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Heterotrophic soil respiration in relation to environmental factors and microbial biomass in two wet tropical forests

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Abstract

We examined the correlation between fungal and bacterial biomass, abiotic factors such as soil moisture, carbon in the light soil fraction and soil nitrogen to a depth of 0–25 cm and heterotrophic soil respiration using a trenching technique – in a secondary forest (*Myrcia splendens*, *Miconia prasina* and *Casearia arborea*) and a pine (*Pinus caribeae*) plantation in the Luquillo Experimental Forest in Puerto Rico. Soil respiration was significantly reduced where roots were excluded for 7 years in both the secondary forest and the pine plantation. Microbial biomass was also significantly reduced in the root exclusion plots. In root exclusion treatment, total fungal biomass was on average 31 and 65% lower than the control plots in the pine plantation and the secondary forest, respectively, but the total bacterial biomass was 24 and 8.3% lower than the control plots in the pine plantation and the secondary forest, respectively. Heterotrophic soil respiration was positively correlated with fungal biomass ($R^2 = 0.63$, $R^2 = 0.39$), bacterial biomass ($R^2 = 0.16$, $R^2 = 0.45$), soil moisture ($R^2 = 0.41$, $R^2 = 0.56$), carbon in light fraction ($R^2 = 0.45$, $R^2 = 0.39$) and total nitrogen ($R^2 = 0.69$, $R^2 = 0.67$) in the pine plantation and the secondary forest, respectively. The regression analysis suggested that fungal biomass might have a greater influence on heterotrophic soil respiration in the pine plantation, while the bacterial biomass might have a greater influence in the secondary forest. Heterotrophic soil respiration was more sensitive to total N than to carbon in the light fraction, and soil moisture was a major factor influencing heterotrophic soil respiration in these forests where temperature is high and relatively invariable.

Introduction

Soil respiration, measured as soil-surface CO_2 efflux, produces about 80 Pg of CO_2–C annually at a global scale (Raich et al., 2002), which is about one tenth of the total atmospheric CO_2 stock and more than 11 times the current rate of fossil fuel combustion (Marland et al., 2000). The carbon stock in global soils is twice the size of atmospheric carbon pool and 70% of the soil carbon is stored in forest soil. Tropical forests are of particular importance in global carbon cycle because tropical forests account for 20 % of the world's carbon stocks of terrestrial ecosystems and the carbon turnover rate in tropical forests is much faster than in the temperate and boreal forests (Dixon et al., 1994; Schlesinger,

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1997). Therefore, the study of soil respiration in tropical forests is critical to the understanding of global carbon dynamics, the response of terrestrial ecosystem to global change, and the feedback effect of terrestrial ecosystem to future atmospheric CO_2 concentration (Amatya et al., 2002; Lugo, 1992; Tufekcioglu et al., 2001).

Total soil respiration includes autotrophic root respiration (e.g., root respiration and associated rhizospheric microbial respiration) and heterotrophic microbial respiration (e.g., fauna respiration and the respiration from microorganisms that are not associated with the rhizosphere and obtain their energy source from different materials). It is believed that heterotrophic respiration is mainly driven by microbial activities and environmental factors, such as soil temperature and moisture, while autotrophic respiration is additionally affected by above-ground photosynthesis (Högberg et al., 2001; Wang et al., 2003) and plant physiological processes (Tang, 2003). Therefore, partitioning the total soil respiration into autotrophic and heterotrophic respiration is important to understand the mechanisms controlling carbon exchange between soil and the atmosphere. This partition is also indispensable for the projection of ecosystem carbon dynamics in response to future global warming because these two respiration processes may respond differently to environmental factors, such as temperature (Boone et al., 1998; Epron et al., 2001; Xu and Qi, 2001). Despite the growing body of information on total soil respiration, studies on heterotrophic respiration have been rarely reported in the wet tropical forests (Giardina and Ryan, 2000; Hanson et al., 2000; Trumbore et al., 1996).

Soil temperature and moisture are the major abiotic factors determining soil respiration in most ecosystems and are commonly used in modeling soil respiration. However, the strong interaction between soil temperature and moisture makes it very difficult to separate the temperature and moisture effect (Davidson et al., 1998; Howard and Howard, 1993; Xu and Qi, 2001). Finding a natural ecosystem where either soil temperature or soil moisture is stable may greatly enhance our ability to examine the effect of each factor on soil heterotrophic respiration. The wet tropical forests in Puerto Rico is ideal for this purpose because the diurnal and seasonal temperature variations are <3 °C, while soil moisture may vary from 40 to 80% (gravimetric water content).

