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Sensitivity of Soil Restoration Indicators during Páramo Succession in the High Tropical Andes: Chronosequence and Permanent Plot Approaches

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Abstract

The aim of this study was to analyze indicators of soil restoration during secondary succession in a heterogeneous valley in the high tropical Andes. A combination of chronosequence and permanent plot methods was used to detect changes in this heterogeneous matrix. Thirty-six plots with different fallow times (1–9 years) and four non-cultivated plots with natural vegetation (páramo) were sampled twice in a 3-year interval (1996 and 1999). The following soil properties were determined: total C and N, pH, exchangeable bases, cation exchange capacity, and microbial biomass N (MB-N). Using the chronosequence approach, successional increases in soil pH and Mg were detected, pointing to these variables as indicators of soil restoration during the fallow period. Comparing the non-cultivated páramo with the fallow plots, a significant decrease in MB-N was found, suggesting that this is a sensitive agricultural disturbance indicator. The permanent plot analysis failed to detect successional trends in any of the study variables, probably as a result of a lack of sensitivity of the indicators used within the 3-year interval. Nevertheless, a strong acidification was detected by the permanent plot method when fallow plots were cultivated. We conclude that the size of important soil components such as total soil organic matter or microbial biomass is not a sensitive soil restoration indicator in these heterogeneous mountain systems but that other integrative variables such as pH could be more sensitive to successional changes in key soil processes (e.g., nitrification or nutrient losses).

Key words: disturbance, fallow agriculture, microbial biomass, nitrogen, páramo, pH, soil organic matter, spatial heterogeneity.

Introduction

The search for, and evaluation of, sensitive indicators for monitoring dynamic processes in terrestrial ecosystems has become an important issue in recent years due to the increasing pace of local, regional, and global changes in land use and climate. Monitoring changes in soil physicochemical and biological properties under different environmental scenarios, such as global warming, agricultural conversions, or recovery from disturbance, is of particular importance due to the role that soil state variables play in controlling key aspects of ecosystem function and stability (e.g., water dynamics, nutrient cycling, and soil fertility). Some of the desirable characteristics of an ecological indicator include (1) ease of measurement, (2) stress sensitivity, (3) fast and predictable response, (4) low spatio-temporal variability, and (5) providing an integrative measure of changes in the whole ecosystem (Grabherr & Pauli 2004).

Traditional agriculture with long fallow periods is a unique study system for analyzing ecosystem restoration after human disturbance. Two main approaches have been used: the chronosequence or synchronic analysis, where plots in different seral stages are studied simultaneously, and the less common diachronic approach, based in following permanent plots over time. This latter strategy has the obvious disadvantage of requiring longer study periods but avoids the confounding effect of spatial heterogeneity inherent to the interpretation of synchronic data, in which time is substituted by space (Pickett 1989).

Secondary succession in terrestrial ecosystems has been associated with clear temporal trends in soil components such as organic matter and available mineral nutrients (Odum 1969; Gorham et al. 1979; Vitousek & Walker 1987). These changes in soil components are dynamically linked with trends in vegetation structure and function (Bush & Van Auken 1986; Chapin et al. 2002). Old-field succession has been studied in detail in the traditional long-fallow agroecosystems of the lowland tropics. Successional increases in soil organic matter and nutrient availability in these systems have been linked to soil fertility restoration after agricultural abandonment (Nye & Greenland 1960; Aweto 1981; Ewel 1986; Ramakrishnan 1992, 1994; Davidson et al. 2007).

In the alpine belt of the tropical northern Andes, locally known as *páramo*, long-fallow agricultural systems are still used for the production of potatoes and cereals, providing

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an interesting study system to evaluate restoration dynamics in mountain environments, where spatial heterogeneity is exacerbated, and consequently monitoring soil changes is particularly challenging. In these páramo areas, farmers alternate periods of cultivation of 2–3 years with fallow periods of 5 to more than 10 years. This management system generates a landscape mosaic in which natural vegetation areas and plots under cultivation coexist with plots in different seral stages. The dynamics of vegetation restoration during the fallow period have been described in several páramos of Colombia (Ferwerda 1987; Jaimes & Sarmiento 2002) and Venezuela (Sarmiento et al. 2003). These studies have identified clear successional trends in plant species dominance, with relatively fast changes in vegetation structure and in the life-form spectrum. However, when the focus shifts to the detection of soil changes, two factors complicate the interpretation of successional trends. The first factor is the high spatial heterogeneity of these environments, where finding plot series with similar environmental conditions is extremely difficult due to continuous variations in slope, altitude, aspect, stoniness, geomorphology, topography, and land use history. This large spatial heterogeneity complicates the application of a synchronic approach (or space-for-time substitution), as many other sources of variation, unrelated with successional time, generate a large variability in the parameters under evaluation (Sarmiento & Llambí 2005). The second limiting factor is the possible lack of sensitivity of the variables analyzed within the timescale of secondary succession. For example, the high organic matter content of páramo soils masks the small variations that could be expected to occur. Hence, there is a need to identify more sensitive restoration indicators, with response times within the temporal scale of secondary succession. An ideal solution would be to find soil parameters with higher sensitivity to successional change than to spatial heterogeneity.

