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Original article

Soil CO_2 efflux rates in different tropical vegetation types in French Guiana

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Abstract – Soil CO_2 efflux rates were measured from July to September 1994 in three vegetation types (primary forest, hardwood plantation and clear-cut) near Sinnamary, French Guiana (5°15' N, 52°55' W), using a portable closed-chamber infrared gas analysis system. Mean soil CO_2 efflux rates were: 2.3 $\mu mol\ m^{-2}\ s^{-1}$ in the primary forest versus 2.5 $\mu mol\ m^{-2}\ s^{-1}$ in the clear-cut and 2.9 $\mu mol\ m^{-2}\ s^{-1}$ in the plantation. Diurnal patterns of soil CO_2 efflux in the primary forest and hardwood plantation did not show significant ($P \leq 0.05$) changes. No correlation between soil CO_2 efflux rate and soil temperature was detected in these two vegetation types. In the clear-cut, a very pronounced peak in soil CO_2 efflux rate occurred, which was strongly correlated with soil temperature. In all three sites, the range of average soil CO_2 efflux rates among collars (spatial differences) largely exceeded the range observed among daily means (temporal variation). We investigated the correlation between soil CO_2 efflux and several biotic or abiotic variables: soil temperature, water content of upper soil, root density, litter quantity, carbon content and C/N ratio. The only variable that was significantly correlated with the spatial variations in soil CO_2 efflux was root density. (© Inra/Elsevier, Paris.)

carbon cycle / infrared gas analysis / soil CO_2 efflux / humid tropical ecosystems

Résumé – Flux de CO_2 du sol dans trois types tropicaux de végétation en Guyane française. La respiration du sol a été mesurée de juillet à septembre 1994 dans trois types de végétation (une forêt primaire, une plantation de bois dur et une coupe claire) près de Sinnamary, Guyane Française (5°15' Nord, 52°55' Ouest), en utilisant un système portable d'analyse de gaz infrarouge. Les valeurs moyennes de flux de CO_2 du sol ont été de 2.3 $\mu mol\ m^{-2}\ s^{-1}$ dans la forêt primaire, de 2.9 $\mu mol\ m^{-2}\ s^{-1}$ dans la plantation et de 2.5 $\mu mol\ m^{-2}\ s^{-1}$ dans la coupe claire. Les changements journaliers de flux de CO_2 du sol dans la forêt et dans la plantation de bois dur nont pas montré de variations significatives. Aucune corrélation entre la respiration du sol et la température du sol n'a été détectée dans ces deux types de végétation. Dans la coupe claire, un pic très

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prononcé dans la respiration du sol sest produit dans l'après-midi. Celui-ci a été fortement corrélé avec la température du sol. Dans chacun des trois sites, la variation spatiale de la respiration du sol a dépassé la variation temporelle. Nous avons étudié la corrélation entre la respiration du sol et plusieurs variables biotiques et abiotiques: la température du sol, lhumidité du sol, la densité des racines, la quantité de litière, le contenu en matière organique, et le ratio C/N de la matière organique. Seulement la densité des racines a été corrélée avec les variations spatiales de flux de CO_2 du sol. (© Inra/Elsevier, Paris.)

cycle du carbone / analyse de gaz infrarouge / flux de CO_2 du sol / écosystèmes tropicaux humides

1. INTRODUCTION

Soils play a key role in the global carbon cycle, as well as within the carbon cycle of any ecosystem [1]. Next to photosynthesis, soil CO_2 efflux is the largest carbon flux in forest ecosystems [16]. Soil CO_2 efflux is driven by two major processes, i.e., root respiration and microbial respiration. Both are controlled by various biotic and abiotic factors such as soil temperature [11, 19], soil moisture [8, 10], litter quantity and quality [18], root activity [4] and several others [18]. The impact of these biotic and abiotic factors on soil CO_2 efflux rates is often unclear, mainly because of the multiple interactions between the controlling factors and because of the complexity of soil carbon processes. Consequently, the soil compartment often remains a black box in ecosystem carbon research [1]. Although research on soil CO_2 efflux has received more attention over the last decades, detailed data are still scarce, especially in the tropics [2, 12, 16].

Within this context, the objectives of the present study were 1) to quantify and compare the soil CO_2 efflux rates of three different tropical vegetation types, i.e., a primary forest, a plantation of native hardwood species, and a clear-cut, and 2) to evaluate the effects of various biotic and abiotic factors on soil CO_2 efflux.

