

Nutrient stocks and phosphorus fractions in mountain soils of Southern Ecuador after conversion of forest to pasture

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Abstract Understanding pasture degradation processes is the key for sustainable land management in the tropical mountain rainforest region of the South Ecuadorian Andes. We estimated the stocks of total carbon and nutrients, microbial biomass and different P fractions along a gradient of land-uses that is typical of the eastern escarpment of the Cordillera Real i.e., old-growth evergreen lower montane forest, active pastures (17 and 50 years-old), abandoned pastures 10 and 20 years old with bracken fern or successional vegetation. Conversion of forest to pasture by slash-and-burn increased the stocks of SOC, TN, P and S in mineral topsoil of active pasture sites. Microbial growth in pasture soils was enhanced by improved availability of nutrients, C:N ratio, and increased soil pH. Up to 39 % of the total P in mineral soil was stored in the microbial biomass indicating its importance as a dynamic, easily available P reservoir at all sites. At a 17 years-old pasture the stock of NH_4F extractable organic P, which is considered to be mineralisable in the short-term, was twice as high as in all other soils. The importance of the NaOH extractable organic P

pool increased with pasture age. Pasture degradation was accelerated by a decline of this P stock, which is essential for the long-term P supply. Stocks of microbial biomass, total N and S had returned to forest levels 10 years after pasture abandonment; soil pH and total P 20 years after growth of successional bush vegetation. Only the C:N ratio increased above forest level indicating an ongoing loss of N after 20 years. Soil nutrient depletion and microbial biomass decline enforced the degradation of pastures on the investigated Cambisol sites.

Keywords Land-use change · Soil organic matter · Soil microbial biomass · Tropical soils · Phosphorus availability · Sulphur

Introduction

In South America the conversion of tropical forests to agricultural land is the main factor for the worldwide highest net annual loss of forests (FAO 2010). Fires are set frequently in tropical regions to remove the slashed forest and to prepare the sites for crop or pasture establishment (Nye and Greenland 1960). This slash-and-burn practice is also widespread in the South Ecuadorian Andes. In the valley of Rio San Francisco (study area), about half of the natural montane forest on slopes below 2,200 m asl has been converted to

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pasture land over the last 50 years (Göttlicher et al. 2009; pers. com. M. Richter). About 2/3 of the pasture area has been abandoned due to the suppression of the pasture grass *Setaria sphacelata* by invasion of the tropical bracken fern *Pteridium arachnoideum* (Beck et al. 2008). The sprouting of *P. arachnoideum* was observed a few weeks after burning the sites for pasture establishment. To eliminate the growing bracken fern, farmers repeatedly set fires of low to medium intensity. However, this management practice favours the growth of bracken fern (Hartig and Beck 2003) due to the following reasons: (i) rhizomes of *Pteridium arachnoideum* are heat tolerant (up to 70 °C); (ii) the production of fronds from short shoots is enhanced at temperatures between 40 and 60 °C; and (iii) the lifespan of the fronds produced directly after fire is longer compared to the lifespan of fronds produced without fire (Roos et al. 2010). Repeated burning is one of the important factors leading to pasture degradation in the study area. In addition, soil degradation may be contributing to pasture degradation. However, this topic has not been investigated systematically so far.

Several studies conducted in Latin America have shown that pasture degradation is not always accompanied by a decline in soil quality (Feigl et al. 2006; Müller et al. 2004). Insufficient and/or inappropriate weed control, especially during the initial stages of pasture establishment led to agricultural degradation of pastures in the Western Amazon region of Brazil (Feigl et al. 2006). However, although weeds competed with grass for nutrients and light, the capacity of the soils to provide nutrients for the production of plant biomass was not decreased (Feigl et al. 2006; Müller et al. 2004). Pastures were degraded but soils were not. Other studies of the Brazilian Amazon (Numata et al. 2007) and Costa Rica (Cleveland et al. 2003) reported the decline of soil quality as a key for decreasing pasture productivity, subsequent weed infestation and the progressive decrease of forage quality. The reasons for the discrepancies in the relationship between weed encroachment and soil nutrient status in different study areas remain unclear.

If soil degradation proceeds with weed encroachment, depleted soil nutrient stocks will be an additional difficulty for sustainable land management. Throughout the tropics successful reforestation on abandoned pastures is mainly restricted by an inappropriate soil nutrient status and the competition for

light. In the lowland moist forest region of Colombia, forest regeneration on abandoned pastures is mainly limited by low levels of exchangeable Ca, Mg and P (Aide and Cavellier 1994). On abandoned pastures in Southern Ecuador (Günter et al. 2009) as well as in Puerto Rico (Aide et al. 1995), fern and bush vegetation hinders the re-establishment of light demanding native tree species. Understanding the interactions between burning, invasion of pioneer plants (fern, bushes) and soil biogeochemical processes is crucial for maintaining existing pastures as well as for re-establishing or reforesting of abandoned pastures.

Burning of slashed forests leads to a partial loss of carbon and nutrients to the atmosphere and to a redistribution of carbon and nutrients within the terrestrial ecosystem. Depending on fire severity between 29 and 80 % of C stored in the pre-fire aboveground biomass is lost together with main nutrient elements like N, S, K, Ca and Mg (Kauffman et al. 2009). However, the extent of nutrient loss varies considerably. After burning of a tropical lowland rainforest almost all K, Ca and Mg present in the vegetation was stored in the pool of exchangeable cations in the mineral topsoil (Nye and Greenland 1964). The availability of nutrients in the soil increases immediately after burning. In acidic, highly weathered tropical soils an increase of P availability is particularly of interest, since P is often a deficient nutrient for plants. In the study area of Southern Ecuador the content of total P in the soils of the tropical montane forest is low (Günter et al. 2009; Makeschin et al. 2008; Wilcke et al. 2003). A substantial part of the soil P (33–82 %) is organic P which is only available to plants after mineralisation to inorganic $\text{PO}_4\text{-P}$ (Chen et al. 2008; López-Gutiérrez et al. 2004; Rivaie et al. 2008). Burning enhanced the mineralisation of organic P in soils of the Amazonian lowland due to increases in soil pH (McGrath et al. 2001). Further mechanisms explaining an increase of inorganic P after burning are fire effects on the solubilisation of residual inorganic P and ash input (Cade-Menun et al. 2000). However, these post-burning pulses of inorganic P seem to be short-lived and decrease with increasing time after forest to pasture conversion (Cleveland et al. 2003; García-Montiel et al. 2000; McGrath et al. 2001; Townsend et al. 2002). García-Montiel et al. (2000) showed 3–5 years after pasture establishment by slash-and-

burn, that phosphorus was transformed into the less available P forms such as occluded P and organic P. In 20 years-old pasture soils more organic P was present than in forest soils (García-Montiel et al. 2000). Since Ferralsols, Oxisols and Ultisols are the main soil types in the Amazonian lowland region, these results may not be directly transferable to the tropical mountain rainforest region in Southern Ecuador. There, Cambisols frequently occur on pasture sites.

