Global Change Biology (2004) **10**, 833–843, doi: 10.1111/j.1529-8817.2003.00776.x

CO_2 flux from soil in pastures and forests in southwestern Amazonia

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Abstract

Stocks of carbon in Amazonian forest biomass and soils have received considerable research attention because of their potential as sources and sinks of atmospheric CO_2. Fluxes of CO_2 from soil to the atmosphere, on the other hand, have not been addressed comprehensively in regard to temporal and spatial variations and to land cover change, and have been measured directly only in a few locations in Amazonia. Considerable variation exists across the Amazon Basin in soil properties, climate, and management practices in forests and cattle pastures that might affect soil CO_2 fluxes. Here we report soil CO_2 fluxes from an area of rapid deforestation in the southwestern Amazonian state of Acre. Specifically we addressed (1) the seasonal variation of soil CO_2 fluxes, soil moisture, and soil temperature; (2) the effects of land cover (pastures, mature, and secondary forests) on these fluxes; (3) annual estimates of soil respiration; and (4) the relative contributions of grass-derived and forest-derived C as indicated by $\delta^{13}CO_2$. Fluxes were greatest during the wet season and declined during the dry season in all land covers. Soil respiration was significantly correlated with soil water-filled pore space but not correlated with temperature. Annual fluxes were higher in pastures compared with mature and secondary forests, and some of the pastures also had higher soil C stocks. The $\delta^{13}C$ of CO_2 respired in pasture soils showed that high respiration rates in pastures were derived almost entirely from grass root respiration and decomposition of grass residues. These results indicate that the pastures are very productive and that the larger flux of C cycling through pasture soils compared with forest soils is probably due to greater allocation of C belowground. Secondary forests had soil respiration rates similar to mature forests, and there was no correlation between soil respiration and either forest age or forest biomass. Hence, belowground allocation of C does not appear to be directly related to the stature of vegetation in this region. Variation in seasonal and annual rates of soil respiration of these forests and pastures is more indicative of flux of C through the soil rather than major net changes in ecosystem C stocks.

Keywords: Amazon Basin, Brachiaria, deforestation, global carbon cycle, soil carbon, soil respiration

Received 11 January 2002; revised version received 10 August 2003 and accepted 12 November 2003

Introduction

Carbon cycling in the tropics, especially in the Amazon basin, has received considerable research attention since the recognition that deforestation for cattle ranching and other agricultural uses is an important source of greenhouse gases to the atmosphere (Fearnside, 1985; Lugo & Brown, 1986). Carbon stocks in Amazonian forest biomass (Houghton *et al.*, 2001) and in soils (Batjes & Dijkshoorn, 1999) are well studied, although uncertainties in values for both reservoirs are still large. On the other hand, carbon fluxes from soil to the atmosphere are still poorly understood, in terms of seasonal variation and of amounts of carbon respired in different land covers. Some authors have addressed these questions, but with little spatial or temporal repetitions (Medina *et al.*, 1980; Feigl *et al.*, 1995; Meir *et al.*, 1996; Davidson *et al.*, 2000; Fernandes *et al.*, 2002). It is well known that soil respiration is affected by soil temperature (Kirschbaum, 1995), soil water content (Davidson *et al.*, 2000), and inputs of C belowground

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(Trumbore *et al.*, 1995), but the relative importance of these factors is likely to vary regionally. Soil respiration has been used as a proxy for estimating belowground C allocation in forest soils (Raich & Nadelhoffer, 1989; Davidson *et al.*, 2002a), and it may also provide an indication of C allocation in pasture soils. Degraded pasture soils might be expected to exhibit low rates of soil respiration, whereas productive pastures may have higher rates of soil respiration.

In search of a better understanding of spatial and temporal patterns in CO_2 fluxes from soils, in this paper we address the following questions: (1) What is the seasonal pattern in CO_2 flux from soil to atmosphere in pastures, mature and secondary forests and how does that seasonality relate to patterns of precipitation and temperature? (2) Are the CO_2 fluxes different among these land covers? (3) What are the annual CO_2 fluxes? (4) What fraction of the CO_2 respired from pasture soils is derived from pasture plants and what fraction from remaining organic matter from the former forest soil?

Materials and methods

Study area

The study areas (Table 1) are located in the south-western corner of the Brazilian Amazon Basin, near the city of Rio Branco in the state of Acre, Brazil, where most of the deforestation in that state is taking place. The regional climate has a mean annual temperature of 26 °C; rainfall of 1940 (± 230) mm with a well-defined dry season (with less than 50 mm per month from June through August); mean annual relative humidity of 85% (Duarte *et al.*, 2000). The soils are classified as dystrophic and eutrophic Ultisols with patches of Oxisols (RADAMBRASIL, 1976; Eufran do Amaral, pers. commun.).

Natural vegetation is classified as Ombrophilous Open Forest (RADAMBRASIL, 1976) with patches of bamboo-dominated forest (Silveira, 1999). Where natural forests have been converted, 60% is now used for cattle ranching and agriculture, and almost 40% is in some stage of secondary succession (Salimon, Brown, and Stone, unpublished).

Specifically, this study was conducted in two secondary forests at the Zoobotanical Park at the Federal University of Acre, Rio Branco, Acre State, hereafter referred to as PZ, and also at two government-sponsored settlements, (1) Peixoto Settlement Project and (2) Humaitá Settlement Project, hereafter referred to as Peixoto and Humaitá. In both settlements the main animal products are cattle and chickens and the principal crops are manioc, maize, banana, and rice (INCRA/AC, 2001). The typical land holding is about 120 ha located along access roads.

