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Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon

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[1] This study explored biotic and abiotic causes for spatio-temporal variation in soil respiration from surface litter, roots, and soil organic matter over one year at four rain forest sites with different vegetation structures and soil types in the eastern Amazon, Brazil. Estimated mean annual soil respiration varied between 13–17 t C ha^{-1} yr^{-1}, which was partitioned into 0–2 t C ha^{-1} yr^{-1} from litter, 6–9 t C ha^{-1} yr^{-1} from roots, and 5–6 t C ha^{-1} yr^{-1} from soil organic matter. Litter contribution showed no clear seasonal change, though experimental precipitation exclusion over a one-hectare area was associated with a ten-fold reduction in litter respiration relative to unmodified sites. The estimated mean contribution of soil organic matter respiration fell from 49% during the wet season to 32% in the dry season, while root respiration contribution increased from 42% in the wet season to 61% during the dry season. Spatial variation in respiration from soil, litter, roots, and soil organic matter was not explained by volumetric soil moisture or temperature. Instead, spatial heterogeneity in litter and root mass accounted for 44% of observed spatial variation in soil respiration ($p < 0.001$). In particular, variation in litter respiration per unit mass and root mass accounted for much of the observed variation in respiration from litter and roots, respectively, and hence total soil respiration. This information about patterns of, and underlying controls on, respiration from different soil components should assist attempts to accurately model soil carbon dioxide fluxes over space and time.

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1. Introduction

[2] Soil respiration (R_s) releases 75–80 billion tons of C each year [*Schlesinger*, 1977; *Raich and Potter*, 1995; *Raich et al.*, 2002]. This efflux is more than 11 times the recent rate of C produced from human combustion of fossil fuels [*Marland and Boden*, 1993]. So even a slight proportional change in global R_s could significantly alter atmospheric CO_2 levels, and hence climate. R_s usually accounts for a large proportion of terrestrial ecosystem respiration [*Lavigne et al.*, 1997; *Janssens et al.*, 2001] and variation in R_s may determine whether an ecosystem is a net source or sink of CO_2 [*Valentini et al.*, 2000; *Davidson et al.*, 2006]. Yet despite its clear importance for global C cycling and climate change, understanding of the processes controlling spatial and temporal variation in R_s is limited. This is largely because soil is a complex and spatially heterogeneous mixture of different compounds (e.g., ground surface organic litter, live roots, and soil organic matter pools). Understanding the individual responses of these compounds to environmental change and the net effect upon R_s remains a key objective for research into ecosystem C cycling and biosphere-atmosphere interactions.

[3] R_s is derived from autotrophic respiration by roots (R_r) and heterotrophic respiration by microorganisms that decompose ground surface organic litter (R_l) and soil organic matter or SOM (R_{som}). In this study, R_{som} also includes CO_2 derived from microbial decomposition of root tissue and exudates, and contributions from mycorrhizal fungi. These different sources of soil CO_2 may respond to environmental change in different ways, whilst estimates of the autotrophic component of R_s range between 12–93%

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Table 1. Key Vegetation and Soil Features for Each Site Surveyed[a]

Site Characteristics	Sand	Dry	Clay	Fertile
Vegetation				
Tree density (stems ha^{-1})[b]	434	421	419	544
Stem basal area (m^2 ha^{-1})[b]	24	24	25	37
Leaf area index (m^2 m^{-2})[c]	5 (4, 7)	5 (3, 6)	6 (4, 7)	—
Soil[d]				
Clay content (%)	18	13	42	20
C content 0–0.05 m depth (g kg^{-1})	9	12	27	49
Carbon stocks				
Total 0–1 m depth (t ha^{-1})	100 (94, 111)	103 (98, 108)	109 (103, 117)	206 (201, 216)
Surface litter (t ha^{-1})	2 (1, 4)	2 (1, 3)	2 (0, 3)	3 (1, 6)
Roots 0–0.3 m depth (t ha^{-1})[e]	6 (2, 13)	5 (2, 8)	7 (4, 12)	5 (2, 10)
Roots 0–1 m depth (t ha^{-1})[e,f]	8 (3, 17)	6 (2, 10)	9 (5, 16)	6 (3, 13)
Soil 0–0.3 m depth (t ha^{-1})[d]	35	44	45	111
Soil 0–1 m depth (t ha^{-1})[d]	90	95	98	197

[a]Values indicate mean and, where possible, 5th and 95th percentiles around the mean (in parentheses).
[b]All individuals over 0.1 m diameter at breast height, measured in January 2005.
[c]Means of 25 replicate measurements taken each month at each site in 2005 ($25 \times 12 = 300$ replicates), no data are available for the Fertile site.
[d]Calculated from data in *Ruivo and Cunha* [2003] and *Sotta* [2006], percentiles could not be calculated because neither data source presents error estimates.
[e]Roots less than 5 mm diameter.
[f]Calculated from root depth profile data presented by *Fisher et al.* [2007]. Profiles were available only for the Sand and Dry sites. Therefore, the root profile for the Sand site was applied to estimate stocks in the Clay and Fertile sites.