Microbial biomass has been suggested as a sensitive early indicator of changes in soil organic matter quality and soil fertility, showing faster response than organic matter as a whole (Powlson et al. 1987; Coleman et al. 1989; Turco et al. 1994; Connell et al. 1995; Gregorich et al. 1995; Carter 2002). In temperate ecosystems, successional increases in microbial biomass have been reported by several authors (Insam & Domsch 1988; Insam & Hasselwandter 1989).

The objective of this study was to combine chronosequence and permanent plot methods to analyze (1) the successional changes of soil microbial biomass and other soil physicochemical properties, evaluating their sensitivity as indicators of soil restoration in these heterogeneous environments, and (b) the effect of agricultural disturbance on páramo soils by comparing fallow plots with noncultivated natural páramo areas. Given these objectives, 36 plots with different fallow times, between 1 and 9 years, and 4 areas of noncultivated páramo (NCP) were compared (chronosequence approach) at a 3-year interval (permanent plot approach).

Methods

Study Area

The study was carried out in the Páramo de Gavidia of the Venezuelan Andes, located in the Sierra Nevada National Park, in the state of Mérida (lat 8°35′N, long 70°55′W). The area is a narrow glacial valley with well-drained inceptisols (*Ustic Humitropept*) of a sandy loam texture, low pH, and high organic matter levels but low mineral nutrient contents (Llambí & Sarmiento 1998; Abadín et al. 2002). Agricultural activity in this area occurs between 3,200 and 3,800 m above sea level on steep slopes or on small alluvial or colluvial deposits and hanging valleys. The precipitation regime is unimodal, with a dry season between December and March and a peak of rainfall between June and July. The mean annual temperature ranges between 9 and 5°C, and the mean precipitation is 1,300 mm. The land use system is long-fallow agriculture. Potatoes are grown during an agricultural phase lasting 2–3 years. Agricultural practices include the incorporation of successional vegetation as green manure, mineral fertilization with an average dose of 1.8 t ha^{-1} yr^{-1} of NPK, and plowing two or three times per year. After the cultivation period, the fields are abandoned and the succession–restoration period begins. Occasionally, fields are cultivated with cereals before being abandoned (Sarmiento et al. 1993). The current average fallow length is 4.6 years, but there is large variability, with times ranging from 2 to more than 15 years (Sarmiento et al. 2002). During the fallow, fields are used for extensive cattle and horse grazing. Grazing loads are variable, with an estimated average of 0.1 animal units/ha (Pérez 2000).

During succession, there are relatively rapid changes in vegetation structure, with introduced forbs dominating the initial stages and being replaced as dominants after 5–6 years by the characteristic páramo life-forms: sclerophylous shrubs and giant rosettes (Fig. 1). Hence, after about 9 years, vegetation physiognomy is similar to that found in the NCP. However, vegetation succession is divergent: similarity in vegetation composition between plots in the same seral stage decreases during succession, probably as a result of spatial heterogeneity (see Sarmiento et al. 2003, for details).

From the end of the nineteenth century, with the onset of human settlement, up until the 1950s, the valley was divided, with the higher areas dedicated to extensive grazing of cattle, horses, and sheep and the lower areas dedicated to small-scale cultivation of wheat. Potato was cultivated only in small plots adjacent to the farmhouses. Population densities were much lower than today. After the 1950s, as population started to increase, potato cultivation replaced wheat and expanded from the valley bottom into the slopes, beginning the long-fallow system still in use today (Smith 2003).

Soil Sampling

A spatial database, containing information on fallow lengths of 1,200 fields, was used for plot selection (Smith

