collector on an occasional basis (every 1–3 months or seven times during the measurement period) in conjunction with litter fall measurements. Litter was collected within a 25 × 25 cm quadrat that was randomly placed adjacent to each litter fall collector, washed with distilled water, dried at 65–70°C for 72 h, and weighed on a digital balance. Litter fall estimates are expressed as the dry mass per unit ground area over a period of one month (Mg ha^{-1} month^{-1}), while litter pool estimates are expressed as the dry mass per unit ground area (Mg ha^{-1}).

[9] Air temperature and vapor pressure were measured at the top of a tower 40 m tall tower using a combination relative humidity/temperature sensor equipped with a radiation shield (HMP-35, Vaisala, Inc., Helsinki, Finland). Precipitation data were obtained from the Fazenda Continental located 5 km SE of the study site. Meteorological data were averaged every 30 min from observations made every 60 s and stored using a solid-state data logger (CR-10X, Campbell Scientific, Inc., Ogden, Utah).

2.3. Data Analysis

[10] Over seasonal time scales the relationship between soil CO$_2$ efflux, soil temperature, soil water content, and leaf litter fall was analyzed using linear and nonlinear regression. An exponential relationship in the form of $R = R_o e^{\alpha T}$ was used to relate soil CO$_2$ efflux to soil temperature,

where R is the soil respiration rate (μmol m^{-2} s^{-1}), T is the soil temperature (°C), R_o is the soil respiration rate at a temperature of 0°C, and α is the rate constant [*Fang and Moncrieff*, 2001; *Lloyd and Taylor*, 1994]. From the rate constant α, the Q_{10}, or the coefficient that relates the relative increase in soil respiration for each 10°C increase in temperature, was estimated as $Q_{10} = e^{10\alpha}$ [*Fang and Moncrieff*, 2001; *Lloyd and Taylor*, 1994].

[11] The combined effects of soil moisture and temperature on CO$_2$ efflux were assessed using a model described by *Bunnell et al.* [1977], $R(W, T) = (W/a + W)(b/b + W)cd^{((T-10)/10)}$, where W is the soil moisture, T is the temperature (air or soil), and a, b, c, and d are constants estimated using nonlinear regression. For this model the a value represents the soil moisture where microbial activity is half its maximum value, b represents the soil moisture when the soil CO$_2$ diffusion is half its maximum value, c represents a CO$_2$ efflux at a 10°C temperature, and d is the value of Q_{10} [*Bunnell et al.*, 1977]. The term $(W/a + W)$ suggests that microbial activity increases as the microbial water requirements become less limiting, while the term $(b/b + W)$ suggests that CO$_2$ diffusion becomes progressively more limited as water content increases the proportion of blocked soil pores [*Bunnell et al.*, 1977]. The final portion of the model ($cd^{((T-10)/10)}$) relates CO$_2$ efflux as an exponential function of temperature.

[12] Litter decomposition was calculated monthly using a mass balance approach [*Wieder and Wright*, 1995; *Xu and Hirata*, 2002]. The change in the surface litter pool over each month (dLP/dt) was calculated as the difference between aboveground litter inputs (LF) minus the mass of litter lost from decomposition ($k*LP$):

$$dLP/dt = LF - k*LP. \tag{1}$$

Setting dLP/dt = 0, the litter decomposition rate constant (k) was estimated from LF and LP as

$$k = LF/LP. \tag{2}$$

This approach provided estimates of k over monthly intervals and assumes that litter decomposition over submonthly intervals was negligible, an assumption that might be violated in tropical environments where warm and wet conditions facilitate rapid litter decomposition [*Wieder and Wright*, 1995]. Unfortunately, the potential for litter in litter fall traps and the surface litter pool to be lost over submonthly time steps cannot be determined with the data provided. With estimates of dLP/dt and k, the mass of surface litter for the current month (LP_t) was calculated as

$$LP_t = LP_{t-1} + dLP/dt_{t-1}, \tag{3}$$

where LP_{t-1} was the litter pool mass of the previous month and dLP/dt_{t-1} was the change in the litter pool mass during the previous month. Monthly rates of net decomposition (D_t) were calculated as

$$D_t = LP_t + LF_t - LP_{t+1}, \tag{4}$$

where LP_t and LF_t are the current month's litter pool biomass and litter fall, respectively and LP_{t+1} is the litter pool of the next month [*Wieder and Wright*, 1995].

3. Results

3.1. Microclimate

[13] Rainfall varied between 270 and 385 mm month^{-1} between February and April 2003 and rapidly declined into May (Figure 1a). Between May and September, total monthly rainfall was <60 mm, and no measurable rainfall was recorded in June and August (Figure 1a). Assuming that the dry season comprises the number of consecutive months with a total monthly rainfall <100 mm (May–September), the dry season length during the study period was 5 months. Rainfall increased in October, and between October 2003 and January 2004 rainfall varied between 280 and 460 mm month^{-1} (Figure 1a). Total annual rainfall for the entire study period was approximately 2500 mm, which is nearly 500 mm higher than the long-term (30 year) average for the region [*Vourlitis et al.*, 2002]. Nearly half (220 mm) of the excess rainfall occurred in October–November 2003.

[14] The temporal trend in surface (0–30 cm) soil water content was highly correlated with the temporal trend in rainfall ($r = 0.95$; $p < 0.05$), and maximum soil moisture was observed in January 2004 (15.3%) while minimum soil moisture was observed in August 2003 (4.8%, Figure 1a). The soil moisture reported here is lower than that reported for other Amazonian forests [*Davidson et al.*, 2000; *Sotta et al.*, 2004] presumably because the soil at Sinop is almost entirely composed of sand (94%), which has a low water holding capacity [*Teepe et al.*, 2003].