depending upon the ecosystem studied and the method used to estimate R_r [*Hanson et al.*, 2000]. R_l and R_{som} are directly driven by microbial activity, which, in turn, is strongly affected by temperature [*Davidson et al.*, 1998; *Fang and Moncrieff*, 2001] and available moisture [*Davidson et al.*, 1998; *Sotta et al.*, 2004]. This explains frequent observations, particularly in temperate and boreal regions where diurnal and seasonal fluctuations in temperature are greatest, that R_s rises as soil becomes warmer and wetter [e.g., *Savage and Davidson*, 2001]. However, both R_l and R_{som} are also partly decoupled from local soil conditions because they are affected by the supply and quality of substrate from above-ground in the form of organic litter and root exudates [*Melillo et al.*, 1982; *Högberg et al.*, 2001]. R_r is also partly a product of the level of metabolic activity within root tissue, affected by factors such as soil temperature [see *Atkin et al.*, 2000, and references therein], water availability [*Bouma et al.*, 1997; *Burton et al.*, 1998], N supply [*Ryan et al.*, 1996; *Zogg et al.*, 1996], and the supply of photosynthate from above-ground [*Högberg et al.*, 2001; *Nordgren et al.*, 2003], influenced by ecosystem GPP and plant allocation strategy. Thus, R_s and its component fluxes may display substantial spatial and temporal variability which is not readily attributable to changes in soil temperature and moisture. This variation reflects changes in both the total amount of respiring tissue (e.g., root mass) or available substrate, (e.g., surface litter mass) and the rate of respiration per unit mass of tissue or substrate (specific root respiration: *SRR*, specific litter respiration: *SLR*). Understanding the extent and causes of this variability represents an important step towards accurately modelling ecosystem C cycling, and up-scaling localized measurements across larger spatial scales for comparison with top-down measurement systems (e.g., satellites, flux towers). The overall objectives of this study, therefore, were to (1) partition R_s into R_l, R_r and R_{som} over one full seasonal cycle at four rain forest sites with contrasting vegetation and soil types in the eastern Amazon; (2) investigate potential biotic (roots, ground surface litter) and abiotic (soil moisture, soil temperature) causes for observed differences in respiration within and between sites and seasons; and (3) quantify the contributions of component mass and respiration per unit mass to total R_r and R_l.

[4] We focused upon sites in the Amazon because the region plays an important role in global biogeochemical cycles [*Houghton et al.*, 2001; *IPCC*, 2001], and displays a high degree of spatial heterogeneity in terms of many ecosystem properties [*Williams et al.*, 2002], but may experience an increase in drought conditions over this century due to a possible increase in El Niño-Southern Oscillation events [*Trenberth and Hoar*, 1997; *Schöngart et al.*, 2004] driven by global climate change, and reductions in rainfall caused by regional deforestation [*Shukla et al.*, 1990] and fire [*Andreae et al.*, 2004].

2. Materials and Methods

2.1. Site and Experimental Design

[5] The experimental site is located in the Caxiuanã National Forest, Pará State, north-eastern Brazil (1°43′3.5″S, 51°27′36″W). The forest is a lowland *terra firme* rain forest with a high annual rainfall (~2500 mm) and a pronounced dry season [*Fisher et al.*, 2006]. Across the entire year, mean soil surface temperature is ~25°C (±5°C), whilst diurnal variation is typically 1–2°C. The most widespread soil type is a highly weathered yellow Oxisol (US Department of Agriculture soil taxonomy). There are also patches of relatively fertile soil, called anthropogenic dark earths (ADE) or *Terra Preta do Indio*, which were modified by indigenous populations of pre-Columban inhabitants [*Da Costa and Kern*, 1999; *Lehmann et al.*, 2003]. To represent regional variation in soil type, one-hectare measurement sites (see Table 1 for additional site details) were located on a well drained sandy Oxisol (Sand site), a clay-rich Oxisol

(Clay site), and an ADE (Fertile site). In January 2002, a fourth one-hectare measurement site, also on sandy Oxisol soil, was modified by the installation of plastic panels at two meters height to exclude a proportion of incident rainfall (Dry site). The perimeter of the Dry site was trenched to a mean depth of one meter to minimize lateral flow of water into the site. Data from the fourth year of the rainfall exclusion on the Dry site were used to examine R_s under drier conditions than currently exists naturally. A detailed site inter-comparison, before the imposition of the drought treatment on the Dry site, indicates that soil and vegetation characteristics on the Sand and Dry sites were similar (P. Meir et al., manuscript in preparation, 2007).

2.2. Measurements

[6] Monthly measurements of R_s were made at 25 replicate points, at 20 meter intervals along a regularly spaced grid, within each site using an Infra-Red Gas Analyzer or IRGA (EGM-4 and SRC-1 chamber, PP Systems, Hitchin, UK.). Two months prior to the initiation of the measurement program plastic collars were inserted into the soil at each measurement location, to a depth of approximately 2 cm, to ensure a good seal between the IRGA chamber and soil. R_s (kg CO_2 m^{-2} s^{-1}) was calculated as:

$$R_s = \frac{\Delta C}{\Delta T} \bullet \frac{P}{1000} \bullet \frac{273}{t+273} \bullet \frac{44.01}{22.41} \bullet \frac{V_{ch}}{A} \quad (1)$$

where $\Delta C/\Delta T$ represents the change in CO_2 within the chamber (ppm) per unit time (seconds), P is atmospheric pressure (Pa), t is the temperature of the air within the chamber (°C), V_{ch} is the total internal volume of the chamber (m^3) and A is the ground area covered by the chamber (m^2). All measurements showed a positive linear relationship between C and T, indicating a constant rate of CO_2 release from the soil into the atmosphere.