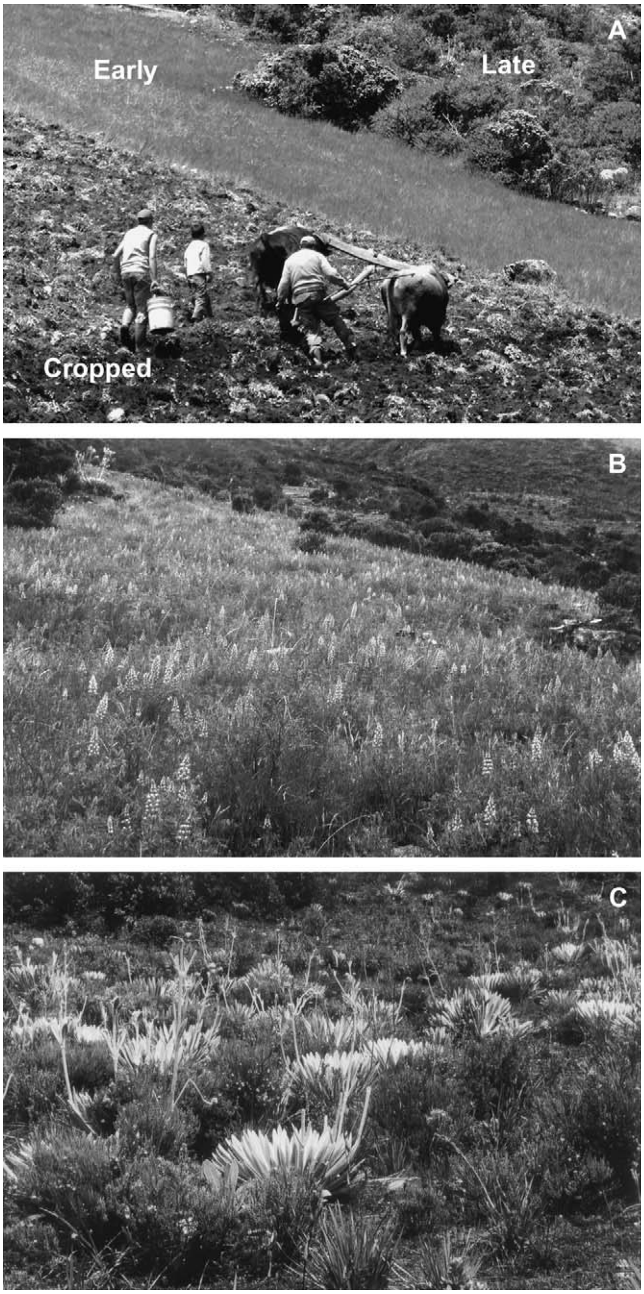

Figure 1. Three views of changes in vegetation physiognomy during succession in Gavidia, Venezuela. (A) Landscape mosaic including cultivated, early-successional, and late-successional plots. (B) Detail of an early-succession plot dominated by introduced and native herbs (3 years). (C) Detail of late-successional plot dominated by giant rosettes and sclerophyllous shrubs (10 years).

1995, updated up to 1999). This large database allowed extensive spatial replication: 36 plots with 1–9 years of fallow (4 plots/yr) and 4 NCP areas, which had never been incorporated into the cultivation–fallow system, were randomly selected. To reduce between-plot heterogeneity, we excluded (1) areas near farmhouses, as they present extreme levels of grazing and tend to have a long history of cultivation, (2) areas in the valley bottom, as soils are generally boggy, and (3) plots in which vegetation cover suggested overgrazing.

The 40 plots selected were sampled twice: in July 1996 and July 1999. In each case, sampling was done within the shortest time possible (2–3 days). In the second sampling period, 16 of the 36 plots that were in fallow in 1996 had been cultivated, whereas the rest were still in succession. Of the cultivated plots, four were still planted with potatoes and the rest had started a new fallow phase. In all cases, the sampling date corresponded to the peak of the rainy season when microbial biomass shows maximum values (Sarmiento 1995).

For sampling, a 2-m band at the edge of each plot was excluded and 10 points were randomly located (average plot size was 2,166 ± 1,645 m^2). At each point, a soil monolith of 10 cm diameter and 20 cm depth was collected. Soil from the 10 points was thoroughly mixed to obtain a composite sample of 4–6 kg of soil per plot. This was intended to provide a representative sample from each plot. Soils were stored at 4°C for no more than 15 days before analysis.

Microbial Biomass

Microbial biomass N (MB-N) was determined using the fumigation–extraction method (Brookes et al. 1985). Soil was sieved at 4 mm, and three replicates of fresh soil equivalent to 40 g of dry soil were fumigated with alcohol-free chloroform for 18 hours. After removing the chloroform, the fumigated soils and three nonfumigated controls were extracted with 0.5M K_2SO_4 (soil solution ratio of 1:5). Total N of the control and fumigated extracts was determined through digestion and distillation using the Kjeldahl method. MB-N was calculated as the difference in total N between fumigated and control extracts divided by a K_N factor of 0.45 (Brookes et al. 1985).

Soil Chemical Analysis

Soils were dried and sieved at 2 mm, and the following soil properties were determined: pH in water by potentiometry, total soil N (N+) by Kjeldahl, total organic C (C+) by Walkley–Black, exchangeable cations (Ca, Mg, K, and Na) extracted with ammonium acetate 1M at pH 7 and measured by atomic absorption spectrophotometry, and cation exchange capacity (CEC) by extraction with ammonium acetate (IGAC 1978).

Data Analysis

Before statistical analysis, plots were grouped into five land use classes: cultivated (only in the second sampling date), early fallow (1–3 years), intermediate fallow (4–6 years), late fallow (7 years or more), and NCP. To analyze differences between classes, one-way analysis of variance (ANOVA) and Tukey's honest test for multiple comparisons were used (both sampling dates were analyzed separately). The assumptions of the ANOVA were evaluated in each case (normality and homogeneity of variance) and nonparametric methods used when the assumptions were not satisfied (Kruskal–Wallis ANOVA and Duncan's *C* multiple comparison test).

Short-term diachronic changes were evaluated by comparing soil characteristics within each plot in 1996 and 1999. The change in soil variables was calculated as the difference between the final value in 1999 and the initial value in 1996 divided by the initial value (expressed in %). The values for each variable in 1996 and 1999 for each land use class were compared using a general linear model (GLM) for repeated measurements. For those variables that showed significant differences between sampling years (1996–1999), the differences within each land use class were evaluated using a paired *t* test.

For an integrated analysis of the patterns of variation for all soil variables in the 40 plots sampled in 1996 and 1999, principal components analysis (PCA) was used. Data for each variable were centered and standardized. Pearson's correlation coefficient was used to evaluate the correlation of each soil variable with the first three ordination axes. A two-way ANOVA was used to evaluate if there were significant differences in the plots' ordination scores between land use classes and between sampling years (1996 and 1999). Given that significant differences were detected between the NCP areas and the rest of the plots for the first two principal components, the PCA was repeated including only the cultivated and fallow plots. This allowed evaluation of successional trends, excluding the effects on the ordination of the nondisturbed páramo areas.