[15] Soil temperature measured in the upper 5 cm of soil during respiration measurements was highly correlated to average monthly air temperature ($r = 0.9$; $p < 0.05$; Figure 1b). Soil and air temperature tended to be lowest in July (22.1° and 23.3°C, respectively), which corresponds to the peak of the dry season, and highest between March–May (25.1° and 26.3°C, respectively), which corresponds to the transition between the wet and dry seasons (Figure 1b).

3.2. Soil Respiration

[16] The average (±SE) soil CO$_2$ efflux reached a minimum value of 4.3 ± 0.4 g C m^{-2} d^{-1} in July and August during the peak of the dry season and a maximum value of 11.1 ± 0.7 g C m^{-2} d^{-1} in December during the rainy season (Figure 1c). Averaged over seasonal periods, mean (±95% CI) was 9.15 ± 0.90 g C m^{-2} d^{-1} during the wet season and 6.19 ± 1.40 g C m^{-2} d^{-1} during the dry season (Table 1).

[17] Temporal trends in soil CO$_2$ efflux were coincident with seasonal trends in air and soil temperature, soil moisture, and rainfall. Soil respiration increased exponentially as a function of average monthly temperature (Figure 2a); however, the Q_{10} value calculated from this relationship was large (12.2) and is considerably higher than values reported for other Amazon forests [*Meir et al.*, 1996; *Sotta et al.*, 2004]. A model that combined seasonal variations in soil moisture and temperature [*Bunnell et al.*, 1977] explained over 60% of the variation in average monthly soil CO$_2$ efflux (Figure 3). After accounting for
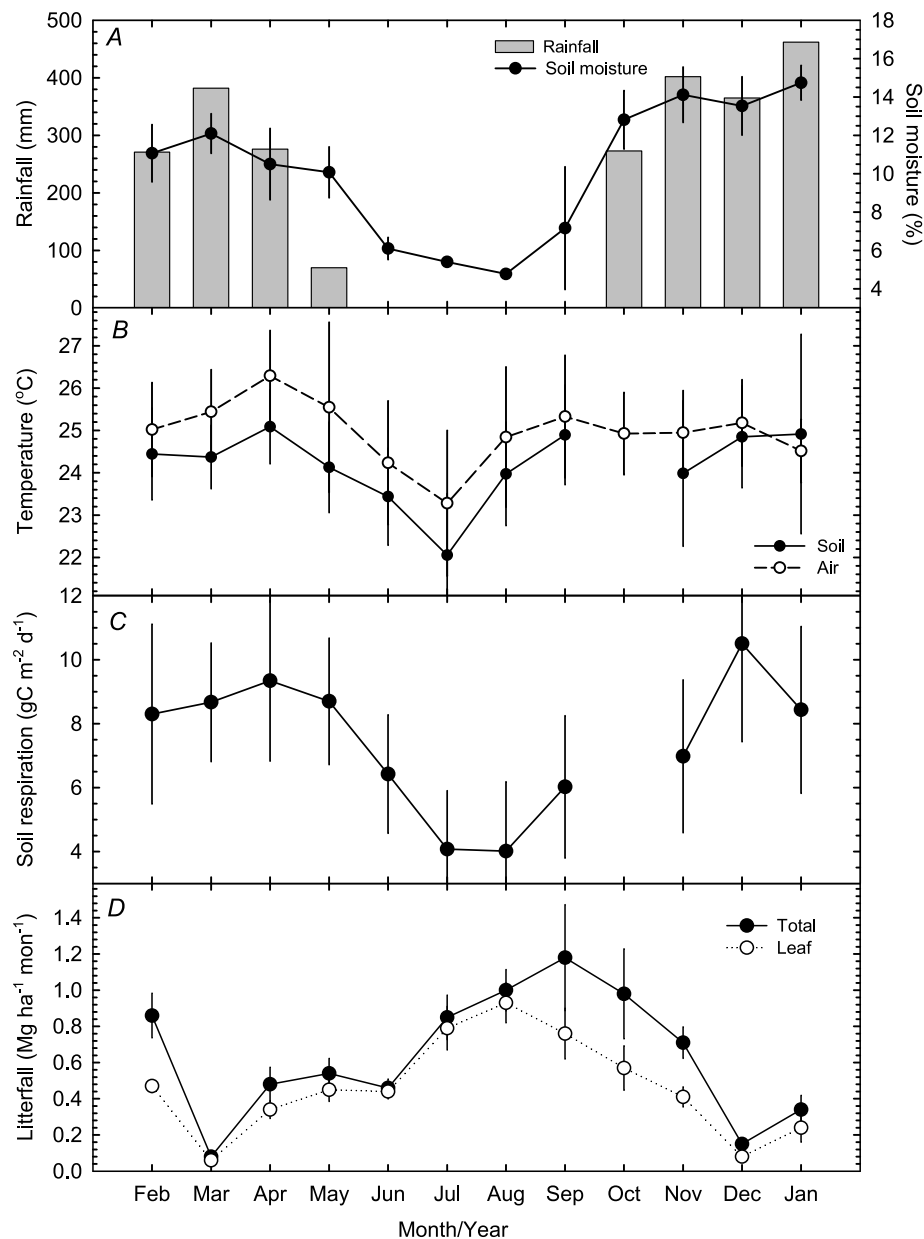
Figure 1. (a) Seasonal variation in total monthly rainfall (bars) and the average (±1 SD) surface (0–30 cm) volumetric soil moisture, (b) average monthly (±1 SD) air temperature (closed circles, dashed line) and average instantaneous (±1 SE; $n = 20$) soil temperature (open circles), (c) average (± SE, $n = 20$) seasonal trend in soil respiration, and (d) the average (±1 SE; $n = 20$) monthly total (closed circles, solid line) and leaf litter fall (open circles, dotted line) for a transitional tropical forest located near Sinop, Mato Gross, Brazil. Air temperature data were measured at the top of a 40-m-tall tower. Precipitation data were obtained from the Fazenda Continental located 5 km SE of the study site. Surface (0–30 cm) soil moisture was measured adjacent to the tower using time domain reflectometry ($n = 1$).