The aim of this study was to assess the effect of land-use change on (i) total stocks of organic C and nutrients (N, P, S), (ii) the pool of microbial biomass C (MBC) and nutrients stored in the microbial biomass (N, P) and (iii) P stored in fractions of different availability in topsoil of the mountain rainforest region of Southern Ecuador. Thereby, we wanted to determine whether nutrient depletions of soils are connected with the degradation of pastures. Five sites (~2,000 m asl) covering the gradient of land-use that is typical of the study area were examined: old-growth evergreen lower montane forest, 17 and 50 years-old active pastures, about 10 years-old abandoned pasture with bracken as dominant plant species and about 20 years-old abandoned pasture with vegetation succession of a variety of herbs and shrubs.

Materials and methods

Sites and soil sampling

The study sites in Southern Ecuador are located close to the “Estación Científica San Francisco”, about halfway between the provincial capitals Loja and Zamora, in the Cordillera Real, an Eastern range of the South Ecuadorian Andes. The climate is characterised by a mean annual air temperature of 15.3 °C and a mean annual precipitation of 2,176 mm (Bendix et al. 2006). The land-use history was reconstructed using ortho-aerial photographs and Landsat Enhanced Thematic Mapper data from 1987 and 2001 (Göttlicher et al. 2009; Meyer 2010), interviews with local farmers, knowledge of experts active in the area for more than 10 years (Beck and Müller-Hohenstein 2001; Beck et al. 2008), and our own observations. It was impossible to find replicate sites of similar age with the same history of burning and a priori site conditions. To overcome this problem and to derive

reliable conclusions from the data, all sites included in the study had to encompass a large area. Hence, sites were selected according to the following criteria (i) most homogeneous expansion on an area of at least 0.25 ha (up to 0.5 ha), (ii) most reliable reconstruction of land-use history, (iii) proximity to the other sites, and (iv) permission of landowner for soil sampling. Based on analysis of non-weathered rock, weathered rock and mineral soil, Makeschin et al. (2008) showed that selected sites are comparable in a priori soil mineralogy. Clay schists, metasilstones, sandstones and quartzites are the soil parent materials (Makeschin et al. 2008). In November 2007 soil sampling was conducted along a land-use gradient of old-growth evergreen lower montane forest (0.25 ha)—17 years-old pasture (0.5 ha)—50 years-old pasture (0.25 ha)—abandoned pasture (0.5 ha)—succession (0.5 ha) at an elevation of about 2,000 m asl (Table 1). Slopes at all sites had a gradient of about 25°–30°. The topographical position of all sites was similar. The soil types were classified as Cambisols according to WRB 2006 (FAO 2006) (for details see Table 1). At the 50 years-old pasture, soils showed a thick Ah horizon (>20 cm) and therefore were classified as Mollic Cambic Umbrisols. At all sites the soil texture was dominated by silt (Table 2).

The site characteristics of old-growth forest, 17 years-old pasture and abandoned pasture are described in more detail in Potthast et al. (2011), those of 50 years-old pasture and succession in Makeschin et al. (2008). The old-growth forest had been converted to pasture by planting the grass *Setaria sphacelata* after clear cut and slash burn 17 years or 50 years prior to soil sampling, respectively. *S. sphacelata* was the dominant plant species which covered more than 95 % of the area (Table 1). Leguminous plant species did not occur in pastures (pers. com. J. Gawlik). No further agricultural practices, apart from cutting and burning, were applied by the farmers on pasture sites. The 17 years-old pasture had not been burnt since the initial clearing in 1990 (pers. com. of the local farmer family). According to the local farmer no fire had occurred at the 50 years-old site since 1990. Fire frequency during the 1960–1990 s is unknown. Livestock density of dairy cattle was one cow per ha. A rotational grazing system is used by farmers based on grazing periods of 15–30 days followed by a period of 2–3 months for pasture regrowth (Schneider 2000). The 50-years old

Table 1 Site characteristics and land-use history

	Elevation (m asl)	Coordinates	Soil type (WRB 2006)	Vegetation	Slash- and- burn	Repeated fire	Last fire
Forest	1,890	03°58'35"S 79°04'65"W	Folic Endogleyic Cambisol (Alumic, Humic, Dystric, Siltic)	Old-growth, evergreen montane forest with high species diversity: <i>Graffenrieda emarginata</i> and <i>Miconia</i> (Melastomataceae, 31 %) ^a , <i>Ocotea</i> (Lauraceae, 13 %) ^a , <i>Alchornea</i> (Euphorbiaceae) ^a , <i>Palicourea</i> (Rubiaceae) ^a , <i>Clethra</i> (Clethraceae) ^a	No	No	
Pasture 17a	1,930	03°57'26"S 79°02'19"W	Haplic Cambisol (Humic, Siltic)	<i>Setaria sphacelata</i> (>99 %)	Yes	No	1990
Pasture 50a	2,080	03°57'53"S 79°04'37"W	Mollic Cambic Umbrisol (Humic, Siltic)	<i>Setaria sphacelata</i> (>95 %)	Yes	Yes	Before 1990
Abandoned Pasture	2,100	03°57'51"S 79°04'37"W	Haplic Cambisol (Humic, Siltic)	<i>Pteridium arachnoideum</i> (approx. 85 %) <i>Setaria sphacelata</i> (approx. 15 %)	Yes	Yes	2004
Succession	2,150	03°58'30"S 79°05'19"W	Folic Cambisol (Alumic, Humic, Dystric, Siltic)	<i>Pteridium arachnoideum</i> (approx. 50 %) <i>Baccharis latifolia</i> and <i>Ageratina</i> <i>dendroides</i> (Asteraceae) ^b , <i>Monochaetum lineatum</i> (Melastomataceae) ^b	Yes	Yes	Before 1992

^a Moser (2008)^b Hartig and Beck (2003)

pasture was included, since it is one of the oldest pastures found in the region representing an end-member of land use, which was not burned at least during the last 17 years (Table 1). The abandoned pasture was a former *S. sphacelata* pasture, which had been abandoned 10 years ago due to the invasion of the tropical bracken fern *P. arachnoideum*. The area had been burned irregularly during the past. The last fire occurred in 2004 (pers. observation). Since about 1990 the sites under succession had been abandoned due to severe infestation by bracken fern. Now the vegetation was dominated by different herb and shrub species mainly of the families *Asteraceae* and *Melastomataceae* (Hartig and Beck 2003; Beck et al. 2008) (see also Table 1). All these sites set the frame for the range of changes in land use in the study area. In the natural, old-growth forest the taxonomic diversity of

trees, shrubs, herbs and epiphytes was extremely high. Dominant tree species belonged to the genera *Lauraceae*, *Rubiaceae* and *Melastomataceae* (Homeier and Werner 2007; Moser 2008). The forest was classified as evergreen lower montane forest.