All statistical analyses used SPSS 12.0 and CANOCO for Windows 4.02 (Ter Braak & Smilauer 1998).

Results

Synchronic Analysis

The synchronic analysis of changes in soil restoration indicators for plots in different fallow stages showed successional increases for pH and Mg but only significant increases for data collected in 1999 (Tables 1 & 2). In the case of pH, significantly higher values were detected in late-successional plots, whereas for Mg, there were significant increments in both intermediate and late fallow stages. Contrary to what was expected, no significant increases for MB-N were detected between fallow stages.

Plots under potato cultivation in 1999 showed similar average values to fallow plots for all variables except for pH and Mg, which had lower average values than intermediate- and late-successional plots (Table 2). For all soil parameters, there was large within-group variability (Tables 1 & 2).

The NCP areas had significantly higher average values for MB-N, MB-N/Nt, and pH in both sampling years than the plots under fallow agriculture (Tables 1 & 2). In páramo areas, the size of the MB-N component was almost twice that in the cultivated and fallow plots. In the páramo, N immobilized in microbial biomass corresponded to 2.9–3.0% of total soil N, whereas in cultivated and fallow plots, it ranged between 1.5 and 1.9%. In addition, differences between páramo and fallow plots were significant for total N but only in 1996, whereas for Mg, they were significant in 1999.

Diachronic Analysis

The diachronic analysis of the percent variation of soil properties in each plot between 1996 and 1999 showed significant changes for pH and K (Table 3). On the one hand, pH values measured in 1999 were consistently lower than those recorded in 1996 ($p < 0.001$, GLM test for repeated measurements). The values in 1999 were on average between 2.2 and 9.3% lower than those measured in 1996 for the different plot classes. There was also a significant interaction between sampling year and land use class (Table 3) so that in some cases (plots incorporated into cultivation after 1996), the decrease in pH was much more pronounced. A paired *t* test showed a significant decrease in pH in the plots incorporated into cultivation. There was also a significant but less marked decrease in pH in the

Table 1. Average and standard deviation of soil variables determined for plots in three fallow stages and in NCP areas in 1996.

	Early ($n = 12$)	*Intermediate* ($n = 12$)	*Late* ($n = 12$)	*NCP* ($n = 4$)	*ANOVA* ($\alpha = 0.05$)
pH	4.75 (0.32)a	4.71 (0.23)a	4.9 (0.30)ab	5.17 (0.14)b	$p = 0.03$
Ct (%)	8.8 (2.7)	9.4 (2.9)	8.4 (3.0)	11.2 (3.6)	ns
Nt (%)	0.42 (0.09)a	0.50 (0.11)a	0.44 (0.12)a	0.60 (0.18)b	$p = 0.04$
C/N	20.4 (2.0)	18.7 (1.9)	18.8 (2.9)	18.4 (1.9)	ns
CEC (meq/100 g)	20.3 (5.9)	23.2 (5.7)	23.2 (5.8)	23.9 (5.3)	ns
Ca (meq/100 g)	3.0 (1.0)	3.7 (1.2)	3.7 (1.6)	7.6 (6.8)	ns (KW)
Mg (meq/100 g)	0.37 (0.18)	0.34 (0.24)	0.48 (0.39)	1.21 (1.10)	ns (KW)
K (meq/100 g)	0.35 (0.11)	0.28 (0.09)	0.32 (0.18)	0.38 (0.15)	ns
Base sat (%)	20.0 (6.1)	19.9 (7.3)	22.1 (14.5)	38.2 (27.1)	ns (KW)
MB-N (mg N/kg)	69.9 (28.7)a	76.1 (18.4)a	73.8 (16.1)a	176.5 (48.3)b	$p = 0.02$ (KW)
MB-N/Nt (%)	1.70 (0.69)a	1.58 (0.42)a	1.85 (0.75)a	2.95 (0.52)b	$p = 0.005$

Letters indicate significant differences ($p < 0.05$) based on Tukey's (parametric) and Duncan's *C* (nonparametric) multiple comparison tests. ns, nonsignificant differences; *n*, number of replicate plots for each group; KW, Kruskal–Wallis.

Table 2. Average and standard deviation of soil variables determined for plots in three fallow stages, cultivated plots, and NCP areas in 1999.