2. MATERIALS AND METHODS

2.1. Site description

The study site Paracou (tropical experimental station managed by CIRAD-forêts) is located in Sinnamary, in the equatorial lowland rainforest of French Guiana (5°15' N, 52°55' W). Mean annual rainfall for the region amounts to 2 200 mm [9]. Rainfall is seasonal, with a long dry period from September to November, and a short dry season in February or March [9]. Mean daily temperatures do not vary much through the year, and fluctuate around 26 °C, with daily minima around 21 °C and daily maxima around 32 °C [20]. The three sampling sites chosen were in close proximity. The soil type was a well drained oxisol on Precambrian bedrock with a microaggregated structure and with continuously increasing clay contents from a sandy upper layer to sandy-clay below 150 cm [9].

The forest site was chosen in a climax rainforest with a closed canopy. LAI at the site was 8.6 ± 0.7 [5], so undergrowth in the plantation was scarce and only small changes in soil temperature occurred (ca. 1 °C). Mean soil temperature (at 5 cm deep) during the measurements was 24.9 °C. As in most tropical forests [21], surface litter was present in small amounts: less than 10 tons ha^{-1} (*table I*).

The selected plantation was ca. 10 years old and had three different, fast growing native hardwood species of the Vochysiaceae family, i.e., *Vochysia tomentosa* D.C., *Vochysia densiflora* Spruce and *Vochysia* *surinamensis* Stafleu. As in the primary forest the canopy was closed. Mean soil temperature during the measurements was 25.0 °C, and diurnal changes were small (ca. 1 °C). Undergrowth was scarce and consisted of grasses and other herbaceous species. Surface litter was also present in small amounts (*table I*).

The sampling site in the clear-cut was dominated by Cyperaceae and Poaceae, and the soil surface was much more exposed to solar radiation. Due to this direct and strong insolation, mean soil temperature was higher (26.3 °C) and showed pronounced diurnal changes (ca. 6.5 °C), with minima around 8 a.m. and maxima around 4 p.m. The surface litter layer was nearly not existing.

2.2. Soil CO_2 efflux rates

Soil CO_2 efflux was measured with a portable closed chamber infrared gas analysis system (EGM-1 with SRC-1, PP Systems, UK). Permanent PVC collars were used to reduce the disturbance created by placing the gas exchange chamber on the soil surface. Eight collars were installed in the primary forest and the clear-cut, and six collars were installed in the hardwood plantation. Each collar was considered as an individual replicate. The SRC-1 soil chamber was adapted to seal the collars, which had a diameter of 12 cm and a depth of 25 cm, and were inserted 5 cm deep in the soil. To avoid interference from the metabolism of plants in the collars during gas exchange measurements, the above-ground parts of all herbs and shrubs were removed well before every measurement.

Measurements were made over 7 days in each site, during the period July–September 1994. Most measurements were made between 7 a.m. and 7 p.m., and one full diurnal cycle of soil CO_2 efflux was measured per site.

2.3. Biotic and abiotic factors

Soil temperature in each site was continuously monitored with a Cu-Const thermocouple at a depth of 5 cm. Soil temperature next to each collar was also registered during each gas exchange measurement. This was measured with a thermistor connected to the gas analyser (EGM-1), which was inserted 5 cm deep in the soil next to the collar to give an indication of the spatial variation in soil temperature.

At the end of the study period, the litter and soil (upper 15 cm) was removed from all collars and was analysed for bulk density, organic carbon, nitrogen, water content, litter quantity and root density. All samples were dried for 24 h at 105 °C. Root biomass (< 1 cm) and litter quantity were determined by hand-picking all litter and roots out of the oven-dried soil samples. Soil water content was determined gravimetrically. Soil organic carbon and nitrogen content were determined for each sample according to the procedures of Houba et al. [7]. Carbon to nitrogen ratio (C/N) for each collar was calculated from these results and total organic carbon content in the upper 15 cm of the soil was obtained using the bulk density data.

2.4. Statistical analysis

Student's t-test was used to test the significance of diurnal changes in soil CO_2 efflux and temperature, and to test the differences between the mean values of the biotic and abiotic factors of each sites. We also used t-test to test the significance of correlations between soil CO_2 efflux and the various biotic and abiotic factors. All analysis were conducted using StatMost (DataMost Corporation, 1994). Differences are reported significant at $P \leq 0.05$.

