SOIL–CO_2 EFFLUX IN SIMPLE AND DIVERSE ECOYSTEMS ON A VOLCANIC SOIL IN COSTA RICA[1] /

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Resumen

*El flujo de CO_2 de un suelo relativamente fértil fue medido en nueve ecosistemas. Los ecosistemas tenían de 0,8 a 10 años de edad e incluyeron un suelo libre de vegetación, monocultivos de melina (*Gmelina arborea*) y yuca (*Manihot esculenta*), y comunidades sucesionales que contenían de 80 a > 150 especies. Los flujos de CO_2 se midieron en 6 u 8 repeticiones a intervalos de 4 horas durante períodos continuos de 24 horas, empleando cámaras cerradas con álcali absorbente. Los flujos medios de CO_2 oscilaron entre aproximadamente 9 y 18 g m^{-2} d^{-1}; los patrones diurnos fueron inconsistentes. Los insecticidas no redujeron las tasas de emanación de CO_2 en los dos ecosistemas donde fueron aplicados. El suelo libre de vegetación produjo las menores cantidades de CO_2; sin embargo, otras diferencias en producción de CO_2 entre ecosistemas no se relacionaron claramente con variaciones en cuanto a edad de la vegetación, estatura, riqueza de especies o área superficial de raíces finas. La temperatura del suelo no contribuyó en las diferencias de flujo de CO_2, mientras que el incremento del agua en el suelo fue asociado con una liberación más rápida de CO_2, probablemente debido a un estímulo en la actividad de los microorganismos del suelo y/o de las raíces. Se incluye un resumen de datos sobre flujos de CO_2 de suelos tropicales.*

Introduction

Soils receive organic matter produced by the aboveground plant community and, through numerous pathways, convert much of it to CO_2. This process-soil respiration-releases energy to the soil community and results in the liberation of nutrients for use by plants. Organic matter catabolism is therefore a major ecosystem process upon which the entire plant/soil community depends.

Measurement of CO_2 efflux from the soil surface is probably the most widely used system of estimating the rate of soil respiration *in situ*. However, soil respiration and soil-CO_2 efflux are not synonymous, although they are often assumed to be so. Soil respiration is the oxidation of organic matter in the soil, and includes the respiration of roots and soil biota, as well as the physical oxidation of organic matter (19). Soil-CO_2 efflux is the release of CO_2 into the atmosphere, and therefore depends both on CO_2 production in the soil and the physical process of gas flow out of the soil. However, most CO_2 produced in a soil is eventually released into the atmosphere, so soil-CO_2 efflux measured over relatively long periods reflects soil respiration. In seasonal climates the time lag between respiration and subsequent CO_2 efflux may be months long, resulting in CO_2 buildups and fluctuations in the soil (7). In relatively aseasonal environments, however, fluctuation in soil-CO_2 concentrations should be damped, and CO_2 efflux should track soil respiration more closely.

The purpose of our study was to compare rates of CO_2 release from the same soil occupied by different kinds of young, fast-growing tropical vegetation. It was our broad working hypothesis that soil-CO_2

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[1] Received for publication on May 21, 1984
This study was part of a cooperative research project being conducted by the University of Florida and the Centro Agronómico Tropical de Investigación y Enseñanza, and was supported by National Science Foundation grants DEB 78-10721 and DEB 80-11136. We thank W. Cropper for comments.

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efflux would increase as soil microbes, organic matter, and roots increased, and as the surface-soil microclimate was ameliorated by the overtopping plants. Specifically, we predicted that soil-CO_2 efflux would 1) be lower in ecosystems whose soil had been treated with insecticide than in ecosystems of comparable complexity that had not been treated, 2) increase with vegetation age, and 3) increase with increasing vegetation complexity (i.e. stature and/or species richness).

Materials and methods

Soil-CO_2 efflux was measured on nine sites, all located within the Florencia Norte forest of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), at Turrialba, Costa Rica (9° 53'N, 83° 40'W). All ecosystems were within 200 m of one another and at an elevation of approximately 650 masl. Mean annual rainfall in the area is about 2700 mm and the dry season extends from December through March. The native forest is evergreen, and the area falls within the Tropical Premontane Wet Forest life zone (36) or the Tropical Ombrophilous Submontane Forest formation (37). The study-area soil is a Typic Dystrandept of the Colorado series (2).