Microbial communities contributing to soil heterotrophic respiration are mainly composed of bacteria and micro-fungi (Smith and Paul, 1995). Micro-fungi are the most active decomposers of plant residues in soils while bacteria play a secondary role despite their high numbers (Kjoller and Struwe, 1994). The contribution of soil fauna to total soil respiration accounts for $<3\%$ of the total CO_2 respired (e.g. Holt et al., 1990). Previous studies found bacteria and micro-fungi were considerably different in terms of biomass and functional activity among different ecosystems, suggesting they may play different roles in decomposing soil organic carbon. Therefore, differentiating the total soil microbes into bacteria and micro-fungi and investigating their relationships with heterotrophic soil respiration will significantly improve our understanding on soil carbon dynamics. In addition, vegetation type may also affect heterotrophic soil respiration through its effect on litter production and litter quality, microbial communities, and soil microclimate (Davidson and Ackerman, 1993; Elberling et al., 2003). By synthesizing a global database on soil respiration, Raich (2000) found that vegetation types could significantly influence soil respiration and decomposition.

In this study, using a trenching technique we examined the relationships among heterotrophic soil respiration, environmental factors and microbial biomass in a 20-year-old pine plantation and a secondary forest originated from the same abandoned banana farmland in the wet tropics in Puerto Rico. The environmental factors examined include soil moisture, total soil organic carbon, soil organic carbon in the light fraction and total soil N content. We also differentiated the total microbial biomass into bacteria and micro-fungi biomass. The main objectives of the present study were to examine: (1) how different environmental factors affect soil heterotrophic respirations; (2) how bacteria and micro-fungi affect heterotrophic respiration differently; and (3) how the above relationships vary in the pine plantation vs. the secondary forest.

Material and methods

Study sites

The study was conducted on two sites that were within 100 m of each other. One site was in a pine plantation and the other was in a secondary forest. Both sites were located at the Guzman sector of the Luquillo Experimental Forest in northeastern Puerto Rico (18°18′ N, 65°50′ W). The plantation and the secondary forests originated from the same abandoned agricultural land with the same cropping system and management/disturbance history (Lugo, 1992). The sites are characterized by wet tropical climate with mean annual precipitation of 3920 mm and mean annual air temperature of 22.3 °C (Lugo, 1992). The temperature is mild and stable with diurnal and seasonal temperature ranges of 3–4 °C. Precipitation shows a seasonal variation, with a dry season from February to April and a wet season from August to October (Scatena, 2001). Soils are classified as mixed isothermic tropohumult in both the plantation and the secondary forest. The sites are relatively flat with a slope of <5° and an elevation of about 400 m above sea level. The tree plantation was established on an abandoned cropland in 1976 as part of a reforestation program of the United States Forest Service (Lugo, 1992). The secondary forest has naturally developed on the same abandoned cropland since the same year. The plantation is dominated by *Pinus caribeae* with small trees and grass species underneath the canopy. The secondary forest is characterized by a sparse overstory and a dense understory with abundant shrubs and grasses. The dominant canopy species in the secondary forest include *Myrcia splendens*, *Miconia prasina* and *Casearia arborea*, and the major understory species include *Casearia sylvestris*, *Miconia mirabilis* and *Tabebuia heterophylla*.