The four pastures studied were all between 12 and 15 years old, dominated by *Brachiaria brizantha* and had from zero to three burning events. The eight secondary forests were more heterogeneous in age, ranging from 3 to 18 years old, and were also diverse in previous use, from rice to manioc plantation. The four mature forests have no historical sign of clear-cutting, but are all used for rubber tapping, Brazil nut extraction and for game hunting. Details for each site are given in Table 1.

Soil sampling

In order to characterize soils at the Peixoto and Humaitá sites, we sampled soils from each land cover from 0 to 60 cm depth. For this purpose, three trenches (60 × 60 × 60 cm) were dug in each of the following sites: Secfor 11, Secfor 3a, Pasture 13 and Matfor at Peixoto, and in Secfor 3b, Pasture 14 and Matfor at Humaitá (site codes in Table 1). Physical and chemical analyses were carried out at the Soil Laboratory at Escola Superior de Agronomia, following van Raij *et al.* (2001). Carbon concentration in soil was determined at the Isotopic Ecology Laboratory at the Centro de Energia Nuclear na Agricultura, University of São Paulo, using an Element Analyzer Carlo Erba, model 1110 CNHS. The number of samples per depth was 12, 6, 3, and 3 for 0–5, 5–10, 20–30 and 50–60 cm, respectively. In order to calculate C stocks, we estimated soil bulk density by sampling twelve intact soil cores at each sampling depth (same as for the C samples) using a steel cylinder 8.25 cm of diameter by 6 cm height (Blake & Hartge, 1986).

The amount of C_4 originated carbon in pasture soils was calculated using an isotopic mixing model, Eqn (1):

$$\%C_4 = \frac{\delta^{13}C_{sample} - \delta^{13}C_{reference}}{\delta^{13}C_A - \delta^{13}C_{reference}} \times 100, \qquad (1)$$

where C_A stands for the C_4 plant value and $C_{reference}$ stands for the C_3 plant value.

Because of the large number of sample sites and frequent sample dates, we did not take samples to measure soil water content routinely. The relationship between soil respiration and soil water content was evaluated on one date in the dry season (June 2001) and one date in the wet season (February 2002) in all of the pasture and forest sites in the Humaita1 and Peixoto1 area. Soil respiration measurements were made on these dates as described below, and five randomly distributed samples of the top 0–5 cm soil were taken from each field. Samples were stored in plastic bags until they were oven dried at 105 °C for 72 h. Water-filled pore space (WFPS) was calculated as in the

Table 1 Description of the study sites

Sampling sites		Lat/long					
		S	W	History of site	Previous use	Litterfall C (Mg C ha^{-1} $^{-1}$)	Annual CO_2 flux (Mg C ha^{-1} a^{-1})
PZ	Secfor 12a	9°56′59″S	67°52′18″W	Secondary forest 12 years old	Agriculture and pasture	6.3 (± 1.1)	18.8 (± 0.6)
	Secfor 18	9°56′59″S	67°52′18″W	Secondary forest 18 years old	Agriculture and pasture	5.2 (± 0.8)	17.1 (± 0.6)
	Pasture 13	9°52′ 27.6″S	67°4′19.2″W	Pasture 13 years old	Mature forest	–	18.4 (± 0.4)
	Secfor 11	9°52′32.5″S	67°4′17.7″W	Secondary forest 11 years old	Pasture	No data	18.3 (± 1.1)
Peixoto 1	Secfor 3a	9°52′30.1″S	67°4′26.9″W	Secondary forest 3 years old	Manioc plantation	6.1 (± 0.8)	15.4 (± 0.5)
	Secfor 3b	9°52′31.3″S	67°4′24″W	Secondary forest 3 years old	Manioc plantation	No data	13.5 (± 0.5)
	Matfor	9°52′36.7″S	67°4′37.9″W	Mature forest	–	8.7 (± 2.2)	14.9 (± 0.9)
	Pasture 12	9°56′38.9″S	67°6′56.7″W	Pasture around 12 years old	Mature forest	–	26.2 (± 0.3)
Peixoto 2	Secfor 12b	9°56′35.6″S	67°6′56.4″W	Secondary forest 12 years old (lianas; cattle enters the area)	Manioc plantation	No data	16.9 (± 0.8)
	Matfor	9°56′52.9″S	67°7′30.8″W	Mature forest		7.8 (1.3)	17.3 (± 0.8)
	Pasture 14	9°46′12.8″S	67°39′28.7″W	Pasture 14 years old	Mature forest	–	22.8 (± 0.5)
Humaitá 1	Secfor 3c	9°46′14.9″S	67°39′27.9″W	Secondary forest 3 years old	Plantation of rice and/or beans	6.5 (± 1.2)	16.9 (± 0.8)
	Matfor	9°46′13.5″S	67°39′29.1″W	Mature forest	–	5.5 (± 0.6)	14.7 (± 0.6)
Humaitá 2	Pasture 6	9°50′30.7″S	67°46′30.4″W	Pasture 6 years old	Mature forest	–	27.5 (± 0.5)
	Secfor 18	9°50′40″S	67°46′35.7″W	Secondary Forest 18 years old	Plantation (not specified)	No data	15.1 (± 0.7)
	Matfor	9°50′23.7″S	67°46′33.8″W	Mature forest	–	6.4 (± 1.0)	17.7 (± 1.0)

Secfor means secondary forest; matfor means mature forest; numbers after the names stand for the age (i.e. Secfor 18, secondary forest with 18 years of age). Error terms (in parentheses) represent standard error among replicate litterfall traps ($n = 5$) and flux chambers per site ($n = 8$).

following equation:

$$WFPS = \frac{\%_{volumetric\ water}}{\%_{soil\ porosity}}$$
$$\%_{soil\ porosity} = 1 - \left(\frac{soil\ bulk\ density}{2.65}\right), \qquad (2)$$

where 2.65 is the assumed particle density.

