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Carbon and nitrogen dynamics in two soils with different fallow times in the high tropical Andes: indications for fertility restoration

Lina Sarmiento [a,*], Pierre Bottner [b]

[a] *Facultad de Ciencias, Instituto de Ciencias Ambientales y Ecológicas, Universidad de los Andes, Mérida 5101, Venezuela*
[b] *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 05, France*

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Abstract

In the upper agricultural belt of the tropical Andes, above 3000 m of altitude, long fallow agriculture is commonly used to produce potatoes and cereals. This agricultural system alternates short intervals of production (2–4 years) with long fallow periods (generally 5–10 years or more). In order to analyse soil changes related to the rapid fertility loss during the production interval and soil fertility restoration during the fallow period, the soils of two adjacent but contrasting plots were compared. One plot had passed through 15 years of fallow (restored) and the other had been cultivated with potatoes for three consecutive years after a 12 years fallow period (depleted). The soils were analysed for fresh C- and N-microbial biomass, inorganic N and physical–chemical properties. Then, the soils were incubated under controlled laboratory conditions for 81 days, with and without the addition of ^{14}C labelled wheat straw. During the incubation, periodic measurement of C– and ^{14}C–CO_2 release, C- and ^{14}C-microbial biomass, N-microbial biomass and inorganic N were performed. The most pronounced difference between the fresh soils was in the microbial biomass, which was almost double the amount in the restored soil with respect to the depleted soil. During the incubation, the total amounts of soil native C and N mineralised were significantly higher in the restored soil. Also the mineralisation of the added ^{14}C-labelled straw was faster in the restored than in depleted soil. These results suggest that the fallow period leads to an increase in the labile C and N pools and microbial biomass, which represent more carbon and nitrogen availability for microorganisms and plants and could be related to fertility restoration. A very high stability of the organic matter in these mountain soils was also revealed and its implications for agricultural sustainability are discussed.

Keywords: Secondary succession; Fallow agriculture; Microbial biomass; C and N mineralisation; Microbial activity; Decomposition

1. Introduction

In the northern Andes (paramo ecosystem), above 3000 m, a long fallow agricultural system is commonly used for the cultivation of potatoes and cereals. This type of agriculture is characterised by short periods of cultivation (two–four consecutive years) during which the soil fertility declines rapidly, followed by long fallow periods, extending from 5 to more than 10 years, that allows fertility restoration. When the fields are cultivated, after the fallow period, the successional vegetation is ploughed into the soil as green manure. Despite the economical importance and widespread

* Corresponding author. Tel.: +58-274-2401255; fax: +58-274-2401286.
E-mail addresses: lsarmien@ciens.ula.ve (L. Sarmiento), bottner@cefe.cnrs-mop.fr (P. Bottner).

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use of fallow agriculture in the Andes, little attention has been paid to the processes involved in the fast decline of fertility during cultivation and its progressive restoration under the fallow periods. Also the role of the incorporated fallow vegetation on fertility recovery has been little investigated.

This agricultural system is similar to the slash and burn agriculture practised in lower altitudes in the tropics, with the difference that plant residues are not burned. The mechanisms of restoration during the fallow period have been investigated in tropical forests (Nye and Greenland, 1960; Aweto, 1981; Jordan, 1985, Lessa, 1998), in mountain ecosystems of India (Mishra and Ramakrishnan, 1983a,b; Ramakrishnan, 1992) and in African savannas and dry forests (Floret et al., 1993). Under low altitude conditions, the soil organic matter content is generally low and an increase in soil organic matter and available nutrients during the fallow period has frequently been reported. However, in the humid tropical mountains, where soils have higher organic matter contents, similar increases have not been observed. Studies carried out in the high Andean mountains of Colombia and Venezuela, have not shown an increase in the total soil carbon or nitrogen content, or an increased availability of soil nutrients, like mineral N, exchangeable cations and available phosphorus during the fallow period (Ferwerda, 1987; Sarmiento et al., 1990, 1993; Sarmiento and Monasterio, 1993; Aranguren and Monasterio, 1997; Llambí and Sarmiento, 1998). In these soils, the expected increase of total C and N during the fallow period is probably masked by the large size of the organic matter pool and by the spatial heterogeneity of mountain soils. Therefore, the labile fractions of nitrogen and carbon must be explored to understand the mechanisms of fertility loss and restoration, since these pools are expected to show a dynamic response at the time scale of the fallow and cultivation periods.

The main objective of this study is to detect soil changes that can be associated with fertility restoration. Total, microbial, mineral and potentially mineralisable carbon and nitrogen were analysed in two adjacent plots at contrasting stages of the fallow-cultivation cycle. Differences in decomposition of fresh plant residues were also studied, since the incorporation of the successional plant biomass into the soil and its subsequent decomposition appears to be an important component of fertility restoration.

2. Materials and methods

2.1. Study area and plot selection

The study area was in the Páramo de Gavidia, located at 3400 m of altitude in Mérida State, Venezuela (8°35′–8°45′N, 70°52′–70°57′W), with an average annual precipitation of 1329 mm and a mean annual temperature of 8.5 °C. In this area, a long fallow agricultural system is practised to cultivated potatoes and cereals. The fields are cropped with potatoes for an average of two consecutive years and then are abandoned for 5 to more than 10 years, until the farmer considers that fertility is restored.