3. RESULTS

3.1. Differences between vegetation types

No significant diurnal changes in soil CO_2 efflux were observed in both the primary forest and the plantation (*figure 1b*). In the primary forest, maximum soil CO_2 efflux rate did not occur when soil tem-

Table I. Biotic and abiotic factors influencing soil CO_2 efflux in three tropical vegetation types. Soil water content, litter quantity, root mass density, organic carbon content, carbon to nitrogen ratio (C/N) and average soil temperature are presented.

	Soil water content (wt%)	Litter (kg m^{-2})	Root density (g dm^{-3})	Org. C (g dm^{-3})	C/N ≥ ratio	Soil temp. (°C)
Forest						
Mean	15.8	0.94	12.7	34.2	12.0	24.9
c.v. (%)	11	66	93	16	6	11
r	0.69 (ns)	0.52 (ns)	0.81 (*)	0.19 (ns)	−0.08 (ns)	0.17 (ns)
Plantation						
Mean	15.7	0.72	4.9	43.5	14.7	25.0
c.v. (%)	9	61	105	16	10	12
r	0.67 (ns)	0.60 (ns)	0.89 (*)	0.66 (ns)	0.65 (ns)	
Clear-cut						
Mean	8.7	0.09	0.7	31.1	11.6	26.3
c.v. (%)	6	75	70	15	10	5
r	0.19 (ns)	0.55 (ns)	0.60 (ns)	0.62 (ns)	0.59 (ns)	

Means are averages of 6–8 samples per site and refer to the upper 15 cm of soil.
c.v.: Coefficients of variation; r: correlation coefficients for each variable with soil CO_2 efflux (ns = not significant at $P < 0.05$, * = significant at $P < 0.05$).

perature was highest (*figure 1a*), but during the night, and there was no obvious correlation between soil CO_2 efflux and soil temperature. In the clear-cut, soil CO_2 efflux showed a distinct diurnal pattern (*figure 1b*), that was strongly correlated with soil temperature (*figure 2*). Because of these significant diurnal changes in the clear-cut, a comparison between the sites using only daytime flux data would lead to a serious overestimation in the clear-cut site. A meaningful comparison between the sites could only be performed with daily averages. We therefore needed a simple regression model to predict the missing night-time soil CO_2 efflux data, and calculate daily averages.

A remarkable feature of *figure 2* is the reversal of the lag between soil temperature and CO_2 efflux. Normally soil CO_2 efflux lags soil temperature. In this study the reverse was found, which may indicate that in the clear-cut most respiratory activity occurred above the depth at which soil temperature was measured (5 cm). In relation to this time lag, a hysteresis is observed when plotting a complete diurnal cycle of soil CO_2 efflux versus soil temperature (*figure 3*). CO_2 efflux rates are higher in the morning and early afternoon, when soil temperature is increasing compared to the rates measured in the late afternoon or evening at the same soil temperature. To model the missing night-time flux data, we therefore calculated temperature response functions using only soil CO_2 efflux data when temperature was decreasing. Because of the large spatial variability inherent to soil CO_2 efflux, a separate temperature response function was fitted for every collar. We used only exponential functions of the form $y = a + b*e^{T/c}$ to model soil CO_2 efflux (*figure 4*), and every fit was significant (y is the soil CO_2 efflux, T the soil temperature, a, b and c are regression constants).

Daily mean soil CO_2 efflux rates were then calculated, using the measured daytime fluxes, and the modelled night-time fluxes. From the daily means of 7 days, and 68 collars per site, the total mean soil CO_2 efflux of every site was calculated (*table II*). Mean soil fluxes in the plantation (2.87 μmol m^{-2} s^{-1}) were significantly higher than in the other sites, while no significant differences were detected between the clear-cut and the forest site (respectively, 2.45 and 2.29 μmol m^{-2} s^{-1}).

For all sites, the range of soil CO_2 efflux rates among collars was larger than the range of soil CO_2 efflux rates among daily means.