[7] An additional 18 locations (9 each in November 2004 and June 2005, corresponding to the peaks of the dry and wet seasons respectively) were selected at 30 meter intervals along a regularly spaced grid, in each site to: (1) estimate the percentage contribution of surface litter, roots, and soil organic matter (SOM) to total R_s, and (2) examine factors controlling spatial and temporal variation of R_s in greater detail. At these points, R_s was measured twice with the IRGA: once with surface organic litter and once without. We defined surface litter as identifiable plant material on the ground surface which did not pass through a 0.5 mm mesh diameter sieve. Collected litter was carefully cleaned of inorganic detritus, roots, and mycorrhizae. The area of soil measured by the IRGA was then extracted as a soil core (diameter = 0.14 m, depth = 0.3 m) using opposable semi-circular cutting blades, and the roots were carefully removed by hand and cleaned of detritus. Fresh roots from each core were then placed into a cuvette which was connected to an IRGA that measured the rate of CO_2 accumulation within the cuvette. Root and litter samples were then dried at 70°C to constant mass and weighed. Two mass measurements were made for root samples: 1) roots less than five mm diameter, and 2) total. At all R_s measurement locations, instantaneous measurements of volumetric soil moisture (CS616 probe, Campbell Scientific, Loughborough, U.K.) and soil temperature (Testo 926 probe, Testo Ltd., Hampshire, U.K.) were taken at a soil depth of 0.3 m.

2.3. Data Analysis

[8] For each core, R_l (g m^{-2} hr^{-1}) was estimated as the difference between the first (with litter) and second (without litter) IRGA measurements. *SLR* (g g^{-1} hr^{-1}) was calculated by dividing R_l by sample dry litter mass. *SRR* (g g^{-1} hr^{-1}) was calculated by dividing the respiration rate of fresh root samples placed in the cuvette by sample dry mass of roots less than five mm diameter. R_r (g m^{-2} hr^{-1}) was then estimated by multiplying *SRR* by $1/A$. Estimates of R_r, following this method, integrated both root growth and maintenance respiration, and are likely to be conservative because they consider only the contribution from roots in the 0–0.3 meter soil layer and ignore the contributions of mycorrhizae and microbes dependent upon root exudates [*Nguyen*, 2003; *Jones et al.*, 2004]. Instead, in this analysis, these sources of CO_2 were ascribed to R_{som}. No consistent change in *SRR* over time since root excision was found (data not shown), so we propose that our estimates of *SRR* are not likely to be strongly biased by root excision [*Amthor*, 1994; *Burton et al.*, 1998]. R_{som} (g m^{-2} hr^{-1}) was estimated as the difference between measured R_s and the sum of estimated R_l and R_r, for each measurement point.

[9] Monthly measurements of R_s were used to estimate total monthly and annual R_s, while detailed core measurements (in November 2004 and June 2005) were used to partition R_s into R_l, R_r and R_{som}, for each site. To do this, we made several assumptions. Estimates of the proportional contribution of individual soil components derived from the June 2005 measurements were applied to monthly R_s measurements during June, April and May. Estimates of contributions taken in November 2004 were applied to monthly R_s measurements during November, October and December. The intervening two three-month R_s measurement periods were assigned values of the proportional contribution of soil components intermediate to the June and November measurement periods. This approach clearly simplifies reality but provides approximate estimates of seasonal and annual R_l, R_r and R_{som}. All measurements were made during the day. However, no significant difference between overall day (07:00–19:00) and night time (19:00–07:00) respiration values was found ($P = 0.48$, $n = 9$), and diurnal temperature variation at the site was minimal (1–2°C).

[10] Linear regression was used to assess whether spatial heterogeneity in soil moisture, soil temperature, litter mass and root mass could explain observed variation in R_s and its component fluxes. It was assumed that CO_2 flux from any individual component of R_s (e.g., roots, surface litter) was adequately described by:

$$R_c = C_m \bullet C_{rr} \bullet \frac{1}{A} + E, \quad (2)$$

where R_c is component respiration (g m^{-2} hr), C_m is component mass (g), C_{rr} is component respiration rate per unit mass (g g^{-1} hr^{-1}), and E is measurement error. In this study, R_r was not directly measured, but was calculated as solely the product of root mass and *SRR*. In addition, *SLR* was estimated as the residual variation in R_l, once variation