Field and laboratory measurements

This study was a part of a long-term experiment known as 'Soil Organic Matter Dynamic' (SOMD) in the Luquillo Experimental Forest. Measuring plots were arranged in a square plot of 0.25 ha in each of the plantation and secondary forest initially established by the SOMD project in 1990. Root exclusion treatment was applied by trenching soil along the four sides of the plot to a depth of 1 m and burying a car tarp sheet into soil to keep roots from entering the plots. Both control and root exclusion treatment featured three replicates and each replicate was located on a subplot of 3 m × 3 m, which was randomly located in the 0.25 ha plot. The plots of root exclusion treatment were monitored frequently after the initial trenching to ensure no plants growing in it. The control plots were clearly marked and kept under natural condition. Soil sampling in both the plantation and secondary forest was conducted in August of 1996 and in March of 1997. Four soil samples (0–25 cm) were collected by coring the soil at the corners of each 3 m x 3 m replicate plot to measure microbial biomass, soil pH, soil moisture, and carbon and nitrogen content. The data from these soil samples were independently used in the regression analysis. We measured these soil physical and chemical properties in August of 1996 and March of 1997, representing the wet and dry seasons respectively. Additionally, a soil sample from seven cores (3.75 cm in diameter) from each plot was collected to a depth of 10 cm and weighed for soil bulk density determination. Approximately 15–20 g of each soil sample was oven-dried at 105 °C for 3 days for determination of soil moisture. Total C and N in soils were obtained using a Perkin Elmer CHN analyzer. Carbon in the light fraction of soil organic carbon was determined using the density fractionation method of Sollins et al. (1984). Air-dried soils were passed through a 2 mm mesh sieve and then 1 g of the sieved soil was suspended in 20 ml of NaI solution adjusted to a density of 1.85 g/ml. The suspension was then sonicated for 15 min at a medium energy level, vacuumed (70 kPa) for 10 min, and then left to settle over night at room temperature to separate light and heavy fractions. The light fraction at the surface of the density liquid was aspirated and trapped onto a filter (GF/A), rinsed with deionized water, and then analyzed for total organic C and N. Soil moisture contents were determined by oven-drying 10 g of fresh soil at 105°C for 48 h. Soil pH was measured by using a paste of 1:1 ratio of fresh soil and deionized water.

Soil respiration was measured using the alkali trap method (Carter, 1993). A plastic chamber

with an opening area of 102.5 cm^2 and a height of 20 cm and a plastic cup with a diameter of 5 cm and a height 7.5 cm were used for soil respiration measurements at each location. The chamber and the cup were made of polyethylene and the CO_2 absorption/emission by the chamber wall was negligible. At each measurement location a trap unit was prepared by pipetting 15 ml 1.0 M NaOH solution into a plastic cup and placing it on the soil surface. A chamber was immediately placed over the alkali cup and its edge was pressed into soils for 2 cm to ensure the chamber was well sealed. Another cup was filled with the same solution and tightly sealed and placed outside of the chamber as the control to consider the CO_2 absorption during the solution transport. After 24 h, the cup was removed, enclosed with a lid, and taken to the laboratory for analysis. In the laboratory, alkali solutions were titrated with 1 M HCl solution to the phenolphthalein end point to determine the amount of NaOH left after excess $BaCl_2$ was added to the NaOH solution to precipitate the carbonate as insoluble $BaCO_3$. Soil respiration was measured six times between August 1996 and June 1997. Soil respiration mean values in August 1996 and March 1997 were used for regression analysis.

Total microbial biomass, fungal biomass and bacterial biomass were measured in August 1996 and March 1997, which represented a wet and a dry season, respectively. Total microbial biomass was measured using a fumigation-incubation procedure (Jenkinson and Powlson, 1975). Two sets of soil samples were prepared: one as a control and the other for fumigation treatment. Each sample contained 30 g of soil was placed into a 100 ml beaker. For the fumigation treatment, beakers were placed in a clean glass vacuum desiccator that was lined with moistened filter paper. A beaker containing 40 ml of alcohol-free chloroform was placed into the desiccator, which was then evacuated for 2–3 min. During the evacuation period, the chloroform was boiled vigorously until the vapor in the desiccator was near saturation. Samples were left in the desiccator for 18–24 h. The fumigated samples were vacuumed for three times to extract the remaining chloroform in soil. Each sample was inoculated with 1.0 g well mixed inoculum and then placed into a 2-L wide-mouth glass jar. A beaker containing 20 ml of 1 M NaOH was placed into each jar. The jars were closed using lids with rubber septa and incubated for 10 days at 25 °C. The quantity of NaOH that remained in each beaker was titrated with 1 M HCL with phenolphthalein as an indicator. The same soil sample was incubated with another 20 ml of 1 M NaOH for another 10 days and the remaining NaOH was titrated with HCl at the end of the incubation. Biomass of active and total fungi was estimated using the agar film techniques (Lodge and Ingham, 1991). Biomass of active and total bacteria was obtained using fluorescein isothiocyanate techniques (Zou and Bashkin, 1998).