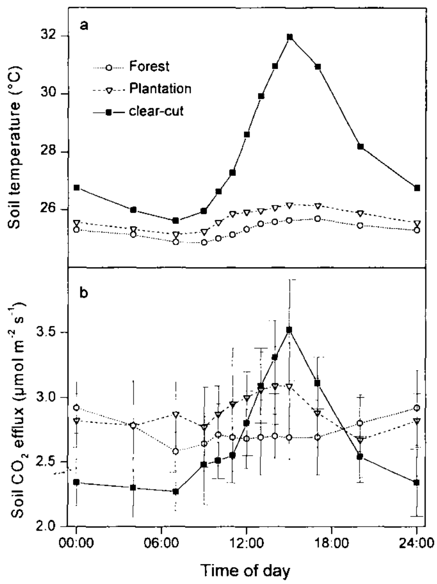

Figure 1. a) Typical diurnal cycles of soil temperature (not simultaneously measured) in three tropical vegetation types, i.e., primary rainforest, plantation of native hardwood species and clear-cut. b) Corresponding diurnal cycles of soil CO_2 efflux rate in three tropical vegetation types. Error bars indicate 1 SEM (wide caps on error bars for clear-cut, small caps for primary forest).

3.2. Biotic and abiotic factors

To explain this large spatial variation, all collars were analysed for water content, root biomass, litter quantity, organic carbon, carbon to nitrogen ratio (C/N) and average soil temperature during the measurements (*table I*). In the plantation and the primary forest, only one of these variables was significantly correlated with the spatial changes of soil CO_2 efflux, i.e., root biomass. No significant correlation of soil CO_2 efflux was found with either soil temperature, soil water content, litter mass or soil organic matter content. Attempts to fit a multiple regression did not result in a significant model. In the clear-cut site, no significant correlation was found between soil CO_2 efflux and any of the biotic or abiotic variables.

4. DISCUSSION

In all sites spatial variation in soil CO_2 efflux was very large. This large spatial variability seems to be inherent to soil CO_2 efflux [3, 15, 17]. In none of the three study sites were spatial differences in soil CO_2 efflux rates correlated with soil temperature, probably because the spatial variability in soil temperature was very small compared to the large variability in the other factors that influence soil CO_2 efflux. In the clear-cut site, no correlations were found with either of the investigated variables. In the plantation and the primary forest, root density was the only factor with which soil CO_2 efflux was significantly correlated. This correlation may indicate that root respiration explained most of the spatial vari-

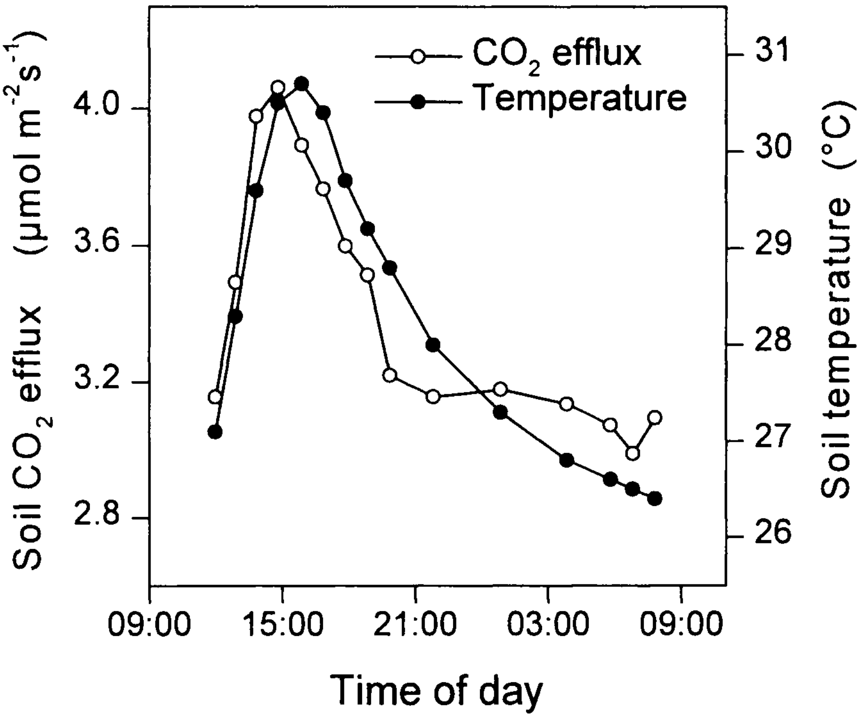

Figure 2. Typical diurnal cycle of soil CO_2 efflux rate (data from one collar) and soil temperature (at 5 cm depth) in the clear-cut site.