According to US Soil Taxonomy (Soil Survey Staff, 1994), the soil is an *Ustic Humitropepts*, sandy–loamy, well drained, rather acid (pH between 4.3 and 5.5) with a high organic matter content (up to 20%) (Llambí and Sarmiento, 1998).

Two adjacent plots of approximately 2000 m^2, with similar conditions of slope, stoniness, soil texture and other physical and chemical soil characteristics, but at different stages in the fallow-cultivation cycle were selected. One plot had passed through a 15 years fallow period (restored soil) and the other had been cultivated with potatoes for three consecutive years after a previous 12 years fallow period (depleted soil). Before cultivation both plots formed one field with the same history.

One of the difficulties of using a synchronic approach to study the changes that take place during the fallow period is that the spatial coexistence of sites in different stages of development do not necessarily represent the real time course of the ongoing succession (Scheu, 1990). Spatial heterogeneity in the environment can introduce differences between plots due to other factors than fallow time. To minimise the effects of spatial variability, the plots investigated have to be chosen very carefully. To evaluate the suitability of the selected plots for a synchronic analysis, a previous soil analysis was carried out. In each plot, 10 soil samples of 1 kg were randomly taken in the ploughing layer (0–20 cm) and analysed for texture (Bouyocos method), pH (measured in 1/1 soil–water

Table 1
Physical, chemical and biological characteristics of the restored and depleted soils (mean ± S.D.)[a]

		Restored soil	Depleted soil
Texture (%)	Sand	48.0 ± 1.4 a	48.0 ± 1.4 a
	Silt	39.2 ± 2.3 a	38.4 ± 1.7 a
	Clay	12.8 ± 1.8 a	13.6 ± 2.6 a
Soil–water retention (%)	1/3 bar	46.0 ± 0.20 a	45.5 ± 0.30 a
	15 bar	24.1 ± 0.25 a	24.5 ± 0.51 a
pH		5.0 ± 0.2 a	4.7 ± 0.3 a
Total C ($g\,kg^{-1}$)		105.4 ± 0.7 a	103.1 ± 1.3 b
Total N ($g\,kg^{-1}$)		6.9 ± 0.4 a	6.6 ± 0.6 a
Microbial biomass ($mg\,kg^{-1}$)	C	604.3 ± 80 a	313.2 ± 34 b
	N	54.2 ± 7.4 a	26.37 ± 1.5 b
Mineral nitrogen ($mg\,kg^{-1}$)	NH_4	2.8 ± 0.4 a	1.7 ± 0.3 b
	NO_3	3.1 ± 0.6 a	4.4 ± 0.5 b
	Total	5.9 ± 0.3 a	6.1 ± 0.3 a

[a] Different alphabets indicate significant differences between soils ($n = 10$, $P < 0.05$, HSD).

mixture using a pH meter), soil–water retention at 1/3 and 15 bar (pressure plate extraction method, Klute, 1986), total C (dry combustion and Carmhograph 12A, manufactured by Wosthoff Bochum Germany), and total N (micro Kjeldalh, Bremmen and Mulvaney, 1982). The results of this preliminary survey showed that soil texture and water retention capacity were not significantly different between the soils (Table 1), and confirmed their similarity with respect to important soil parameters that are not expected to be affected by the fallow time. Other soil characteristics such as soil C and N content, are susceptible to be influenced by the fallow time, but a small modification is expected within the 3 years interval during which the management of the plots was different. In Table 1, we can see that total soil carbon was slightly but significantly ($P < 0.05$) higher in the restored than the depleted soil and total N content was not significantly different, confirming again the adequacy of the selection.

2.2. Fresh soil analysis

After plot selection, 10 individual soil samples were taken at random (0–20 cm) in each plot, sieved (<4 mm) and analysed for C- and N-microbial biomass and mineral nitrogen (NH_4 and NO_3). Then, the soils were air-dried, composed to obtain a unique sample by plot, and stored before incubation.

2.3. Incubation of soils unamended and amended with ^{14}C plant material

For each soil, 44 sub-samples (40 g air dry soil) were incubated aerobically in a dark room for 81 days at 26 °C. Each replicate was moistened to 80% of the water holding capacity using a fine spray and placed in a 100 ml beaker inside a hermetically sealed 1 l flask. The flasks were opened weekly to maintain aerobic conditions and adjust soil moisture. For each soil, half of the sub-samples (22) were amended with 0.4 g of uniformly ^{14}C-labelled mature wheat straw (46% C, 0.49% N, C/N 94, specific activity $2.59\,kBq\,mg^{-1}$ C) cut into 3–5 mm pieces. The added material amounted to 1% of the soil weight and 4.9% of the soil native C. The soils were pre-incubated for 24 h before the labelled material was added.

For the treatments amended (+S) or not (−S) with ^{14}C-labelled straw, the CO_2 release was measured on 10 replicate soils. The other 12 replicates were used for destructive measurements of C- and N-microbial biomass and mineral nitrogen.