Soil temperature was measured at 10 cm depth by inserting a temperature probe near each soil respiration chamber while each flux measurement was in progress.

CO_2 flux measurements

Fluxes were measured once per month from June 1999 to July 2000 at all sites, except for October when no measurement was made. Eight CO_2 flux measurements were made at each site and date.

Carbon dioxide flux from soil to atmosphere was measured using an infrared gas analyzer (IRGA), LICOR-6252, coupled to a vented dynamic chamber system (identical to the system shown in Fig. 3 in Davidson *et al.*, 2002b). Eight PVC rings (20 cm diameter × 10 cm height) were inserted 3 cm into the soil at each site. At the time of sampling, a PVC opaque chamber, with an ID at the bottom just slightly larger than the OD of the ring, was placed snuggly over the ring, and air was circulated between this chamber (volume of ring + the top was 7.1 L) and the IRGA with an air pump at 0.5 L min^{-1}. A vent (5 cm long, 2.16 mm ID stainless steel tube) was installed in the chamber top through a Swaglok fitting to equalize pressure with the atmosphere.

CO_2 concentrations in the chamber were recorded every 12 s for 5 min and were stored in an HP 200 XL palmtop connected to the IRGA. With one exception for a diel study, measurements were always conducted between 00:09 hours to 14:00 hours. In order to evaluate whether the time of sampling was representative of soil respiration during the day, we also conducted diel samplings at 1 h intervals in pasture, mature and secondary forests in June and July 2000, with five flux measurements at each site and hour.

The flux was calculated from linear regression of the difference of CO_2 concentration over time. The first few measurements during the first minute were discarded from the regression to avoid any artifact of closing the chamber, and only the data showing a linear increase in CO_2 concentration (usually during a 1–5 min interval) were used to calculate fluxes. The IRGA was calibrated every morning by using 'zero' air that had been run through a soda lime scrubber and by using a White Martins certificated standard gas of 610 (± 2%) ppmv of CO_2 (nitrogen as the balance gas).

Annual fluxes for each flux measurement ring were calculated by multiplying the hourly fluxes for each month by the number of hours and days of that month. Fluxes for October 1999, when no data were available, were estimated by averaging values from the previous and the following months (this interpolation was used only for annual flux calculations). After calculating monthly fluxes for all rings at all sites, we summed the monthly values into annual fluxes for each ring and calculated the mean and standard error of the annual flux for each site.

$\delta^{13}C$ of respired CO_2 in pasture and mature forest

We used isotopic measurements in two situations. First, we sampled air effluxing directly from the soil *in situ*, using a soil flux chamber, to determine $\delta^{13}C$ of total soil respiration (both root and microbial). These measurements were made twice in pastures and once in a mature forest. Second, we sampled air evolved from laboratory incubations of a pasture soil, which was sieved and had no roots or grass leaves in it. Hence, the $\delta^{13}C$ values of the CO_2 in this laboratory measurement were related to heterotrophic respiration alone.

In order to determine the $\delta^{13}C$ of the CO_2 respired from pasture and mature forest soils, we collected time series of eight samples of air in 100 mL pre-evacuated bottles from a 65 L chamber attached to the soil. Wetted soil from nearby was used to seal the chamber to the soil to avoid any air leak from or to the chamber. Each sample was taken after a 50 ppm increase in CO_2 concentration inside the chamber. A small fan kept air well mixed inside the chamber throughout the period of sampling, which lasted for about 5–10 min. We also used a tube with magnesium perchloride between the sampling bottle and the chamber to avoid water vapor in the air samples. CO_2 concentrations of each sample were determined with an IRGA (as described in Bowling *et al.*, 2001).

Samples were then taken to the Isotopic Ecology Laboratory at CENA/USP for $\delta^{13}C$ determination of CO_2 of each bottle within two weeks of field sampling. Isotopic ratios were determined in an isotopic ratio mass spectrometer, model Finnigan DeltaPlus (Thermo Electron Cooperation, Bremen, Germany). Analytical precision during the time of measurements was 0.3‰. Soil from the same pasture and forest sites was also sampled for $\delta^{13}C$ determination of soil carbon. Plant tissues (leaves) from pasture and forests were also sampled for $\delta^{13}C$ determination of the sources of carbon to the soil.

We then calculated a linear regression of the inverse of the CO_2 concentration with its $\delta^{13}C$ – usually referred to as *Keeling plot* (Keeling, 1958). The intercept of the equation that describes that function is equal to the $\delta^{13}C$

of the CO_2 that is coming from the soil, and we use that number to estimate the sources of carbon being respired; that is, whether it is from C_3 or C_4 plants (Ometto *et al.*, 2002).

For laboratory incubations, five soil samples from 0 to 10 cm deep were taken from the pasture, and then mixed into a composite sample. This composite sample was divided into eight subsamples of 20 g of sieved soil that were placed in eight 600 mL jars. These jars had valves to allow connection with pre-evacuated bottles and to an IRGA for monitoring CO_2 concentration inside the jars. Because a gas sample of 100 mL had to be removed from the headspace of a jar for isotopic analysis of the CO_2, each small jar could be sampled only once. Therefore, one of the eight jars was destructively sampled every hour for 8 h in order to calculate a concentration gradient over time among the eight subsamples of each soil sample. Keeling plots were calculated from these data as described for the field data.

Litterfall measurements

Litter traps were constructed of 1 × 1 m squares of 5 mm nylon mesh suspended 30 cm above the soil surface. Five traps were installed in each of the mature forests and in four of the secondary forests (secfor3a, secfor3b, secfor12a, and secfor18; see Table 1). Litter was collected monthly, stored in paper bags, sorted for removal of coarse material with diameter >5 cm, dried at 70 °C for 72 h, and then weighed.

