



Decomposition of standard plant material along an altitudinal transect (65–3968 m) in the tropical Andes

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Abstract

The dynamics of plant decomposition in the soil were analysed in an altitudinal transect from 65 to 3968 m under tropical conditions. Six sites were studied, with a mean annual temperature ranging from 5.5 to 27.4°C, and an annual precipitation from 790 to 1992 mm. A ¹⁴C-labelled standard plant material was incubated in situ, at 5 cm depth, over a period of 1.5–3 years, depending on the altitude. The aim was to determine the contribution of climate (temperature and moisture) and of other factors, such as soil properties, to explaining the differences in mineralisation between the sites. Data analysis was performed using two-compartment models with first-order kinetics. To evaluate the effect of climate on decomposition, a response function to temperature (τ) and a response function to moisture (μ) were calculated. The kinetics of the remaining ¹⁴C were adjusted to the two-compartment first-order model considering successively time, τ_{cum} (cumulated τ), and $\tau\mu_{\text{cum}}$ (cumulated $\tau\mu$) as independent variables. The assumption was that if the introduction of a climatic component into the explanatory variable reduces the distances between the decomposition curves of the sites, the differences are related to this factor. If the distance is not reduced, other factors in addition to climate must influence decomposition and/or the climatic response to altitude is not linear. The results show a clear decrease in decomposition with increasing altitude. Nevertheless, the altitudinal effect is not equal for the two fractions estimated using the two-compartment model. The size of the labile fraction decreased with altitude, whereas the recalcitrant fraction increased. The labile fraction decomposed very quickly, independently of the altitude, whereas the rate of decomposition of the recalcitrant fraction decreased with altitude. When τ_{cum} is used as the independent variable, the distance between the curves diminishes, indicating the great effect of temperature on decomposition, but in the high mountain sites, additional factors act. Using $\tau\mu_{\text{cum}}$ the difference between sites was not reduced, showing that the moisture effect is low or that the moisture response function is not appropriate. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

As a consequence of increases in the atmospheric concentrations of gases from burning fossil fuels, the global mean temperatures are expected to rise between 1.5 and 4.5°C during the 21st century (Houghton et al., 1990). The soil organic matter (SOM) represents the largest C reservoir of the terrestrial ecosystems and global warming is expected to modify this soil carbon storage potential (Melillo et al., 1990). Many studies have shown that soil C mineralisation increases exponentially with increasing temperature (e.g. Schleser, 1982) and a positive feedback is expected between the liberation of soil carbon

and the temperature rise. The potential net transfer of CO₂ to the atmosphere depends on the imbalance between the rates of decomposition and net primary production. Previous studies have shown that in tropical ecosystems decomposition is considerably more sensitive to temperature than net primary production (Brown et al., 1994), probably because production is more strongly limited by nutrient availability. As a consequence, the imbalance between decomposition and production in a scenario of temperature rise should be greater in these regions. Therefore, tropical soils are likely to release relatively large amounts of carbon into the atmosphere despite the less pronounced warming expected in equatorial regions (Townsend et al., 1992).

The dynamics of organic matter in tropical soils, particularly the response to temperature, are insufficiently understood, and it is still not clear if there are differences

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with respect to temperate areas. As a consequence, it is difficult to predict the effects of climatic change in these areas and their possible contribution as sources of CO₂. Additionally, in tropical areas, soil fertility and sustainability are particularly related to the organic matter content (Woomer et al., 1994). Therefore, a better knowledge of decomposition behaviour under a tropical climate is essential in the context of both the evaluation of agricultural sustainability and the prediction of global change.

The effects of soil temperature and moisture on SOM decomposition and soil respiration have been widely studied in controlled conditions (e.g. Bunnell et al., 1977; Ross and Cairns, 1978; Seto and Yanagiya, 1983; Honeycutt et al., 1988; Joergensen et al., 1990; Holland et al., 1995; Winkler et al., 1996). Field approaches without climate manipulations such as the incubation of plant residues in climatic transects are closer to the real world, but more difficult to interpret due to the effect of several sources of variation. The use of a standard plant material can reduce the variability and select climate and soil properties as the main controlling factors (Berg et al., 1993; Bottner et al., 2000; Coûteaux et al., 2001).

Most multi-compartment SOM models have defined functions to describe the effects of temperature and moisture on C transfers (Parton et al., 1987; Jenkinson, 1990; Rodrigo et al., 1997). For temperature, the van't Hoff response function is widely used (Jansson and Berg, 1985; Andr n and Paustian, 1987; Townsend et al., 1992; Lloyd and Taylor, 1994; Coûteaux et al., 2001). Moisture response functions are based on soil moisture content or water potential (Jansson and Berg, 1985; Andr n et al., 1992) or derived from potential evapotranspiration and precipitation (Parton et al., 1987; Coûteaux et al., 2001). These functions produce reduction factors ranging from 0 to 1. The combined temperature and moisture response function is generally the product of both functions and constitutes a reduction factor for all transfer rates in modelling applications.