2.4. Analysis

Evolved CO_2 was absorbed in 20 ml 0.25N NaOH, which was replaced at each sampling date. Total CO_2 was determined by titration (0.05N HCl) and $^{14}CO_2$ by liquid scintillation counting after 3, 6, 10, 14, 21, 27, 37, 46, 55, 69 and 81 days of incubation. C- and N-microbial biomass and mineral nitrogen were determined by destructively sampling of four replicates of each treatment after 33, 53 and 80 days of incubation. C- and N-microbial biomass were measured using the fumigation-extraction technique (Brookes et al., 1985). Each replicate was divided in two equivalent portions (20 g dry soil), one was fumigated for 18 h with alcohol-free chloroform and the other was the unfumigated control. Both fumigated and unfumigated soils, were shaken for 1 h with 1N KCl (soil:solution 1:5) and centrifuged. The supernatant was analysed for total dissolved organic carbon using wet combustion by persulphate and a CO_2 analyser (Carmhograph 12A, Bottner and Warembourg, 1978). The ^{14}C in supernatants was determined by liquid scintillation counting. The N-microbial biomass was measured in 70 ml of the extract by micro-Kjeldahl digestion and distillation (Bremmen and Mulvaney, 1982). A k_{EC} value of 0.45 and a k_{EN} of 0.54 were used to calculate the C and N content of the microbial biomass, respectively (Joergensen, 1996; Joergensen and Mueller, 1996). N–NH_4 and N–NO_3 were measured colorimetrically in the unfumigated KCl extracts using Devarda's alloy to reduce NO_3 to NH_4 (Keeney and Nelson, 1982). Total soil C was determined by dry combustion at 1000 °C and Carmhograph 12A was used to measured the evolved CO_2, whereas total soil nitrogen was determined by Kjeldahl digestion.

2.5. Kinetic parameters

To estimate the kinetic parameters of C mineralisation, the cumulative curves of the released native soil carbon–CO_2 were fitted to a double exponential function (Ellert and Bettany, 1988),

$$C_t = C_0(1 - e^{-kt}) + C_r(1 - e^{-ht}) \quad (1)$$

where C_t is the cumulative C–CO_2 released after time t, C_0 is the labile C pool, C_r the recalcitrant pool (calculated as the difference between total and labile C pools), k and h are the mineralisation rates of the labile and recalcitrant pools, respectively.

For the estimation of the carbon mineralisation rate of the ^{14}C-labelled straw (d), a simple exponential model was utilised,

$$^{14}C = {}^{14}C_0(1 - e^{-dt}) \quad (2)$$

where ^{14}C is the cumulative C–CO_2 mineralised from the ^{14}C-labelled straw and ^{14}Co is the potentially mineralisable carbon of the straw.

The potentially mineralisable nitrogen was calculate by fitting the cumulative mineralised nitrogen of the unamended treatment to an exponential model (Stanford and Smith, 1972),

$$N = N_0(1 - e^{-mt}) \quad (3)$$

where N is the cumulative nitrogen mineralised and N_0 is the potentially mineralisable nitrogen.

Finally, to estimate the decay rate of the labelled microbial biomass, a simple exponential function was fitted to the C-microbial biomass.

2.6. Metabolic quotient of the microbial biomass

The metabolic quotient (qCO_2) represents the CO_2 production per unit of C-microbial biomass and unit of time (Insam and Haselwandter, 1989). A low metabolic quotient indicates a high quality of the substrate used by microorganisms or a low microbial maintenance requirements.

2.7. Statistic

Statistical comparisons were made by using one way analysis of variance and Tukey's honestly significant difference test (HSD) for post-hoc comparisons of the means. Differences were considered significant at 0.05 level. The STATISTICA 4.5 package was used for the statistical analysis.

3. Results

3.1. Microbial biomass and inorganic nitrogen in fresh soils

The most pronounced initial difference between the soils appeared in the fresh C- and N-microbial

biomass, which doubled the amount in the restored soil compared to the depleted soil (Table 1). C-microbial biomass represented 0.64 and 0.34% of the total soil carbon pool, while N-microbial biomass represented 1.14 and 0.53% of the total soil nitrogen, in the restored and depleted soil, respectively.

Total mineral nitrogen was very low in both soils, without significant differences between them (Table 1). Nevertheless, the percentage of nitrate with respect to total mineral nitrogen ($NO_3/(NH_4 + NO_3)$) was significantly greater ($P > 0.05$) in the depleted soil (72%) than in the restored soil (52%).

3.2. Mineralisation of the native soil carbon

The native C–CO_2 release was higher in the restored soil in respect to the depleted soil with significant differences during the whole incubation period (Fig. 1). In Table 2, the total native C mineralised after 12 weeks of incubation and the mineralisation parameters derived from the double exponential adjustment (Eq. (1)) are shown. In the treatment without ^{14}C-labelled plant material, the estimated C_0 was 55% greater in the restored soil than in the depleted soil. The mineralisation rate of this labile organic C pool (k) was lower in the restored soil than in the depleted soil, corresponding to half-lives of 5.5 and 3.7 days, respectively. The mineralisation rate of the recalcitrant organic C pool (h) was similar in both soils, with an average half-life of 21.5 years.

The addition of ^{14}C-labelled straw did not change the amount of native C mineralised from soils after the 12 weeks incubation but decreased the mineralisation rate (Table 2).

The total C mineralised during the incubation represented a very small percentage of the total soil C: 1.25–1.41% depending on the treatment.

3.3. Decomposition of ^{14}C-labelled plant material

The decomposition of the labelled straw was slightly faster in the restored soil compared to the depleted soil (Fig. 2). The percentage of the added ^{14}C mineralised after the 12 weeks incubation was 43.9% in the restored soil and 42.9% in the depleted soil. The cumulative ^{14}C–CO_2 release fitted well to Eq. (2) ($r^2 > 0.99$ for both soils), with decomposition rates (d) of 0.045 and 0.041 per day for the restored and depleted soil, respectively ($P < 0.05$, HSD).