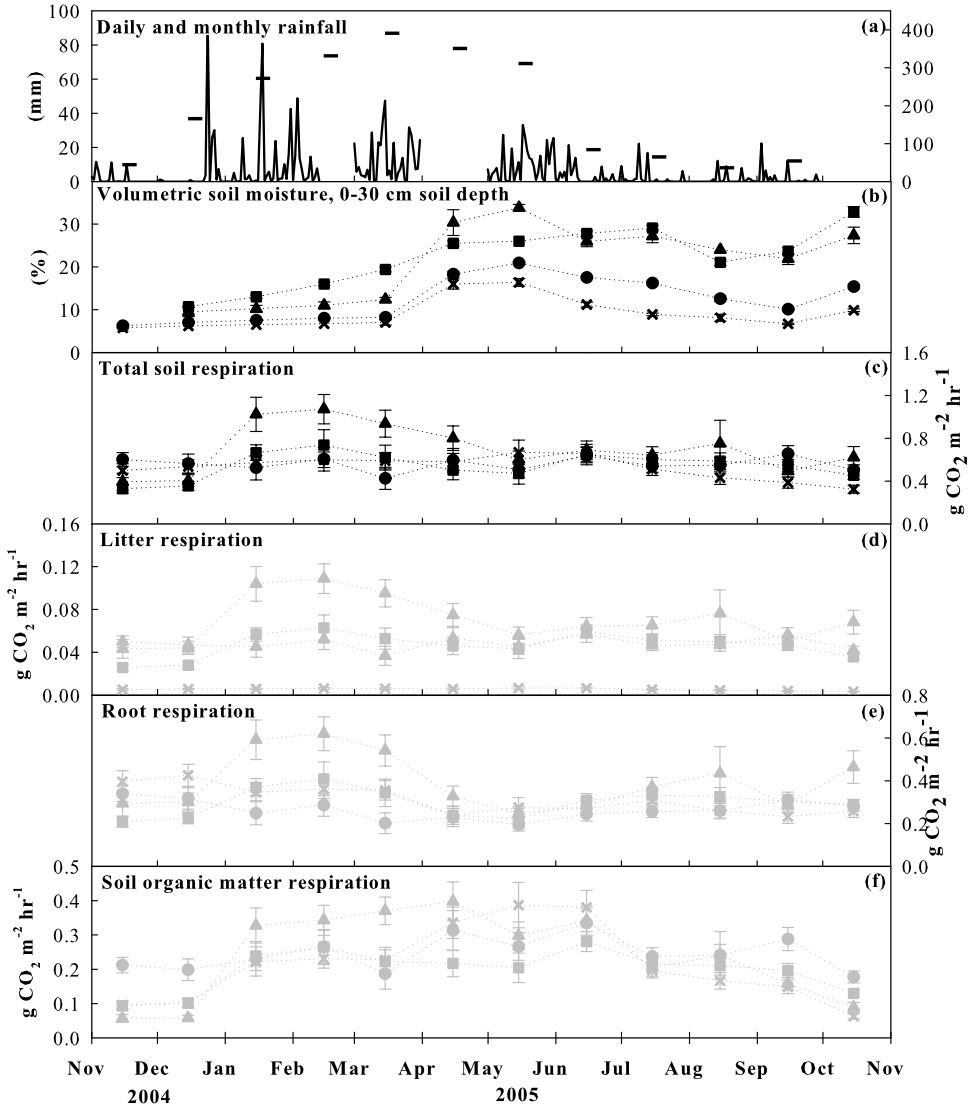

Figure 1. Temporal trends in (a) rainfall, (b) volumetric soil moisture, respiration from (c) soil, (d) litter, (e) roots, and (f) soil organic matter on all sites. Black symbols, directly measured data; grey symbols, estimated data from combination of directly measured (1) R_s (Figure 1c) and (2) contribution of R_l, R_r and R_{som} to R_s recorded in November 2004 and June 2005 (Table 2). Sites: circles, Sand; crosses, Dry; squares, Clay; triangles, Fertile. Error bars indicate SE of the mean, n is 25.

in litter mass was accounted for. Therefore, our estimates of R_r and *SLR* are likely to include some component of measurement error. A stepwise regression was performed which quantified the individual and combined contributions of estimated C_m and C_{rr} to R_c of roots and litter. Statistical analysis was carried out using SPSS 13.0 for Windows (SPSS Inc., Chicago, U.S.A). Data were subject to a natural logarithmic transformation, where necessary, to conform to the assumptions of parametric analysis.

3. Results

3.1. Spatial and Temporal Variation in Respiration From Soil and Its Components

[11] There was substantial variation between sites in the respiration variables recorded (Table 2 and Figure 1). Estimated mean annual site R_s varied between 13–17 t C ha^{-1} yr^{-1}, which was partitioned into 0–2 t C ha^{-1} yr^{-1} from litter, 6–9 t C ha^{-1} yr^{-1} from roots, and 5–6 t C ha^{-1} yr^{-1} from soil organic matter (Table 2). On average, 51% of the total range in R_s values recorded across all sites and measurement periods was also observed within each site and period. A large proportion of the recorded variation in R_s was, therefore, caused by within-site spatial heterogeneity, rather than systematic changes between sites and measurement periods. Site mean fluxes ranged between 5–13%, 40–75%, and 14–54% of total R_s for litter, roots, and SOM, respectively (Table 2). Mean R_{som} contribution declined from 49% during the wet season to 32% in the dry season (Figure 1f), while R_r contribution displayed the opposite trend: increasing from 42% in the wet season to 61% during the dry season (Figure 1e). In contrast, R_l

Table 2. Annual Respiration From Soil and Its Components, Contribution of Surface Litter, Roots, and Soil Organic Matter to Total Soil Respiration, and Specific Respiration of Litter and Roots, for Each Site[a]

	Sand	Dry	Clay	Fertile
Annual respiration				
Total soil (t C ha^{-1} yr^{-1})	13 (9, 20)	13 (8, 18)	13 (10, 18)	17 (13, 30)
Litter (t C ha^{-1} yr^{-1})	1 (1, 2)	0 (0, 1)	1 (1, 2)	2 (1, 4)
Roots (t C ha^{-1} yr^{-1})	6 (4, 9)	7 (4, 9)	7 (6, 10)	9 (8, 17)
SOM (t C ha^{-1} yr^{-1})	6 (4, 10)	5 (4, 8)	5 (4, 6)	6 (4, 9)
Litter contribution				
Nov 2004 (%)	9 (0, 29)	6 (0, 15)	9 (0, 23)	13 (0, 42)
Jun 2005 (%)	10 (2, 19)	5 (0, 14)	10 (2, 25)	11 (0, 25)
Root contribution				
Nov 2004 (%)	48 (19, 81)	55 (30, 85)	64 (42, 85)	75 (50, 91)
Jun 2005 (%)	38 (19, 60)	41 (9, 69)	48 (32, 66)	41 (26, 59)
SOM contribution				
Nov 2004 (%)	46 (4, 81)	39 (11, 60)	28 (4, 54)	14 (6, 28)
Jun 2005 (%)	51 (31, 70)	54 (31, 81)	42 (23, 60)	48 (33, 67)
Specific respiration rate				
Litter (g CO_2 kg^{-1} hr^{-1})	0.3 (0, 0.6)	0.2 (0, 0.5)	0.3 (0, 0.7)	0.4 (0, 1.5)
Roots (g CO_2 kg^{-1} hr^{-1})	0.4 (0.2, 0.8)	0.5 (0.2, 0.9)	0.3 (0.2, 0.6)	0.7 (0.3, 1.2)

[a]Values indicate mean (5th percentile, 95th percentile), n is 18, except estimates of percentage contribution from components where n is 9.

contribution showed no clear seasonality, though experimental precipitation exclusion on the Dry site was associated with an apparent reduction in R_l of approximately 90% relative to the unmodified sites (Table 2 and Figure 1d).