The aim of this study is to enlarge the knowledge of mechanistic processes regulating decomposition in tropical soils, specially of those concerning the response to temperature and moisture. We attempt to explain the variation in C mineralisation of a ¹⁴C-labelled standard plant material over a period of 1.5–3 years in an altitudinal transect (65–3968 m) of tropical conditions including sites with a mean annual temperature ranging from 5.5 to 27.4°C, and an annual precipitation from 790 to 1992 mm. We try to determine whether differences in ¹⁴C mineralisation between sites are completely explained by the climate or also by other factors and if the climate acts similarly on the different SOM compartments. The data analysis was performed using a two-compartment model with first-order kinetics in order to understand the SOM stabilisation process.

2. Material and methods

2.1. Site description

In the tropical Andes of Venezuela, six sites along an altitudinal climatic transect from 65 to 3968 m were selected. The sites cover a large bioclimatic vegetation gradient including: (1) tropical rain forest; (2) seasonal savannah; (3) seasonal montane forest; (4) cloud montane forest; and (5) paramo (Table 1). The sites were selected either in natural herbaceous formations or managed grasslands to minimise the variability of introducing different kinds of vegetation. Tables 1 and 2 present the site and soil characteristics.

The lowest site is El Vigia, A(65), situated west of the Andes and characterised by a tropical rainforest climate, without a pronounced dry season. The original vegetation is a tropical rain forest but the area has been recently deforested and is now intensively used for cattle raising and agriculture. The study plot was situated in a managed grassland dominated by the African grass *Brachyaria humidicola*.

The other low altitude site is Barinas, A(165), located on the opposite flank, East of the Andes. This site is characterised by a typical tropical wet and dry climate with a pronounced dry season of 4–5 months, during which soil water in the surface layers is below the permanent wilting point. The vegetation is a seasonal savannah, dominated by perennial tussocks and isolated trees, with *Axonopus purpusii*, *Leptocoryphium lanatum* and *Trachypogon vestitus* as the dominant grass species. The experimental plot was situated in a natural savannah.

The other four sites are located in interandean valleys. Tovar, A(780), is characterised by a seasonal mountain climate with four dry months. The natural vegetation is a seasonal montane forest, dominated by deciduous trees, which has almost completely been transformed into coffee plantations and managed grasslands. The study plot was situated in a secondary grassland vegetation.

The site in Merida, A(1800), is situated in the lower limit of the cloud forest. The climate is characterised by a high precipitation, without a pronounced dry period, high cloudiness together with fogs, mist, low insolation and high relative humidity. The study plot had a grassland vegetation dominated by the African grass *Melinis minutiflora*.

Gavidia, A(3400), with a seasonal high-altitude tropical climate, is located in a glacial valley near the upper limit of agriculture. The climate is characterised by large daily temperature fluctuations and frequent night frosts concentrated in the dry season between November and March. The typical vegetation is the paramo, dominated by the giant rosettes of *Espeletia schultzii*, several species of shrubs (*Hypericum laricoides*, *Baccharis prunifolia*, *Acaena elongata*, *Stevia lucida*) and grasses as *Calamagrostis pittieri*, *Bromus carinatum*, *Nassella mucronata* and *Trisetum irazuense*. The study plot was situated in an old fallow field.

Table 1
Characteristics of the studied sites

Site	Code	Latitude	Longitude	Altitude (m)	Natural vegetation type	Actual vegetation type	Temperature ^a (°C)	Precipitation ^a (mm)	AET ^a (mm)	Water deficit ^a (mm)	Surplus ^a (mm)
El Vigia	A(65)	8°37'33"N	71°40'6"W	65	Tropical rain forest	Managed grassland	27.4	1825	1711	31	115
Barinas	A(165)	8°36'55"N	70°12'15"W	165	Seasonal savannah	Natural savannah	26.8	1565	1297	457	268
Tovar	A(780)	8°20'43"N	71°43'13"W	780	Seasonal montane forest	Managed grassland	23.2	1112	1054	95	58
Merida	A(1800)	8°37'37"N	71°9'17"W	1800	Cloud montane forest	Managed grassland	17.4	1992	785	0	1206
Gavidia	A(3400)	8°40'47"N	70°55'47"W	3400	Paramo	20 year fallow	8.4	1338	557	23	965
El Banco	A(3968)	8°49'00"N	70°54'50"W	3968	Paramo	Natural paramo	5.5	790	515	16	275

^a Long-term annual mean.