The nine experimental ecosystems ranged from 0.8 to 10 yr old, were 0 to 18 m tall, and contained 0 to > 150 plant species (Table 1). All of them except the young forest and the melina (*Gmelina arborea* Roxb.) plantation were established after parts of the young forest were felled and burned in early 1979. The impacts of the slash and burn (including impacts on soil-CO_2 efflux) were described previously (12). The cassava planting (*Manihot esculenta* Crantz) had been preceded by two crops of maize (*Zea mays* L.) following the burn. The 1.5-yr-old succession contained natural colonists only; its composition had not been manipulated by the investigators. The enriched succession consisted of successional vegetation to which seeds of other species ($\geqslant$10 000 seeds comprised of $\geqslant$ 20 species per 225 m^2 plot per month) had been added. The imitation was an ecosystem designed to mimic the structure and function of naturally occurring successional vegetation, but was comprised of species-both wild and cultivated-chosen by the investigators; natural colonists were weeded out. The vegetation-free plot contained some living roots connected to plants whose stems were outside the plot boundary. Detailed descriptions of vegetation structure, including roots, are reported by Berish (4, 5), Brown (6) and Ewel *et al.* (11).

Two of the vegetations-enriched succession and cassava monoculture-had been treated with insecticides as part of herbivore-reduction experiments (6). The insecticide treatments began in early 1979 and consisted of twice-weekly (or weekly only, in the dry season) applications of diazonone to the foliage and twice-yearly (most recently in May, 1980) applica-

Table 1. Characteristics of the ecosystems where soil-CO_2 efflux was measured.[a]

Ecosystem	Species Richness	Age (yr)	Leaf Area Index	Canopy Height (m)	Root Area Index[b]
Young forest	>150[c]	∿10	6.0[d]	18 [c]	3.2
Enriched succession	159	1.5	5.0	3.7	1.9
Enriched succession plus insecticide	81	1.5	5.4	3.7	no data
Succession	121	1.5	4.4	3.5	1.0
Imitation of succession	82	1.5	3.6	3.1	0.5
Melina monoculture	1[e]	3.2	5.1	11[c]	1.0
Cassava monoculture	1	0.8	2.9	2.9	0.1
Cassava monoculture plus insecticide	1	0.9	3.3	2.9	0.1
Vegetation-free	0	1.5	0	0	0.5

[a] Source: Berish (4, 5), Brown (5) and Ewel *et al.* (11).

[b] Surface area of roots <5 mm in diameter, to a depth of 25 cm per m^2 of ground.

[c] Estimated value

[d] Based on measurement 19 mo earlier (12)

[e] Not including herbaceous ground cover, which accounted for 6% of leaf area

tions of aldrin to the soil. Diazonone is a broad-spectrum, non-persistent organophosphate that has low phytotoxicity and aldrin is a persistent, chlorinated hydrocarbon.

Three sets of measurements were made, all in August-September 1980, during the rainy season. A set of measurements consisted of measuring soil-CO_2 efflux at 4-h intervals for a continuous 24-h period at six (first and third sets) or eight (second set) randomly selected locations within each of several of the ecosystems described in Table 1. Soil temperatures were measured every 4 h beside a randomly selected subset of the locations in each site. Temperatures were measured with mercury thermometers pushed 1 cm into the soil. On the bare plot the thermometers were shaded with cardboard, to underestimate the actual soil temperatures reached in the open. Soil moisture was also monitored as a potentially important factor influencing CO_2 efflux. Six samples were collected from each treatment four times during each set of measurements: at the beginning, at dusk, at dawn, and at the end. Soil moisture was determined gravimetrically (oven-drying at 110°C) on soil samples taken from the surface 5 cm next to each sample location.

The first set of measurements was designed to answer two questions: 1) Did the insecticides affect soil metabolism? 2) If so, was a relatively simple ecosystem affected more than a relatively complex one? Two vegetations (treated and untreated plots of each) were used for this set of measurements: the cassava monoculture and the 1.5-yr-old enriched successional vegetation.

The second and third sets of measurements involved CO_2 efflux as a function of vegetation age and complexity. The purpose of the second set of measurements was to compare soil metabolism of a young monoculture with that of an older monoculture, and to compare the soil metabolism of these two monocultures with that of a diverse community. The three ecosystems chosen for these comparisons were the cassava (young monoculture), the melina (older monoculture) and the 1.5-yr-old successional vegetation.