seasonal variation is soil moisture, the Q_{10} of the soil respiration temperature response (4.3) was closer to previous estimates of tropical forest soil CO$_2$ efflux [*Meir et al.*, 1996; *Sotta et al.*, 2004]. Soil respiration exhibited an optimum response to soil moisture with maximum rates of respiration at a soil moisture equivalent to 12% (Figure 2b).

3.3. Litter Production

[18] The average (±1SE; $n = 20$) rate of total litter fall (leaves, twigs, flowers, and fruits) was 0.86 ± 0.12 Mg ha^{-1} month^{-1} in February 2003, but this rate declined substantially the following month (Figure 1d). Total litter fall increased between March and August when the maximum monthly rate of total litter fall was observed (1.18 ± 0.29 Mg ha^{-1} month^{-1}). After September, total litter fall declined to 0.15 ± 0.03 Mg ha^{-1} month^{-1} by December but increased in January 2004 to a value of 0.34 ± 0.08 Mg ha^{-1} month^{-1} (Figure 1d). The seasonal trend in leaf litter fall followed the seasonal trend in total litter fall until August 2003 (Figure 1d). The rate of leaf litter fall was $0.47 \pm$

Table 1. Transitional Tropical Forest Statistics[a]

Variable	Units	Wet Season	Dry Season	Annual
Total litter fall	Mg ha^{-1} month^{-1}	0.51 ± 0.22	0.80 ± 0.22	0.64 ± 0.19
Leaf litter fall	Mg ha^{-1} month^{-1}	0.31 ± 0.14	0.67 ± 0.16	0.46 ± 0.14
Measured litter pool[b]	Mg ha^{-1}	6.0 ± 2.8	5.4 ± 1.1	5.7 ± 2.2
Estimated litter pool	Mg ha^{-1}	5.8 ± 0.3	5.2 ± 0.4	5.5 ± 0.3
Estimated k	month^{-1}	0.07 ± 0.01	0.19 ± 0.02	0.12 ± 0.04
Soil Respiration (R)	g C m^{-2} d^{-1}	9.15 ± 0.90	6.19 ± 1.40	7.91 ± 1.16
Decomposition (D)	g C m^{-2} d^{-1}	0.66 ± 0.08	1.65 ± 0.10	1.07 ± 0.27
D/R		0.07 ± 0.01	0.29 ± 0.07	0.16 ± 0.06

[a]Mean (±95% confidence interval) total and leaf litter fall, litter pool, estimated litter decomposition rate constant (k), average daily soil respiration, litter decomposition, and the ratio of decomposition to soil respiration (D/R) during the wet (n = 7 months) and dry (n = 5 months) seasons and over an annual basis. The wet season is defined as the number of consecutive months with precipitation >100 mm.

[b]Number of months (n) = 4 months for the wet season, 3 months for the dry season, and 7 months for the annual average.

0.04 Mg ha^{-1} month^{-1} in February 2003 and declined to 0.06 ± 0.01 Mg ha^{-1} month^{-1} in March 2003. Leaf litter fall reached a seasonal peak of 0.93 ± 0.11 Mg ha^{-1} month^{-1} at the end of the dry season in August and declined to a value of 0.08 ± 0.01 Mg ha^{-1} month^{-1} during the wet season in December (Figure 1d). Between March and August 2003, leaf litter fall comprised on average 86% the total litter fall; however, after August 2003 leaf litter fall
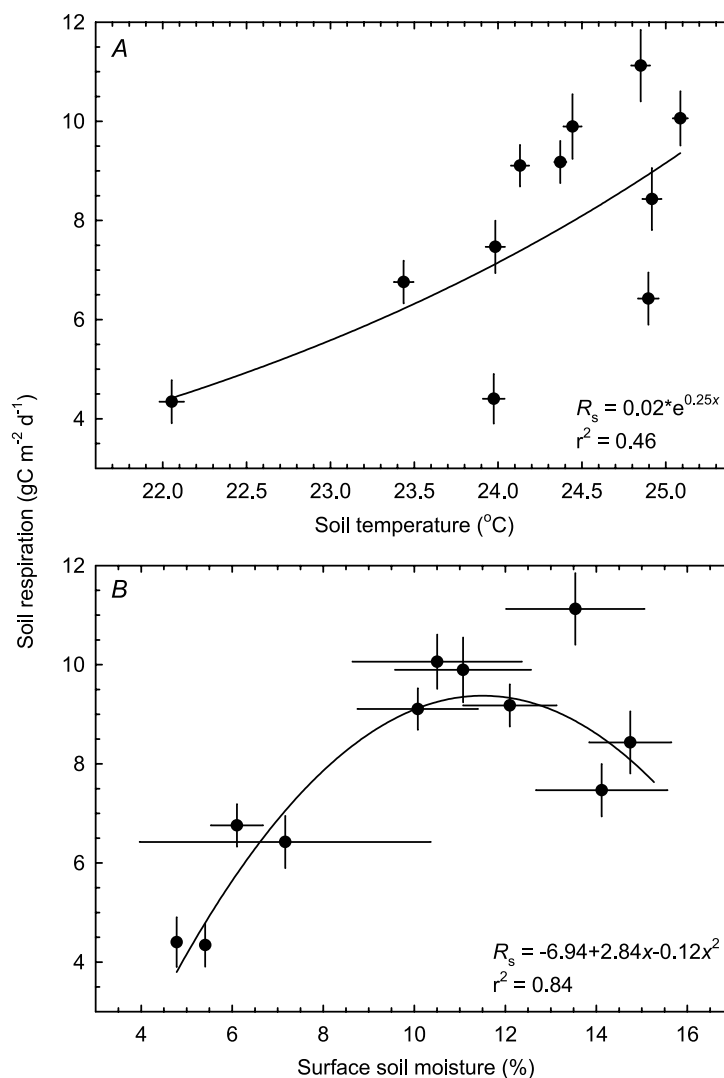