Results and discussion

Soils

Soils at Peixoto are on average more dystrophic (i.e. pH in 0.01 M $CaCl_2$ from 3.2 to 4.1 and base saturation from 6% to 34%) and clayey (50%) than at Humaitá (pH from 3.9 to 5.5; base saturation from 23% to 74%; and clay 40%). Carbon stocks in soil differed significantly between pastures and forests only at 0–5 and 5–10 cm at Peixoto, whereas in Humaitá, there was no significant difference in carbon stocks among land uses and depths (Table 2). An increase in surface C stocks has also been observed in pastures of other western Amazonia sites (Moraes *et al.*, 1996; Fernandes *et al.*, 2002).

Temporal variation of CO_2 flux

No consistent diel variation in CO_2 fluxes was observed in either pasture or forests (Fig. 1). It is possible that with a greater number of replicates and/or with an automated flux measurement system, a small but detectable diel pattern may appear (Savage & Davidson, 2003). However, it is clear from our data that the diel variation in soil respiration, if it exists, is not large.

Seasonal variation in CO_2 flux (Fig. 2a) was related to precipitation (Fig. 2b) and soil water content (Fig. 3). On the other hand, seasonal variation in air temperature was not as large (Fig. 2c). Soil temperatures at 10 cm depth ranged from 22 °C to 35 °C in pastures, 23 °C to 33 °C in secondary forests, and 20 °C to 26 °C in mature forests. Soil temperature was not a good predictor of CO_2 flux (Fig. 4). This was the case for all data combined ($R^2 = 0.18$), for pasture sites only ($R^2 = 0.05$), for secondary forest sites only ($R^2 = 0.02$), or for mature forest sites only ($R^2 = 0.11$). Temperature plays a key role in soil respiration rates globally and in many locales (Kirschbaum, 1995), but in low latitudes and where precipitation is strongly seasonal, the seasonal variation of temperature is not large compared with variation in soil water content. Observations of interactions of temperature and moisture effects (Xu & Qi, 2001) and confounding of temperature and moisture effects (Davidson *et al.*, 1998) are common and could also be important at our study site. However, we were unable to detect temperature dependency given our sampling regime and the large seasonal variation in soil water content.

The highest fluxes at all sites were observed during the rainy season (November to May), with peaks in January and February. The lowest fluxes were in August 1999, which was one of the driest months. The same seasonality was observed by Davidson *et al.* (2000) in forest and pastures of eastern Pará.

The CO_2 flux increased sharply between the August and September sampling dates at all sites, which corresponded to the transition from dry to wet seasons (Fig. 2), when both precipitation and air temperature increased. In most cases, soil respiration increased with increasing soil moisture across sites and dates (expressed as WFPS, in Fig. 3). Although one site exhibited reduced soil respiration at a 62% WFPS, others showed increases up to 80% WFPS. We cannot explain why respiration did not decline in all of the very wet soils that had water contents above the reported optimum of about 60% WFPS for soil microbial respiration in the laboratory (Linn & Doran, 1984) and soil respiration in some field studies (Kiese & Butterbach-Bahl, 2002). It is possible that root respiration continued at high rates or that the water content was not uniform throughout the soil cores used for bulk density and water content measurements.

CO_2 flux comparison among land covers

Pastures showed on average higher fluxes than mature and secondary forests ($P < 0.05$, the Kruskal–Wallis

Table 2 Soil bulk density, concentration, cumulative stocks and $\delta^{13}C$ of soil carbon in Peixoto and Humaitá

		Depth (cm)	Soil bulk density ($g\,cm^{-3}$)		Soil C ($mg\,C\,g^{-1}$)		Soil C stock ($Mg\,C\,ha^{-1}$)		$\delta^{13}C$ (‰)		%C C4
Peixoto	Pasture13	0–5	1.1	(0.01)	**44.7**	**(3.1)**	**24.6**	**(5.6)**	**−21.4**	**(0.2)**	41.9
		5–10	1.2	(0.03)	**17.4**	**(0.3)**	**10.4**	**(0.7)**	**−24.2**	**(0.2)**	16.8
		20–30	1.2	(0.01)	12.5	(0.3)	**7.5**	**(0.4)**	−24.4	(0.1)	8.8
		50–60	1.3	(0.03)	7.9	(0.1)	**5.2**	**(0.3)**	−24	(0.2)	4.9
	Secfor11	0–5	1.1	(0.01)	27.1	(1.4)	14.9	(2.4)	−28.3	(0.1)	–
		5–10	1.3	(0.02)	12.9	(0.5)	8.4	(0.9)	−27.3	(0.0)	–
		20–30	1.3	(0.04)	9.2	(0.5)	6	(0.7)	−26.3	(0.2)	–
		50–60	1.4	(0.02)	5.4	(0.8)	3.8	(0.9)	−25.4	(0.3)	–
	Secfor3a	0–5	1	(0.07)	20.5	(1.2)	10.3	(2.9)	−27.2	(0.3)	–
		5–10	1.3	(0.01)	12.7	(0.4)	8.2	(0.6)	−26.2	(0.3)	–
		20–30	1.2	(0.02)	7.9	(0.4)	4.7	(0.6)	−25.5	(0.1)	–
		50–60	1.2	(0.01)	6.4	(0.8)	3.9	(0.7)	−25.1	(0.2)	–
	Matfor	0–5	1.1	(0.08)	26.2	(1.7)	14.4	(3.7)	−28.2	(0.1)	–
		5–10	1.3	(0.02)	12.4	(1.3)	8.1	(1.8)	−26.7	(0.4)	–
		20–30	1.4	(0.03)	8.4	(0.1)	5.9	(0.4)	−25.6	(0.1)	–
		50–60	1.4	(0.03)	6	(0.3)	4.2	(0.6)	−24.6	(0.1)	–
Humaitá	Pasture14	0–5	**1.2**	**(0.04)**	28.2	(1.1)	16.9	(2.2)	**−19.4**	**(0.3)**	52.8
		5–10	1.4	(0.05)	15.2	(2)	**10.7**	**(2.9)**	**−22.2**	**(0.3)**	22.0
		20–30	1.4	(0.01)	7.6	(0.4)	**5.3**	**(0.5)**	**−22.4**	**(0.5)**	23.9
		50–60	1.4	(0.00)	5.7	(0.4)	**4**	**(0.4)**	**−23.1**	**(0.3)**	11.7
	Secfor3c	0–5	1	(0.06)	28.5	(2.4)	14.3	(4.8)	−28.2	(0.1)	–
		5–10	1.2	(0.01)	12.5	(1.5)	7.5	(1.9)	−27.1	(0.2)	–
		20–30	1.4	(0.02)	6.9	(0.4)	4.8	(0.5)	−25.8	(0.1)	–
		50–60	1.4	(0.03)	4.7	(0.4)	3.3	(0.7)	−24	(0.3)	–
	Matfor	0–5	1.1	(0.02)	21.3	(2.5)	11.7	(4.6)	−27.6	(0.1)	–
		5–10	1.2	(0.01)	11.2	(2.9)	6.7	(3.7)	−26.5	(0.1)	–
		20–30	1.4	(0.01)	5.1	(0.5)	3.6	(0.5)	−25.7	(0.1)	–
		50–60	1.3	(0.03)	4.1	(0.2)	2.7	(0.4)	−24.5	(0.3)	–