The third set of measurements was designed to compare soil-CO_2 efflux from a broad array of ecosystems that differed with respect to vegetation age and community complexity. Six ecosystems (listed in order of decreasing vegetation complexity) were compared: 10-yr-old forest, 1.5-yr-old enriched succession, 1.5-yr-old succession, imitation of succession, cassava monoculture, and a soil maintained free of vegetation since early 1979.

Soil-CO_2 efflux was measured using a modification (12) of Haber's (14) method. Carbon dioxide released from the soil surface was trapped in an inverted, 2-liter plastic tub and absorbed with 25 ml of 1.0 N Na OH. The Na OH was supported 5 cm above the soil surface in a Petri dish on a wire stand. The plastic tub covered 186 cm^2 of soil surface, and the Na OH had an exposed surface area of 62.2 cm^2. Six to eight such set-ups were used in each site during each experiment. The rim of each tub was pushed 2 cm into the soil to prevent atmospheric contamination of the samples. Each tub was left in place for 4 h, at which time it was removed, the alkali was replaced with fresh solution, and the tub was carefully repositioned. Measurements continued for 24 h.

All samples were kept in air-tight containers both before and after absorption. In addition, blanks were run to account for CO_2 absorption during storage and handling. Blanks were samples that were poured into the Petri dish and then immediately back into their air-tight cannisters; their absorbing time was therefore zero. Two blanks were run at each 4-h interval. Samples and blanks were titrated to the end points of phenolphthalein and methyl orange with 0.5 N HCl. The average amount of CO_2 absorbed by the blanks was subtracted from each 4-h sample, and this value was used as a measure of soil-CO_2 evolution. No factor was used to account for CO_2 not absorbed by the alkali, as has been utilized by others (21, 22, 32, 39, 40).

Results

The data, summarized in Table 2, were subjected to analysis of variance using the SAS (30) general linear model procedure. Rates of CO_2 efflux from the soil surface varied significantly ($P < 0.05$) among some treatments within days, from day to day within the 1.5-yr-old successional vegetation, and among times within days. Diurnal patterns of soil-CO_2 evolution were not consistent, however, perhaps because the range of temperatures encountered was not great. In most cases the diurnal difference between maximum and minimum soil temperatures was 6°C or less, a value exceeded only in one of the three sets of measurements in the cassava monoculture (8.4°C) and in the vegetation-free soil (11.9°C). Comparisons below are based on the total amount of CO_2 absorbed beneath each tub during each 24-h set of measurements.

Neither the vegetation type nor the insecticides significantly affected soil-CO_2 efflux during the first set of measurements. At the time of these measurements soil moisture was significantly greater in the enriched succession (mean of 52.8%) than in the cassava monoculture (mean of 42.8%).

Table 2. **Soil-CO_2 efflux, soil moisture, and soil temperatures.** Values are means ± standard deviations.

Ecosystem	CO_2 efflux (g m^{-2} d^{-1})	Moisture (%)	Temperature (°C) min. max. diff.
FIRST SET OF MEASUREMENTS			
Cassava	$^{a}12.1 \pm 1.2$	$^{a}41.1 \pm 5.6$	20.6 29.0 8.4
Cassava plus insecticide	$^{a}11.2 \pm 2.6$	$^{a}44.5 \pm 2.5$	20.6 25.0 4.4
Enriched succession	$^{a}12.0 \pm 3.0$	$^{b}55.6 \pm 0.8$	21.3 24.3 3.0
Enriched succession plus insecticide	$^{a}12.6 \pm 3.8$	$^{b}50.0 \pm 1.5$	21.0 24.5 3.5
SECOND SET OF MEASUREMENTS			
Succession	$^{a}17.5 \pm 5.1$	$^{a}61.3 \pm 1.8$	21.0 24.1 3.1
Cassava	$^{b}12.4 \pm 1.5$	$^{b}54.3 \pm 1.8$	21.5 25.0 3.5
Melina	$^{b}11.4 \pm 2.4$	$^{b}51.3 \pm 3.8$	21.0 23.0 2.0
THIRD SET OF MEASUREMENTS			
Young forest	$^{a}17.9 \pm 1.6$	$^{a}60.8 \pm 0.9$	21.6 24.0 2.4
Enriched succession	$^{b}13.7 \pm 0.7$	$^{a}60.5 \pm 2.2$	21.5 23.8 2.3
Succession	$^{c}12.7 \pm 3.4$	$^{a}58.0 \pm 1.1$	21.3 27.0 5.7
Imitation of succession	$^{c}12.4 \pm 2.4$	$^{b}50.6 \pm 1.9$	22.4 27.5 5.1
Cassava	$^{c}12.7 \pm 2.1$	$^{c}44.1 \pm 1.4$	22.3 26.7 4.4
Vegetation-free	$^{d}9.2 \pm 2.3$	$^{d}33.7 \pm 2.8$	24.1 36.0 11.9