3.2. Factors Affecting Total Soil Respiration

[12] Several non-linear models were fitted to the monthly R_s data, but none explained above 0.07% of observed variation in R_s. So the data were log-transformed and analyzed with a linear regression. Soil temperature did not contribute significantly to the model, and so was removed. There was a significant relationship between volumetric soil moisture and monthly R_s (Figure 2, $F = 30$, d.f. = 1, 763, $R^2_a = 0.04$, $p < 0.001$). Given the low R^2_a, the significance of the relationship between R_s and soil moisture probably reflects the large sample size, rather than strong evidence of any causal link.

[13] A subset of R_s measurements, made in November 2004 and June 2005, were used to examine factors affecting R_s in more detail. Based upon these data, with a smaller sample size, neither soil temperature nor volumetric soil moisture (Figure 3a) could explain observed variation in R_s. Instead, regression analysis revealed that ground surface litter and root mass in the surface 0.3 meter soil layer together were more useful predictors of R_s, accounting for 44% of observed spatial variation in R_s (Figures 3b and 3c, $F = 17$, d.f. = 1, 68, $R^2_a = 0.44$, $p < 0.001$). The majority of this variation (31%) was attributable solely to heterogeneity in soil surface root mass (Figure 3c), while litter mass accounted for the remaining 13% (Figure 3b).

3.3. Factors Affecting Respiration From Litter, Roots, and Soil Organic Matter

[14] Based upon the subset of measurements made in November 2004 and June 2005, there was no significant relationship between volumetric soil moisture and R_l, R_r and R_{som} (data not shown). Heterogeneity in ground surface litter mass accounted for 25% of observed variation in R_l (Figure 4b). The majority of variation in R_l was, therefore, attributed to differences in *SLR* and measurement error (Figure 4a). In contrast, fine root mass explained 73% of variation in R_r, (Figure 5b) while changes in *SRR* accounted for 16% (Figure 5a).

[15] Volumetric soil moisture had no clear effect upon R_l ($F = 2$, d.f. = 1, 45, $R^2_a = 0.02$, $p = 0.16$) or litter mass ($F = 0.1$, d.f. = 1, 69, $R^2_a = -0.01$, $p = 0.75$). Root mass, in contrast, increased significantly with soil moisture (Figure 6a, $F = 17$, d.f. = 1, 70, $R^2_a = 0.19$, $p < 0.001$), while *SRR* decreased (Figure 6b, $F = 13$, d.f. = 1, 69, $R^2_a = 0.15$, $p = 0.001$). The net outcome of these two opposing patterns

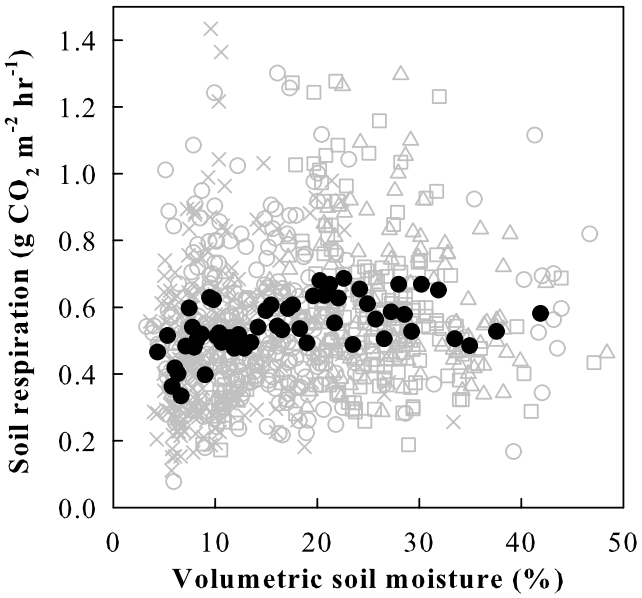

Figure 2. Relationship between monthly soil respiration and volumetric soil moisture. Data from all sites and months have been pooled. Data: grey symbols, individual values; black symbols, mean of 15 values. Sites: grey circles, Sand; grey crosses, Dry; grey squares, Clay; grey triangles, Fertile.

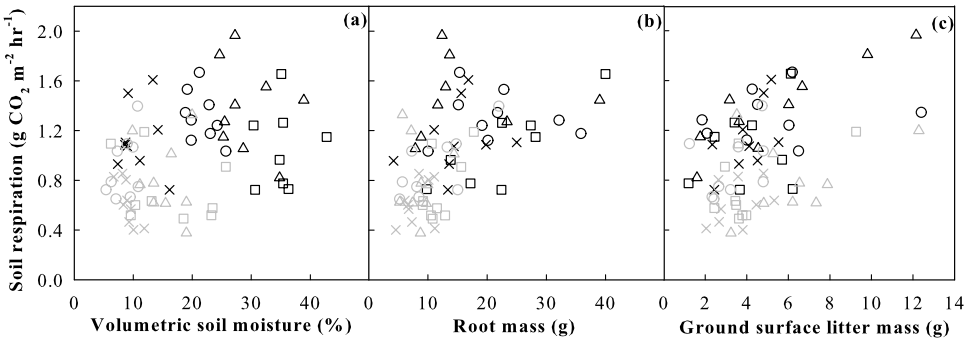

Figure 3. Relationship between soil respiration and (a) volumetric soil moisture, (b) root dry mass and (c) surface litter dry mass. Root mass represents the quantity of root material (<5 mm diameter) retrieved from a 0.3 m deep soil core corresponding to the area enclosed by the IRGA chamber (area = 154 cm^2). Litter mass represents the quantity of organic material retrieved from the ground surface within the IRGA chamber. Measurement periods: grey symbols, November 2004; black symbols, June 2005. Sites: circles, Sand; crosses, Dry; squares, Clay; triangles, Fertile.