The distance of all sites selected for soil sampling was within 4 km from the Estación Científica San Francisco. Soil samples were taken with a soil auger (diameter: 6 cm) at five randomly chosen replicate plots for each land-use type from 0 to 5, 5 to 10 and 10 to 20 cm depth (Makeschin et al. 2008; Potthast et al. 2011). In addition, at forest and succession sites samples from the Oi and OeOa layer were collected with a 100 cm² frame. A mixed soil sample consisting of 8–10 sub-samples was taken at replicate plots. All plots were situated more than 10 m apart from each other and the subsamples per plot were about 3 m

Table 2 Chemical and physical soil characteristics

	Sand (%) ^a	Silt (%) ^a	Fine soil density (g cm ⁻²)/(g cm ⁻³)	pH (H ₂ O)	SOC (g kg ⁻¹)	C:N
Forest						
Oi	nd	nd	0.11 (0.02)	5.8 (0.3)	461.6 (18.8)	26.2 (2.4)
OeOa	nd	nd	0.41 (0.13)	4.9 (0.7)	407.7 (38.0)	19.0 (1.2)
0–5 cm	32.6 (5.7) ^a	45.7 (4.3) ^a	0.49 (0.12) ^a	4.2 (0.4) ^a	85.3 (24.2) ^a	16.6 (0.5) ^{bc}
5–10 cm	29.9 (7.2) ^a	43.3 (6.1) ^a	0.67 (0.08) ^a	4.2 (0.4) ^a	62.8 (14.6) ^a	16.8 (1.6) ^b
10–20 cm	29.7 (8.9) ^a	46.4 (6.2) ^a	0.69 (0.24) ^a	4.3 (0.4) ^a	54.7 (8.6) ^a	18.5 (1.1) ^b
Pasture 17a						
0–5 cm	28.5 (9.0) ^a	37.8 (7.8) ^a	0.43 (0.07) ^a	5.3 (0.1) ^c	115.7 (18.8) ^b	13.3 (0.7) ^a
5–10 cm	28.8 (5.1) ^a	39.7 (7.0) ^a	0.74 (0.06) ^a	5.3 (0.2) ^b	55.1 (6.2) ^a	12.5 (0.5) ^a
10–20 cm	28.9 (7.7) ^a	40.7 (9.1) ^a	0.93 (0.09) ^{ab}	5.1 (0.3) ^c	36.1 (5.2) ^a	13.0 (0.4) ^a
Pasture 50a						
0–5 cm			0.59 (0.10) ^a	4.6 (0.4) ^b	116.4 (31.7) ^b	15.5 (1.4) ^{ab}
5–10 cm	29.1 (3.3)	46.4 (1.4)	0.93 (0.25) ^a	4.6 (0.3) ^a	65.2 (21.8) ^a	16.4 (1.3) ^b
10–20 cm	27.2 (8.7) ^a	48.7 (4.1) ^a	0.99 (0.28) ^b	4.6 (0.2) ^{ab}	39.0 (16.0) ^a	18.6 (2.6) ^b
Abandoned pasture						
0–5 cm	29.8 (1.5) ^a	41.4 (7.0) ^a	0.58 (0.15) ^a	5.2 (0.4) ^c	79.5 (14.1) ^a	17.9 (1.4) ^c
5–10 cm	28.7 (2.9) ^a	45.2 (2.0) ^a	0.76 (0.15) ^a	5.1 (0.3) ^b	60.4 (7.3) ^a	18.5 (1.1) ^b
10–20 cm	28.2 (2.1) ^a	46.1 (2.8) ^a	0.92 (0.18) ^{ab}	4.9 (0.2) ^{bc}	48.1 (8.7) ^a	19.8 (1.3) ^b
Succession						
Oi	nd	nd	0.02 (0.01)	5.3 (0.3)	449.7 (104.6)	45.0 (5.2)
OeOa	nd	nd	0.50 (0.21)	4.1 (0.2)	370.8 (72.5)	23.0 (1.7)
0–5 cm			0.60 (0.12) ^a	4.0 (0.1) ^a	82.8 (28.5) ^{ab}	24.4 (0.8) ^d
5–10 cm	21.5 (8.9)	53.9 (6.7)	0.93 (0.24) ^a	4.2 (0.1) ^a	57.3 (15.1) ^a	25.3 (1.2) ^c
10–20 cm	22.1 (9.9) ^a	56.2 (5.2) ^b	1.10 (0.18) ^b	4.5 (0.2) ^{ab}	32.0 (14.8) ^a	25.4 (1.9) ^c

Means with standard deviations in parenthesis, *different letters* within one column indicate significant differences at $p < 0.05$ between the study sites for the respective soil depth interval, nd: not detectable, $n = 5$

^a For Pasture 50a and Succession only mean values for 0–10 cm are available and shown in italics

apart from each other. Greatest possible representativeness was achieved with this sampling design on a large area. Main resting places of cattle and trails were excluded from soil sampling.

Stones, coarse woody debris and roots were removed carefully immediately after sampling. The remaining soil was used for further analysis. Volumetric soil samples were taken to determine bulk density. The fresh weight, the dry weight (105 °C) and the weight of stones, coarse woody debris and roots were measured. Density of fine earth fraction was determined by correcting the bulk density for the content of coarse-fragments (>2 mm) and roots. For each soil layer, the fine soil density was used to calculate nutrient element stocks based on a hectare [$t\ ha^{-1}$] (Guo et al. 2008).

Determination of pH, texture, SOC, TN, total P, total S and microbial biomass

An aliquot of all samples was dried at 40 °C for determination of soil pH, texture, soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (P) and sulphur (S). The soil pH was measured potentiometrically in deionised water at a soil:water ratio for mineral soil of 1:2.5 and for organic layer of 1:10. Soil texture was analysed by sieving and sedimentation (Schlichting et al. 1995). An aliquot of the dried samples was finely ground for determination of SOC, TN, total P and S. SOC and TN were analysed with a CNS-analyser (Vario EL, Heraeus). Strong acid digestion was used to determine total P and S. Briefly, 200 mg dry weight soil were digested

with $\text{HNO}_3/\text{HF}/\text{HClO}_4$ in a microwave heated to a final temperature of 200 °C within 30 min according to Kingston and Jassie (1986). Digestion aliquots were analysed for bulk elemental chemistry with ICP-OES (CIROS, Spectro).

All other analyses were carried out on field moist soil samples. The determination of microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) is described in detail in Potthast et al. (2010) and followed the protocol of the chloroform-fumigation extraction method of Vance et al. (1987). The amount of C present in the microbial biomass is considered as measure of soil microbial biomass. Various studies have shown that MBC correlates well with other measures of microbial biomass like total phospholipid fatty acids and total DNA for a wide range of soils (e.g. Joergensen and Emmerling 2006; Leckie et al. 2004; Paul and Clark 2007). Nitrogen stored in the microbial biomass represents a dynamic, easily available N pool (Brookes 2001).

Phosphorus fractions

In addition to the total amount of P in the soils, different P fractions were analysed. Due to limited laboratory capacity for the time consuming P fractionation only the end-members of the land-use gradient (forest, succession) as well as both active pasture sites were included into this analysis. On acidic soils it has been shown that $\text{NH}_4\text{F}/\text{HCl}$ is a suitable extractant to determine available P (Cade-Menun and Lavkulich 1997) and P stored in the microbial biomass (Chen and He 2004) (details are given below). For more resistant P pools an analytical protocol has been developed based on the comparison of four sequential extraction schemes in the frame of the Standards Measurements and Testing Program of the European Commission using NaOH and HCl (Ruban et al. 1999, 2001). In all these extracts molybdate reactive P was measured photometrically with a continuous flow auto analyser at 880 nm (Skalar Analytik GmbH, Germany) to assess the amount of orthophosphate P, an inorganic P (Pi) form which can be taken up by plant roots. Note that in the presence of inorganic polyphosphates the true Pi pool is underestimated, because inorganic polyphosphates

do not react with molybdate (Doolette and Smernik 2011). Pi is also underestimated because phosphate interacts with humic substances in alkaline extracts (Turrion et al. 2010). The total P(Pt) content in all extracts was determined by ICP-OES (CIROS, Spectro). The fraction of molybdate unreactive P was calculated as $\text{Pt}-\text{Pi}$ and is considered to represent mainly organic P (Po). Note that the contribution of Pi to this fraction can not be excluded completely. However, inorganic polyphosphates have to be hydrolysed to orthophosphate prior to plant uptake by most plant roots (Torres-Dorante et al. 2006a, b) such as organic P. All methods to determine P fractions and Po have some disadvantages and need to be developed further (Cade-Menun and Lavkulich 1997; Doolette and Smernik 2011, Kirkby et al. 2011).