Last column is the percentage of C4 carbon in pasture soils. For details on site description, see Table 1. Values in parenthesis stand for standard errors. Pasture values that are in bold are statistically different from forests at $p < 0.05$ for the same depths within the same region (Peixoto or Humaitá).

test). Feigl *et al.* (1995) and Fernandes *et al.* (2002) have also presented similar results where pastures had higher fluxes than forests in southwestern Amazonia, but this was generally not the case in eastern Amazonia (Davidson *et al.*, 2000). The dry season is shorter in southwestern Amazonia compared with eastern Amazonia and some of the soils are also more fertile in southwestern Amazonia due to proximity to the Andes. We have anecdotally observed that the pastures of the present study appeared more productive than those studied by Davidson *et al.* (2000) in Paragominas, Pará.

Annual fluxes were estimated by extrapolating measurements to monthly fluxes and summing them for a year. The limited seasonal variation in temperature and the lack of a clear diel effect make the common approach of extrapolation with a temperature function untenable in this case. Monthly sampling probably under-represents the effects of wetting events (Savage & Davidson, 2003), but the use of automated chambers that can capture such rapid responses was beyond the scope of this study. Although there are inevitable uncertainties in annual extrapolations based on 12 monthly measurements, year-round measurements with even this frequency are still not common in the literature for tropical regions.

A correction for annual flux estimates was required for the pasture sites. The dense cover of grasses in the pastures made it difficult to avoid including some leaves within the chambers. In order to evaluate the influence of these leaves inside the chamber in pasture measurements, we sampled leaf biomass inside the rings and correlated that with soil CO_2 flux. During the dry season, there was no significant difference between fluxes of chambers with leaves and without leaves ($n = 5$; Sign test, $P > 0.07$). During the wet season, however, when leaf biomass can reach up to 30 g (dry

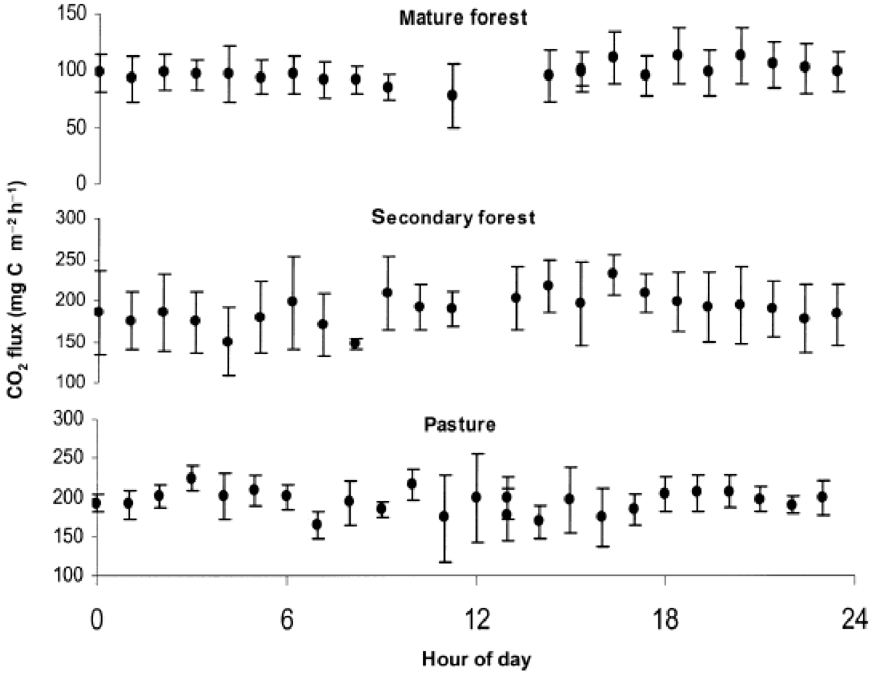

Fig. 1 Diel variation in CO_2 fluxes for the three land covers. Secondary forest data were sampled in June 2000; pasture and mature forest data were sampled in July 2000. Error bars represent standard deviation for spatial term variation ($n = 5$).