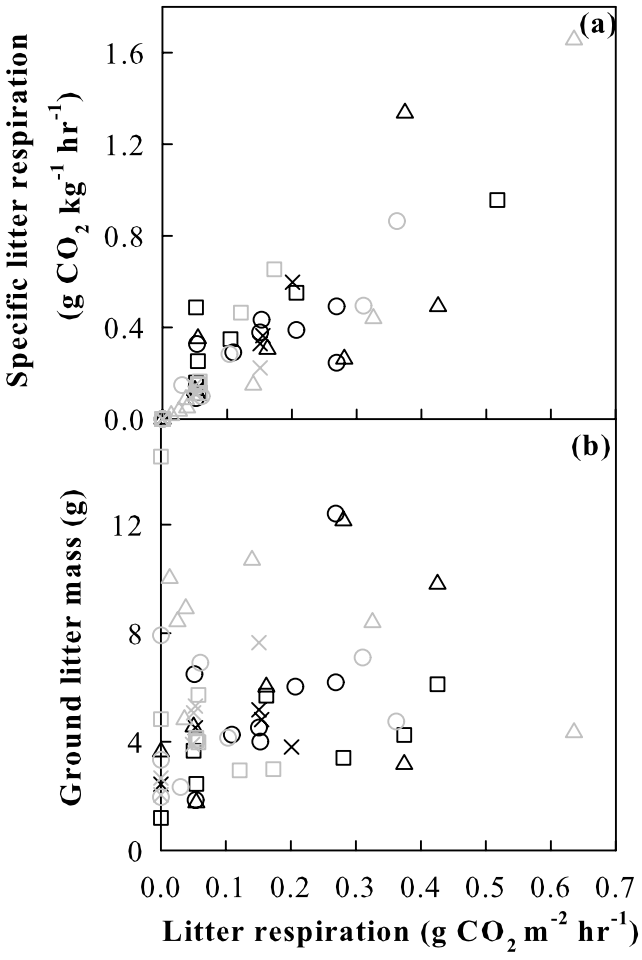

Figure 4. Relationship between surface litter respiration and (a) specific litter respiration and (b) litter dry mass. Litter mass represents the quantity of organic material retrieved from the ground surface within the IRGA chamber (area = 154 cm^2). Measurement periods: grey symbols, November 2004; black symbols, June 2005. Sites: circles, Sand; crosses, Dry; squares, Clay; triangles, Fertile.

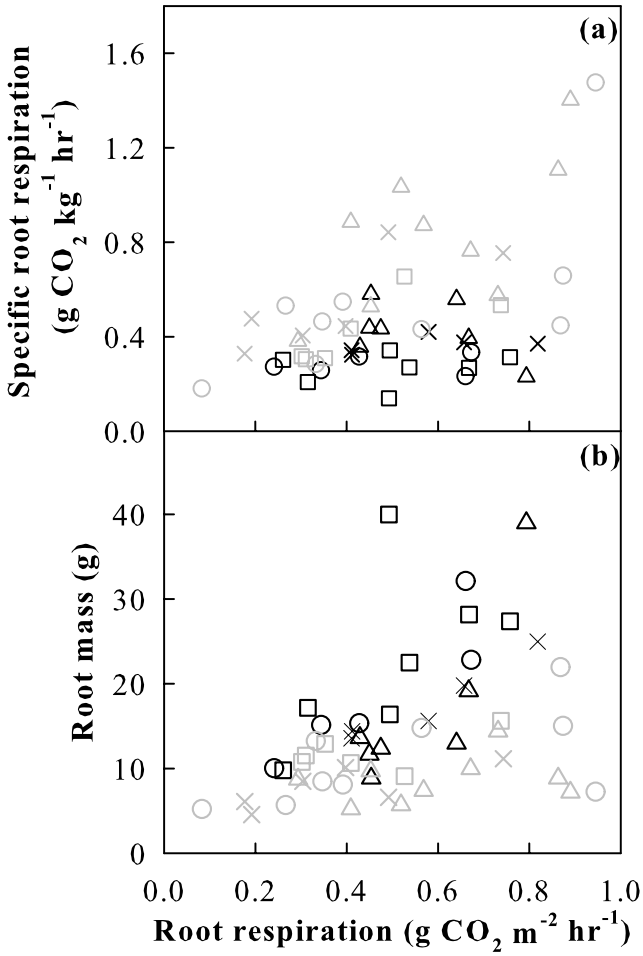

Figure 5. Relationship between root respiration and (a) specific root respiration and (b) root dry mass. Root mass represents the quantity of root material (<5 mm diameter) retrieved from a 0.3 m deep soil core corresponding to the area enclosed by the IRGA chamber (area = 154 cm^2). Measurement periods: grey symbols, November 2004; black symbols, June 2005. Sites: circles, Sand; crosses, Dry; squares, Clay; triangles, Fertile.