3.4. Mineralisation of nitrogen

Irrespective of the sampling time significantly higher mineral nitrogen was measured in the unamended restored soil compared to the depleted soil (Table 3). The addition of plant material with high

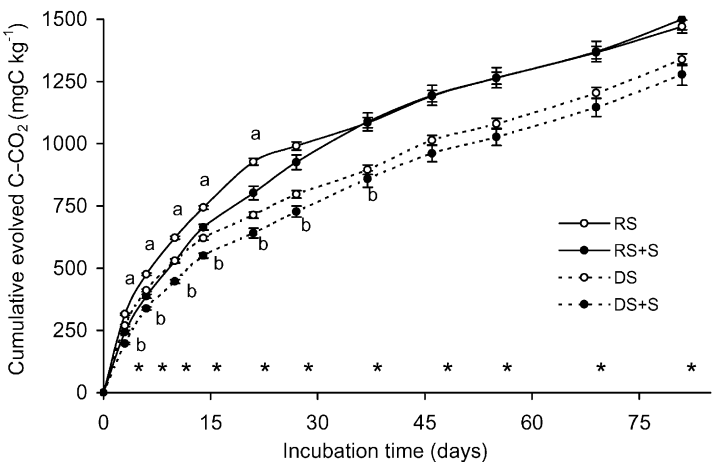

Fig. 1. Cumulative unlabelled C–CO_2 evolved from the restored (RS) and the depleted soil (DS), amended (+S) and unamended (−S) with ^{14}C-plant material. Sampling dates indicated with an asterisk had significantly ($P < 0.05$, HSD) more C evolved from restored than depleted soil. Sampling dates indicates with a letter had significantly difference between +S and –S treatments (a for the restored and b for the depleted soil).

Table 2
Soil native carbon mineralised after 12 weeks of incubation (C) and mineralisation parameters using a double exponential model[a,b]

Treatment	C ($g\,kg^{-1}$)	C_0 ($g\,kg^{-1}$)	k (per day)	$t_{1/2}$ of C_0 (day)	$h \times 10^4$ (day^{-1})	$t_{1/2}$ of C_r (year)	r^2
RS	1.49 ± 0.09 a	0.790 a	0.125 a	5.5 a	0.8 a	24 a	0.997
RS + S	1.54 ± 0.07 a	0.826 a	0.078 b	8.9 b	0.9 a	21 a	0.998
DS	1.34 ± 0.05 b	0.513 b	0.189 c	3.7 c	1.0 a	19 a	0.998
DS + S	1.29 ± 0.09 b	0.449 c	0.142 d	4.9 d	1.0 a	19 a	0.998

[a] RS, restored soil; DS, depleted soil; +S amended with ^{14}C-plant material. C_0, labile C pool; k, mineralisation rate of C_0; C_r, recalcitrant C pool ($C_0 + C_r$= total soil C); h, mineralisation rate of C_r; $t_{1/2}$, half-life
[b] Different alphabets indicate significant differences within each column ($P < 0.05$, HSD).

C/N ratio (+S) considerably inhibited nitrogen mineralisation in the two soils, mainly at the beginning of the incubation.

The total amount of nitrogen mineralised corresponded to 1.16–2.70% of the total soil nitrogen, depending on the treatment. The potentially mineralisable nitrogen was estimated at $0.58\,g\,kg^{-1}$ for the restored soil and $0.24\,g\,kg^{-1}$ for the depleted soil using Eq. (3).

3.5. C- and N-microbial biomass during the incubation

In both soils maximum amounts of autochthonous microbial biomass (not labelled and consequently not involved in ^{14}C-straw decomposition) were measured after 33 days of incubation and decrease thereafter (Table 3). After day 33, the differences in C- and N-microbial biomass between the two soils was not significant (Table 3). A clear decrease in microbial biomass was observed throughout the incubation, tending to stabilise towards the end of the studied period.

The zymogenous or labelled microbial biomass was not significantly different between the soils with the exception of the second date of measurement, when it was significantly greater in the restored soil (Table 3). The labelled microbial biomass represented around 30% of the total soil biomass. The decay rate of this ^{14}C-microbial biomass, calculated by fitting the biomass data to an exponential model, was significantly lower ($P < 0.05$) in the restored soil (0.0056 per day) than in the depleted soil (0.010 per day). Therefore, the half-life of the labelled microbial biomass was 124 and 68 days in the restored and depleted soils, respectively.

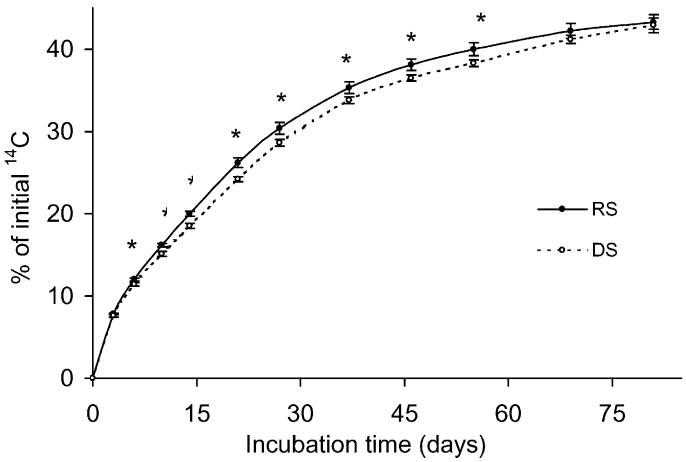

Fig. 2. Cumulative labelled ^{14}C–CO_2 evolved from the restored (RS) and the depleted soil (DS) expressed as percentage of initially added ^{14}C. Significantly ($P < 0.05$, HSD) more C was evolved from restored than depleted soils on sampling dates indicated with an asterisk.