Based on these considerations, the following six P fractions have been distinguished: (i) inorganic P extractable with NH_4F [Pi (NH_4F)] which represents $\text{PO}_4\text{-P}$ available to plants and is loosely attached to the surfaces of Fe and Al oxides; (ii) organic P extractable with NH_4F [Po (NH_4F)] which can be easily mineralised and thus contributes to plant available P in the short term; (iii) P bound in the microbial biomass [MBP] which is considered as dynamic, easily available P pool; (iv) inorganic P extractable with NaOH [Pi (NaOH)] which is more resistant and associated with oxides and hydroxides of Al, Fe and Mn; (v) organic P extractable with NaOH [Po (NaOH)] which is Po associated with humic and fulvic acids and considered to be involved in long term P transformations; and vi) total P extractable with HCl [Pt (HCl)] containing mainly Pi associated with Ca (apatite P) as stable P pool (Cross and Schlesinger 1995; Pardo et al. 2003; Solomon et al. 2002).

Available P

Five g dry weight equivalent (dw) of mineral soil and 2.5 g dw organic layer, respectively, were extracted with 50 ml of a solution containing 0.03 M $\text{NH}_4\text{-F}$ and 0.025 M HCl following the Bray-P method (Bray and Kurtz 1945). Samples were shaken at 180 rpm for one minute before they were filtered (Schleicher and Schuell 512 $\frac{1}{2}$). These extracts were used to determine Pi ($\text{NH}_4\text{-F}$) and Po ($\text{NH}_4\text{-F}$) as described above.

Microbial biomass P

Phosphorus in the microbial biomass was determined by chloroform-fumigation extraction method (Chen and He 2004). The extraction procedure before and after fumigation as well as the extracting agent (0.03 M NH_4F and 0.025 M HCl) were the same as described for available P determination. Additionally, a correction factor (k_p) was determined to account for the possible adsorption of P_i to soil colloids during extraction of fumigated samples. To obtain k_p a P-spike of 25 μg $\text{KH}_2\text{PO}_4\text{-P}$ was added per g of soil followed by immediate extraction. The recovery of the P-spike added was measured (Brookes et al. 1982). Total microbial biomass P was calculated as $\text{MBP} = ((\text{F}-\text{B}) \times k_p)/k_{\text{EP}}$. F represents the amount of P in samples after fumigation and B represents the amount of P in samples before fumigation. The k_{EP} factor used was 0.4.

NaOH and HCl extractable P

NaOH and HCl extractable P was determined by sequential extraction following the analytical protocol of Ruban et al. (1999, 2001). Briefly, 2 g dw equivalent samples were extracted with 200 ml of 1 M NaOH overnight (16 h shaking at 180 rpm) before they were centrifuged. 100 ml of the supernatant were mixed with 40 ml of 3.5 M HCl, stirred for 20 s and allowed to stand overnight (16 h) and centrifuged. Then, P_i and P_t were measured in the supernatant. The cake of the first centrifugation was washed two times with 120 ml 1 M NaCl. Thereafter, the cake was extracted with 200 ml of 1 M HCl overnight (16 h shaking at 180 rpm). After centrifugation, P_i and P_t were measured in the supernatant. In addition, the contents of Al, Fe and S were determined by ICP-OES. In the following only the P_t values of the HCl extract are reported since there was no significant difference between P_i and P_t values.

Statistics

Statistical analysis was performed with SPSS 17.0. Significant differences between mineral soil samples of the different sites were identified at $p < 0.05$ with a one-way ANOVA (Tukey test for variables with similar variances and Tamhane-T2 for variables with non-similar variances). A t test for unpaired groups

was used to compare organic layers of forest and succession. Relationships between variables were assessed by Pearson correlation coefficients.

Results

Highest pH values were measured in the 17 years-old pasture and abandoned pasture soils with 5.3 and 5.2 (in 0–5 cm depth), respectively. These values for the mineral topsoil were about one pH unit higher compared to forest and succession (Table 2) and are due to the introduction of alkaline ashes by the burning processes. The total stock of soil organic carbon (SOC), including organic layer and mineral topsoil (0–20 cm depth), did not change significantly along the land-use gradient (Fig. 1a). A significant increase of the SOC stock was only evident in 0–5 and 5–10 cm depth of the 50 years-old pasture. On average, up to 21 t SOC ha^{-1} was stored additionally in the 0–10 cm depth interval compared to all other sites. This increase was due to an increase of the SOC content in mineral soil of the 50 years-old pasture rather than to the slight, non-significant increase in the density of the fine soil (Table 2). SOC stocks in 10–20 cm depth were not affected by land-use change (Fig. 1a). In 10–20 cm depth, the density of the fine soil fraction was lowest at the forest site (Table 2). Since the stone content was highest in the forest soil, the probability of methodological errors was highest. This most likely caused an underestimation of the true density of the forest soil (Gutachterausschuss Forstliche Analytik 2009). Hence, no effect of cattle grazing was detected. This was expected, since livestock densities were very low and main resting places and trails were excluded from soil sampling. The stocks of total nitrogen (TN) in the mineral soil (0–20 cm) were significantly highest in the 17- and 50 years-old pasture (Fig. 1b). Compared to the forest, the TN pools increased about 1.9 and 2.2 t ha^{-1} , respectively. As indicated by the narrow C:N ratio of 13 in the 17 years-old pasture (Table 2), the increase of the N stock was disproportional to the increase of the C stock. After pasture abandonment the C:N ratio increased with time above the forest level. Under succession the highest C:N ratio in mineral soil detected was 25 (Table 2). The narrow C:N ratio in the 17 years-old pasture might contribute to the strong increase of microbial biomass in the mineral soil. Compared to the forest, the stocks of