Table 2
Characteristics of the studied soils before the addition of the straw

Site	Soil type	pH _{H₂O}	C (%)	N (%)	C:N	CEC $\mu\text{mol}_c \text{g}^{-1}$	Sand (% DW)	Silt (% DW)	Clay (% DW)	WHC (% DW)	Wilting point (% DW)
A(65)	Inceptisol	5.1	2.87	0.288	10.0	13.9	67.3	24.0	8.7	31.15	17.15
A(165)	Alfisol <i>Oxic tropustalf</i>	5.7	1.87	0.093	20.0	5.2	77.0	14.0	9.0	10.80	7.52
A(780)	Mollisol <i>Hapludoll</i>	6.1	4.32	0.390	11.1	13.1	62.0	31.3	6.7	28.13	19.22
A(1800)	Inceptisol <i>Typic humitropepts</i>	5.2	11.29	0.698	16.2	26.5	69.3	25.3	5.3	42.75	36.01
A(3400)	Inceptisol <i>Ustic humitropepts</i>	4.6	9.63	0.540	17.8	24.8	40.0	42.0	18.0	40.74	20.77
A(3968)	Entisol	4.7	4.66	0.288	16.2	12.1	62.0	30.0	8.0	25.81	11.01

Table 3
Experimental design and response functions

Sites	Oven dried weight (g bag ⁻¹)	Added labelled plant material (g)	Duration (months)	Mean τ	Mean μ	Mean $\tau\mu$
A(65)	188.24	1.08	18	1	0.98	0.98
A(165)	224.35	1.08	18	1	0.65	0.65
A(780)	150.47	0.84	24	0.86	0.94	0.81
A(1800)	112.27	0.84	31	0.55	1.00	0.55
A(3400)	160.49	0.48	38	0.28	0.99	0.28
A(3968)	182.21	0.48	38	0.21	0.99	0.21

The highest site is El Banco, A(3968), with a high altitude tropical climate characterised by frequent night frosts throughout the year. With an annual precipitation of 790 mm, it is the driest of the study sites. The seasonal rain pattern leaves four dry months. The mean annual temperature is 5.5°C, with more pronounced daily fluctuation than in A(3400). Giant rosettes of *Espeletia schultzii* and shrubs of *Hypericum laricoides* dominate the vegetation.

Together, these sites form a transect with contrasting conditions. The carbon content at 0–10 cm depth varies from 1.87% in A(165) to 11.29% in A(1800) and the C:N ratio from 10 in A(65) to 20 in A(165) (Table 2). The long-term mean annual air temperature ranges from 5.5°C in A(3968) to 27.4°C in A(65). The mean annual precipitation ranges from 790 in A(3968) to 1992 mm in A(1800). The annual actual evapotranspiration (AET), water deficit (DEF) and surplus (SUR) were calculated using the WATERBUD model designed by Sharpe and Prowse (1983).

2.2. Experimental design

The decomposition of a standard plant material was measured using soil bags with an envelope shape (14 × 15 cm) containing soil from the top 5–10 cm layer of the different sites. The soil weight per bag was calculated to reproduce the natural bulk density with a volume of 210 cm³ (Table 3). The mesh of the top part of the bag was 1 mm to allow mesofauna to access the bags and the bottom part was a mesh of about 0.1 mm to minimise soil losses during manipulation. The soils were labelled by adding a standard plant material, which had a high ¹⁴C activity. The labelled plant material was wheat straw grown in a labelling chamber controlled for temperature, radiation, moisture, and CO₂ concentration. The wheat was grown from seed to maturity for four months under a ¹⁴C labelled atmosphere and on a low NPK + micro-nutrients solution. The C content of the straw was 39.44% and its specific activity was 0.875 kBq mg C⁻¹. The straw was roughly ground and the largest particles did not exceed 5 mm. In order to avoid modifying the physical and chemical characteristics of the soil organic matter, the added plant material carbon (Table 3) ranged from 1.4 to 9.0% of the initial native C in the soil, except for A(165) where it was

11.6% because of the very low initial native C content. The decomposition of this standard plant material reflected the activity of the total decomposer community, giving a comparative figure of the biological activity throughout the climatic transect.

From 23 November to 6 December 1994, a total of 240 labelled soil-bags were buried at 5 cm depth (10 sampling occasions × 4 replicates × 6 sites). At installation, the soil-bags were moistened with 200 ml of deionised water. The soil-bag exposure time ranged from 18 to 38 months depending on the altitude (Table 3). The first sampling took place 1 month after the installation and the interval increased with time to reach 6 months at the end of the experiment for the highest sites.

2.3. Chemical analyses

The ¹⁴C and total carbon concentrations in the original straw and in the labelled soil samples were determined on four replicates using dry combustion (Carmograph 12A carbon analyser, Wosthoff, Bochum, Germany) and liquid scintillation counting (Bottner and Warembourg, 1976). The calculated number of disintegrations per minute (DPM) of a soil sample was divided by the corresponding value of the labelled straw at the beginning of incubation to obtain the fraction of labelled material still remaining in the soil. Total soil N was determined using micro Kjeldahl. pH was determined on a 1:1 (V/V) soil/water mixture using a pH meter calibrated to buffers pH 4 and 7. CEC was measured after extraction with 1 M NH₄OAc, pH 7.