Table II. Comparison of soil CO_2 efflux rates in three tropical vegetation types.

	Primary forest	Plantation	Clear-cut
Mean CO_2 efflux	2.3	2.9	2.5
Range	2.0–2.7	2.5–3.2	2.4–2.7
c.v. among days	10.5	9.3	4.9
c.v. among collars	24.4	16.3	12.6

Values shown are averages and ranges of 7 daily means and 6–8 measurement collars. Efflux rates are in µmol m^{-2} s^{-1}; c.v.: coefficients of variation (%).

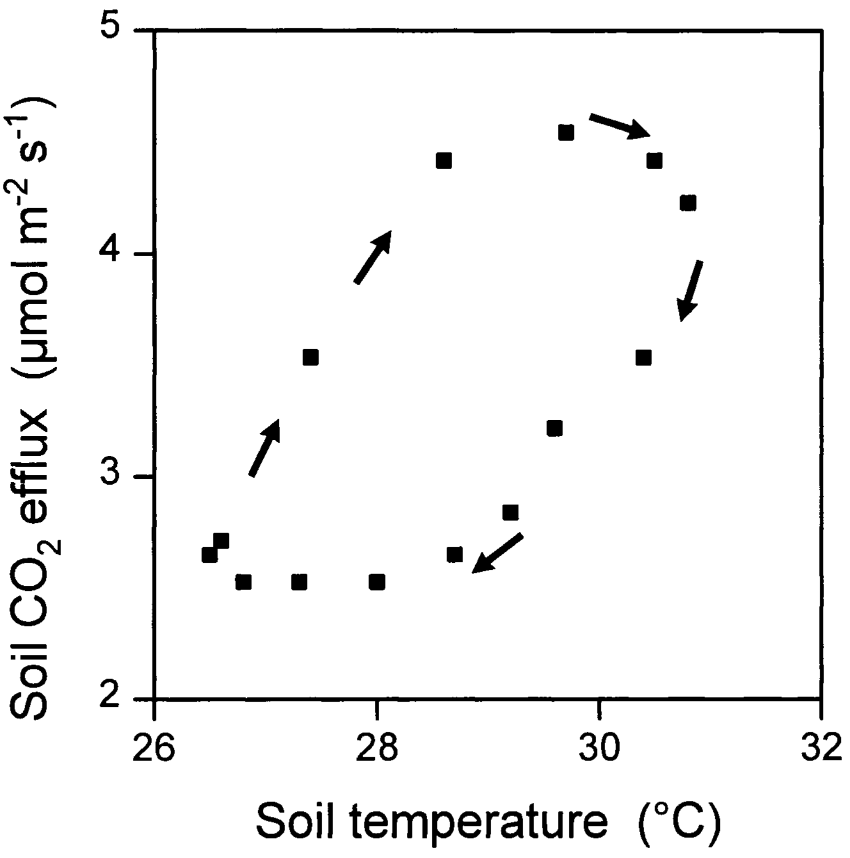

Figure 3. Soil CO_2 efflux rate in relation to soil temperature (at 5 cm deep) for the clear-cut site. Data from one collar over a 24 h period are shown, diurnal evolution is indicated by the arrows.

ability in soil CO_2 efflux, and that root density gave a good reflection of root respiration.

Due to the small temporal variation of soil temperature with time, no correlation of soil CO_2 efflux with soil temperature was found in the primary forest and hardwood plantation, and soil respiration did not change significantly during the day. In the primary forest maximum soil CO_2 efflux rate did not even occur in the afternoon when soil temperature was highest, but during the night. The same observation was made by Kursar [10] in a rainforest in Panama. In the clear-cut, however, temporal differences of soil CO_2 efflux rate were strongly correlated with soil temperature, which resulted in a pronounced diurnal pattern of soil CO_2 efflux.

Mean soil CO_2 efflux rates reported for moist tropical forests range from 0.7 to 5 μmol m^{-2} s^{-1} [2, 14] with an average value of 1 μmol m^{-2} s^{-1} [16]. The average value for the primary forest in this study (2.3 μmol m^{-2} s^{-1}) was well within this range, but was lower than the values reported by Buchmann et al. [2] for the same site (3–5 μmol m^{-2} s^{-1}).