Figure 2. Instantaneous soil respiration as a function of (a) instantaneous soil temperature and (b) average monthly surface (0–30 cm) soil moisture. Data are means (±1 SE; n = 20) except for soil moisture where data are means (±1 SD). Regression lines were estimated using nonlinear least squares regression. Also shown are the estimated model coefficients and the coefficient of determination (r^2).
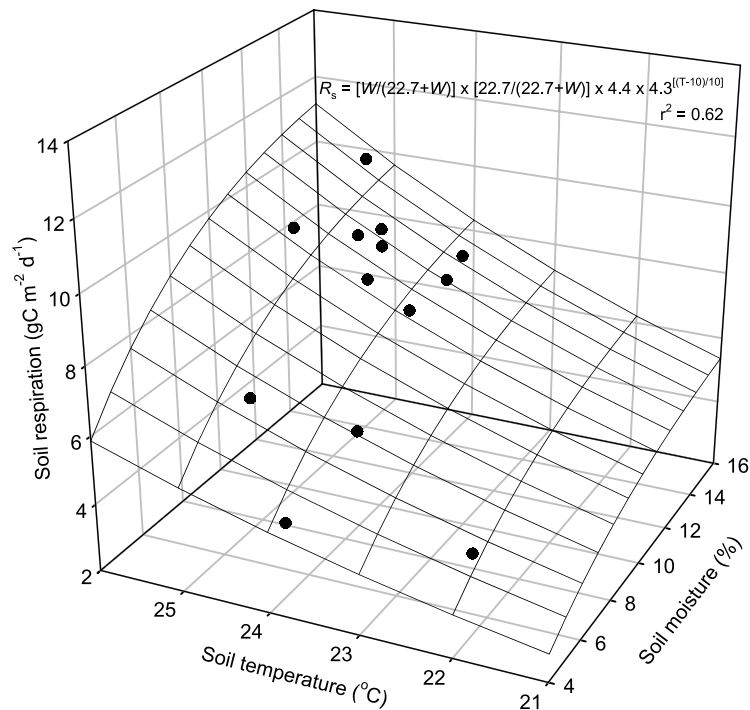
Figure 3. The soil respiration response as a function of surface (0–30 cm) soil moisture and soil temperature calculated using the model by *Bunnell et al.* [1977]. Also shown are the measured monthly soil respiration (closed circles), model coefficients, and the coefficient of determination (r^2).

comprised 58% of the total litter fall and the contribution of flowers and fruits to the total litter production became larger.

[19] Mean (±95% CI) total litter fall was 0.51 ± 0.22 Mg ha^{-1} month^{-1} during the wet season and 0.80 ± 0.22 Mg ha^{-1} month^{-1} during the dry season, while the average total litter production for the study period was 0.64 ± 0.19 Mg ha^{-1} month^{-1}, which corresponds to an annual rate of 7.0 Mg ha^{-1} (Table 1). Similarly, mean (±95% CI) leaf litter fall was 0.31 ± 0.14 and 0.67 ± 0.16 Mg ha^{-1} month^{-1} during the wet and dry seasons, respectively, and 0.46 ± 0.14 Mg ha^{-1} month^{-1} over the study period, corresponding to an annual rate of 5.2 Mg ha^{-1} (Table 1).

[20] Leaf and total litter fall declined as a function of total monthly rainfall and average monthly soil moisture; however, in most cases, litter fall was correlated more with the rainfall and soil moisture of the previous month (Figure 4). For example, total litter fall was not significantly correlated with rainfall of the current month ($r^2 = 0.31$; $p > 0.05$) but declined significantly as a function of rainfall of the previous month ($r^2 = 0.63$; $p < 0.01$; Figure 4a). In contrast, leaf litter fall was strongly correlated with rainfall of the current and previous month (Figure 4b). With soil moisture as the independent variable, total litter fall was not significantly correlated with soil moisture of the current month ($r^2 = 0.24$; $p > 0.05$) but was highly negatively correlated to soil moisture of the previous month ($r^2 = 0.70$; $p < 0.005$; Figure 4c). Leaf litter fall was significantly negatively correlated with soil moisture of the current and previous month; however, the correlation was higher if soil moisture was lagged by 1 month (Figure 4d).