2.4. Decomposition response function to climate

The temperature decomposition response function (τ) was calculated as a function of the mean air temperature (T_d). Below the optimal temperature (T_{opt}), a van't Hoff function (τ , Eq. (1)) ranging from 0 to 1 was used

$$\tau = Q_{10}^{(T_d - T_{opt})/10}, \quad (1)$$

when $T_d < T_{opt}$, where Q_{10} is the increase in the rate when temperature increases by 10°C. T_{opt} was fixed at 25°C (Lomander et al., 1998) and Q_{10} at 2.2 (Coûteaux et al., 2001). The assumption of a constant value of Q_{10} could be questionable because it has been shown that Q_{10} decreases with temperature (Schleser, 1982; Kirschbaum, 1995;

Dalias et al., 2001a,b). Nevertheless, Coûteaux et al. (in press) comparing the validity of the response function to temperature using a fixed Q_{10} and a mobile Q_{10} , related to daily temperature and based on published data, did not find any improvement in the explanatory value of the response function and suggested that the simplest procedure should be used for calculation. Kätterer et al. (1998) also showed that a Q_{10} of 2 is adequate for describing the temperature dependence of decomposition in the temperature range of the present study. Above T_{opt} , the decomposition function was assumed constant $\tau = 1$, when $T_d > T_{opt}$.

A moisture response function (μ), ranging from 0 to 1, was calculated as a function of the water deficit (DEF), i.e. the difference between the potential evapotranspiration (PET), according to the procedures of Thornthwaite and Mather (1957) and the actual evapotranspiration (AET).

$$DEF = PET - AET, \quad (2)$$

and

$$\mu = \frac{DEF_{lim} - DEF}{DEF_{lim}}, \quad (3)$$

with $\mu = 0$ when $DEF > DEF_{lim}$, where DEF_{lim} is the water deficit threshold over which the response function is zero. DEF , the actual water deficit, was generated by the WATERBUD model (Sharpe and Prowse, 1983). The responses functions were calculated on a monthly basis and then converted on a daily basis to be adjusted to the sampling intervals.

2.5. Two-compartment models

A two-compartment, first-order model was adjusted to the kinetics of the remaining ^{14}C (Eq. (4)) by an iterative regression procedure:

$$RC = Ae^{-k_a t} + Be^{-k_b t}, \quad (4)$$

where RC is the remaining ^{14}C expressed as percent of the initial ^{14}C . A and B are the initial ^{14}C proportions (in percent) of the fast and the slow decomposing compartments, respectively, ($A + B = 100$); k_a and k_b are the decay rate constants for the A and B fractions, respectively, and t is time in days.

Two other two-compartment, first-order models were fitted to the remaining ^{14}C data in order to weight the kinetic model by the climate response function (Eq. (5)). One of these models considers the time cumulated value τ_{cum} of τ (Eq. (1)) as the independent variable

$$RC = A'e^{-k'_a \tau_{cum}} + B'e^{-k'_b \tau_{cum}}, \quad (5)$$

where k'_a and k'_b are the decomposition rates per τ unit of the A' and B' fractions respectively ($A' + B' = 100$). The other model (Eq. (7)) considers the time cumulated product

$\tau\mu_{cum}$ (Eq. (6)) of τ and μ (Eqs. (1) and (3)) as the independent variable

$$\tau\mu_{cum} = \sum \tau\mu. \quad (6)$$

Then

$$RC = A''e^{-k''_a \tau\mu_{cum}} + B''e^{-k''_b \tau\mu_{cum}}, \quad (7)$$

where k''_a and k''_b are the decomposition rates per ($\tau\mu$) unit of the A'' and B'' fractions, respectively, ($A'' + B'' = 100$).

Differences between fitted parameters were considered significantly different when their confidence interval did not overlap ($P < 0.05$). By using successively time, τ_{sum} , and $\tau\mu_{sum}$ as the independent variable, we hypothesise that, if the introduction of a climatic component into the explanatory variable reduces the distances between the decomposition curves of the soils in the transect, the difference between these decomposition kinetics is related to climate. To test the modification of this distance with the independent variables, a common non-linear regression curve was fitted to the combined data from all sites for each of the three independent variables. Then, we used a Newman–Keuls test to compare the residuals of each set of soil data with respect to this common curve. If the climatic parameters have an explanatory value, the residual differences should become non-significant. At least, the mean difference between the residuals should decrease with the introduction of temperature and moisture compared to that with time as the independent variable.