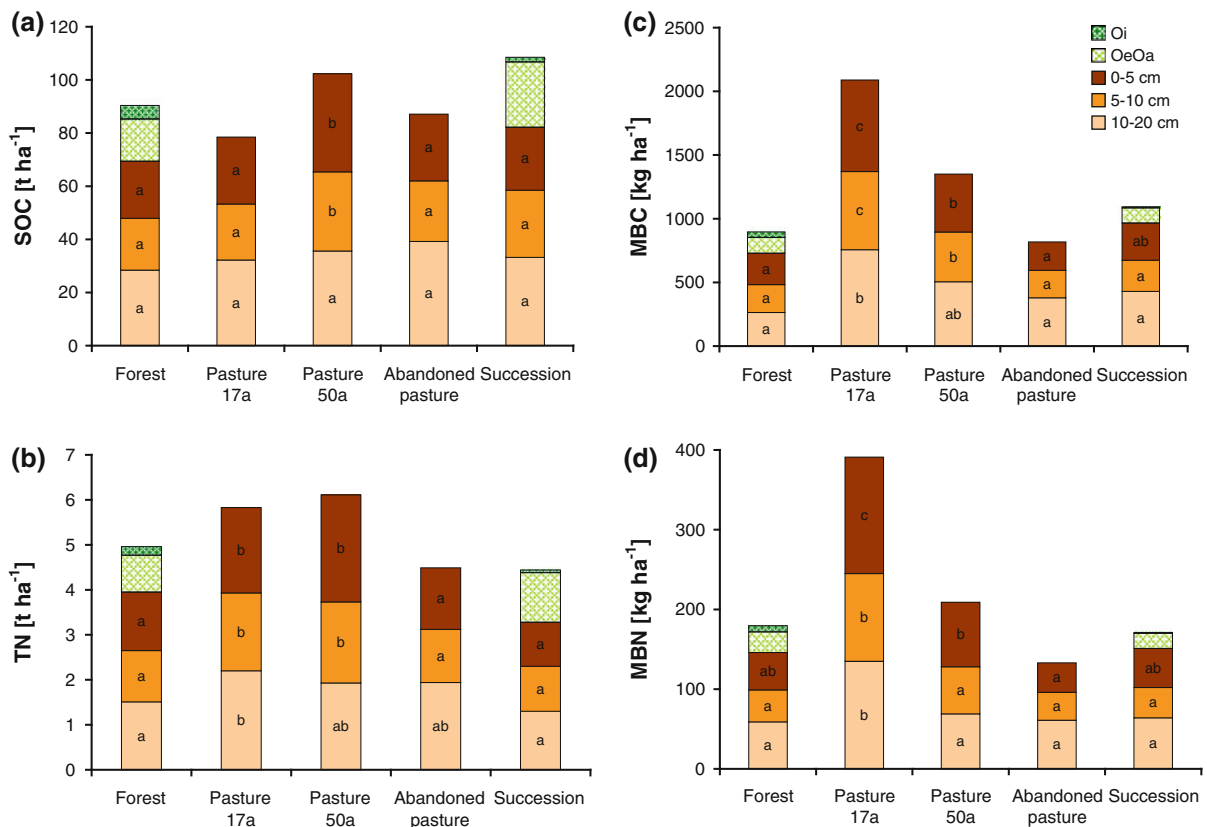


Fig. 1 Stocks of soil organic carbon (a), total nitrogen (b), microbial biomass carbon (c) and microbial biomass nitrogen (d) in mineral topsoil (0–5, 5–10, 10–20 cm depth) and organic layer (Oi, OeOa) along the land-use gradient (mean values,

$n = 5$, different letters indicate significant differences between sites for the respective depth interval of the mineral soil at $p < 0.05$, no significant differences were detected between organic layers of forest and succession)

microbial biomass C and N (Fig. 1c, d) and microbial biomass P (Fig. 3c) were about 2 times higher in the 17 years-old pasture soil. Also the 50 years-old pasture soil showed significant higher stocks of microbial biomass carbon in 0–20 cm depth than forest, abandoned pasture and succession (Fig. 1c); microbial biomass N (Fig. 1d) and P stocks (Fig. 3c), however, were only significantly higher in 0–5 cm depth.

The total stocks of other major nutrients such as P and S were also significantly highest in the mineral topsoil (0–20 cm) of the 17 years-old pasture followed by the 50 years-old pasture (Fig. 2). While the S stocks in the mineral soil of the abandoned pasture returned to forest values, the stocks of total P remained significantly higher. No significant differences were detected between forest and succession (Fig. 2).

The highest stocks of all measured P fractions occurred in the mineral soil of the 17 years-old pasture (Fig. 3). However, taking into account the amount of P

stored in the organic layer of forest and succession sites no significant difference was detected for available Pi (Fig. 3a). Compared to the forest and succession, the 50 years-old pasture had elevated stocks of NaOH extractable Po and Pi and of HCl extractable Pt (Fig. 3d–f). Not only was the absolute amount of NaOH extractable Po highest within all depth intervals of the 50 years-old pasture soil, but also its relative fraction of total P (Table 3). In contrast, the percentage of Po extractable with NH_4F was significantly lowest. The fraction of P stored in the microbial biomass decreased with increasing soil depth, on average, from about 30 % in 0–5 cm to 8 % in 10–20 cm depth. In the forest mineral soil, the proportion of MBP remained stable at about 20 % (Table 3). The sequential extraction with NaOH and HCl resulted in total P of mineral soil which ranged between 52.4 % (forest 0–5 cm) and 72.0 % (pasture 50a). The non-extractable remaining P may represent

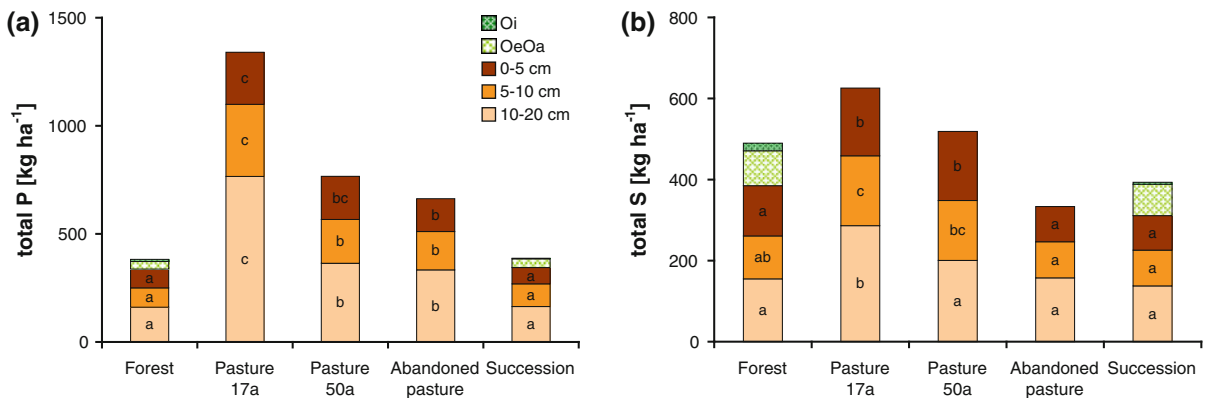


Fig. 2 Stocks of total phosphorus (a) and sulphur (b) in mineral topsoil (0–5, 5–10, 10–20 cm depth) and organic layer (Oi, OeOa) along the land-use gradient (mean values, $n = 5$, different letters indicate significant differences between sites

occluded P (García-Montiel et al. 2000; Pardo et al. 2003). In the NaOH extracts of all mineral soil samples, on average, 1.9 % of the total Fe and about 50 % of S were detected. The recovery of Al in the NaOH extracts differed. NaOH extractable Al was about three times higher in forest mineral soil and decreased to 13 % in pasture and succession soils. Using subsequent HCl extraction 4.9 % of the total Al, 31.9 % of the total Fe and 1.2 % of the total S was detected.