3.4. Litter Decomposition and the Surface Litter Pool

[21] Estimates of the litter decomposition constant (k) estimated from mass balance (equations (1) and (2)) declined exponentially with rainfall ($r^2 = 0.86$; Figure 5), and this relationship was used to provide monthly estimates of k for the study period. The decay constant increased from the wet to the dry season and varied from 0.044 month^{-1} in January to 0.209 month^{-1} in June–August (Figure 6a). When averaged over the study period, k was 0.07 ± 0.01 month^{-1} during the wet season, 0.19 ± 0.02 month^{-1} during the dry season, and 0.12 ± 0.04 month^{-1} (1.45 a^{-1}) for the study period (Table 1).

[22] Litter decomposition rates were generally between 0.5 and 1.0 g C m^{-2} d^{-1} during the wet season and between 1.5 and 2.0 g C m^{-2} d^{-1} during the dry season (Figure 6b). On a seasonal basis, mean (±95% CI) daily litter decomposition was significantly higher during the dry season (1.67 ± 0.10 g C m^{-2} d^{-1}) than during the wet season (0.66 ± 0.08 g C m^{-2} d^{-1}), and averaged over the study period, litter decomposition was estimated to be 1.07 ± 0.27 g C m^{-2} d^{-1} (Table 1).

[23] The seasonal trend in the ratio of litter decomposition to soil respiration (D/R) followed the trend in litter decomposition closely (Figure 6b). During the dry season, decomposition accounted for approximately 30% of the soil CO$_2$ efflux, while during the wet season litter decomposition accounted for only 7% of the average daily soil respiration (Table 1). On an annual basis, litter decomposition accounted for approximately 16% of the soil respiration.

[24] The seasonal pattern for the measured surface litter pool was markedly different to that estimated using mass balance (Figure 6c). Measured litter pool biomass declined
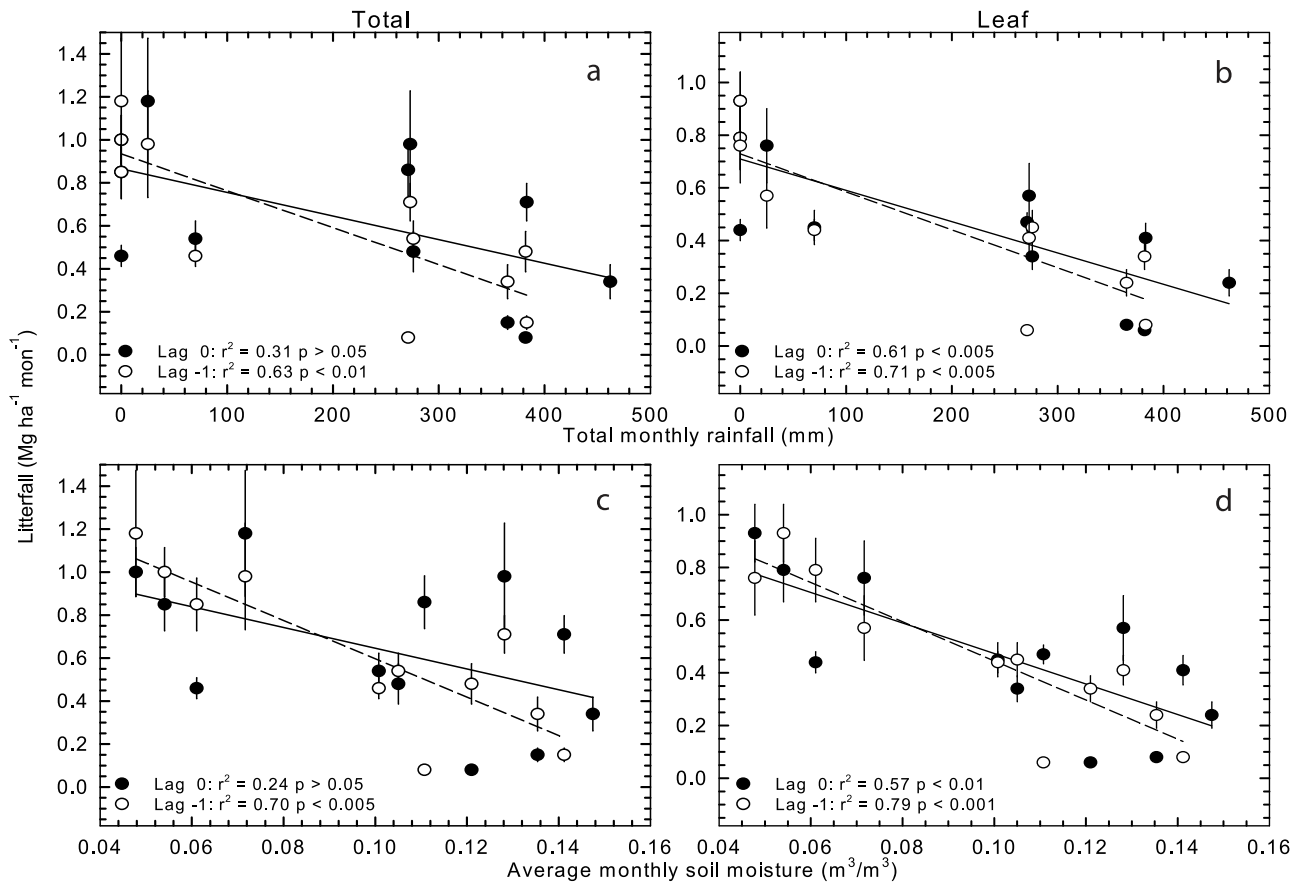
Figure 4. The relationship between (a) total and (b) leaf litter fall as a function of rainfall of the current (closed circles) and previous month (open circles), and the relationship between (c) total and (d) leaf litter fall as a function of mean surface soil moisture of the current (closed circles) and previous month (open circles). Also shown are the regression lines calculated using linear least squares for current rainfall or soil moisture (solid lines) and rainfall or soil moisture of the previous month (dashed lines), the coefficient of determination (r^2), and probability of type 1 error.
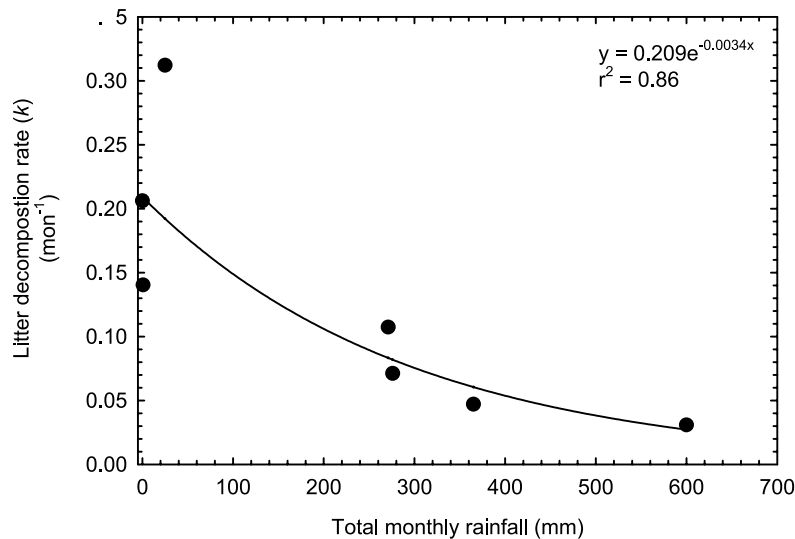