3. Results

3.1. Remaining ^{14}C versus time

The decomposition rates decreased with increasing altitude (Fig. 1A, Table 4). Three groups appeared: (1) A(65) and A(165), where 50% of the straw was decomposed within 1–2 months and after the first year about 75% of ^{14}C was lost; (2) A(780) and A(1800), where 50% decomposition was reached within 3–4 months and after the first year about 65% of ^{14}C was lost; and (3) A(3400) and A(3968), where 50% decomposition was reached within almost 2 years and after the first year about 40% of ^{14}C was lost. The differences between the residuals of the data for each soil compared to the common fitted curve are significantly different between these three groups (Newman–Keuls test, $P < 0.05$, Table 5).

The two-compartment, first-order model (Eq. (4)) fitted to all sites except A(165) for which we did not obtain convergence (Table 4). The size of the A fraction ranged from 31 to 37% at A(3968), A(3400) and A(780) and from 44 to 51% at A(65) and A(1800), with a tendency to be lower in high altitudes. Except for the A fraction of A(3400) which was significantly different from that of A(65) and A(1800), the

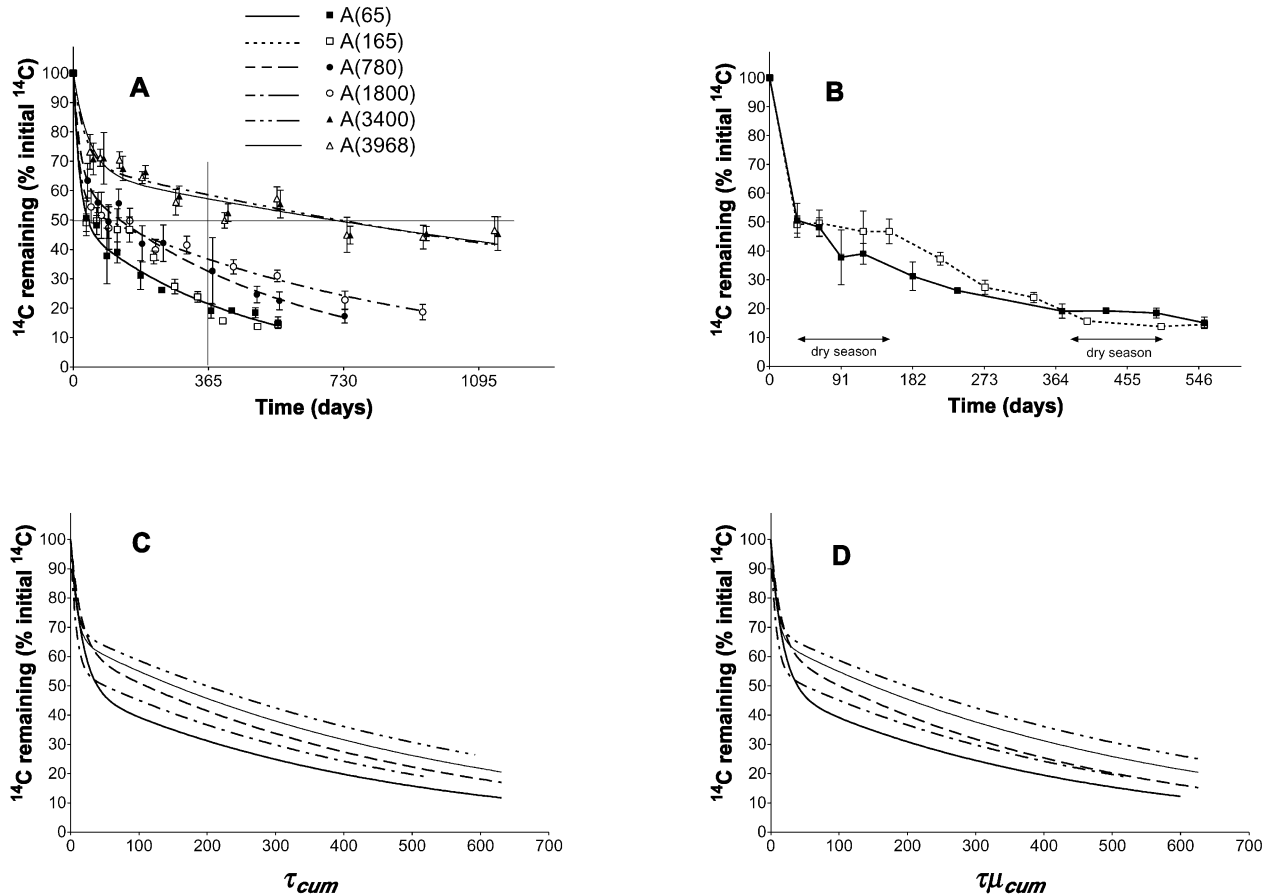


Fig. 1. Remaining ^{14}C (% of the initial ^{14}C) versus (A) time for all the sites, (B) time for A(65) and A(165) (C) τ_{cum} for all the sites and (D) $\tau\mu_{cum}$ for all the sites.

other A fractions were similar. The k_a values ranged from 0.02 to 0.07% day $^{-1}$ with the lowest values also in high mountains. Nevertheless, because of the large range of variation of the fitting error, they were not significantly different. The k_b values ranged from 0.0004 to 0.0023% day $^{-1}$ with a clear decreasing trend with increasing altitude. The range of variation of k_a and k_b from the smallest to the highest value was 2.75 and 5 times, respectively.