Data analysis

Soil respiration rate was calculated using the following formula (Carter, 1993): Milligrams of C or CO_2 = (B–V) NE, where B = volume (milliliters) of acid needed to titrate the NaOH in the beakers from the control sample, V = volume (milliliters) of acid needed to titrate the NaOH in the beakers from the CO_2 enriched samples, N = normality of the acid, and E = equivalent weight. To express the data in terms of carbon, $E = 6$; to express it as CO_2, $E = 22$. Significant differences among means were determined by Scheffe's multiple range test at $\alpha = 0.05$. Linear regression analysis was used for examine the relationship between heterotrophic soil respiration and environmental factors and microbial biomass.

Results

Root and heterotrophic soil respiration

The mean root respiration (e.g. subtracting heterotrophic soil respiration from total soil respiration) was 1.31 ± 0.21 g C m^{-2} d^{-1} in the pine plantation and 1.85 ± 0.12 g C m^{-2} d^{-1} in the secondary forest, accounting for 56 and 69% of the total soil respiration respectively in these forests. The mean heterotrophic soil respiration was 0.8 ± 0.15 g C m^{-2} d^{-1} in the pine plantation and 1.02 ± 0.17 g C m^{-2} d^{-1} in the secondary forest, 41% higher in the secondary forest than the plantation. Figure 1.

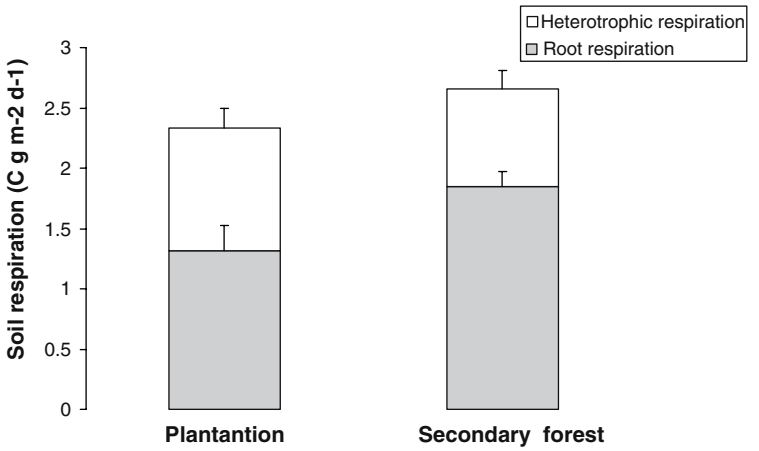

Figure 1. Mean heterotrophic soil respiration (g C m^{-2} day^{-1} ± SE) and mean root respiration (g C m^{-2} day^{-1} ± SE) in the pine plantation and the secondary forest from August 1996 to June 1997 (bimonthly) (n = 6). The root respiration was determined by subtracting heterotrophic soil respiration from total soil respiration.

Soil properties and microbial biomass

Soil organic carbon in the light fraction and soil pH were significantly higher in the pine plantation than in the secondary forest (Table 1). Total soil organic carbon, total nitrogen and soil moisture did not differ between the pine plantation and the secondary forest. Fungal biomass was significantly higher in the pine plantation than in the secondary forest but the bacterial biomass was significantly higher in the secondary forest than in the pine plantation (Table 1). Bacterial biomass was much lower than fungal biomass in both the plantation and the secondary forest.

Effects of environmental factors on heterotrophic soil respiration

Heterotrophic soil respiration was highly correlated with fungal biomass in both the plantation ($R^2 = 0.63$, $P = 0.01$) and the secondary forest ($R^2 = 0.39$, $P = 0.05$) (Table 2), indicating the critical contribution of the fungal community to soil decomposition in these tropical forests. Heterotrophic soil respiration was also strongly correlated with bacterial biomass in the secondary forest ($R^2 = 0.45$, $P = 0.02$), but the correlation was weak in the pine plantation ($R^2 = 0.16$, $P = 0.08$).

We also found that heterotrophic soil respiration and soil moisture were highly correlated in both the plantation ($R^2 = 0.67$, $P < 0.01$) and the secondary forest ($R^2 = 0.56$, $P = 0.03$) (Table 2). Meanwhile, the correlation between soil pH value and the heterotrophic soil respiration was very weak with correlation coefficients close to zero in both forests (data not shown).