	Cultivated ($n = 4$)	*Early* ($n = 12$)	*Intermediate* ($n = 11$)	*Late* ($n = 9$)	*NCP* ($n = 4$)	*ANOVA* ($\alpha = 0.05$)
pH	4.43 (0.27)a	4.27 (0.21)a	4.59 (0.33)ab	4.72 (0.28)b	4.91 (0.10)b	($p = 0.001$)
Ct (%)	8.0 (2.0)	9.2 (2.4)	10.1 (3.2)	9.8 (3.9)	11.9 (2.7)	ns
Nt (%)	0.42 (0.09)	0.50 (0.12)	0.49 (0.13)	0.47 (0.14)	0.56 (0.14)	ns
C/N	19.0 (0.9)	19.1 (6.6)	21.0 (5.8)	22.5 (11.0)	21.8 (3.5)	ns (KW)
CEC (meq/100 g)	24.1 (5.4)	22.8 (4.4)	20.7 (5.4)	19.6 (6.2)	23.7 (5.7)	ns
Ca (meq/100 g)	4.2 (0.7)	2.8 (2.6)	3.7 (1.7)	4.6 (2.1)	5.6 (1.4)	ns
Mg (meq/100 g)	0.47 (0.19)a	0.31 (0.32)a	0.50 (0.32)b	0.61 (0.36)c	1.71 (0.50)d	$p = 0.0001$
K (meq/100 g)	1.15 (0.94)	1.03 (0.75)	0.88 (0.80)	0.98 (0.60)	1.43 (1.66)	ns (KW)
Base sat (%)	26.5 (13.5)	18.0 (13.5)	25.7 (11.0)	35.7 (19.3)	38.2 (7.0)	ns
MB-N (mg N/kg)	76.7(22.8)a	75.2 (27.3)a	84.1(26.5)a	78.7(23.1)a	157.9 (27.2)b	$p = 0.0001$
MB-N/Nt (%)	1.82 (0.27)a	1.54(0.52)a	1.74(0.37)a	1.71(0.30)a	2.93(0.52)b	$p = 0.01$ (KW)

Letters indicate significant differences ($p < 0.05$) based on Tukey's (parametric) and Duncan's *C* (nonparametric) multiple comparison tests. ns, nonsignificant differences; *n*, number of replicate plots for each group; KW, Kruskal–Wallis.

nondisturbed páramo areas. However, no significant differences in this variable were detected in the plots that where still in fallow after 3 years. The decrease in pH in the cultivated plots confirms the strong acidification processes triggered by cropping. On the other hand, K values in 1999 were consistently larger than those measured in 1996 ($p < 0.001$, GLM test, no significant interaction term between sampling year and land use), with higher average percent variations than for pH. In this case, the increase in K was significant (paired *t* test) in all groups except for the NCP.

Multivariate Analysis

The integrated analysis of all soil variables in the 40 plots, including both sampling dates, using PCA (Table 4, Fig. 2), shows a strong positive association between base saturation, Ca, Mg, and pH with the first ordination axis (representing 31.5% of total variance). This first axis is negatively associated with total C, C/N ratio, and CEC. The second principal component, accounting for 25.3% of total variation, had a strong positive association with total C and N, CEC, and MB-N. In the third axis, C/N and pH are the most important variables (Table 4). Hence, the first two axes of variation seem to be responding to two relatively independent gradients, one associated with variations in pH and the availability of soil bivalent cations (Ca, Mg) and the other related to changes in soil organic matter, MB-N, and CEC.

Noncultivated páramo plots (triangles in Fig. 2) were located in the upper-right quadrant of the ordination, strongly associated with high values for MB-N, Ca, Mg, base saturation, pH, total C, and N (Fig. 2). The ordination scores on the first and second principal components were significantly different for plots in different land use classes (two-way ANOVA, $p < 0.001$), with no significant effect of sampling year ($p = 0.973$) and no significant interaction term ($p = 0.595$). A Tukey's honest test confirmed that páramo plots had significantly different scores than successional plots, but the seral stages did not show significantly different scores among themselves.

Table 3. Average and standard deviation of the percent variation between 1996 and 1999 for soil variables for plots in three fallow stages, under cultivation, cultivated and left in fallow, and NCP areas.

	Cultivated ($n = 4$)	*Cultivated (1999 Early)* ($n = 12$)	*Early* ($n = 8$)	*Intermediate* ($n = 6$)	*Late* ($n = 6$)	*NCP* ($n = 4$)	*GLM*	
							SY	*SY × LU*
pH	−9.9 (2.9)*	−9.1 (5.1)*	−3.5 (5.6)	−2.2 (3.5)	−3.4 (5.4)	−4.9 (1.1)*	$p < 0.001$	$p = 0.03$
Ct	4.3 (15.2)	−5.3 (18.4)	15.2 (34.2)	14.6 (12.6)	46.1 (90.6)	9.3 (14.1)	ns	ns
Nt	1.0 (8.0)	0.9 (21.3)	16.9 (19.2)	5.2 (7.4)	18.7 (44.5)	−6.7 (15.1)	ns	ns
C/N	2.9 (7.7)	−0.3 (36.2)	0.0 (32.9)	9.3 (14.6)	34.7 (80.6)	18.5 (16.2)	ns	ns
CEC	20.5 (24.0)	6.1 (52.1)	2.2 (26.0)	−7.1 (11.4)	−12.4 (23.2)	3.5 (34.9)	ns	ns
Ca	19.5 (13.5)	−22.8 (52.7)	35.8 (90.7)	20.9 (30.9)	46.9 (142.2)	17.6 (77.7)	ns	ns
Mg	62.6 (68.3)	3.1 (45.0)	57.5 (93.3)	36.9 (36.2)	40.6 (91.4)	122.0 (125.6)	ns	ns
K	336.6 (345.9)*	266.6 (318.0)*	218.7(304.6)*	90.0 (105.1)*	447.6(451.7)*	522.8 (955.7)	$p < 0.001$	ns
Base sat	19.5 (35.0)	−4.6 (42.0)	40.9 (61.1)	35.3 (46.8)	91.8 (150.6)	51.6 (120.3)	ns	ns
MB-N	4.6 (27.9)	4.9 (29.9)	20.0 (60.2)	118.2 (289.3)	9.1 (43.2)	−6.9 (19.6)	ns	ns