A(165) did not converge because of the strong inhibiting effect of the dry season during the first year as compared to A(65), but by the end of the incubation, the remaining ^{14}C reached the same level (about 15% of the initial ^{14}C) in both sites (Fig. 1B).

3.2. Remaining ^{14}C versus temperature response function

When the data were fitted by the second model (Eq. (5), where τ_{cum} was the independent variable), in order to obtain lower fitting errors, the A' fraction size was fixed at the value obtained when time was taken as the independent variable. Again, we did not obtain convergence for A(165). A reduction of the distances between the curves can be observed (Fig. 1C, Table 4). The Newman–Keuls test still shows significant differences between the residuals

of the data for each soil compared to the common fitted curve (Table 5). It also shows a clustering into three groups but the range of variation of their value was reduced from 32 to 15%. In A(65) and A(165), the temperature effect was optimum ($\tau = 1$, Table 3). In A(1800), τ described the effect of temperature satisfactorily as its curve did not differ significantly from the curve of A(65), their residuals were not significantly different (Table 5). In the other sites, the significant differences between the residuals indicates that the response function τ was higher than expected if temperature would explain kinetic differences. Other factors must be taken into account in addition to the temperature effect.

The number of heat units (τ_{sum}) needed to reach 50% of decomposition ranged from 40 to 223 (Table 4). The higher the size of the A fraction, the less heat is needed.

The k'_a value ranged from 0.059 to 0.130 (Table 4). Two groups were significantly different: (1) A(65) with the lowest values; and (2) A(1800), A(3400) and A(3968) with the highest values. A(780) had an intermediate position. The k'_b value ranged from 0.0016 to 0.0023. The differences were not significant except for A(3400), meaning that for most sites the decomposition of the recalcitrant fraction was controlled by temperature.

Table 4
Parameter values and coefficients of determination (R^2) for the two compartment first order model with time, τ_{cum} and $\tau\mu_{cum}$ as independent variables, first year ^{14}C -loss, τ_{cum} and $\tau\mu_{cum}$ at 50% ^{14}C -loss. Different letter indicates significant differences (Student t -test, $P < 0.05$)

A	Time		τ_{cum}		$\tau\mu_{cum}$		First year ^{14}C -loss ^a	τ_{cum} at 50% ^{14}C -loss	$\tau\mu_{cum}$ at 50% ^{14}C -loss	R^2
	k_a	k_b	k'_a	k'_b	k''_a	k''_b				
A(65)	0.059a	0.0023c	0.059a	0.0023b	0.058a	0.0023b	78.7	40	40	0.97
A(165)	Did not converge	Did not converge	Did not converge	Did not converge	Did not converge	Did not converge	76.6 ^a	42 ^a	63 ^a	
A(780)	0.054a	0.0018c	0.067ab	0.0021b	0.070ab	0.0023b	67.5	108	109	0.95
A(1800)	0.066a	0.0011b	0.130b	0.0021b	0.130b	0.0021b	62.9	49	50	0.96
A(3400)	0.032a	0.0004a	0.130b	0.0016a	0.130b	0.0016a	40.4	223	202	0.91
A(3968)	0.024a	0.0004a	0.124b	0.0019ab	0.123b	0.0019ab	42.8	150	152	0.90

^a Approximated.

Table 5

Mean differences between the residuals compared to the common fitted curves. SE = standard error, Different letters indicates significant difference (Newman–Keuls test, $P < 0.05$)

	Time	SE	τ_{cum}	SE	$\tau\mu_{cum}$	SE
A(65)	-15.01	1.52a	-6.96	1.15a	-5.37	1.11b
A(165)	-12.15	3.15a	-4.64	1.19a	-13.48	0.79a
A(780)	-4.12	2.57b	2.30	0.82b	2.76	0.85d
A(1800)	-3.89	2.00b	-3.68	1.10a	-1.60	1.03c
A(3400)	16.83	1.64c	8.43	1.39c	10.71	1.17f
A(3968)	16.10	1.78c	4.07	1.56b	6.70	1.39e

3.3. Remaining ^{14}C versus the combined temperature and moisture response function

The mean annual moisture response function was higher than 0.9 in all sites except in A(165), which was strongly affected by the dry season (mean annual $\mu = 0.65$). Thus, except in A(165), the temperature effect was dominant (Table 3).

The third model (Eq. (7), where $\tau\mu_{cum}$ is the independent variable), was fitted to the data. The A'' fraction size was also fixed at the value obtained when time was taken as independent variable. No convergence was obtained for A(165). The distances between the curves were similar to the previous fit (Fig. 1D). The Newman–Keuls test showed significant differences between the residuals of the data for each soil compared to the common fitted curve (Table 5). In A(165), a significant mass loss of 10% occurred within 2 months (between the 336th day on 6 November 1995 and the 404th day on 13 January 1996) just before the dry season showing SOM instability even during this late stage of decomposition.