Additionally, we found heterotrophic soil respiration and total soil organic carbon content were moderately correlated both in the pine plantation ($R^2 = 0.26$, $P = 0.06$) and in the secondary forest ($R^2 = 0.37$, $P = 0.06$). Heterotrophic soil

Table 1. Soil moisture, pH, TOC (total organic carbon), LF-OC (soil organic carbon in the light fraction), TN (total nitrogen), FB (fungal biomass), BB (bacterial biomass), TMB (total microbial biomass) at 0–25 cm soil depth in the pine plantation and the secondary forest

	Soil moisture (%)	pH	TOC (kg m^{-2})	LF-OC (kg m^{-2})	TN (g m^{-2})	FB (mg C kg^{-1})	BB (mg C kg^{-1})	TMB (mg C kg^{-1})
Plantation	49.5 (6.6) a	4.5 (0.3) b	5.59 (0.22) a	3.45 (0.12) a	61.8 (7.4) a	673 (43) a	38 (2) b	711 (47) a
Secondary forest	48.6 (5.4) a	5.3 (0.2) a	5.68 (0.16) a	2.13 (0.14) b	68.4 (9.7) a	547 (35) b	71 (3) a	618 (34) b

Common letters within a column indicate no significant difference between the treatments according to the Tukey's test at a = 0.05 (N = 12).

Table 2. Linear regression between soil CO_2 efflux (g C m^{-2} day^{-1}) and fungal biomass (mg C kg^{-1} soil), bacterial biomass (mg C kg^{-1} soil), soil moisture, total SOC (kg m^{-2}), SOC in light fraction (C in LF, kg m^{-2}), total N (g m^{-2}) in the pine plantation and the secondary forest ($n = 12$)

Ecosystem type	Factors	Regression equation	R^2	P
Plantation	Fungal biomass	y = 0.0009x + 0.4131	0.63	0.01
	Bacterial biomass	y = 0.009x + 0.7594	0.16	0.08
	Soil moisture	y = 0.0304x + 0.5295	0.67	0.00
	TOC	y = 0.229x + 0.812	0.26	0.06
	C in LF	y = 0.2829x + 0.2919	0.45	0.02
	Total N	y = 0.0555x − 2.5042	0.69	0.00
Secondary forest	Fungal biomass	y = 0.0007x + 0.4108	0.39	0.05
	Bacterial biomass	y = 0.0023x + 0.6672	0.45	0.02
	Soil moisture	y = 0.0108x + 0.3160	0.56	0.03
	TOC	y = 0.1307x + 0.0499	0.37	0.06
	C in LF	y = 0.1927x + 0.2628	0.38	0.04
	Total N	y = 0.016x − 0.2742	0.67	0.00

respiration was also significantly correlated with carbon in light fraction in both the plantation and the secondary forest with a slightly stronger correlation in the pine plantation ($R^2 = 0.45$, $P = 0.02$) than in the secondary forest ($R^2 = 0.38$, $P = 0.04$). Finally, we found heterotrophic soil respiration was highly correlated with the total soil nitrogen content in both the plantation ($R^2 = 0.69$, $P < 0.01$) and the secondary forest ($R^2 = 0.67$, $P < 0.01$) (Table 2).

Discussion

Some previous studies showed that total soil respiration varied considerably among the vegetation types and was generally positively correlated with above-ground litter production in tropical forests (Gunadi, 1994; Raich, 1998). In the present study, our result that heterotrophic soil respiration varied substantially between the plantation and the secondary forest confirmed that vegetation type is an important factor in influencing heterotrophic respiration in the wet tropical forests. Although the above-ground litter production was higher in the pine plantation than in the secondary forest (Li et al., 2005), heterotrophic soil respiration was significantly higher in the secondary forest than in the pine plantation. This is because the plantation has accumulated a large amount of C on forest floor, while the secondary forest relocated more C to the belowground as soil organic carbon.

Fungal biomass was significantly higher in the pine plantation than in the secondary forest while bacterial biomass was significantly higher in the secondary forest than in the pine plantation in both the control plots and the root exclusion plots, suggesting that different microbial functional groups may regulate the decomposition processes under different vegetation types. Our results that heterotrophic soil respiration had a higher correlation with fungal biomass ($R^2 = 0.63$) than with bacterial biomass ($R^2 = 0.16$) in the pine plantation and a higher correlation with bacterial biomass ($R^2 = 0.45$) than with fungal biomass ($R^2 = 0.39$) in the secondary forest, suggested that bacteria may play a more important role in the decomposition processes in the secondary forest while fungi maybe more critical to decomposition in the pine plantation.