Table 3
Mineral nitrogen, N- and C-microbial biomass, metabolic quotient (qCO_2), ^{14}C microbial biomass and $q^{14}CO_2$ during the incubation (mean ± S.D.)[a]

	Treatment	33 days	53 days	80 days
Mineral nitrogen ($mg\,kg^{-1}$)	RS	89 ± 2 a	112 ± 5 a	178 ± 12 a
	RS + S	17 ± 2 b	27 ± 7 b	95 ± 15 b
	DS	76 ± 7 c	80 ± 15 c	129 ± 6 c
	DS + S	30 ± 2 d	26 ± 4 b	83 ± 8 b
C-microbial biomass[b] ($mg\,kg^{-1}$)	RS	476 ± 55 a	426 ± 44 a	428 ± 34 a
	RS + S	616 ± 59 b	504 ± 28 b	443 ± 25 a
	DS	431 ± 49 a	383 ± 41 a	419 ± 62 a
	DS + S	572 ± 20 b	427 ± 8 a	400 ± 28 a
N-microbial biomass[c] ($mg\,kg^{-1}$)	RS	56 ± 8 a	54 ± 7 a	48 ± 5 a
	RS + S	137 ± 5 b	80 ± 34 a	74 ± 18 a
	DS	50 ± 14 a	50 ± 13 a	45 ± 10 a
	DS + S	107 ± 4 c	101 ± 4 a	70 ± 31 a
qCO_2 ($mgC\text{-}CO_2\,h^{-1}\,g^{-1}$ microbial-C)	RS	0.9 ± 0.2 a	0.8 ± 0.2 a	0.8 ± 0.2 a
	RS + S	1.2 ± 0.2 b	0.7 ± 0.2 a	1.0 ± 0.1 a b
	DS	1.2 ± 0.2 b	0.8 ± 0.2 a	1.1 ± 0.2 b
	DS + S	1.0 ± 0.3 a b	0.8 ± 0.1 a	1.1 ± 0.1 b
^{14}C-microbial biomass ($mg\,kg^{-1}$)	RS + S	201 ± 16 a	185 ± 10 a	154 ± 14 a
	DS + S	222 ± 20 a	147 ± 13 b	145 ± 19 a
$q^{14}CO_2$ ($mg^{14}C\text{-}CO_2\,h^{-1}\,g^{-1}$ microbial-^{14}C)	RS + S	4.7 ± 0.2 a	2.0 ± 0.2 a	1.1 ± 0.1 a
	DS + S	4.5 ± 0.3 a	2.5 ± 0.3 b	1.4 ± 0.1 b

[a] Different alphabets indicate significant differences within each column ($n = 4$, $P < 0.05$, HSD). RS: restored soil; DS: depleted soil; +S with ^{14}C-plant material.
[b] Include only the unlabelled microbial biomass.
[c] Includes also the N-biomass derived from the added labelled material.

3.6. Metabolic quotients of the autochthonous and zymogenous microbial biomass

The qCO_2 of the unlabelled microbial biomass was significantly lower in the restored than depleted soil (Table 3). The addition of plant material induced the development of a zymogenous microbial biomass with a $q^{14}CO_2$ roughly higher than the qCO_2 of the autochthonous biomass, mainly at the beginning of the incubation (Table 3). As for the qCO_2, the $q^{14}CO_2$ was significantly lower ($P < 0.05$) in the restored than depleted soil after 53 and 80 days of incubation (Table 3).

4. Discussion

Potato yields in the high tropical Andean mountains is largely determined by the length of the fallow period and the number of consecutive years of cultivation. Sarmiento (1995); analysing 47 farmer plots, showed that the potato yield decreases from an average of $18\,t\,ha^{-1}$ in the first year of cultivation to $10\,t\,ha^{-1}$ during the second year and only $5\,t\,ha^{-1}$ after 4 years of consecutive cultivation. The same study showed that yield was significantly lower in fields which had passed through fallow periods less than 5 years, compared to fields with longer fallow periods. Other studies carried out in these agricultural systems have not detect soil changes explaining the loss of fertility during the cultivation and its progressive recovery during the fallow period (Ferwerda, 1987; Sarmiento et al., 1990, 1993; Hervé, 1994; Aranguren and Monasterio, 1997; Llambí and Sarmiento, 1998, 1999), probably due to: (a) the spatial heterogeneity in mountains that limit the application of a synchronic analysis, (b) small changes in soil organic matter are not easily detected when the soil organic matter pool is very large, and (c) the rapid uptake of available nutrients by the fallow vegetation prevents nutrient accumulation in the soil. In this study, carried out on adjacent and homogeneous plots that differed only in their fallow lengths, we were able to detect initial significant differences in several soil properties. Particularly, soil biological properties,

as microbial biomass, seem to have a greater potential than chemical or physical properties in this mountain heterogeneous context to indicate soil fertility because they are more sensitive to land use changes.