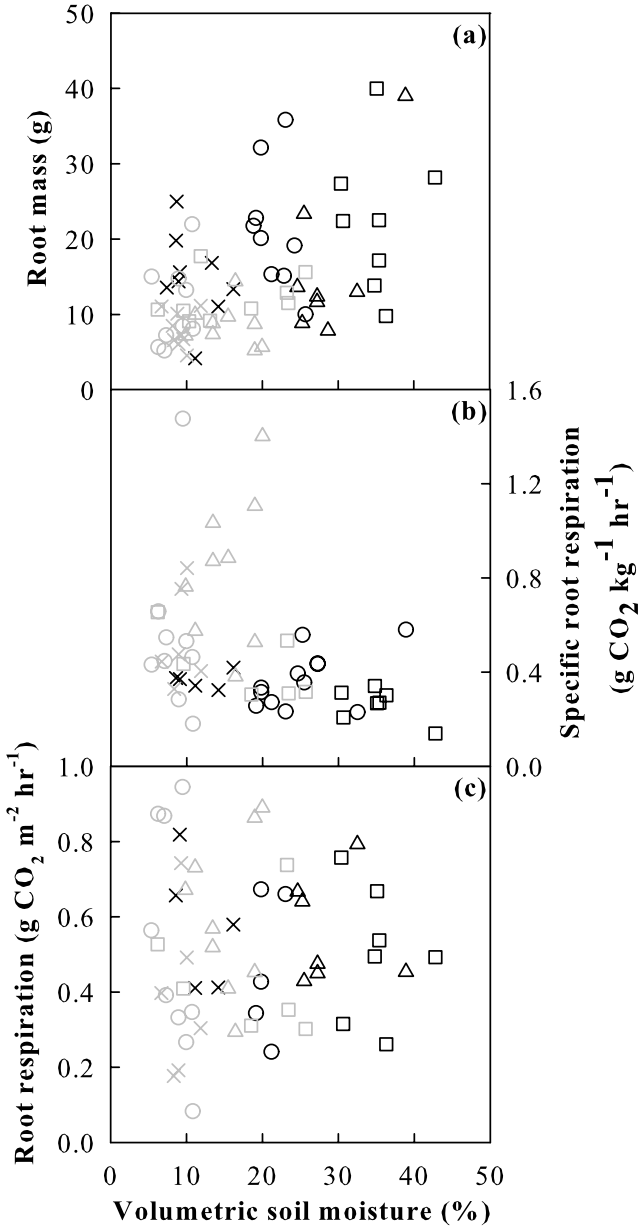

Figure 6. Relationship between volumetric soil moisture and (a) root dry mass, (b) specific root respiration and (c) root respiration. Root mass represents the quantity of root material (<5 mm diameter) retrieved from a 0.3 m deep soil core corresponding to the area enclosed by the IRGA chamber (area = 154 cm^2). Measurement periods: grey symbols, November 2004; black symbols, May 2005. Sites: circles, Sand; crosses, Dry; squares, Clay; triangles, Fertile.

was that R_r was not clearly affected by soil moisture (Figure 6c, F = 0.1, d.f. = 1, 70, $R^2_a = -0.01$, p = 0.79).

4. Discussion

4.1. Annual Respiration Estimates

[16] Based upon a global review of R_s partitioning across biomes [*Subke et al.*, 2006] we estimated mean R_s in tropical deciduous forests of 14 t C ha^{-1} yr^{-1} (ranging from 8–24 t C ha^{-1} yr^{-1}, from 10 studies reviewed), compared to values from this study of 13–17 t C ha^{-1} yr^{-1} (Table 2). Across all sites surveyed in this study, estimated mean annual heterotrophic contribution to total R_s was 40–52%, compared to a mean of 51% (ranging from 27–76%) from other studies in the same ecosystem [*Subke et al.*, 2006]. By comparison, temperate broadleaf and boreal coniferous forests appear to have lower mean R_s of 9 and 7 t C ha^{-1} yr^{-1} respectively, and slightly higher mean heterotrophic contribution to R_s (~57%), compared to tropical forest ecosystems [*Subke et al.*, 2006].

[17] The quantity of C respired from each soil component relative to C stocks in each component provides clues about the rate of soil C cycling on each site. For example, while the total amount of litter on the Dry site was similar to the Sand site (2 t C ha^{-1}, Table 1), R_l on the Dry site was ~90% lower. On both sites, the measured C input into surface organic litter (4 and 3 t C ha^{-1} yr^{-1} on the Sand and Dry sites respectively; D. B. Metcalfe, unpublished data, 2007) was higher than the estimated quantity of C released via R_l. There are several explanations for this apparent imbalance: (1) the system is not in steady state and therefore surface litter stocks should accumulate on both sites, or steady state conditions do exist but (2) C is removed from the surface litter (~3 t C ha^{-1} yr^{-1} on both sites) through mechanisms other than respiration (e.g.: conversion into SOM, leaching), and/or (3) R_l has been underestimated in this study. We propose that additional measurements; including repeated measurement of litter stocks over time, sampling of dissolved organic C in soil, direct measurement of litter decomposition with litter bags [*Nepstad et al.*, 2002; *Cleveland et al.*, 2006], and R_l measurement at sufficient temporal frequency to capture short-lived surges in respiration after rainfall events [*Lee et al.*, 2002; *Savage and Davidson*, 2002], could distinguish between these different explanations.