n, number of replicate plots for each group; Cultivated, plots incorporated into cultivation still being cultivated in 1999; Cultivated (1999 Early) = plots incorporated into cultivation but early successional by 1999; Early, Intermediate, and Late, plots in that seral stage in 1996 still in succession after 3 years; ns, nonsignificant differences. Significance of a GLM for repeated measurements test indicated for sampling year (SY) and the interaction term between sampling year and land use (SY × LU). Significant differences ($p < 0.05$) between the two sampling dates for each group of plots (paired *t* test) are indicated *.

Table 4. Pearson correlation coefficients for each soil variable for the first three axes of variation of a PCA (centered and standardized) for the 40 plots sampled in 1996 and 1999.

	Axis		
	First	*Second*	*Third*
pH	0.575**	−0.038	0.569**
Ct	−0.469**	0.716**	0.406**
Nt	−0.275**	0.781**	−0.305**
C/N	−0.326**	0.077*	0.853**
CEC	−0.320**	0.689**	−0.144
Ca	0.812**	0.397*	−0.038
Mg	0.837**	0.369*	0.103
K	0.182*	−0.021	−0.210
Base sat	0.928**	0.001	0.002
MB-N	0.240	0.793**	−0.029

Significant correlations are indicated * $p < 0.05$; ** $p < 0.01$.

To evaluate more directly the response of soil variables to changes during succession, we repeated the PCA excluding the NCP plots, which had a strong influence on the ordination. As in the previous case, the position of the plots along the first three components did not differ between fallow stages, nor between sampling years (two-way ANOVA).

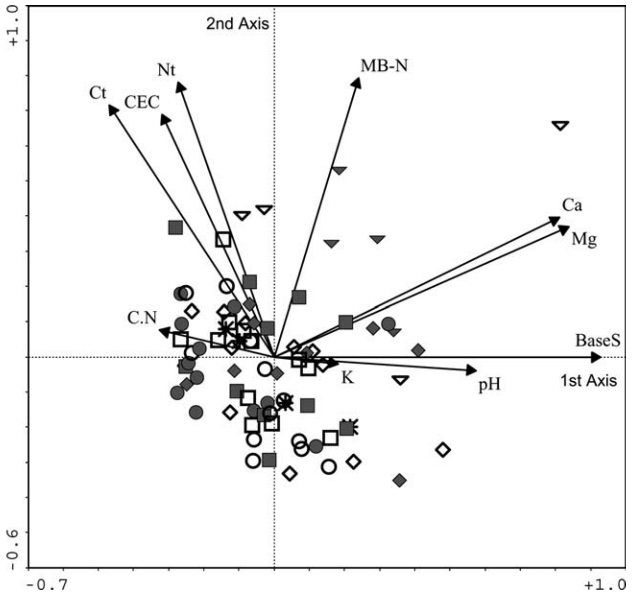

Figure 2. Ordination biplot (PCA, centered and standardized) of soil variables in the 40 studied plots sampled in 1996 and 1999. The first and second axes are presented, absorbing 31.5 and 25.3% of the total variance, respectively. Open symbols: values in 1996; closed symbols: values in 1999. Circles, early-succession plots; squares, intermediate-succession plots; diamonds, late-succession plots; triangles, NCP areas; stars, cultivated plots.

Discussion

Synchronic Analysis

In this study, the synchronic approach revealed that two variables, pH and Mg, displayed significant increases during the fallow phase of the agricultural cycle, suggesting these as sensitive indicators of successional status despite the very heterogeneous environment where this succession takes place. Abadín et al. (2002) also reported a decrease in soil acidity during the fallow period in another chronosequence of the same area, whereas Ferwerda (1987), analyzing a chronosequence in a Colombian páramo, found a significant increase in soil Mg. Other studies of secondary succession after potato agriculture in the high tropical Andes did not reveal significant variations in standard soil properties (Hervé 1994; Aranguren & Monasterio 1997; Jaimes 2000; Pestalozzi 2000). In all previous studies that included a large number of replicate plots, there was high between-plot variability, complicating the identification of successional trends.

The successional changes in pH and Mg found in this study could be associated with the restoration of soil fertility during the fallow period. As pH increases, the concentration of H^+ and Al^{+3} in the soil complex decreases, contributing to enhanced nutrient retention while decreasing aluminum toxicity. The magnitude of the decrease in pH, comparing the natural ecosystem to the cultivated plots, was 0.48 units for 1999, similar to the decrease of 0.50 reported by Abadín et al. (2002). The restoration pH during the fallow period was 0.29 units for 1999 (comparing cultivated and late-successional plots) and 0.15 units for 1996 (comparing early- and late-successional plots). These results indicate that during the agricultural cycle, strong acidifying processes occur (probably due to the stimulation of mineralization and nitrification or changes in rates of plant uptake or nutrient losses), whereas during the fallow phase, the buffering index of the soil is progressively but not completely restored. The acidification of the soil induced by cultivation can be interpreted as a temporal decoupling of the ion cycle, as a net flow of ions is connected with the production or consumption of protons (Ulrich 1987).