weight) inside the measurement rings, grass leaves caused an average increase of 52% in soil CO_2 fluxes in pastures. This increase was estimated from the difference between the average CO_2 flux with leaves inside the chambers (550 mg C m^{-2} h^{-1}) and the *y*-intercept of the linear regression of the flux with the leaf dry biomass (365 mg C m^{-2} h^{-1}; 95% CI of *y*-intercept = 167; $n = 16$; $P < 0.001$, Fig. 5). To be conservative, we set the upper limit for soil CO_2 fluxes in pasture chambers to 365 mg C m^{-2} h^{-1} in the pasture annual estimates. Even with this correction, the soil respiration rates were still significantly higher in pastures than in forests (the Kruskal–Wallis test, $P < 0.01$). Only if the low end of the 95% confidence interval of the *y*-intercept of this function (204 mg C m^{-2} h^{-1}) is used as the estimate of soil respiration, would the pasture fluxes be the same as the forest sites. However, this lower estimate for soil respiration in the pastures is probably unrealistic because soils usually contribute >60% of total ecosystem respiration (Sanderman *et al.*, 2003). Therefore, we conclude that our estimate of higher respiration in the pastures compared with the forests is robust despite uncertainties in correction for respiration of grass leaves in the chambers.

Average annual soil respiration in pastures, corrected for leaf respiration, was 24 (± 0.7) Mg CO_2–C ha^{-1} a^{-1}. Average annual rates were 17 (± 0.3) and 16 (± 0.5) Mg CO_2–C ha^{-1} a^{-1} in mature and secondary forests, respectively. These values for forest soil respiration fall within the range of other published estimates of tropical forests (Davidson *et al.*, 2002a). Annual fluxes for each site are given in last column of Table 1.

Aboveground live biomass increases with age of secondary forests, from about 25 Mg C ha^{-1} in 6-year-old forests to about 65 Mg C ha^{-1} in 30-year-old forests in this region (Salimon & Brown, 2000). We observe a similar or even greater growth in biomass C with increasing age among the secondary forests in the present study, from 15 Mg C ha^{-1} in 3-year-old forest to 80 Mg C ha^{-1} in 18-year-old forests. In contrast, the annual CO_2 flux did not increase significantly with forest age, showing no covariation of age and soil respiration. The mean annual flux of 3-year-old secondary forests was 15 (± 0.4) Mg ha^{-1} a^{-1} ($n = 3$), while the 18-year-old secondary forest's mean annual flux was 16 (± 0.3) Mg ha^{-1} a^{-1} ($n = 2$). Similarly, annual litterfall in secondary forests varied only from 5.2 to 6.5 Mg C ha^{-1} a^{-1} (Table 1), with no correlation between annual litterfall and annual soil respiration or forest age. Therefore, increases in aboveground biomass during secondary forest succession are not accompanied by concomitantly large and obvious changes in soil respiration. The foliar canopy and rates of litterfall increase very rapidly in secondary forests during the first few years after agricultural abandonment, and then change only modestly throughout the remaining stages of secondary succession (Vieira *et al.*, 2003). With

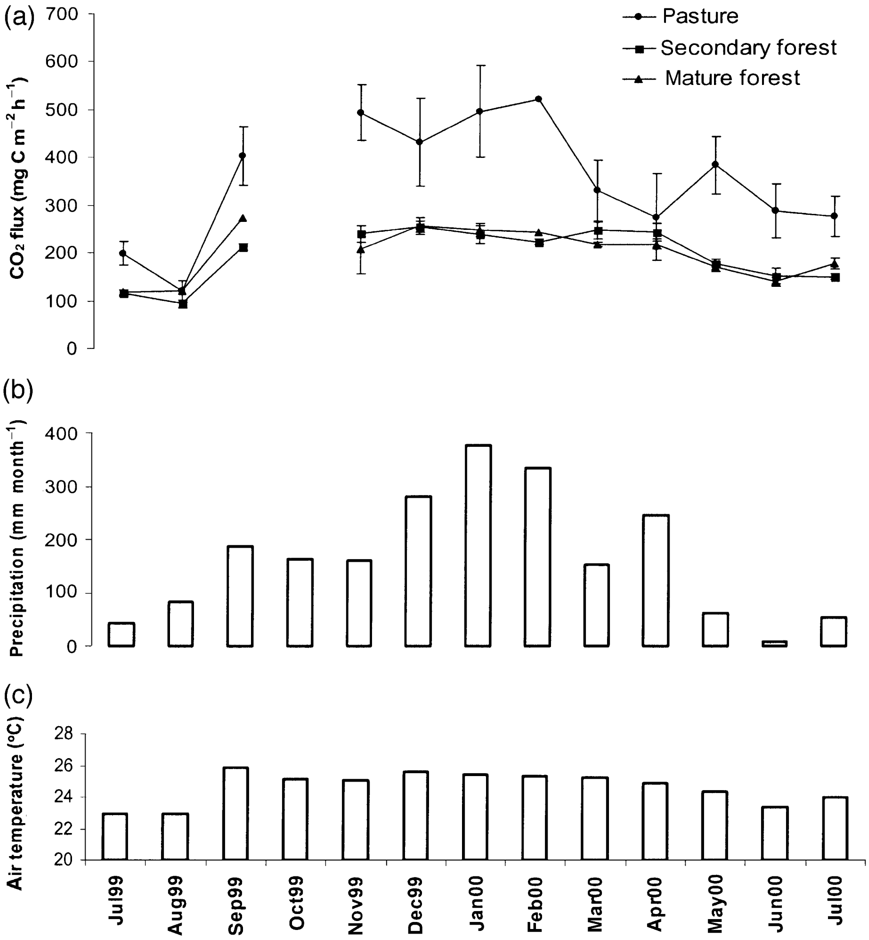

Fig. 2 (a) Seasonal variation of CO_2 flux from soil in Western Amazonia. Data from all sites of each land cover type are combined into a single mean for each sampling date. Error bars represent standard deviation for spatial variation – secondary forests ($n = 64$), mature forests ($n = 32$), pastures ($n = 32$). (b) Precipitation, extracted from Duarte *et al.* (2000). (c) Mean monthly air temperature (Duarte *et al.*, 2000).

similar rates of soil respiration and litterfall measured among the forest sites, allocation of C belowground cannot vary widely across the forests of this study, despite large differences in aboveground biomass.