[18] Estimated R_{som} on the Fertile site was similar to the other sites (Table 2), even though estimated soil C stock in the 0–0.3 meter soil layer was over twice as large. This suggests that a relatively large proportion of the soil C stock at the Fertile site may be recalcitrant, compared to the other sites. This interpretation is consistent with much of the few existing data on this unusual soil type [*Da Costa and Kern*, 1999; *Lehmann et al.*, 2003]. Given the sensitivity of most Amazonian soils to many current forms of agriculture, there is substantial interest in how these soils have sustained such a high level of fertility after hundreds, sometimes thousands, of years of cultivation, and potentially how to recreate them across the Amazon again [see *Mann*, 2002]. Within this context, this study provides insights into how, and why, the ADE or *Terra Preta do Indio* soil on the Fertile site differs from the more widespread highly weathered Oxisol soils on the other sites.

[19] Our estimates of R_r did not include contributions from roots below 0.3 meter soil depth. Other studies in the Amazon estimated that up to 20% of total R_s was produced below 1 meter depth, and attributed this to substantial respiration from live roots and root-derived SOM in deeper soil layers [*Davidson and Trumbore*, 1995; *Trumbore et al.*, 1995]. However, based upon soil CO_2 production profile data recorded at the Sand and Dry sites [*Sotta*, 2006], we estimate that soil below 1 meter depth accounted for only 12% of total respiration (within the upper 3 meter soil layer) at these sites, while the 0–0.3 meter soil layer sampled in

this study produced approximately 75% of total respiration. We suggest, therefore, that the extent of R_r underestimate in this study is likely to be relatively minor. Clearly, though, further work is required to resolve the contribution of deep roots to C cycling in this ecosystem.

4.2. Factors Affecting Respiration From Soil, Litter, Roots, and Soil Organic Matter

[20] In this study, an asymptotic response pattern of R_s to moisture was recorded (Figure 2) which is consistent with results from other studies [e.g., *Davidson et al.*, 2000; *Schwendenmann et al.*, 2003; *Sotta et al.*, 2006], but the observed trend was weak (Figure 2). Neither was there a strong relationship between volumetric soil moisture and R_l, R_r and R_{som} estimated from the subset of measurements recorded in November 2004 and June 2005 (data not shown), despite the fact that both R_r and R_{som} contributions to total R_s changed substantially between the wet and dry seasons and R_l was consistently lower on the Dry site (Table 2 and Figure 1). Though, the respiration time series presented in this study (Figure 1) should be interpreted with caution, given the assumptions inherent in the analysis (see the methods section). Surface soil temperature was relatively invariant at the study site and thus could not account for the observed level of spatio-temporal variation in R_s and its component fluxes.

[21] Several studies in the region have reported a relationship between R_s and soil temperature and/or soil moisture [*Meir et al.*, 1996; *Davidson et al.*, 2000; *Sotta et al.*, 2004, 2006]. For example, *Meir et al.* [1996] found that soil temperature at five cm soil depth accounted for 76–88% of variation in R_s, at a rain forest site in the south-western Amazon. *Sotta et al.* [2004] reported a significant effect of both soil temperature and moisture on R_s from a forest in the central Amazon. However, these results were based upon short-term temporal trends (days-weeks) in R_s, whereby repeated measurements were taken from the same locations. *Sotta et al.* [2004] concluded that "temperature and soil water content. . ..can mostly only explain temporal variation (in R_s), especially in relatively uniform ecosystems." We suggest that, in addition to spatial patterns in R_s, longer-term temporal (seasonal and inter-annual) trends in R_s, may be confounded by changes in root and litter mass or respiration rate of these components. This is potentially important because seasonal changes in temperature and moisture often coincide with major shifts in leaf litter and root activity [*Gosz et al.*, 1972; *Vose and Ryan*, 2002]. Spatial and temporal models of soil and ecosystem C cycling could, therefore, be significantly improved through incorporation of litter and root dynamics.

[22] In this study, spatial heterogeneity in litter and root mass (in the surface 0.3 meter soil layer) were more useful predictors of spatial variation in R_s (Figure 3): together accounting for 44% of observed spatial variation in R_s. In particular, variation in *SLR* and root mass accounted for much of the variation in R_l and R_r respectively (Figures 4 and 5), and hence R_s. The two determinants (mass and respiration rate per unit mass) of component respiration represent different C flux pathways which may each respond to environmental variation in different ways (see Figure 6). For example, increased drought-like conditions in the Amazon may cause increased leaf litter fall [*Neilson and Drapek*, 1998; *Nepstad et al.*, 2002] and thus surface litter mass, but an associated drop in litter moisture [*Couteaux et al.*, 1995] or litter quality [*Melillo et al.*, 1982] could drive a decline in *SLR*. Results from this study (Figure 4) suggest that if this happened, a drought-induced decline in *SLR* would have a much greater impact on the contribution of litter to R_s. These preliminary findings could be improved through the simultaneous application of alternative methodologies for partitioning R_s (e.g.: trenching [*Silver et al.*, 2005]; tree girdling [*Högberg et al.*, 2001]; isotopic tracers [*De Camargo et al.*, 1999]) to compare the resultant estimates of R_l, R_r and R_{som}.

5. Conclusions

[23] This study examined spatial and temporal variation in respiration from soil and its components. There was substantial variation in respiration within and between sites and seasons. Neither volumetric soil moisture nor soil temperature could explain this heterogeneity even though both R_r and R_{som} contributions to R_s changed between the wet and dry seasons, and R_l was consistently lower on the Dry site. Instead surface litter and root mass accounted for much of the observed spatial variability in R_s. Specifically, variation in *SLR* and root mass accounted for much of variation in R_l and R_r respectively, and hence R_s. This information about the underlying controls upon respiration from different soil components has important implications for modeling soil CO_2 fluxes over space and time.

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