a, b, c, d Within a given set of measurements, means in the same column accompanied by the same superscript do not differ significantly

The diverse, successional ecosystem had significantly higher soil-CO_2 efflux (and moister soil) than did either the cassava monoculture or the melina plantation during the second set of measurements. The rates of soil-CO_2 evolution in the two monocultures were about the same.

Soil-CO_2 efflux and soil moisture were both significantly affected by the type of vegetation during the third set of measurements. The 10-yr-old secondary forest had higher rates of soil-CO_2 evolution and more soil moisture than did all other sites. The vegetation-free plot had the lowest rates of soil-CO_2 evolution as well as the driest soil. Mean daily soil-CO_2 efflux during the third set of measurements ranged, from highest to lowest: secondary forest > enriched succession > succession = cassava = imitation of succession > vegetation-free soil. Soil moisture varied in a slightly different manner: enriched succession = young forest = succession > imitation of succession > cassava > vegetation-free soil.

Daily soil-CO_2 efflux was significantly ($P < .001$) correlated with soil moisture by the following equation:

$$Y = .24X + .76 \qquad (r^2 = .61)$$

where: Y = mean soil-CO_2 efflux (g m^{-2} d^{-1}) and X = mean soil moisture (%). Dry-season data, collected in the same location and with the same methodology (12), were included in this regression.

Discussion

Rates of soil-CO_2 evolution on the sites reported here (9.2 to 17.9 g m^{-2} d^{-1}) are in the upper range of values reported from other tropical areas, with the exception of a few apparent outliers (Table 3). Considering the large number of factors that influence soil-CO_2 evolution rates, the diversity of tropical vegetation types, and the short periods of time over which most of the tropical soil-CO_2-evolution data in the literature are based, the site-to-site variation in Table 3 is understandable. However, it is also likely that methodological differences account for some of the differences. All chamber techniques affect the environment of the soil being measured, if only moderately, and all static systems (which includes most values in Table 3) eliminate air movement over the soil surface, which may be important (24, 33).

Table 3. Soil-CO_2 evolution rates in tropical ecosystems. Values are means or ranges and, unless specified to the contrary, are from closed-chamber systems without air flow.

Location	Reference	CO_2 efflux (g m^{-2} d^{-1})	Vegetation type
Brazil	Coutinho and Lamberti (8)	2.9	Moist forest (white-sand soil)
Costa Rica	Schulze (32)	9.0	Mature dry forest
		32.6	Mature gallery forest
		7.9	Savannah
		38.0	Mature wet forest
		61.3	± 2-yr-old wet-forest regrowth
	Johnson *et al* (15)	14.3	Dry forest
		5.0	Wet forest
	Allen and Lemon (1)	20[1]	60-yr-old wet forest
	Ewel *et al* (12)	12.8	8-yr-old wet forest
		13.3	Cut-and-mulched site
		16.8	Recently burned site
	Raich (27)	12.5	Mature wet forest
		16.9	1-yr-old regrowth
India	Singh *et al.* (35)	0.2 – 2.9	*Zizyphus shrub community*
	Gupta and Singh (13)	1.2 – 10.8	Grassland
	Rai and Srivastava (26)	1.0 – 3.7	Dry forest
	Upadhyaya *et al* (38)	2.7 – 16.5	Grassland (four types)
Indonesia	Wanner (39)	4.1	Lower montane rain forest
	Wanner *et al.* (40)	5.9	Lowland rain forest
		4.4	Strand forest
		5.6	20-yr-old teak plantation
		5.2	Grassland
		5.7	Clump of trees in savannah
		5.8 – 6.7	Montane rain forest (three sites)
Ivory Coast	Lamotte (18)[2]	8	Savannah
Malaysia	Wanner (39)	5.4	Lowland dipterocarp forest
	Wanner *et al.* (40)	6.6	Lowland dipterocarp forest
		6.1	Lowland heath forest
	Ogawa (25)	14.3	Lowland dipterocarp forest
	Anderson *et al* (3)	7.4	Heath forest
		4.5	Alluvial forest
		5.8	Dipterocarp forest
		6.3	Forest on limestone
Puerto Rico	Odum *et al* (24)[3]	0.7 – 11.4	Lower montane rain forest
	Witkamp (44)	0.5 – 1.4	Lower montane rain forest
		1.1	Cloud forest
Thailand	Yoda and Kira (45)	10.6	Dipterocarp savannah forest
		12.3	Dry, monsoon forest
		14.8	Rain forest
		11.5 – 12.1	Three 4-7-yr-old teak forests
	Yoda and Nishioka (46)	9.2	Dry-evergreen forest; dry season
		27.9	Dry-evergreen forest; wet season
Venezuela	Medina and Zelwer (21)	8.3	Moist forest
		4.2	Moist forest
		2.3	Cloud forest
		2.3	Lower montane wet forest