The large flux of CO_2 from the soil of established pastures to the atmosphere is presumably related to commensurately high rates of gross primary productivity (GPP) and probably does not represent a net flux to the atmosphere. A significant fraction of GPP is allocated belowground by grasses. Trumbore *et al.* (1995) showed that increased primary productivity in highly productive pastures can result in both modest C sequestration in the soil and high rates of soil respiration. We also observed higher soil C stocks at one pasture site and higher respiration rates at three pasture sites relative to their respective forests (Table 2). Pasture soil C stocks that are equal to or greater than nearby forest soil C indicated that these pastures appear not to be losing soil C. Therefore, the high rates of soil respiration in pastures must be related to relatively high rates of current inputs of C belowground in the pastures. If and when pasture productivity declines, soil respiration rates might also decline and the previous gain in soil C stocks might be reversed. It should also be noted that the increase in pasture soil C relative to forest soil C (on the order of 10–20 Mg C ha^{-1}) is small relative to the loss of C from aboveground forest biomass (100–300 Mg C ha^{-1}, Houghton *et al.*, 2001).

δ^{13}C of respired CO_2 in pasture

Total CO_2 respired from pasture soils had a δ^{13}C value of −14‰, which is close to −13‰ for *B. brizantha* leaves and higher than −21 to −19‰ of pasture soil C. The CO_2 from the forest soil had a δ^{13}C value of −27.6‰, which is similar to −28‰ for forest leaves and −28‰ for forest soil C (Table 3). This result indicates that most

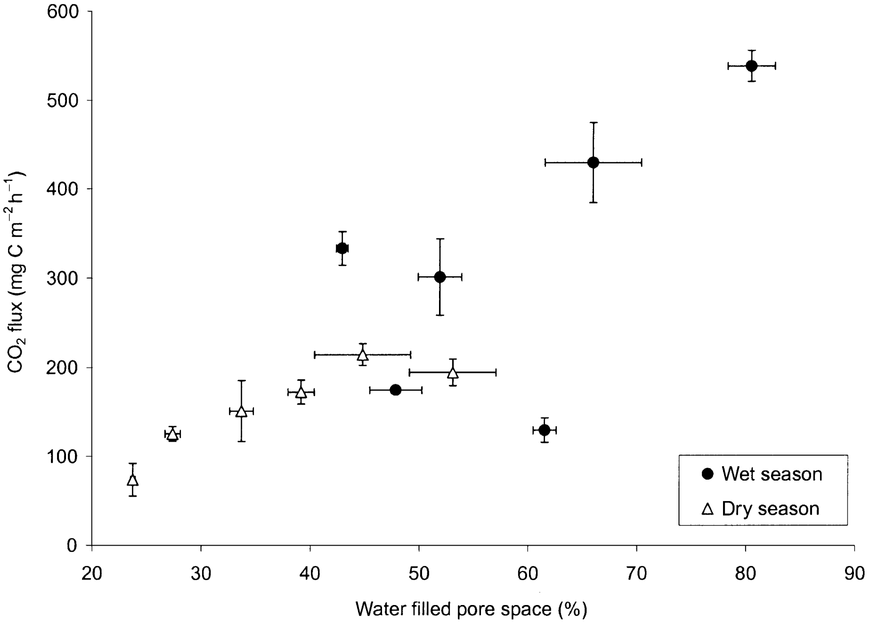

Fig. 3 CO_2 flux from soil as a function of water filled pore space. Dry and wet season data were sampled from all sites at Peixoto 1 and Humaitá 1 in June 2001 and February 2002, respectively.

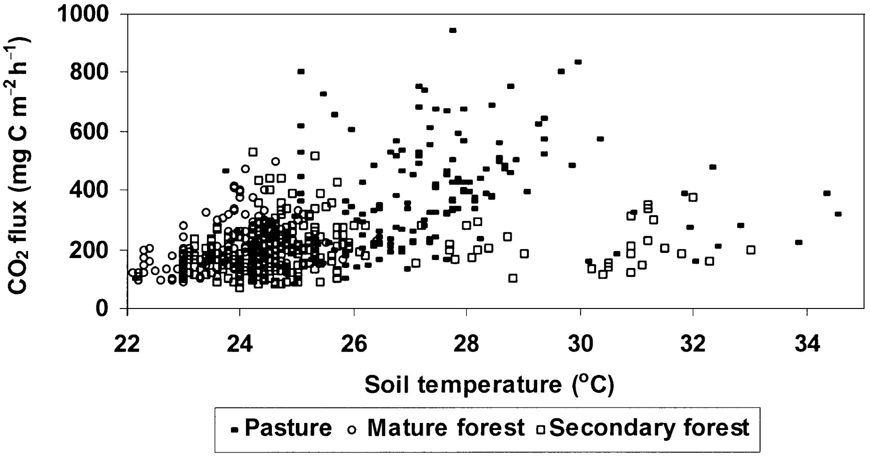

Fig. 4 CO_2 flux from soil as a function of soil temperature (10 cm depth). Data extracted from all sites and all dates of sampling from July 1999 to July 2000.

of the respiration from the pasture soils is either from root respiration of the grasses or from microbial decomposition of C produced by the grasses, and that only a small fraction was contributed by microbial decomposition of old forest soil organic matter.