4.1. Soil biological characteristics

In the examined paramo soils, the C-microbial biomass represented 0.3–0.6% of the total soil carbon. This proportion is very low compared to other arable soils, which generally range from 0.5 to 4.5% (Anderson and Domsch, 1989; Azam et al., 1986; Wardle, 1992), and suggests a high stability of the organic matter.

Expressed in an area basis (considering 100 kg m^{-2} of soil in the upper 20 cm of the soil, Sarmiento, 1995), the fresh N-microbial biomass was 5.4 g m^{-2} in the restored soil compared to 2.6 g m^{-2} in the depleted soil. The importance of this potentially available N pool is highlighted when compared to other N pools in this agroecosystem (e.g. Sarmiento (1995) calculated a total N of 8–9 g m^{-2} in the natural vegetation biomass for a 12 years old fallow plot) and to an estimated total N uptake by the potato crop of 4.5 g m^{-2} for a tuber production of 14 t ha^{-1} (the local average). Thus, the increase in microbial biomass during the fallow period represents an important reservoir of nitrogen and could be an essential component of the fertility recovery.

The inorganic N concentration was by one magnitude lower than the N-microbial biomass and was not significantly different between the soils. Nevertheless, the proportion of nitrate in the mineral nitrogen pool was significantly larger in the depleted compared to the restored soil. A decrease of nitrification during secondary succession has been also observed in other ecosystems (Rice and Pancholy, 1972; Schmitz et al., 1989; Clein and Schimel, 1995). High nitrification during cultivation could have a negative effect on the N budget, since NO_3 is more easily leached than NH_4, and probably contributes to a decline in fertility in this agricultural system.

4.2. Soil incubation

The proportion of soil native carbon mineralised during the 12 weeks incubation period (1.3–1.5%) was lower than other soils incubated under similar conditions (Nicolardot, 1988; Sparrow and Cochran, 1988), suggesting again that soil organic matter in these soils was fairly resistant to decomposition. Also, the potentially mineralisable nitrogen of this soil is low compared to other soils. Stanford and Smith (1972) reported values of N_0 ranging from 10 to 15% of the total nitrogen for a large number of soils. This compares to 9% in the restored and 3% in depleted soil in this study.

Despite the apparent high stability of the soil organic matter, the nitrogen mineralised during the incubation, expressed by unit of area, was 17 g m^{-2} in the restored soil and 12 g m^{-2} in the depleted soil. If the amount of nitrogen mineralised during the incubation is a good estimation of nitrogen availability, these quantities exceed the potato crop requirement to obtain the regional average yield.

Another interesting aspect is that the figure for C_0 are very close to the C-microbial biomass measured in fresh soil. C-microbial biomass usually represents an essential fraction of the labile C. Thus, part of C_0 probably originated from microorganisms that were killed during the drying of the soil before incubation and decomposed when the soil was remoistened and incubated. Many authors report a stimulation of C and N mineralisation during the first days of incubation of dried–remoistened soils (Marumoto et al., 1982; Bottner, 1985; Azam et al., 1986; Beauchamp et al., 1986; Sparling and Ross, 1988; Robertson et al., 1988; Cook and Allan, 1992; Van Gestel et al., 1993). Jawson et al. (1989) found that dead microbial biomass added to soil was decomposed after 4 days, a period similar to our C_0 half-life (4–9 days), supporting our assertion that part of the C_0 originates from dead microorganisms. In natural conditions, the Venezuelan paramos undergo long drought periods, during which the microbial biomass decreases considerably (Sarmiento, 1995). The soil drying–remoistening cycles in the ploughing layer could induce partial mineralisation of the microbial biomass and accelerate the turnover of the microbial nitrogen.

Presumably, microorganisms in the amended treatment utilised the labile part of the straw instead of the native labile soil organic fraction, since the C_0 mineralisation rate was lower in the +S than –S treatment. In the incubation experiment, the low difference between the soils in the rate of straw decomposition compared to the high difference in the mineralisation rate of soil native organic matter is

rather surprising. Compared to the depleted soil, the 15 years fallow resulted in a progressive build up of labile material and microbial biomass which substantially modified the mineralisation parameters of the soil native organic matter (particularly C_0) during the 12 weeks of incubation. However, the decomposition of the freshly added straw was only slightly modified, suggesting that the fallow results essentially in a qualitative modification of soil organic matter. Although, the difference in decomposition between the soils was small, the estimated turnover time of the labelled microbial biomass was greater in the restored than depleted soil, indicating a higher availability of nitrogen.

The mechanisms explaining the successional modification of the soil native organic matter are unknown. One hypothesis is that the increase in plant biomass and diversity during the fallow period (Llambí and Sarmiento, 1999) corresponds to a quantitative and qualitative modification of the plant necromass annually incorporated into the soil. During cultivation, ploughing accelerates the mineralisation of the labile fraction progressively accumulated during the fallow period. An ongoing European program, being carried out in the high tropical Andean mountains (including the study area Páramo de Gavidia), is built on this hypothesis.

The metabolic quotient of the autochthonous and zymogenous biomass was lower in the restored soil, revealing a lower requirement of maintenance energy or higher metabolic efficiency in the utilisation of both the native organic matter and the added plant material. Insam and Domsch (1988) and Insam and Haselwandter (1989), also found that the metabolic quotient was higher in initial primary and secondary successional phases as opposed to more mature ecosystems. They explained the qCO_2 decrease during the succession with the change from "*r*" to "*k*" strategists as the succession progresses and the detritus food webs become more complex. As Insam and Haselwandter (1989) pointed out, the successional decrease in qCO_2 agrees with Odum's (1969) theory of a low maintenance-to-structure ratio in mature ecosystems. Another explanation for the decrease in qCO_2 in the restored compared to depleted soil is that the sources of available nitrogen for microorganisms are more limited in the early stages of the succession. Consequently, more carbon must be mineralised to maintain the microorganism C/N ratio, due to the higher C/N of the substrates and the lack of alternative sources of nitrogen. The high qCO_2 of the zymogenous biomass in the +S treatment can also be explained by the high C/N ratio of the wheat straw.