Continues on page 38

Location	Reference	CO_2 efflux (g m^{-2} d^{-1})	Vegetation type
	Medina *et al.* (22)	0.9	Montane moist forest
		5.0	Dry forest
		2.7	Very dry forest
		4.6	Wet forest on podsol
		1.3	Vegetation-free podsol
		2.7	3 mo after burn; podsol
		3.3	11-mo-old regrowth; podsol
		3.4	13-mo-old regrowth; podsol
		3.7	Wet forest on laterite
		1.2	Vegetation-free laterite
		4.3	1 mo after burn; laterite
		2.0	6-mo-old cassava; laterite
Zaire	Maldague and Hilger (20)[4]	15.3	*Gilbertiodendron* forest
		11.7	*Brachystegia* forest
		11.4	*Scorodophloeus* forest
		12.4	Periodically flooded forest

1 Aerodynamic method

2 Method unknown.

3 Also published much higher values measured in chambers with air flow

4 Oxigen uptake measured with manometer.

Data presented here are most comparable to those of Ewel *et al.* (12) and Raich (27) in Costa Rica, and Maldague and Hilger (20), Ogawa (25) and Yoda and Kira (45) for other warm, moist tropical areas.

Other papers (21, 22, 39, 40) report soil-CO_2 effluxes which are, in general, lower than those reported here, although they were often obtained in similar environments

In comparison with these authors, more hydroxide absorbent was used and a larger surface area of the hydroxide, for better CO_2 absorption (16), was exposed in the present work. Schlesinger's (31) regression line, which relates soil-CO_2 evolution to latitude, predicts a value of about 15 g m^{-2} d^{-1} for the site in which this study was carried out. Mean values for vegetated plots in this site ranged from about 11 to 18 g m^{-2} d^{-1}.

Soil-CO_2 efflux is the result of CO_2 production in the soil and its subsequent diffusion into the atmosphere. Insecticides that kill soil arthropods might be expected to affect rates of CO_2 production, but not diffusion. Although the aboveground insect community was reduced by the spraying (6), any effects on belowground populations were not reflected in the CO_2 efflux data. Most CO_2 released is presumably generated by the activities of microbes and roots, neither of which should have been greatly affected by the insecticides used.

Vegetation can influence soil-CO_2 evolution through its influence on organic matter production (both roots and litter) and on microclimate. The prediction that CO_2 efflux would increase with vegetation complexity was borne out during the second and third sets of measurements, but not the first. At times the monoculture soils yielded as much CO_2 as did those of the more diverse communities. The vegetation-free plot, however, released CO_2 at a substantially lower rate than did any of those with vegetation.

The young forest had the highest root area index (RAI = 3.2, Table 1) and the highest average CO_2 efflux (17.0 g m^{-2} d^{-1}). This relationship did not hold at the other end of the scale: the cassava monoculture had the lowest fine-root biomass (RAI = 0.1), but its rates of CO_2 evolution were intermediate (11.2 to 12.7 g m^{-2} d^{-1}).

Although the rate of CO_2 evolution was greatest from the oldest community studied (young forest), the second-oldest community (melina monoculture) had one of the lowest average rates. It is clear that

CO_2 efflux is not dictated by vegetation age alone. Age in conjunction with vegetation complexity may influence CO_2 efflux, however, through its relationships to root development, litter production, and the soil environment.