Our result that heterotrophic soil respiration was highly positively correlated with soil moisture in both the plantation and the secondary forest, suggested that soil moisture is a major environmental factor regulating heterotrophic soil respiration in these wet tropical forests. This finding was consistent with some other studies in which soil moisture is the major soil respiration controlling variable in wet ecosystems or in regions where temperature are high and relatively invariable (Davidson et al., 2000; Holt et al., 1990; Rout and Gupta, 1989). Generally, soil moisture limits soil respiration when soil moisture is at either extremely high or low levels (Bouma et al., 1997; Howard and Howard, 1993;

Pangle and Seiler, 2002; Xu and Qi, 2001). At this study site, it seemed that soil moisture never reached a high or a low limiting level in both the plantation and the secondary forest during the one-year study period, based on the linear regression analysis between the heterotrophic soil respiration and soil moisture. Soil moisture limits soil respiration through changing aeration status and/or stressing soil microbial activity. Our result that heterotrophic respiration had a higher correlation with soil moisture in the pine plantation than in the secondary forest could be explained by the speculation that fungal biomass might be more sensitive to soil moisture than bacterial biomass since the fungal population in the pine plantation was significantly larger than that in the secondary forest.

The high correlation between heterotrophic soil respiration and the total soil nitrogen content suggested that nitrogen availability may also be critical to the decomposition process in wet tropical forests. The stronger correlation between heterotrophic soil respiration and soil nitrogen than that between heterotrophic soil respiration and microbial biomass also indicates the important role that nitrogen plays in such ecosystems. The effects of nitrogen on total soil respiration have been reported by previous studies with conflicting results. Binkley and Högberg (1997) reported that the response of forest soils to nitrogen input varied depending on soil pH. Microbial activity and microbial biomass are strongly related to soil pH and organic matter substrates (Lee and Jose, 2003). The strong correlations between heterotrophic soil respiration and those environmental variables in both the plantation and the secondary forest make it difficult to give a solid conclusion on nitrogen effects on soil decomposition in tropical forests. In addition, even a good correlation does not imply cause and effect though it could be used in some cases as a predictor. Therefore, further studies are needed on the nitrogen effects on soil heterotrophic respiration by changing the levels of nitrogen inputs while all other factors are held constant.

Our data showed that root respirations accounted for 56 and 69% of the total respiration in the pine plantation and the secondary forest, respectively. These percentages were generally higher than those reported in broad-leaved forests in temperate zone, where root contribution to total respiration was 33–50% (Bowden et al., 1993; Nakane et al., 1996) but they were within the range of 30–93% worldwide published in the literature (Ryan et al., 1997; Thierron and Laudelout, 1996; Xu et al., 2001). By comparing root respiration in different forest types, Nakane et al. (1996) concluded that the proportion of root respiration to soil surface CO_2 efflux may converge to about 50% irrespective of forest types, when the cycle of soil carbon is near a dynamic equilibrium in a forest ecosystem. That root contribution to total soil respiration in both the plantation and secondary forest in our study was slightly higher than the average value might be explained by the aggrading stage of both the plantation and the secondary forest. Root exclusion had a greater effect on reducing soil respiration in the secondary forest (69%) than in the pine plantation (56%), confirmed by our previous study that the secondary forest grew more fine roots than the plantation (Li et al., 2004). The trenching method has been widely used to separate root respiration and heterotrophic soil respiration, despite the concerns about the potential influence of adding C to soil from the dead roots and increasing soil moisture due to the absence of plant transpiration in the trenched plots. Bowden et al. (1993) found that residue root decomposition had little contribution to belowground respiration when measurements were made nine months after the trenching treatment. Our plots were trenched in 1990, 6 years before the initial measurements in this study, the residual root effect on soil respiration was likely minimal. Meanwhile, excluding all the living roots from the trenched plots is difficult and almost impossible. Nepstad et al. (1994) reported that roots might penetrate the soil down to 10 m depth in a study of Amazonian forests. Similar results on root penetration have been reported in other tropical forests (Schwendenmann et al., 2003; Veldkamp et al., 2003). However, most of the root respiration is contributed by the fine roots and previous studies found that most of the fine roots are distributed in the top 30 cm soil layers (Dickmann and Pregitzer, 1992). In addition, the alkali-trap method we used in this study might underestimate soil respiration under conditions of high soil respiration and overestimate soil respiration under conditions of very low soil respiration compared with the infrared

gas analyzer (IRGA) technique (Yim et al., 2002). We do not expect these biases would change our conclusion because the spatial variation of soil respiration in the forests was relatively small.

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