The k''_a and k''_b values were close to those obtained in the previous fit and slightly higher for A(780) which had a lower mean annual μ .

3.4. Correlations with environmental factors

Correlations were calculated between decomposition parameters (the remaining ^{14}C after one year of incubation, the A , k_a and k_b values) and environmental factors (Table 6).

Table 6

Correlations between decomposition parameters and climate or soil characteristics, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

	First year R_C	A	k_a	k_b
Altitude	0.982***	-0.800	-0.846	-0.982**
Temperature*	-0.981***	0.800	0.838	0.983**
AET	-0.878*	0.843*	0.639	0.954*
Mean τ	-0.974***	0.766	0.774	0.995***
Mean $\tau*\mu$	-0.919**	0.795	0.785	0.997***
τ for 50%	0.899*	-0.923**	-0.845	-0.760
$\tau*\mu$ for 50%	0.892*	-0.952**	-0.874	-0.769
C/N	0.880*	-0.673	-0.809	-0.933*
Ca	-0.675	0.571	0.788	0.961**
Mg	-0.721	0.547	0.734	0.940*

Despite the small number of degrees of freedom, significant correlations were found. The remaining ^{14}C after one year of incubation was significantly correlated with altitude, mean annual temperature, mean annual AET, mean annual τ and $\tau\mu$, the number of τ_{cum} and $\tau\mu_{\text{cum}}$ units needed to reach 50% of ^{14}C loss and the C/N ratio of the soil. The *A* fraction was significantly correlated with the mean annual AET and the number of τ_{cum} and $\tau\mu_{\text{cum}}$ units needed to reach 50% of ^{14}C loss. The decomposition rate k_a of the *A* fraction did not show any significant correlation whereas the decomposition rate k_b of the *B* fraction was significantly correlated with altitude, mean annual temperature, mean annual AET, mean annual τ and $\tau\mu$, C/N ratio of the soil and the Ca and Mg concentration.

4. Discussion

Compared to all climatic transect studies, the altitudinal and temperature ranges presented in this study are very wide because of the equatorial situation of the study area (Berg et al., 1993; Vitousek et al., 1994; Holland et al., 1995; Townsend et al., 1995, 1997).

The exponential models used here assume that the straw C is split into two compartments, each decomposing by a first-order process, but one much more quickly than the other. Two options can be taken regarding to the size of these compartments: (1) one can fix them at a given value considering that since the same standard ^{14}C labelled plant material was used in all soils, the initial proportions of the compartments *A* and *B* must be identical (Coûteaux et al., 2001); or (2) one can leave them free in the adjustment considering that the ability of these compartments to be decomposed is the result of the interaction between the straw quality and the microbial community composition. Dalias et al. (2001a) showed, consistently with the present results, that the labile compartment increased with incubation temperature whereas the recalcitrant compartment decreased. The present results also show that the size of the labile compartment (*A*) is positively correlated to AET and that in the sites where this compartment is large, less heat or $\tau\mu$ units are needed to reach 50% of decomposition because of the easy availability of this compartment.

The decomposition rates of both *A* and *B* fractions are controlled by the microbial composition. Cochran et al. (1988) showed two different microbial pools in presence of decomposing straw, one pool unable to utilise the non-soluble component of the straw, but growing rapidly using the readily-available C component and another pool able to use it and growing at a slower rate. The correlation analysis showed no significant relationship between k_a and any environmental factors which is consistent with the fact that there was no significant difference between the sites. So, the decomposition of the *A* fraction is dominated by the straw quality which is the same in all sites. In contrast to the *A* fraction, the decomposition rate of the *B* fraction, k_b , was

influenced by both climatic factors and soil properties. It increased with temperature and AET, showing the thermo-sensitivity of the microbial pool that uses the structural substrate. The stabilisation level of the SOM, i.e. the remaining ^{14}C level at which the decomposition became very slow, was higher in the cold montane sites than in the warm savannah as shown by the higher size of the *B* fraction and the lower k_b rate in the high sites.

