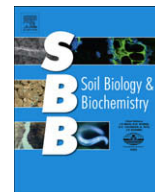




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Short communication

Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest

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ABSTRACT

Respiration of CO₂ from soils (R_s) is a major component of the carbon cycle of ecosystems, but understanding is still poor of both the relative contributions of different respiratory sources to R_s , and the environmental factors that drive diurnal variations in R_s . We measured total and litter-free R_s at half-hourly intervals over full 24 h periods, and thereafter twice a month for 10 months in a tropical montane cloud forest (TMCF) in Peru. Total R_s declined by about 61% during the night as a result of variations in respiration rate in the litter, which were partly correlated with the soil surface air temperature. Most of the diurnal variation of R_s in this TMCF appears to be driven by respiration in the litter layer, which contributed 37% to the total soil CO₂ efflux. Total R_s rates at this particular site would have been overestimated by 60% if derived from daytime measurements that had not been corrected for diurnal variations in R_s .

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Total R_s is the sum of all CO₂ effluxes originating from litter, soil organic matter and roots, controlled by soil faunal activity and environmental drivers such as soil temperature, air temperature, water content and photosynthetically active radiation (PAR) (Luo and Zhou, 2006). As these parameters vary with different amplitudes within a single day, R_s cannot be assumed to be constant over 24 h (Tang et al., 2005; Liu et al., 2006). Diurnal variations in CO₂ effluxes are often assumed to be controlled by diurnal changes in soil temperature (Rayment and Jarvis, 2000; Bajracharya et al., 2000; Xu and Qi, 2001). Different sources of R_s can be separated by various approaches like component integration, exclusion or isotopic methods, as reviewed by Subke et al. (2007) or Hanson et al. (2000), who, distinguishing between autotrophic and heterotrophic respiration, calculated a mean contribution of autotrophic respiration to R_s of 48%. Hardly any studies have been conducted in TMCF that consider differences in day and night-time R_s , and taking into account the different sources of the CO₂ effluxes and the main environmental parameters controlling them. In this study, we quantify for a TMCF the contribution from respiration in the litter to the total respiratory flux from soil and its diurnal variation.

We installed PVC collars (10 cm diameter) on intact and manipulated soil surfaces in an undisturbed TMCF in the Peruvian Andes (13°11'28"S, 71°35'24"E, 3030 m asl, mean annual temperature 12.5 °C) and measured the CO₂ efflux rates half-hourly during full 24 h periods, and as replicated point-measurements fortnightly for the following 10 months.

The soil at the study site consists of a litter layer, a 15 cm thick Oh layer, a 10 cm thick Ah layer and a 60 cm thick B layer overlying the bedrock, with a total C-stock of 27.7 (±3.32) kg m⁻², and has very low pH values throughout the soil profile (Table 1). Dominant tree species are Clusiaceae, Cunoniaceae, Myrsinaceae, Rosaceae, and Clethraceae. In October 2007, three measurement collars were installed with minimum disturbance on intact soil surfaces, and further three collars were installed not more than approx 2–3 m distant but with the entire litter layer carefully removed. The litter-free soil collars were refilled with green glass marbles (diameter 11 mm) up to the adjacent soil surface level to simulate the porosity of the removed material and as protection against splash erosion. The area around these collars was then re-covered with litter. We did not assume any temperature effect caused by the glass marbles, as the sites were under a dense canopy and exposed to very little incoming radiation (<~5%; Chazdon and Pearcy, 1986).

R_s rates were measured with a Licor 8100 closed chamber system (Licor Inc., Nebraska, USA), and temperatures recorded within the measurement chamber (soil surface, T_{surf}) and at 10 cm

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Table 1

Soil properties at the study site at 3030 m asl in Peru, as quantified by replicated sampling with sampling cores of 35 mm in diameter and 50 or 100 mm in length. The litter layer was determined in a square of 50 × 50 cm, pH measured in 0.01 M CaCl₂ solution in a mixing ratio soil to solution of 1:10, and densities calculated for dried fine earth samples after removal of all particles >2 mm.