Incubations of soil samples from which we excluded roots and leaves (column 3 in Table 3) demonstrate that the δ^{13}C of the CO_2 respired by microbes in the pasture soil was 15.7‰; a result similar to the values measured by Feigl (1994) of −18 to −13‰ for the δ^{13}C respired in pastures between 3 and 80 years old in Rondônia. This value is also very close to −13‰ of grass leaves (especially when considering the 1.2‰ of uncertainty from analytical error and natural variability). These results suggest that microorganisms are feeding mainly on recent soil organic matter originated from grasses.

Although 50% of the carbon in the pasture soils was still of forest origin (calculated from the isotopic mixing model; last column in Table 2), this carbon must be in a passive state, since CO_2 from heterotrophs had a strong C_4 signal from grasses. Therefore, high respiration rates in pastures are almost entirely derived from root respiration and decomposition of grass residues and not from loss of remnant forest soil organic matter.

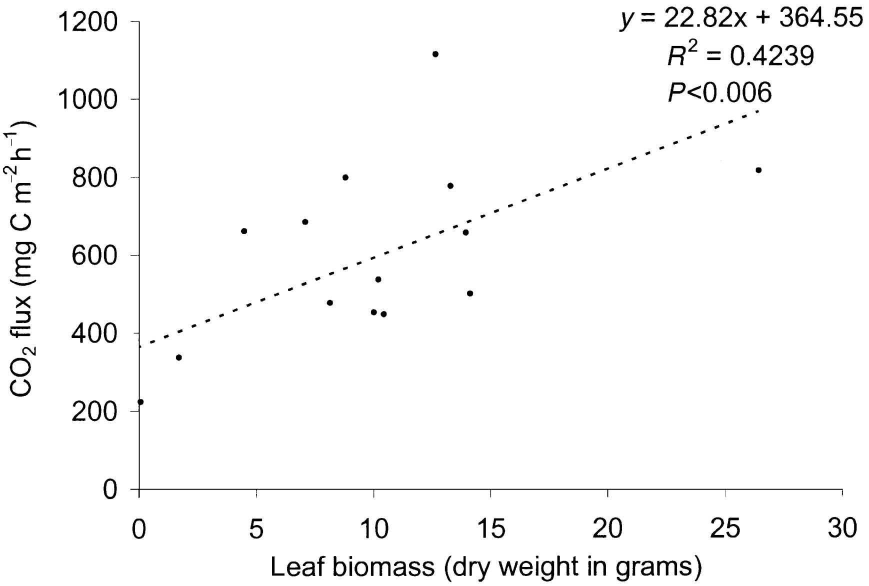

Fig. 5 Regression between CO_2 flux from soil and leaf biomass inside the measurement chambers in November 2002 in a pasture site (Pasture 13, Peixoto 1).

Table 3 $\delta^{13}C$ of respired CO_2 *in situ*, of leaves, and of soil carbon (units in $\delta^{13}C$‰). Also shown is the $\delta^{13}C$ of respired $CO_2$from laboratory incubations of root-free soil of Pasture 13 in jars ("heterotropic" respiration only). Soil $\delta^{13}C$ values are extracted from Table 2. Numbers in parenthesis are standard errors

	Pasture 13_{total}	Pasture 13 (heterotrophic)	Pasture 14_{total}	$Matfor_{total}$
$\delta^{13}C$ of CO_2 ($n = 8$)	−14.0 (0.17)	−15.7 (0.19)	−14.1 (0.06)	−27.6 (0.33)
Vegetation $\delta^{13}C$ ($n = 5$)	−13.6 (0.20)	−13.6 (0.20)	−13.6 (0.20)	−28.4 (0.90)
Soil $\delta^{13}C$ (0–5 cm; $n = 12$)	−21.4 (0.25)	−21.4 (0.25)	−19.4 (0,30)	−28.2 (0.07)
Soil $\delta^{13}C$ (5–10 cm; $n = 6$))	−24.2 (0.17)	−24.2 (0.17)	−22.2 (0.27)	−26.7 (0.44)

Conclusions

Seasonality influences CO_2 fluxes from soil to atmosphere in southwestern Amazonia, with the lowest fluxes being observed in the dry period. Soil respiration rates were poorly correlated with temperature and were positively correlated with soil WFPS. Pastures had greater soil CO_2 fluxes than secondary and mature forests.

We conclude that these pasture lands should not be considered degraded from the point of view of primary productivity. This apparently high pasture productivity is probably also responsible for the modest significant increases in soil carbon stocks in surface layers.

The $\delta^{13}C$ of respired CO_2 shows that most of the carbon respired in pastures comes from the productivity of grasses, including microbial respiration, which is feeding almost entirely from recently incorporated organic matter from these grasses. Also, these results show that the carbon still left from the forest after 12 years of conversion to pasture is in a relatively passive state and mostly not accessible to microorganisms.

Secondary forests had respiration rates similar to mature forests. Forest age and forest biomass did not correlate with rates of soil respiration. Hence, belowground allocation of C does not appear to be directly related to the stature of vegetation in this region. Variation in seasonal and annual rates of soil respiration of these forests and pastures is more indicative of flux of C through the soil rather than major net changes in ecosystem C stocks.

Acknowledgments

We thank Jorcinei Pereira for field work, land owners at Peixoto and Humaitá for letting us work on their lands; the people at Parque Zoobotânico, Federal University of Acre, namely I. Foster Brown; Susan Trumbore for her advise and help; and Jean Ometto for providing the flasks, discussions and advise on the *Keeling Plots*. This work was supported by grants from FAPESP (process 99/03315-3) and NASA LBA-ECO Grant No. NCC5-332 and No. NCC5-686.

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