These results contradict those of Coûteaux et al. (2001) using a similar approach in a European latitudinal climatic transect. They found that decomposition reached about the same level in all sites by the end of the experiment and that under warm conditions, the stabilisation of the organic matter (as indicated by a low k_b) occurred earlier than in a cold climate. Nevertheless, the level of decomposition reached by the end of the experiment needed less heat units in the cold than in the warm zone. The difference between both studies is probably linked to differences in climatic pattern and soil properties. In this study, the continuous warm conditions of the tropics would result in more rapid and complete decomposition of unprotected organic material (Duxbury et al., 1989), whereas the interaction between cationic nutrients or changes in mineralogy may have a specific influence in tropical soils (Oades et al., 1989). The pH of the soils is neutral at low altitudes and becomes acid in the mountain soils (A(3400) and A(3968)). Weathering in acid soils generally generates long-lasting amorphous aluminium and iron compounds. Several authors have demonstrated a depressing effect of these compounds, especially Al hydroxides on the mineralisation rate of soil organic matter (Carballas et al., 1979; Boudot et al., 1989; Boudot, 1992). The protecting effect is explained by the formation of complexes between humified compounds and the Al hydroxides or by the trapping and wrapping of the organic molecules by active Al colloids. This makes the organic compounds inaccessible to soluble enzymes or prevents their migration to immobile enzymatic constituents within microbial cells. This may explain the slow decomposition of the *B* fraction at altitude. Nevertheless, more recently Miltner and Zech (1998) also demonstrated a stabilising effect of Al hydroxides on non-cellulosic and cellulosic polysaccharides that occurs on fresh litter. The mechanism results from the adsorption of Al on the polysaccharides protecting them from microbial degradation. Thus, amorphous Al compounds (and to a lesser extent Fe compounds), which are chemically active and last a long time in acid soils at low temperatures, are an essential factor for retarding organic matter decomposition in two ways: by chemical and/or physical binding and by the toxic effect on the microbiota. Sarmiento and Bottner (in press) also found high soil organic matter stability when they incubated soil from A(3400) under laboratory conditions (temperature constant at 26°C). This supports the idea that soil properties are responsible for the soil organic stability at altitude instead of direct climatic factors.

Seasonal patterns of decomposition were only obvious in A(165) where the dry season consisted of 4 months (January–April) of water deficit greater than 100 mm (from the 27th to 146th day in the first year and from the 392nd to 512th day in the second year). The experiment was set up at the beginning of December and during the first month, 50% of the straw was decomposed (Fig. 1B). Then, until the end of April, decomposition stopped, reflecting the strong effect of the first dry season. Thereafter, the decomposition proceeded again and amazingly, by the end of the first rainy season, a significant enhancement of the decomposition occurred before the final period of stabilisation, which went down 15% of the initial ^{14}C . The plateau of the decomposition curve explains why the exponential model did not fit the data. Weighting time with the climate response function should have given a better fit, but because of the unexpected enhanced ^{14}C loss during the late stage of decomposition (after 1 year), no convergence was obtained. This can be interpreted as the effect of alternate dry and wet events during December, which enhanced decomposition of unprotected SOM (Bottner, 1985; Van Gestel et al., 1993).

As is usually assumed in most modelling applications (e.g. Parton et al. 1987; Jenkinson, 1990; Lomander et al., 1998), the temperature and moisture responses were considered to be equal for all organic fractions. Nevertheless, as shown here by the double exponential models, climate or altitude controlled the decomposition rate of the more recalcitrant fraction. This would mean that the responses to the climate are not equal for all organic fractions and also that for a given organic fraction the climate effect can interact with other factors that counteract or emphasise it. For example, in tropical high mountains such as A(3400) and A(3968), the mean daily temperature of 8.4 and 5.5°C, respectively, do not reflect the high circadian range of variation (up to 30°C of daily variation) compared to lower altitude sites. This daily alternation between freezing nights and warm middays may enhance the negative effect of low temperature on decomposition.

Other studies in wet tropical environments have also found that temperature is the main factor in explaining decomposition and moisture has a secondary role. Brown et al. (1994) summarising the results of the Tropical Soil Biology and Fertility Program project (TSBF), an important project devoted to investigating tropical soil fertility in low altitude conditions, found that temperature explained a greater proportion of the decomposition index (annual litterfall divided by standing litter stock) than did precipitation (61 and 3%, respectively). When temperature and precipitation were combined into a multiple model, 63% of the variation in decomposition was explained. It has to be mentioned that the moisture response function used in this work and based on Thornthwaite and Mather's PET can be questionable because it does not take the effect of altitude on evaporation into account.

5. Conclusions

With this experiment where standard ^{14}C labelled plant material was decomposed in herbaceous sites along an altitudinal transect, we showed the following.

1. The differences between sites are mainly due to climate and especially temperature, as shown by the improved overlap of the two-compartment, first-order model fits when time is weighted by a climatic variable. Nevertheless, the differences between curves remained significant indicating that other factors linked to soil properties and/or climate patterns have to be taken into account.
2. The climate effect is not equal for all organic matter fractions. The A fraction decomposed very quickly independently of climate whereas the decomposition rate of the structural material decreased with altitude.
3. At low altitude under tropical conditions, the SOM appeared to be less protected than under high altitude where stable organo-aluminium complexes can be formed.
4. More research on soil organic matter stabilising processes in high altitude tropical mountains is necessary to improve our understanding concerning the differential impact of climate on different soil organic matter fractions.

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