Layer	Horizon	Thickness (cm)	pH	Density (g cm ⁻³)	C (%)	N (%)	C-stock (kg C m ⁻²)
Litter	L		4.56		45.52	1.67	0.577
Organic layer	Ol	5	2.56	0.048	44.48	2.04	1.44 (±0.70)
Organic layer	Oh	10	2.43	0.070	38.07	1.84	2.62 (±0.48)
Humic layer	Ah	10	2.97	0.306	16.95	0.94	5.17 (±0.27)
Mineral layer	A	10	3.77	0.459	9.88	0.58	4.54 (±0.45)
Mineral layer	B	10	4.00	0.554	7.56	0.44	4.19 (±0.15)
Mineral layer	B	10	4.09	0.606	6.14	0.39	3.72 (±0.22)
Mineral layer	B	10	4.15	0.602	4.89	0.35	2.94 (±0.10)
Mineral layer	B/C	10	4.17	0.576	4.38	0.32	2.56 (±0.95)
Total or weighted mean		75	3.58	0.426	14.68	0.78	27.74 (±3.32)

depth (T_{soil}) with a thermocouple probe. Each of the 6 collars was measured once over a 24 h period on different days/nights without rain in October or November 2007, at least one week after the installation of the collars. Volumetric soil water contents were quantified with a soil moisture probe Echo EC-10 (Degacon, Pullman, USA) installed beneath the organic layer, and varied between 18 and 24% during the 24 h measurement periods. Afterwards, R_s point-measurements of the six collars were taken twice a month until August 2008.

For the 24 h periods, the three measurements for the total R_s and the litter-free R_s , respectively, were averaged for every 30 min and are given (±1SE) in Fig. 1. From November 2007 to August 2008, every collar was measured twice on every occasion, averaged, and the means of the resulting three CO₂ fluxes per treatment are shown in Fig. 2. The fractional litter contribution can then be calculated as the difference between the total R_s and the litter-free R_s divided by the total R_s .

Total R_s followed a distinct diurnal pattern, but showed no trend with time between 11:30 h and 17:30 h. Hereafter, we refer to this stable phase as afternoon R_s , and the subsequent time period at night (23:30 h–05:30 h) as night-time R_s . In the afternoon, the mean CO₂ efflux was 5.08 (±0.08) $\mu\text{mol m}^{-2} \text{s}^{-1}$ and at night 1.99 (±0.06) $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1). In contrast, litter-free R_s showed a much lower diurnal variation with an average R_s of 2.28

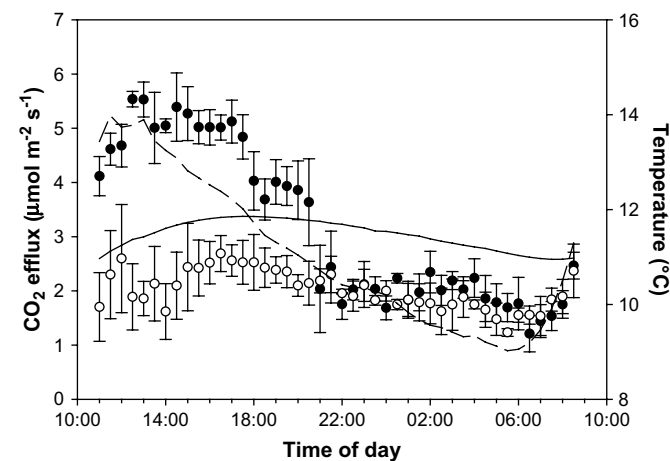


Fig. 1. Diurnal variation of CO₂ effluxes with standard errors for total soil respiration (●) and litter-free soil respiration (○). The solid line is the soil temperature at 10 cm depth and the dashed line the air temperature as measured 5 cm above the soil surface.