Discussion

Dynamics of soil organic carbon

In the mineral soil a significant increase of SOC stocks was detected in the 50 years-old pasture compared to all other sites. The SOC accumulation rate was 420 kg SOC per year on average. Assuming the same SOC accumulation rate for the 17 years-old pasture, about 7.1 t SOC ha⁻¹ should have accumulated since forest to pasture conversion had taken place. In fact, 5.3 t SOC ha⁻¹ accumulated. Due to the high variability of the data, this accumulation was not significant. To overcome the spatial and temporal limitation of data interpretation, the density of data along the land-use gradient needs to be increased. In the future, investigations of pastures of young and intermediate age should be conducted as well. Nevertheless, the results obtained for this tropical mountain rainforest region support the hypothesis of Guo and Gifford (2002) that

for the respective depth interval of the mineral soil at $p < 0.05$, no significant differences were detected between organic layers of forest and succession)

SOC stocks tend to increase after native forests are cleared for pastures in areas receiving 2,000–3,000 mm precipitation per year. The SOC accumulation rate detected for the 50 years-old pasture was high. It falls within the range of rates reported for former agricultural fields converted to grassland (McLauchlan 2006; Post and Kwon 2000), reforested pasture sites (Silver et al. 2000) or improved *Brachiaria* pastures in the Brazilian Cerrado (Batlle-Bayer et al. 2010). The accumulation of SOC occurred in the first 10 cm of the mineral soil. This accumulation was not related to changes in soil density, but to the main rooting zone of *S. sphacelata*. More than 80 % of all fine roots were detected in this depth interval (Potthast et al. 2011). The total amount of organic carbon stored in the fine root biomass was 17.4 t C ha⁻¹ below grass tussocks (Potthast et al. 2011). Thus, a high input of C from decaying roots or root exudates seems to be an important mechanism which contributed substantially to the observed SOC enrichment in pasture mineral soil. A high input of organic substrates which are easily available for soil microorganisms would be expected due to the high root density of *S. sphacelata* (Rhoades et al. 2000). Litter of *S. sphacelata* was utilised rapidly by soil microorganisms as shown by litterbag (Potthast et al. 2011) as well as incubation experiments (Potthast et al. 2010). These processes might have enabled the strong increase of microbial biomass (MBC and MBN) in active pasture soils and resulted in an about three times greater ratio of MBC:SOC in the 17 years-old pasture soil compared to all other soils. The increase in microbial biomass

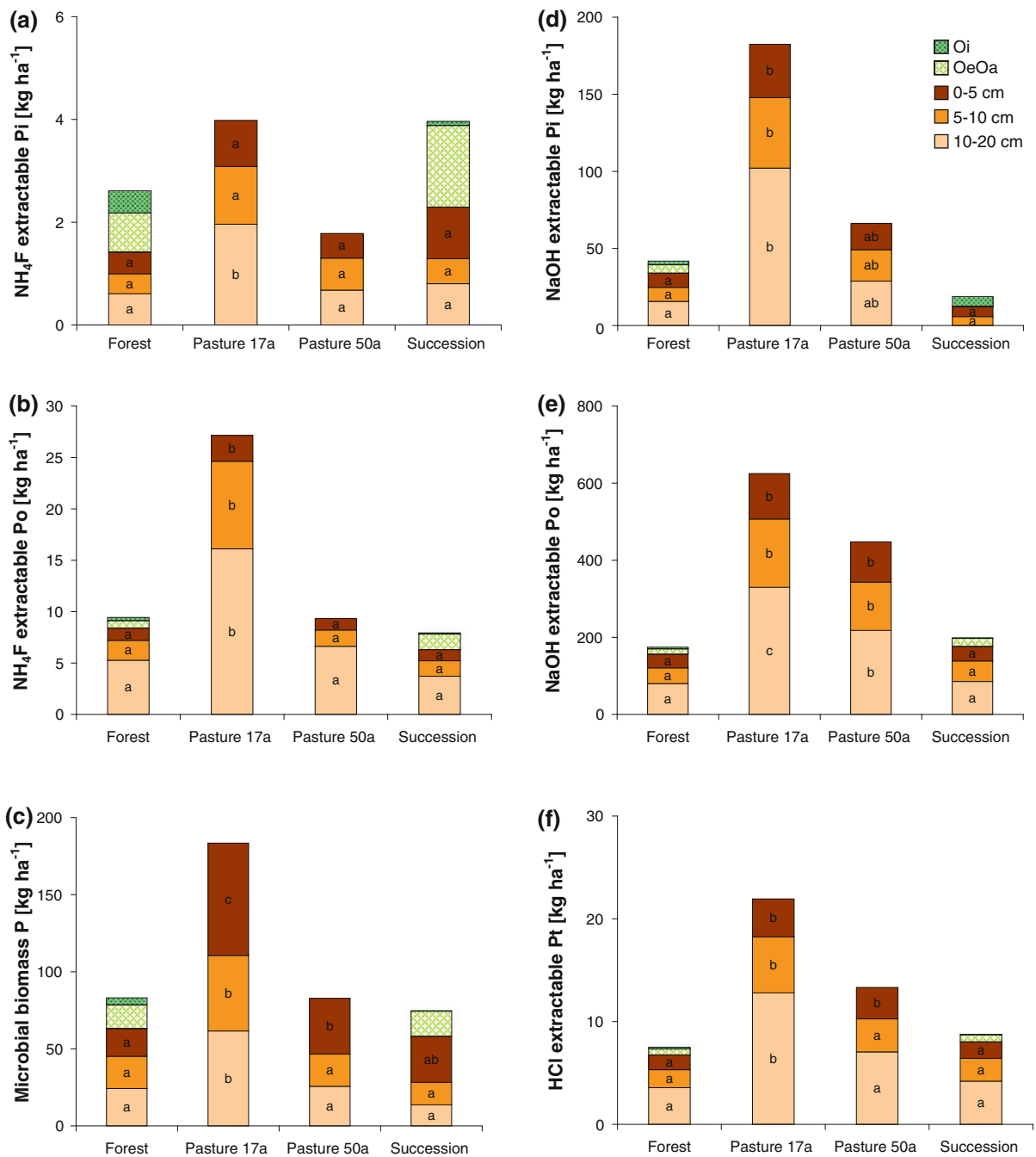


Fig. 3 Stocks of NH_4F extractable inorganic P (a), NH_4F extractable organic P (b), microbial biomass P (c), NaOH extractable inorganic P (d), NaOH extractable organic P (e) and HCl extractable total P (f) in mineral topsoil (0–5, 5–10, 10–20 cm depth) and organic layer (Oi, OeOa) along the land-

use gradient (mean values, $n = 5$, different letters indicate significant differences between sites for the respective depth interval of the mineral soil at $p < 0.05$, no significant differences were detected between organic layers of forest and succession)

was associated with enhanced microbial activity, especially with high rates of microbial N immobilisation (Potthast et al. 2011). The 50 years-old pasture

showed higher microbial biomass stocks in 0–10 cm depth compared to forest, abandoned pasture and succession sites. However, microbial biomass stocks

Table 3 Proportion of NH_4F -extractable and NaOH -extractable fractions of inorganic P (Pi) and organic P (Po), of total HCl-extractable P(Pt) and of microbial biomass P (MBP) in percent of total P in different depth intervals and sites