Figure 5. The relationship between total monthly rainfall and the estimated mean monthly litter decomposition rate constant. The exponential regression line was estimated using nonlinear least squares regression. Also shown are the model coefficients and the coefficient of determination (r^2).
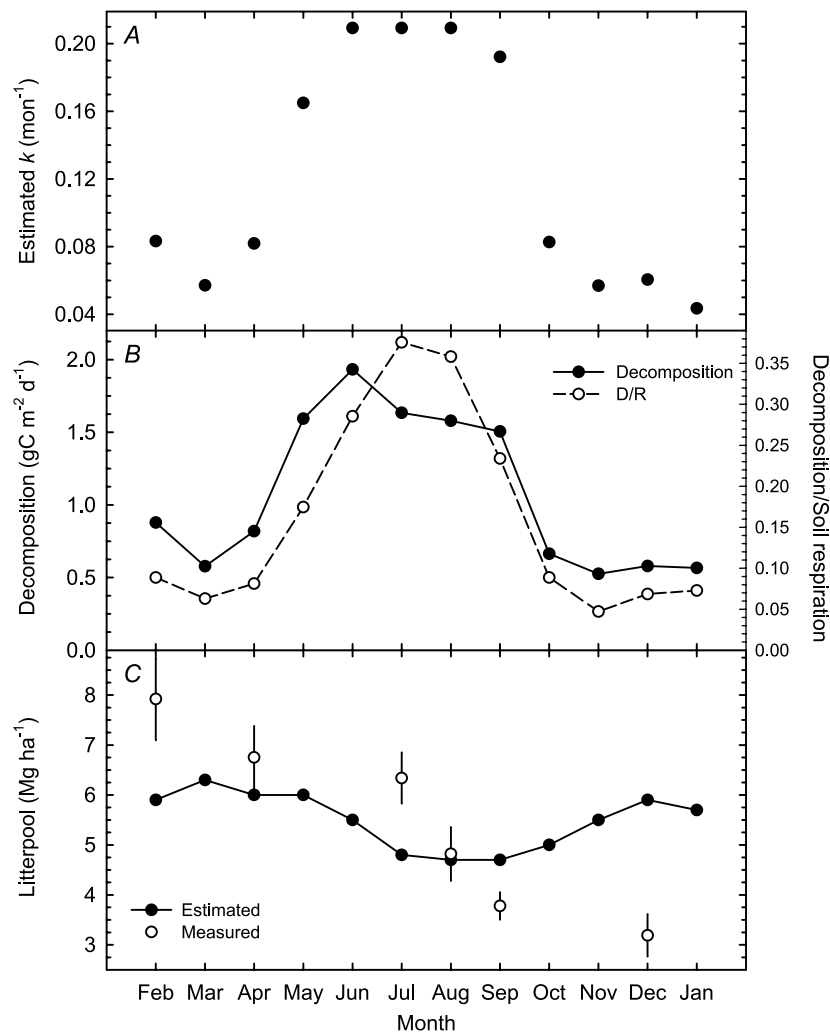
Figure 6. The seasonal trend in (a) the average monthly rate constant for litter decomposition (k), (b) the average monthly litter decomposition rate (left axis, solid circles, solid lines) and the ratio of litter decomposition to soil respiration (right axis, open circles, dashed line), and (c) the average monthly estimated surface litter pool (closed circles, solid line) and the average (± 1 SE, $n = 20$) measured surface litter pool (open circles).

throughout the study period from 7.9 Mg ha^{-1} in February to 3.2 Mg ha^{-1} in December (Figure 6c). In contrast, the estimated litter pool biomass increased slightly until March, declined by 1.6 Mg ha^{-1} by August, and increased to 5.9 Mg ha^{-1} by December (Figure 6c).