(±0.09) $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the afternoon and 1.72 (±0.05) $\mu\text{mol m}^{-2} \text{s}^{-1}$ at night. On a daily basis, the mean total R_s was 3.22 (±0.23) $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the mean litter-free R_s 2.02 (±0.05) $\mu\text{mol m}^{-2} \text{s}^{-1}$, which indicates that 37% of total R_s was litter-derived. During the afternoon, litter contributed to 54.8 (±2.2)% to total R_s , but only 13.6 (±3.4)% at night. Total R_s , if calculated only from R_s measured during the afternoon, would overestimate the average daily R_s by 60%.

The diurnal cycle of total R_s tracked variations in T_{surf} much closer than T_{soil} , and this can be explained by the high proportion of litter contributing the diurnal variation in R_s , which is generally better correlated to T_{surf} (Graf et al., 2008). T_{surf} explained 92% of the diurnal variation in R_s , as calculated with a Lloyd and Taylor (1994) function ($R_s = 18.67 e^{-12.76/(T_{\text{surf}}-3.52)}$) and yielded a Q_{10} value of 3.30. But the rapid drop in R_s at 20:00 h could not be explained by T_{surf} alone. Correlations between litter-free R_s and T_{soil} or T_{surf} were not significant. A possible explanation for this drop might be a light-dependency for the litter component of total R_s , as Tang et al. (2005) reported the importance of tree photosynthesis for diurnal respiration in forests.

As measured during the afternoon across seasons from November 2007 to August 2008 (Fig. 2), R_s was 4.79 (±0.50) $\mu\text{mol m}^{-2} \text{s}^{-1}$, and litter-free R_s was 1.91 (±0.44) $\mu\text{mol m}^{-2} \text{s}^{-1}$. Correlations between respiration rates and temperatures were not significant, probably because other abiotic parameters such as soil moisture and PAR, which are known to have a significant impact on root respiration (Luo and Zhou, 2006), are not considered in the Lloyd & Taylor function.

The volumetric water content at 15–25 cm depth was relatively constant at about 20% from November 2007 to May 2008, but then decreased to <10% in June and August, probably sufficient to limit micro-organism activity (Davidson et al., 1998). Litter-free R_s , in contrast, tended not to change with lower moisture levels, which could mean that soil organic matter and litter are mineralized through micro-organism communities with different moisture vulnerabilities.

Total R_s as measured during the afternoons of the 24 h periods and of the following 10 months were not significantly different (Mann–Whitney rank sum test, $p > 0.05$, $n = 25$), and, combined with the very small seasonal range recorded for soil temperature and soil moisture, suggest that the 24 h measurements in October and November 2007 were representative for the entire year, and thus that the litter contribution of 37% did not change substantially over the course of the year. Vasconcelos et al. (2004) removed all leaf and woody litter in a tropical forest in Brazil, and calculated its

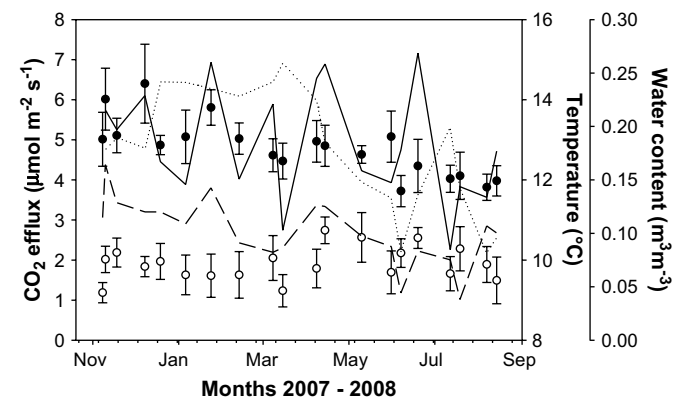


Fig. 2. Variation of CO₂ effluxes with standard errors for total soil respiration (●) and litter-free soil respiration (○) from November 2007 to August 2008. The solid line is the air temperature as measured at the soil surface, the dashed line the soil temperature at 10 cm depth, and the dotted line the volumetric soil water content in 15–25 cm depth.