Even though microbial biomass has been suggested as an early and sensitive indicator of changes in soil organic matter quality and soil fertility (Powlson et al. 1987; Coleman et al. 1989; Connell et al. 1995; Turco et al. 1994; Gregorich et al. 1995; Carter 2002), we did not find significant changes during the first 12 years of succession. As with the other soil parameters evaluated, there was a very high variability in MB-N values within each fallow age class. Other studies using a synchronic approach in the high tropical Andes have found a significant increase in MB-N but evaluated longer fallow times. Whereas Sarmiento and Bottner (2002) reported an increase comparing two adjacent and relatively homogeneous plots in the same area (a first-year fallow plot and a plot with 16 years), Jaimes (2000) reported significant increases only after 12 years in a similar but less heterogeneous long-fallow system in the Colombian páramo. In an Indian mountain system, Arunachalam and Pandey (2003) also detected significant changes in MB-N, this time after 7 years of fallow, but in soils with much lower soil organic matter content.

These results suggest that in the high tropical Andes, the response time of microbial biomass is too slow to explain changes in soil fertility within the fallow times normally used by farmers (which rarely extend beyond 9 years). However, the high spatial heterogeneity could also contribute to mask successional trends using synchronic approaches (Sarmiento & Llambí 2005). In addition, other factors related to land use history could be important sources of between-plot variation, including differences in grazing regimes and the number of cultivation–fallow cycles experienced by different plots. For example, it could be hypothesized that plots incorporated more recently into fallow agriculture could show higher microbial biomass than those that have been cultivated several times. These are important questions for future research.

In summary, the synchronic analysis suggests that the size variation of specific soil components (e.g., soil organic matter or mineral nutrients) is not a good indicator of successional soil fertility restoration. This contrasts with the successional increases in these soil characteristics reported by several studies in long-fallow systems in the lowland tropics (Aweto 1981; Saldariaga et al. 1988). In the highland tropics, the lack of a clear successional response of variables normally associated with soil fertility restoration could be related to (1) high spatial and land use heterogeneity, (2) the relatively short duration of the fallow period, (3) the small expected successional variations compared to the large size of several important soil components (e.g., soil organic matter), and (4) the low accumulation of available nutrients in the soil, probably due to their absorption and accumulation in the successional vegetation (see Uhl 1987, in lowland tropical forests and Montilla et al. 2002, in our study area). An alternative strategy to monitor the soil status could be to analyze key processes related to nutrient cycling and its regulation, such as mineralization, nitrification, denitrification, volatilization, and nutrient leaching. Following this approach, Abadín et al. (2002) found that the δ^{15}N values of the soil organic matter decreased steadily along a crop–fallow chronosequence. The δ^{15}N is an indicator of the extent to which N cycling is closed; its successional decrease suggests a change from "open" to "closed" N cycling. This change toward a more conservative N cycling during early secondary succession has also been reported in lowland tropical forests (Davidson et al. 2007).

Diachronic Analysis of Succession

Contrary to our expectations, the analysis of temporal changes in soil characteristics within each plot after 3 years (diachronic analysis) did not show consistent trends for most variables, including MB-N. Hence, even after eliminating the effect of between-plot heterogeneity, we were not able to identify sensitive indicators of the successional restoration of soil fertility within this relatively short timescale. The only exceptions were pH and K, which showed consistent temporal trends between the two sampling dates. Soil pH was consistently lower in cultivated plots in 1999 and did not show significant differences in successional plots (where the longer-term synchronic analysis showed pH to increase throughout the fallow period). Soil pH also displayed a significant decrease in the noncultivated areas. This suggests that there are other sources of interannual variability, unrelated to agricultural management or successional processes, responsible for this increase in soil acidity. Consistent with this idea, Ulrich (1987) points out that climatic variability can cause important oscillation in soil pH by differentially affecting soil processes such as in mineralization and plant uptake.

One important source of temporal variation could have been climatic differences between sampling years; precipitation during the 2 months prior to the sampling days was 342 mm in 1996 compared to 203 mm in 1999. Lower soil moisture in 1999 could be related to the decrease in pH and microbial biomass observed for this year in the noncultivated areas. We can speculate that nitrification was stimulated by lower moisture (this process requires an adequate oxygen provision), and as a consequence of nitrification, pH could have decreased in 1999.

Other factors that could have an effect on soil chemical and biological properties, and therefore complicate the interpretation of the diachronic analyses, include (1) a possible variable grazing load experienced by the plots between both sampling years, as grazing can have a significant effect on edaphic properties, reducing plant biomass and incorporating feces and urine into the soil, and (2) high within-plot heterogeneity, which could imply that the number of sampling points necessary for obtaining a representative composite sample is higher than the 10 points used here.