4. Discussion

4.1. Soil Respiration

[25] Soil respiration varied considerably over seasonal time scales, and was nearly 3 times higher in the wet season, which is similar to results reported for other Amazonian tropical forests [*Davidson et al.*, 2000; *Meir et al.*, 1996; *Sotta et al.*, 2004]. When averaged over the entire 1 year study period, soil CO$_2$ efflux was 7.9 ± 0.5 g C m^{-2} d^{-1} (Table 1), which is higher than the annual average reported for other tropical forests of the Amazon Basin [*Chambers et al.*, 2004; *Davidson et al.*, 2000; *Meir et al.*, 1996; *Nunes*, 2003]. The higher rates of annual soil CO$_2$ efflux reported here appear to be caused by higher rates of wet season

efflux, as dry season rates of CO$_2$ efflux for the transitional forest were similar to those reported for other Amazonian tropical forests [*Sotta et al.*, 2004; *Trumbore et al.*, 1995]. The higher wet season soil CO$_2$ efflux reported here may be due in part to differences in soil texture and rates of CO$_2$ (and/or O$_2$) diffusion between our site and others in the Amazon Basin. As mentioned above, the transitional forest soil contains 94% sand while many of the tropical forests described in the literature have soils that have substantially higher percentages of clay (e.g., 25–35%, from *Meir et al.* [1996] and 80% from *Sotta et al.* [2004]). Sandy soils have high porosity, and rates of diffusion can be relatively more rapid than in heavier clay soils even during times of high rainfall [*Teepe et al.*, 2003]. Previous studies of Brazilian tropical forest CO$_2$ efflux suggest that rates of CO$_2$ diffusion and/or efflux may be limited in clay-rich soils during the rainy season because of limitations to diffusion and/or the development of anaerobic conditions [*Davidson et al.*, 2000; *Sotta et al.*, 2004].

[26] Tropical forests often exhibit an increase in soil respiration during the wet season, suggesting that soil microorganisms may be water limited during the dry season [*Raich et al.*, 1985]. Seasonal variations in soil water availability can cause rapid fluctuations in microbial growth and activity [*Bunnell et al.*, 1977; *Wieder and Wright*, 1995; *Meir et al.*, 1996], physiological processes such as ion uptake, enzyme activity and concentration, tree growth, and root mortality [*McGroddy and Silver*, 2000; *Ryan*, 1991; *Wright*, 1991], and trigger a variety of phenological processes that alter resource allocation patterns in tropical trees [*Borchert*, 1996]. All of these responses will affect rates of heterotrophic and autotrophic respiration, and ultimately, soil CO$_2$ efflux.

[27] Temporal trends in soil CO$_2$ efflux were coincident with trends in air and soil temperature, soil moisture, and rainfall; which is consistent with results reported for some Amazonian tropical forests [*Meir et al.*, 1996; *Sotta et al.*, 2004; *Davidson et al.*, 2000; *Nunes*, 2003]. However, the Q$_{10}$ values calculated from monthly temperature (Figure 2a) and/or temperature and soil moisture relationships (Figure 3) were considerably higher than values reported for other Amazon forests [*Meir et al.*, 1996; *Sotta et al.*, 2004]. However, our estimate of the Q$_{10}$ should not be viewed as a strict respiratory response to temperature because other processes that also vary seasonally, such as primary productivity, root growth and turnover, and phenological variations in C and nutrient allocation, will also influence seasonal variations in soil respiration [*McGroddy and Silver*, 2000; *Curiel Yuste et al.*, 2004].

4.2. Litter Production

[28] Our estimates of the annual rate of litter production (Table 1) are similar to those published for several lowland tropical forests [*Klinge*, 1977; *Martinez-Yrizar and Sakurhan*, 1990; *Morellato*, 1992; *Luizão et al.*, 2004; *Sundarapandian and Swamy*, 1999] but lower than others [*Chambers et al.*, 2004; *Trumbore et al.*, 1995; *Wieder and Wright*, 1995]. Furthermore, the seasonal pattern in litter production reported here (Figure 4) is typical of many tropical forests [*Sundarapandian and Swamy*, 1999; *Wieder and Wright*, 1995] and suggests that seasonal variation in rainfall acts as a cue for litter production. While leaf and total litter production was highly negatively correlated with water availability, it is unclear whether dry season increases in litter production occur because of drought stress or whether seasonal variations in water availability, in conjunction with other environmental variables that covary with rainfall (temperature, photoperiod), trigger changes in phenology. The increase in flower and fruit litter indicate that the onset of the dry season triggers flower and fruit production [*Borchert*, 1996], but the mechanism for leaf abscission is harder to define. For example, in a field manipulative experiment in a Panamanian rain forest *Wright and Cornejo* [1990] found that plant water status had little to do with the timing of leaf litter fall, suggesting an important role of phenology in triggering leaf litter production.