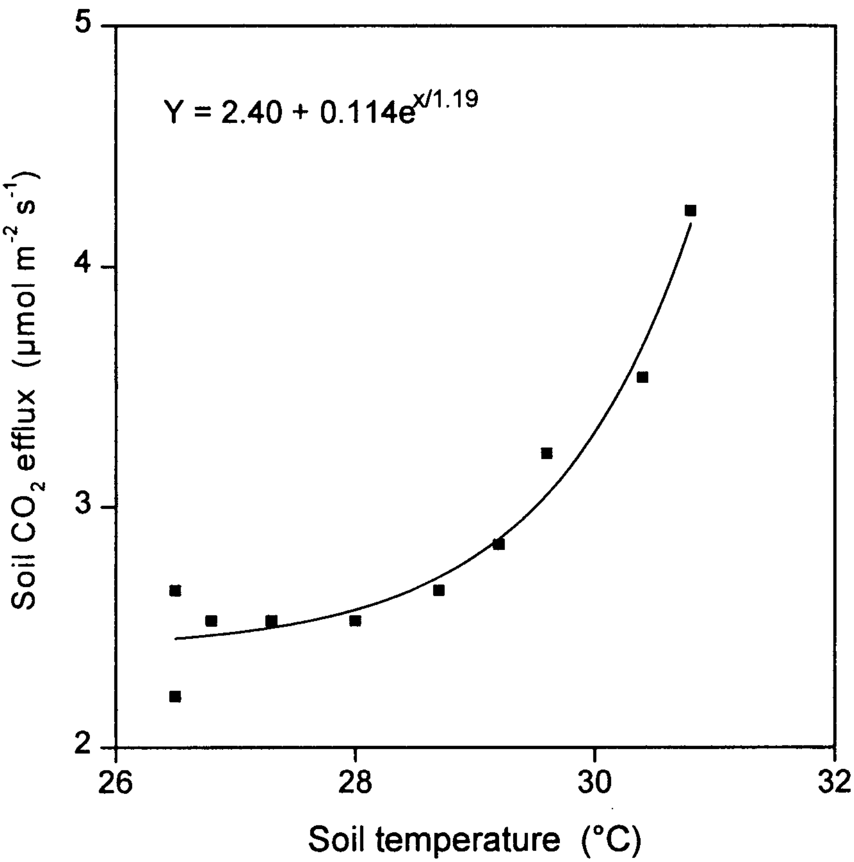

Figure 4. Temperature response of soil CO_2 efflux for one collar in the clear-cut site. Only data from the afternoon and night-time are shown. The fitted regression is significant at $P \leq 0.05$.

Mean soil CO_2 efflux rate in the hardwood plantation was significantly higher compared to the primary forest and the clear-cut. This higher CO_2 efflux was probably due to a higher metabolism of the fast growing trees in the young plantation [13]. In such a young plantation, root systems are still actively expanding and have high nutrient uptake rates to supply the growing trees with nutrients. Root respiration is therefore expected to be quite high. Since root respiration can represent more than 50 % of soil CO_2 efflux in forest ecosystems [4, 6], we speculate that higher specific root respiration rates caused this difference in soil CO_2 efflux between the plantation and the primary forest.

Despite a lower root density and a smaller amount of surface litter (*table I*), soil CO_2 efflux in the clear-cut was not lower than in the primary forest. The fact that root density was much lower in the clear-cut did not mean that root respiration was much lower. The reason for this is that in forested sites, roots lignify and become thicker than the roots in the clear-cut site. In this case it would have been necessary to compare the amounts of live fine roots to compare root activity in the three sites. The higher soil CO_2 efflux in the clear-cut site was probably caused by the higher mean soil temperature (*figure 1a*). A higher soil temperature increases root respiration and enhances decomposition processes. Because the clear-cut in this study was rather recent (ca. 10 years old), the soil was still high in organic matter content (*table I*). Higher soil temperatures and equal amounts of soil organic matter lead to enhanced decomposition and increased soil CO_2 efflux rates. However, this probably is a transient state that will only last until organic matter levels have declined.

In conclusion, differences in soil CO_2 efflux rates among three different tropical ecosystem types were illustrated in this paper, and their relation to a number of biotic and abiotic factors has been examined.

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