contribution to be 28% of total R_s , and Sayer et al. (2007) showed that litter can contribute up to 20% of R_s in a tropical forest in Panama. These studies were conducted in tropical rain forests where mean annual temperatures are about 13 °C higher than at our TCMF site, and soil CO₂ effluxes from litter were estimated solely from daytime measurements (and thus could not be corrected for any diurnal variation). However, diurnal R_s measurements in lowland tropical rain forest appear to show much less pronounced variation between day and night periods (Kiese and Butterbach-Bahl, 2002; Ohashi et al., 2008) and, therefore, diurnal changes in the contribution from litter to R_s might be of less importance in these ecosystems than in TCMF (Cavelier and Penuelas, 1990). The large contribution of litter decomposition to R_s , as observed here, is even more notable considering that only about 2% of the entire soil carbon stock at the study site is stored within the litter layer (Table 1).

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References

- Bajracharya, R.M., Lal, R., Kimble, J.M., 2000. Diurnal and seasonal CO₂-C flux from soil as related to erosion phases in central Ohio. *Soil Science Society of America Journal* 64, 286–293.
- Cavelier, J., Penuelas, M.C., 1990. Soil respiration in the cloud forest and dry deciduous forest of Serrania de Macuira, Columbia. *Biotropica* 22, 346–352.
- Chazdon, R.L., Pearcy, R.W., 1986. Photosynthetic responses to light variation in rainforest species. II. Carbon gain and photosynthetic efficiency during light-flecks. *Oecologia* 69, 524–531.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology* 4, 217–227.
- Graf, A., Weihermüller, L., Huisman, J.A., Herbst, M., Bauer, J., Vereecken, H., 2008. Measurement depth effects on the apparent temperature sensitivity of soil respiration in field studies. *Biogeosciences* 5, 1175–1188.
- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.
- Kiese, R., Butterbach-Bahl, K., 2002. N₂O and CO₂ emissions from three different tropical forest sites in the wet tropics of Queensland, Australia. *Soil Biology and Biochemistry* 34, 975–987.
- Liu, Q., Edwards, N.T., Post, W.M., Gu, L., Ledford, J., Lenhart, S., 2006. Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest. *Global Change Biology* 12, 2136–2145.
- Lloyd, J., Taylor, J.A., 1994. On the temperature-dependence of soil respiration. *Functional Ecology* 8, 315–323.
- Luo, Y., Zhou, X., 2006. *Soil Respiration and the Environment*. Academic Press, 328 pp.
- Ohashi, M., Kumagai, T., Kume, T., Gyokusen, K., Saitoh, T.M., Suzuki, M., 2008. Characteristics of soil CO₂ efflux variability in an aseasonal tropical rainforest in Borneo Island. *Biogeochemistry* 90, 275–289.
- Rayment, M.B., Jarvis, P.G., 2000. Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest. *Soil Biology and Biochemistry* 32, 35–45.
- Sayer, E.J., Powers, J.S., Tanner, E.V.J., 2007. Increased litterfall in tropical forests boosts the transfer of soil CO₂ to the atmosphere. *Public Library of Science ONE* 2, e1299.
- Subke, J.A., Inglisma, I., Cotrufo, M.F., 2007. Trends and methodological impacts in soil CO₂ efflux partitioning: a metaanalytical review. *Global Change Biology* 12, 921–943.
- Tang, J.W., Baldocchi, D.D., Xu, L., 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11, 1298–1304.
- Vasconcelos, S.S., Zarin, D.J., Capanu, M., Littell, R., Davidson, E.A., Ishida, F.Y., Santos, E.B., Araujo, M.M., Aragao, D.V., Rangel-Vasconcelos, L.G.T., Oliveira, F., McDowell, W.H., de Carvalho, C.J.R., 2004. Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochemical Cycles* 18, GB2009.
- Xu, M., Qi, Y., 2001. Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biology* 7, 667–677.