(% of total P)	Forest	Pasture 17a	Pasture 50a	Succession
0–5 cm				
Pi (NH_4F)	0.5 (0.1) ^a	0.4 (0.2) ^a	0.4 (0.6) ^a	1.3 (0.9) ^a
Po (NH_4F)	1.4 (0.2) ^b	1.1 (0.5) ^{ab}	0.6 (0.0) ^a	1.5 (0.4) ^b
Pi (NaOH)	10.4 (1.8) ^a	13.9 (5.2) ^a	9.0 (2.8) ^a	8.3 (2.9) ^a
Po (NaOH)	40.3 (3.1) ^a	49.3 (6.0) ^{ab}	55.2 (13.9) ^b	49.4 (3.2) ^{ab}
Pt (HCl)	1.7 (0.7) ^a	1.5 (0.2) ^a	1.7 (0.6) ^a	2.1 (0.4) ^a
MBP	21.0 (5.3) ^a	30.6 (3.1) ^a	20.6 (10.1) ^a	39.1 (17) ^a
5–10 cm				
Pi (NH_4F)	0.5 (0.2) ^a	0.3 (0.1) ^a	0.3 (0.3) ^a	0.5 (0.3) ^a
Po (NH_4F)	2.2 (0.7) ^{ab}	2.6 (1.3) ^b	0.9 (0.4) ^a	1.5 (0.4) ^{ab}
Pi (NaOH)	10.4 (2.0) ^b	13.8 (2.6) ^b	9.6 (3.0) ^b	3.0 (2.8) ^a
Po (NaOH)	45.6 (4.9) ^a	53.3 (5.6) ^{ab}	60.8 (11.4) ^b	48.0 (4.3) ^{ab}
Pt (HCl)	2.0 (0.4) ^a	1.7 (0.4) ^a	1.6 (0.4) ^a	2.1 (1.0) ^a
MBP	23.7 (9.8) ^a	14.8 (1.7) ^a	12.1 (9.7) ^a	15.4 (7.5) ^a
10–20 cm				
Pi (NH_4F)	0.4 (0.3) ^a	0.3 (0.1) ^a	0.2 (0.1) ^a	0.5 (0.2) ^a
Po (NH_4F)	3.3 (1.2) ^b	2.4 (1.1) ^{ab}	1.9 (0.8) ^a	2.3 (0.8) ^{ab}
Pi (NaOH)	10.5 (3.4) ^a	15.1 (3.7) ^a	7.9 (0.9) ^a	nd
Po (NaOH)	48.8 (4.5) ^a	48.8 (4.0) ^a	58.7 (9.1) ^b	51.5 (7.9) ^a
Pt (HCl)	2.2 (0.4) ^a	1.9 (0.3) ^a	2.0 (0.4) ^a	2.6 (1.2) ^a
MBP	18.8 (6.9) ^a	9.2 (2.5) ^a	7.3 (1.9) ^a	8.8 (4.6) ^a

Means with standard deviations in parenthesis, *different letters* within one row indicate significant differences at $p < 0.05$, nd: not detectable, $n = 5$. The extraction with NaOH and HCl was carried out in sequence

of the 50 years-old pasture were lower compared with the 17 years-old pasture. This pattern is most likely due to the decreasing supply of $\text{PO}_4\text{-P}$ to soil microorganisms, which was highest at the 17 years-old pasture site. The large and active microbial community in pasture soils may be a second mechanism contributing to the SOC enrichment in the mineral topsoil by means of preferential stabilisation of recycled organic matter (OM). Furthermore, in pasture soils fire transformation of plant and soil OM leads to the accumulation of black carbon. The relative importance of these three mechanisms for OM accumulation in pasture soils should be clarified in further investigations. At the 17 years-old pasture site accumulation of black carbon is assumed to be less important than at the 50 years-old pasture, since the 17 years-old pasture was burned only once (Table 1). More charcoal fragments were visible at the 50 years-old pasture site. However, the exact proportion can only be determined by measurements of black carbon in future studies.

Dynamics of nitrogen and sulphur

TN stocks in mineral topsoil increased faster than SOC stocks after forest to pasture conversion, resulting in a significantly lower C:N ratio in the 17 years-old pasture. The TN stock of 17 years-old pasture was about 870 kg ha^{-1} higher than in forest soil. This increase is partly due to the burning of aboveground biomass and the subsequent death of roots. The amount of N stored in the aboveground biomass of tropical mountain and submountain forests ranges between 426 and 998 kg ha^{-1} (Mackensen et al. 2000). Since fires in the study area are of low to medium intensity, only a part of the N stored in aboveground biomass is lost to the atmosphere. According to Soethe et al. (2007) about 208 kg N ha^{-1} is stored in the forest root biomass of the study site. The increase in TN stocks of mineral soils after forest to pasture conversion depends also on the thickness of the forest organic layer. Its thickness is highly variable in the Ecuadorian tropical montane

forest. Therefore, N stocks range from 1 to 3 t N ha⁻¹ (Makeschin et al. 2008; Soethe et al. 2008). Furthermore, N losses decreased due to microbial immobilisation and subsequent incorporation into SOM. After invasion of bracken and abandonment of pastures the C:N ratio increased above forest level indicating a stronger loss of N compared to C. This change can be explained by the plant N-uptake and by repeated burning of this site during former pasture management. Kauffman et al. (2009) reported a loss of 235 kg N ha⁻¹ based on burning of tropical pastures. TN stocks returned to forest level not later than 10 years after pasture abandonment and bracken growth. The same pattern was observed for the stocks of S showing a highly positive correlation with TN stocks ($r = 0.76$, $p < 0.001$). Thus, N and S seem to be important constraints for pasture productivity in the tropical mountain rainforest region of Southern Ecuador. The importance of a balanced supply of tropical forage grasses with N and S has been demonstrated previously (De Bona and Monteiro 2010).

Dynamics of phosphorus

The 17 years-old pasture had the highest total P stock, exceeding that of the forest by 958 kg P ha⁻¹. Since P in mineral topsoil mainly occurs in organic P forms (López-Gutiérrez et al. 2004; Rivaie et al. 2008), a significant positive correlation between SOC and P stocks should exist in the respective depth interval considered. Walker and Adams (1958) reported such positive correlations for 22 grassland soils, which developed from different parent materials, in New Zealand. Similar results have also been shown for soils of Australia (Kirkby et al. 2011) and Canada (Cade-

Menun et al. 2000). However, the Pearson correlation coefficient showed no relationship with data from all sites (Table 4). Significant positive relationships between SOC and P stocks appeared when the data from the 17 years-old pasture were excluded from the analysis (Table 3). A separate regression analysis, including only data of the 17 years-old pasture, also revealed a highly significant positive relationship. The regression lines calculated for each depth interval showed a y-axis intercept (K) other than zero. This is in contrast to those lines calculated when the 17 years-old pasture was excluded (Table 4). This pattern indicates that before land-use change from forest to pasture more P was present in the soil of the 17 years-old pasture. K specifies the size of this P pool. In 0–5 cm depth 64.5 kg P ha⁻¹ existed in addition to the P present at the other sites, in 5–10 cm depth 149.0 kg P ha⁻¹ and in 10–20 cm depth 201.8 kg P ha⁻¹. Thus, the amount of 415 kg P ha⁻¹ must be explained by parent rock material with a higher P content in the unweathered rock. Although much effort was put into the selection of sites with parent material dominated by phyllite, differences in apriori nutrient content can never be excluded. It is known that in the study area the range of the P content in unweathered phyllite is high (175–700 mg kg⁻¹, F. Haubrich, TU Dresden, pers. com.). Nevertheless, the data clearly indicate that the slash-and-burn practice leads to a significant increase of P stocks. At the latest after 20 years of growth of successional bush vegetation on abandoned pastures, P stocks returned to forest level.