If insecticides, vegetation complexity, and vegetation age do not explain the observed differences in CO_2 efflux, what does? The answer seems to be abiotic factors. Numerous authors (10, 15, 17, 28, 41, 42, 43) have demonstrated a significant-and usually positive-relationship between soil temperatures and soil-CO_2 evolution rates, particularly in explaining seasonal trends in temperate environments and day/night differences in rates of CO_2 efflux. However, the highest soil temperatures at the study site occurred in the vegetation-free soil, which also had the lowest soil-CO_2 efflux. This plot had been bare for 1 5 yr at the time of the study, so CO_2 production here may have been substrate limited. Soil temperature variations beneath vegetation were generally modest, and explain relatively little of the variation in the data.

A more likely factor is water. Soil moisture content is well known to influence the rate of soil-CO_2 evolution (9, 23, 28, 34) There are least three ways that soil water content might have influenced CO_2 efflux during the measurements made in the present study.

First, soil respiration might have increased with increasing moisture. This would imply that the soil biota was water-limited, and not substrate-limited, at the lower ranges of soil moisture measured here.

A second, but less likely, possibility is that water might have displaced gas in the soil, increasing the outward flux of CO_2. Such a displacement would have to have been a short-term phenomenon, and could have occurred only as long as soil water content was increasing. The changes in soil moisture observed during our 24-h measurements were not large enough to account for much increase in CO_2 flux due to displacement by water, and the water contents observed were not high enough to fill any but the smallest pores, so this phenomenon is unlikely to have been responsible for most moisture-related differences in CO_2 efflux.

Third, increased soil moisture may have resulted in increased diffusivity of CO_2 out of the soil. The soil at the study site contains shrinking/swelling clays and allophane. Over the range of soil moistures encountered during the study (about 30% to 60%), the bulk density of the study-site soil decreases from 1.00 to 0.85 (29). The resulting increase in pore volume might have increased the rate of CO_2 diffusion out of the soil, but only if the space was occupied by soil atmosphere rather than soil solution, as CO_2 diffuses very slowly in water.

Soil water and temperature –like roots, microbes, and organic matter– are, to some extent, under biotic control. They also vary with season. One might therefore predict that communities with higher transpiration rates would deplete soil moisture faster, resulting in less soil-CO_2 efflux during the dry season. During the wet season (when these measurements were made) differences between high-transpiration and low-transpiration communities would be expected to be small; this fact was observed in the present work.

This study was conducted on a deep, moist, well-drained, relatively fertile soil: perhaps nearly ideal conditions for soil respiration. All of the communities examined (except the vegetation-free plot) were young and very productive. The combination of conducive environmental conditions, year-round growth, abundant fine roots, and high rates of litter production make it likely that soil respiration rates of tropical successional and agricultural ecosystems on good soils are among the highest in the world.

When such sites are cleared –and maintained free of regrowth– they release CO_2 into the atmosphere at a high rate until their soil carbon reserves are much reduced: a process that apparently takes longer than the 1.5 yr that the vegetation-free plot was maintained in this study. Unless they are intentionally kept clear, however, recolonization is rapid. Successional vegetation and plantations of cassava of melina apparently produce sufficient organic matter to fuel soil respiration at rates nearly as high as those of the predisturbance forest.

Summary

Soil-CO_2 efflux was measured from nine ecosystems, all on the same relatively fertile soil. The ecosystems ranged from 0.8 to 10 yr old and included a vegetation-free soil, monocultures of melina (*Gmelina arborea*) and cassava (*Manihot esculenta*), and successional communities containing 80 to > 150 species. CO_2 effluxes were based on replicated ($n = 6$ or 8) measurements at 4-h intervals for continuous 24-h periods, using closed chambers containing alkali absorbent. Mean CO_2 effluxes ranged from about 9 to 18 g m^{-2} d^{-1}; diurnal trends were inconsistent. Insecticides did not reduce rates of CO_2 evolution from the two ecosystems where they were applied. The vegetation-free soil yielded CO_2 at the slowest rate, but other differences among ecosystems were not clearly related to differences in vegetation age, stature, species richness, or fine-root surface area. Soil temperature did not account for differences in CO_2 efflux, but increased soil water was associated with faster CO_2 release, probably because it stimulated the activity of soil microorganisms and/or roots. Soil-CO_2-efflux data from the tropics are tabulated.

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