Hargreaves et al. (2003), analyzing the sensitivity of microbial biomass to changes in soil management, concluded that the high spatial variability associated with this parameter makes it necessary to use very large numbers of replicates to obtain representative samples (350 replicates per plot in their study). These authors indicate that to be able to detect clear responses, changes in the quality and quantity of organic inputs into the soil must be large. In the case of these high mountain ecosystems, the magnitude of the soil organic matter component and its high relative stability could be linked to the limitations on decomposition rates imposed by low temperatures and low-quality litter inputs into the soil (resulting from the scleromorphic nature of the dominant plant species). This could result in a low sensitivity of microbial biomass to successionally induced changes.

Multivariate Analysis

The results of the PCA suggest that other sources of variation independent of successional time (e.g., geomorphology and topography; see Llambí & Sarmiento 1998) could be important in explaining differences in soil characteristics between plots. The main gradient of variation (first principal component) is associated with changes between plots in base saturation, Ca, Mg, and pH (all being positively associated), whereas the second principal component is mainly related with changes in soil organic C and N, CEC, and MB-N. This suggests that total soil organic matter quantity could be an important determinant of the size of the microbial component and for the maintenance of the CEC of these soils. In addition, the negative correlation of total organic C with the first principal component suggests that plots with high soil organic matter levels tend to show relatively low pH values, which could contribute to the loss of Ca and Mg from the cation exchange complex in these areas.

Impact of Long-Fallow Agriculture on Páramo Soils

Our results indicate that the incorporation of natural páramo areas into long-fallow agriculture produces a very clear decrease of MB-N (to about half the original values), accompanied by less marked reduction in total N, Mg, and pH. This suggests that microbial biomass is a particularly sensitive indicator of agricultural disturbance in high tropical mountain ecosystems. Woomer et al. (1994) also reported significant decreases of microbial biomass when comparing cultivated versus natural forest sites across the lowland tropics. These changes could be linked to reduced natural soil fertility, given the importance of MB-N in regulating N immobilization–mineralization dynamics and synchronizing N availability with crop demands (Sarmiento 1995). As discussed above, these negative effects of cultivation on páramo soil properties do not seem to be reversed during the fallow times currently used by the farmers. Hence, the results presented here shed doubts on the long-assumed sustainability of long-fallow agricultural systems in the region. However, the stability of soil organic C in the páramo, with no significant changes after cultivation, suggests that some important properties linked with the magnitude of the soil organic matter component (e.g., water holding capacity, C accumulation, low run-off, and erosion rates) could be relatively resistant to agricultural disturbance.

Conclusions

Identifying sensitive soil restoration indicators is important for improving agricultural management and for the design of ecosystem restoration strategies and integrated monitoring programs. A sensitive indicator can provide farmers with a simple method for evaluating the optimum time for incorporating fallow plots into cultivation, thereby increasing crop productivity. In addition, this research contributes to the identification of strategies to accelerate restoration processes for agricultural production or conservation purposes.

Our results in the high tropical Andes show that potato cultivation in the páramo produces a significant decrease in soil pH that is progressively restored during the fallow period. These changes were detectable in the heterogeneous matrix, suggesting pH as a soil restoration indicator under such conditions, as it possesses the characteristics of being integrative, sensitive, predictable, and easy to measure. However, the increase in soil acidity in the NCP between the two sampling years indicates that pH is also sensitive to other sources of variation unrelated to successional processes such as interannual climatic variability. Other standard soil chemical characteristics were not sensitive to successional changes in soil functioning. Microbial biomass was a good indicator of agricultural disturbance but did not respond to successional changes in a consistent manner. This and other studies in the highland tropics have shown that the size of several important soil components such as total soil organic matter and mineral nutrients is not a sensitive restoration indicator (either because they are too big for detecting significant changes or too dynamic). We recommend focusing on nutrient cycling processes instead of soil component sizes as an alternative approach. Finally, the combined use of synchronic and diachronic approaches did not fully overcome the problem of high spatial heterogeneity. Either the time interval of 3 years was not long enough to detect diachronic changes or the within-plot variability was too high, suggesting the need for a more intensive sampling strategy. Hence, our results illustrate the challenges faced when monitoring soil restoration in heterogeneous mountain ecosystems, pointing to the need for extensive spatial replication and long-term sampling programs in permanent plots.

Implications for Practice

- Soil pH is a sensitive, easy-to-measure and low-cost indicator for farmers interested in evaluating the soil restoration status of successional plots and assessing the time for reincorporating fallow areas into cultivation.
- For practitioners interested in evaluating the conservation status of páramo areas within the framework of conservation or restoration projects, microbial biomass is recommended as a sensitive soil disturbance indicator.
- The lack of successional response of key soil components, such as microbial biomass, within the fallow times used by farmers, questions the viability of long-fallow agriculture in the páramos. Concentrating production in less extensive areas through sustainable intensification could be a better alternative for agricultural production as well as páramo conservation.

- Monitoring and managing these highly heterogeneous mountain ecosystems is a challenging task, as soil properties normally used as indicators are not time sensitive during the first 12 years of succession. Hence, spatiotemporal heterogeneity needs to be explicitly considered in the design of sustainable management and conservation programs.
- The large differences between the natural páramo and plots incorporated into long-fallow agriculture in terms of soil properties associated with soil fertility (e.g., microbial biomass) have probably been one of the key incentives for farmers to extend the agricultural frontier to exploit the more favorable soil conditions of nondisturbed areas. This has important implications for land use planning for páramo conservation.

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