Although forest to pasture conversion significantly increased the total P contents, the P status of these tropical soils has to be classified as low to medium (Landon 1991). This corresponds to values reported for acidic Brazilian forest and pasture soils (Barroso and Nahas 2005). Available P contents, however, were only 1/3 of those in the Brazilian soils. In 0–5 cm depth of the 17 years-old pasture a maximum of 4.5 mg kg⁻¹ available P (Bray-P) was detected. Bray-P [Pi(NH₄-F)] values below 15 mg kg⁻¹ most likely indicate P limitation of plant growth (Landon 1991). Along an elevation gradient in the old-growth forest in the Ecuadorian research area plant growth decreased with decreasing total P contents in the soil organic layer (Soethe et al. 2008). Microbial growth in forest floor samples of the Oe horizon was P limited, too (Maraun et al. 2008). We found about 45 % of the total P in the organic layer of the old-growth forest was

Table 4 Pearson correlation coefficients (r) for the relationship between SOC [t ha⁻¹] and total P [kg ha⁻¹] for all sites, all sites except Pasture 17a and Pasture 17a and intercept (K) from regression analysis of Pasture 17a with total P [kg ha⁻¹] as dependant variable on SOC [t ha⁻¹]

	All sites	All sites except Pasture 17a	Pasture 17a	
	r	r	r	K
0–5 cm	0.197	0.682**	0.561**	64.5
5–10 cm	-0.220	0.414*	0.581**	149.0
10–20 cm	0.286	0.597**	0.760***	201.8

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

stored in the microbial pool. This highlights the importance of the soil microorganisms as P reservoir that can become plant available in the short-term (Brookes 2001). Also in all examined mineral soils along the land-use gradient the most important sink for P is the microbial biomass, especially in 0–5 cm depth where MBP accounts for 21–39 % of total P. This percentage was twice as high as in A horizons of forest soils under beech in Germany (Joergensen et al. 1995) or in unimproved grassland soils of New Zealand (Chen et al. 2008). It may even be higher, since the k_{EP} factor of 0.4 chosen for calculating MBP is a conservative one, presumably underestimating the real amount of MBP in the Ecuadorian mountain soils. According to Bliss et al. (2004) a k_{EP} of 0.34 might be more appropriate for soils often close to field capacity. For acid red soils Chen and He (2004) determined the same low k_{EP} factor. The importance of MBP in the Ecuadorian soils increases further when calculating with the low k_{EP} of 0.34. In the organic layer, values characteristic of *Picea abies* forests in Sweden (Clarholm 1993) and *Pinus radiata* forests in New Zealand (Saggar et al. 1998) are reached with 50–66 % of total P in the microbial biomass. As reviewed by Bünemann et al. (2011) on average 60 % of P in microorganisms is bound in nucleic acids and phospholipids, further 10 % is cytoplasmic organic P. Under P sufficient conditions inorganic P accumulates in microorganisms as polyphosphate. Microorganisms resting in aquatic sediments stored up to 10 % of P in the form of inorganic polyphosphate (Hupfer et al. 2007). Since soils in the present study are P limited, it is likely that Po dominates the pool of MBP and that polyphosphate-P contribution was minor. However, this hypothesis should be verified using e.g. ^{31}P -NMR spectroscopy (Hupfer et al., 2007).

In the 17 years-old pasture the NH_4F extractable Po was identified as further important reservoir of easily mineralisable P. Compared to the other sites its stock was more than two times higher. It is unlikely that inorganic polyphosphates were still important in this P pool, since burning occurred 17 years ago (Table 1). A substantial decline of inorganic polyphosphates has been shown 5 years after burning (Cade-Menun et al. 2000). Inorganic polyphosphates have to be hydrolysed by soil enzymes in order to be available for uptake by most plants (Torres-Dorante et al. 2006a, b). In pasture soils the arbuscular mycorrhiza associated with pasture grasses are effective in P-uptake. They

contribute to the build-up of a large, potentially labile, microbial derived Po pool (Negassa and Leinweber 2009). Thus, it is likely that in active pastures not only the unspecific release of P during SOM mineralisation was higher, but also the selective P release. Phosphatase enzymes which are produced by roots and associated microorganisms selectively release P from SOM through hydrolysis of ester bonds (Clarholm 1993). Fungi capable of solubilizing Fe- or Al-phosphates might be important, too, since more fungal biomass was present in the 17 years-old pasture than in the forest soil (Potthast et al. 2011). The highest number of fungal isolates capable of solubilizing Fe- or Al-phosphates was detected in tropical pasture soils (Barroso and Nahas 2005). In the 50 years-old pasture the NaOH extractable Po was of special importance, since its proportion was significantly higher compared to all other sites. An increase of the Po fraction in old pastures was also found in Brazilian Oxisols (García-Montiel et al. 2000). The same pattern was reported by Townsend et al. (2002) and might suggest changes in the structure and quality of SOM. Obviously, the extractable Po pools (NH_4F and NaOH) are important parameters contributing to an increase of microbial biomass and activity. This, in turn enhances the supply of nutrients for plant growth in active pasture soils. With advanced pasture age the NH_4F extractable pool was exhausted followed by the NaOH extractable pool. Thus, the decline of the NaOH extractable P-pool back to forest level might be of special importance for the degradation of pastures.

Conclusions

From the perspective of pasture productivity, the conversion of forest to pasture on Cambisols of the tropical mountain rainforest region in Southern Ecuador significantly improved the quality of the mineral topsoil in active pastures. The soil pH and stocks of N, S, C and P increased leading to a vigorous growth of microbial biomass especially in the youngest, 17 years-old, pasture soil. Already 20 years after pasture abandonment and development of successional bush vegetation most measured soil properties returned to the old-growth forest levels. The only exception was the C:N ratio which increased above forest level indicating an ongoing depletion of N. The most important parameters connected with the decline

in pasture productivity seem to be the stocks of N and S, which returned to forest levels within 10 years after pasture abandonment. During this time microbial biomass also declined to forest levels which probably was not only related to decreased N and S availability but also to a depletion of the NaOH extractable organic P-pool. Thus, pasture degradation seems to be driven by the interactions of soil nutrient depletion and declined soil microbial biomass. Degradation of pastures, and consequently the establishment of new pastures by deforestation, might be avoided by moderate fertilisation of active pastures. In future investigations, an extended data base would improve the assessment of the dependence of soil quality on pasture management. Pastures of young and intermediate age should be investigated which differ in control measures of bracken fern (fire and/or cutting frequencies; age of bracken fronds at the time of weed control). Nutrient acquisition strategies of bracken versus grass have to be compared and the storage of nutrients in bracken rhizomes has to be considered.

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