5. Conclusion

This study shows several trends of change after a 15 years fallow, which could contribute in explaining the recovery of soil fertility: (a) an increase in soil C- and N-microbial biomass in fresh soil, which could be a source of potentially mineralisable nutrients specially under alternating wet and dry seasons, (b) a decrease in the proportion of nitrate in the mineral N pool, that can minimise the N losses by leaching, (c) an increase in potentially mineralisable C and N, and (d) a less limited microbial community suggested by several indicators like a higher rate of plant material decomposition, a lower energy maintenance cost (qCO_2) of the autochthonous and zymogenous microbial biomass and a higher half life time of the zymogenous biomass in the restored compared to the depleted soil.

The stability of the organic matter is a characteristic of the studied soils and is essential for the sustainability of this agricultural system, favouring infiltration, maintaining a high water holding capacity, cation exchange capacity and minimising erosion (Llambí and Sarmiento, 1998; Sarmiento, 2000). The elimination of the fallow period could lead to a progressive decrease in the soil organic matter, that can endanger agricultural sustainability. In this study, 3 years of consecutive cultivation causes a soil carbon decrease of 2%. For a more intensive but sustainable agriculture the favourable effect of the fallow period in the maintenace of SOM should be replaced by a correct management of organic inputs (e.g. organic manure and crop residues).

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References

Anderson, T.H., Domsch, K.H., 1989. Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil. Biol. Biochem. 21, 471–479.

Aranguren, A., Monasterio, M., 1997. Aspectos de la dinámica del nitrógeno en parcelas con diferente tiempo de descanso en el Páramo de Gavidia (Andes Venezolanos). In: Liberman, M., Baied, C. (Eds.), Desarrollo sostenible en Ecosistemas de Montaña: Manejo de áreas frágiles en los Andes. Universidad de las Naciones Unidas, La Paz, pp. 171–181.

Aweto, A.O., 1981. Secondary succession and soil fertility restoration in south-western Nigeria. J. Ecol. 69, 601–607.

Azam, F., Malik, K.A., Hussain, F., 1986. Microbial biomass and mineralization-inmobilization of nitrogen in some agricultural soils. Biol. Fertil. Soils 2, 157–163.

Beauchamp, E.G., Reynolds, W.D., Blasche-Villeneuve, D., Kirby, K., 1986. Nitrogen mineralization kinetics with different soil pretreatments and cropping histories. Soil Sci. Soc. Am. J. 50, 1478–1483.

Bremmen, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of soil analysis. Part 2. 2nd Edition, Agronomy 9, 595–624.

Bottner, P., 1985. Response of microbial biomass to alternate moist and dry conditions in a soil incubated with ^{14}C- and ^{15}N-labelled plant material. Soil Biol. Biochem. 17, 329–337.

Bottner, P., Warembourg, F., 1978. Method for simultaneous measurement of total and radioactive carbon in soils, soil extracts and plant materials. Plant and Soil 45, 273–277.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17, 837–842.

Clein, J.S., Schimel, J.P., 1995. Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. Soil Biol. Biochem. 27, 743–752.

Cook, B.D., Allan, D.L., 1992. Dissolved organic carbon in old field soils: total amounts as a measure of available resources for soil mineralization. Soil Biol. Biochem. 24, 585–594.

Ellert, B.H., Bettany, J.R., 1988. Comparison of kinetic models for describing net sulphur and nitrogen mineralization. Soil Sci. Soc. Am. J. 52, 1692–1702.

Ferwerda, W., 1987. The Influence of Potato Cultivation on the Natural Bunchgrass Paramo in the Colombian Cordillera Oriental. Internal Report No. 220. Hugo de Vries Laboratory, Department of Palynology and Palaeo/Actuo-Ecology, University of Amsterdam, Amsterdam, p. 83.

Floret, C., Pontanier, R., Serpantier, G., 1993. La Jachère en Afrique Tropicale. Dossier MAB 16, UNESCO, Paris.

Hervé, D., 1994. Respuesta de los componentes de la fertilidad del suelo a la duración del descanso. In: Hervé, D., Genin, D., Rivière, G. (Eds.), Dinámicas del descanso de la tierra en los Andes. IBTA-ORSTOM, La Paz, pp. 155–169.

Insam, H., Domsch, K.H., 1988. Relationships between soil organic carbon and microbial biomass on chronosequence of reclamation sites. Microb. Ecol. 15, 177–188.

Insam, H., Haselwandter, K., 1989. Metabolic quotient of soil microflora in relation to plant succession. Oecologia 79, 174–178.

Jawson, M.D., Elliott, L.F., Papendick, R.I., Campbell, G.S., 1989. The decomposition of ^{14}C-labelled wheat straw and ^{15}N-labelled microbial material. Soil Biol. Biochem. 21, 417–422.

Joergensen, R.G., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the k_{EC} value. Soil Biol. Biochem. 28, 25–31.