4.3. Litter Decomposition and the Surface Litter Pool

[29] Our estimates of the litter decomposition rate constant (*k*) are similar to those published for other tropical or subtropical forests [*Alhamd et al.*, 2004; *Alvarez-Sanchez and*

Enriquez, 1996; *Salamanca et al.*, 2003; *Sundarapandian and Swamy*, 1999; *Wieder and Wright*, 1995]; however, the seasonal trend is opposite of what is typically observed for tropical systems. *Wieder and Wright* [1995] and *Alvarez-Sanchez and Enriquez* [1996] reported significantly higher *k* values during the wet season, and irrigation delivered during the dry season has also been found to stimulate rates of decomposition [*Wieder and Wright*, 1995], suggesting that available soil moisture limits rates of litter decomposition. However, in other field manipulative studies, the rate constant in plots exposed to partial rainfall exclusion (approximately 50% of the total monthly rainfall) was similar to that observed in plots receiving full rainfall [*Salamanca et al.*, 2003], suggesting that moderated reductions in water availability may have little direct effect on *k*. Furthermore, significant rates of litter decomposition can occur in litter humidity and moisture contents as low as 32 and 5%, respectively [*Nagy and Macauley*, 1982], which is lower than the ambient relative humidity and the surface soil moisture during the dry season [*Vourlitis et al.*, 2002, 2008]. Given the large dry season litter production (Figure 1d), it is conceivable that moisture conditions in the surface litter layer during the dry season were conducive for rapid microbial degradation of surface litter.

[30] Another possible explanation for the higher rate of litter decomposition during the dry season is that the nitrogen (N) and phosphorus P content of the litter pool may be higher during the dry season. For example, *Almeida* [2005] found that litter pool N concentration in this forest was more than 5 g kg^{-1} higher during the dry season, suggesting that the dry season litter pool was more N-rich. *Aerts* [1997] reported that litter quality, especially the lignin/N ratio, exerted the strongest influence on litter decomposition rates in tropical forests.

[31] Finally, CH$_4$ evolution reportedly increases by more than twofold during the dry season for this forest, and while the mechanism for this increase is currently unknown, termite activity is the most plausible source of CH$_4$ in upland, *terra firme* tropical forests [*do Carmo et al.*, 2006]. Thus, the increase in dry season litter decomposition (Figure 6a) may in part be explained by increases in termite consumption. Unfortunately, there are no data to test this hypothesis; however, an increase in surface litter degradation by a nonmicrobial agent would reconcile the different seasonal patterns in soil CO$_2$ efflux and litter decomposition.

[32] The seasonal trend in the ratio of litter decomposition to soil respiration (D/R) followed the trend in litter decomposition closely (Figure 6b), and aboveground litter decomposition accounted for approximately 30% of the soil CO$_2$ efflux in the dry season and only 7% of soil respiration during the wet season (Table 1). Our estimate of D/R assumes that all of the litter C is lost as CO$_2$ in soil respiration and that none of the litter C is lost by other processes such as leaching and/or soil C storage; assumptions that are undoubtedly simplistic and not justifiable. Even so our annual average for D/R (16%; Table 1) is remarkably close to that reported for an old-growth coniferous forest (19%) [*Sulzman et al.*, 2005] and a tropical forest near Manaus, Brazil (21%) [*Chambers et al.*, 2004].

[33] The estimated litter pool biomass from mass balanced failed to capture the decline in litter pool observed during the dry-wet season transition (Figure 6c); however,

the measured and estimated aboveground litter biomass was nearly identical when averaged by season and over an annual basis and well within the range of those published for a variety of tropical forests [*Sundarapandian and Swamy*, 1999]. The reason for the discrepancy between the measured and calculated seasonal trend in the surface litter pool is unknown but presumably reflects assumptions of the mass balance model (e.g., estimation of the decomposition rate constant) and/or limited temporal measurement of the surface litter pool.

5. Conclusions

[34] Measurements of soil CO$_2$ efflux, litter production, and the surface litter pool were made over a 1 year period in a tropical transitional forest near Sinop, Mato Grosso, Brazil with the aim of quantifying the seasonal variation in soil respiration and litter decomposition and the contribution of litter decomposition to soil CO$_2$ efflux. Soil CO$_2$ efflux was highest during the November–February wet season and lowest during the May–September dry season, and over 60% of the variation in soil CO$_2$ efflux was explained by the seasonal variation in soil temperature and moisture. However, the underlying mechanisms for this relationship are unknown because seasonal variations in temperature and water availability alter a variety of physiological processes that affect heterotrophic and autotrophic respiration. Total and leaf litter production was higher during the dry season, and 73% of the total litter fall over the study period was composed of leaf litter. Mass balance estimates of litter decomposition revealed that the rate constant for litter decomposition (k) declined exponentially with rainfall, and as a result, rates of litter decomposition were significantly higher during the dry season. The observed seasonal pattern in k and litter decomposition is opposite of what has been reported in the literature and may reflect higher litter quality and/or an increase in termite-induced litter consumption during the dry season. When averaged over the annual measurement period, k was 0.12 month^{-1} (1.45 a^{-1}) and the average litter turnover rate ($1/k$) was 9.5 months (288 days), which is consistent with that reported for other tropical forests. Overall, decomposition comprised on average 16% of the average annual soil respiration, but the contribution of litter decomposition to soil respiration was nearly 2 times higher during the dry season. Average (±95% CI) annual litter pool biomass was estimated to be 5.5 ± 0.3 Mg ha^{-1}, and while the seasonal trend in litter pool biomass estimated from mass balance differed from direct measurements, the estimated annual surface litter pool was similar to the measured pool (5.7 ± 2.2 Mg ha^{-1}). Our results suggest that seasonal variations in water availability (soil moisture and rainfall) had a profound influence on litter production, soil respiration, and surface litter decomposition; however, the degree in which water availability directly affects the kinetics of soil respiration, litter production, and decomposition or indirectly affects these processes though tree phenology is currently unknown.

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