Joergensen, R.G., Mueller, T., 1996. The fumigation-extraction method to estimate soil microbial biomass: calibration of the k_{EN} value. Soil Biol. Biochem. 28, 33–37.

Jordan, C.F., 1985. Nutrient Cycling in Tropical Forest Ecosystems. Wiley, UK, p. 190.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen-inorganic forms. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. 2nd Edition. Agronomy, 643–698.

Klute, A., 1986. Water retention: Laboratory methods. In: Klute, A. (Ed.), Methods of soil analysis. Part 1. Physical and mineralogical methods. Agronomy 9, 635–662.

Lessa, S.N., 1998. Phosphorus dynamics in soils under slash and burn cultivation in the semi-arid northeast of Brazil. Ecotropicos 11, 93–106.

Llambí, L.D., Sarmiento, L., 1998. Biomasa microbiana y otros parámetros edáficos en una sucesion secundaria de los páramos venezolanos. Ecotropicos 11, 1–14.

Llambí, L.D., Sarmiento, L., 1999. Ecosystem restoration during the long fallow periods in the traditional potato agriculture of the Venezuelan high Andes. In: Price, M. (Ed.), Global Change in the Mountains. The Parthenon Publishing Group, New York, pp. 190–192.

Marumoto, T., Anderson, J.P.E., Domsch, K.H., 1982. Decomposition of ^{14}C and ^{14}N labelled microbial cells in soil. Soil Biol. Biochem. 14, 461–467.

Mishra, B.K., Ramakrishnan, P.S., 1983a. Slash and burn agriculture at higher elevations in north-eastern India. I. Sediment, water and nutrient losses. Agric. Ecosystem Environ. 9, 69–82.

Mishra, B.K., Ramakrishnan, P.S., 1983b. Slash and burn agriculture at higher elevations in north-eastern India. II. Soil fertility changes. Agric. Ecosystem Environ. 9, 83–96.

Nicolardot, B., 1988. Evolution du niveau de biomasse microbienne du sol au cours d'une incubation de longue durée: relations avec la mineralisation du carbone et de l'azote organique. Rev. Ecol. Biol. Sol. 25, 287–304.

Nye, P.H., Greenland, D.J., 1960. The Soil Under Shifting Cultivation. Tech. Comm. 51, CAB Farnham Royal, UK, p. 156.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Ramakrishnan, P.S., 1992. Shifting Agriculture and Sustainable Development: An Interdisciplinary Study from north-eastern India, UNESCO, Paris, p. 424.

Rice, E.L., Pancholy, S.K., 1972. Inhibition of nitrification by climax vegetation. Am. J. Bot. 59, 1033–1040.

Robertson, K., Schnurer, J., Clarholm, M., Bonde, T., Rosswall, T., 1988. Microbial biomass in relation to C and N mineralization during laboratory incubations. Soil Biol. Biochem. 20, 281–286.

Sarmiento, L., 1995. Restauration de la fertilité dans un systeme agricole à jachère longue des hautes Andes du Venezuela. Ph.D. Thesis. Université de Paris XI, Paris.

Sarmiento, L., 2000. Water balance and soil loss in fallow agriculture of the high Venezuelan Andes. Mountain Res. Develop. 20 (3), 246–253.

Sarmiento, L., Monasterio, M., 1993. Elementos para la interpretación ecológica de un sistema agrícola campesino en los Andes venezolanos (Páramo de Gavidia). In: Rabey, M. (Ed.), El Uso Tradicional de los Recursos Naturales en Montañas: Tradición y Transformación. IUBS/UNESCO, Montevideo, pp. 55–77.

Sarmiento, L., Monasterio, M., Montilla, M., 1990. Succession, Regeneration and Stability in High Andean Ecosystems and Agroecosystems: the Rest-Fallow Strategy in the Páramo de Gavidia, Mérida, Venezuela. Geographica Bernesia, African Studies Series A8, pp. 151–157.

Sarmiento, L., Monasterio, M., Montilla, M., 1993. Ecological bases, sustainability, and current trends in traditional agriculture in the Venezuelan high Andes. Mountain Res. Develop. 13, 167–176.

Scheu, S., 1990. Changes in microbial nutrient status during secondary succession and its modification by earthworms. Oecologia 84, 351–358.

Schmitz, M.F., Yuste, P., Bermudez de Castro, F., Pineda, F.D., 1989. Microorganisms of carbon and nitrogen cycles: variation during succession in a Mediterranean pasture. Rev. Ecol. Biol. Sol. 26, 371–389.

Soil Survey Staff, 1994. Keys to soil taxonomy U.S.D.A.—Soil Conservation Service. 6th Edition, Washington, DC.

Sparling, G.P., Ross, D.J., 1988. Microbial contributions to the increased nitrogen mineralisation after air drying of soils. Plant and soil 105, 163–167.

Sparrow, S., Cochran, V., 1988. Carbon and nitrogen mineralization in subartic agricultural and forest soils. Biol. Fertil. Soils 6, 33–38.

Stanford, G., Smith, S.J., 1972. Nitrogen mineralization potentials of soils. Soil Sci. Soc. Am. Proc. 36, 465–472.

Van Gestel, M., Merckx, R., Vlassak, K., 1993. Microbial biomass response to soil drying and rewetting. The fate of fast- and slow-growing microorganisms in soils from different climates. Soil Biol. Biochem. 25, 109–123.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soils. Biol. Rev. 67, 321–358.