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• *tropical montane forest - soil development - altitudinal gradients - disturbances*

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Tropical montane rain forest soils
Development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes

Böden unter tropischem Bergregenwald
Bodenentwicklung und Nährstoffstatus entlang eines Höhengradienten in den südecuadorianischen Anden

With 8 figures und 2 tables

Soils are closely linked with the vegetation. They anchor the plant roots and provide most terrestrial plants with water und nutrients. *Vice versa*, soil genesis can be highly affected by feedback mechanisms of the vegetation, e.g., humus formation, mineral weathering, development of soil structure, and soil erosion. Hence, in terrestrial ecosystems soils act as driving variables as well as response variables. Therefore, in modern interdisciplinary approaches to identify the controlling factors in ecosystems, the spatial patterns of environmental resources, the reconstruction of the landscape history, and the influence of anthropogenic disturbance on ecosystems usually include the evaluation and analyses of soils. The results can be interrelated with bio- and physicogeographical, botanical, and plant physiological studies to provide insight into the functioning of ecosystems and to establish resource-saving land management systems.

1. Introduction

The spatial distribution of soil properties in a landscape of homogenous parent material is the result of systematic pedogenetic processes which are controlled by a variety of environmental factors. In tropical mountain regions such as the Ecuadorian Andes, altitudinal changes go along with changes in vegetation cover and climate, which both affect soil formation. Tropical wet forests change substantially with altitude as the forests decrease in stature (*Grubb* 1977, *Whitmore* 1984), growth and productivity (*Tanner* 1980). Several reasons for this altitudinal zonation have been discussed, among them lower temperatures, a decrease in irradiation due to a higher frequency of dense cloud covers (*Grubb* 1977), periodic water shortage (*Whitmore* 1989) and nutrient limitations. *Tanner* et al. (1998) summarized the current knowledge about nutrient limitations in tropical montane ecosystems and concluded that in particular nitrogen might limit the productivity of these forests. However, knowledge about the soil nutrient status along altitudinal gradients is still scarce.

Beneath biotic and abiotic factors, the time of pedogenesis is one of the driving variables that control soil formation and thus affect biological, chemical, and physical soil parameters (*Jenny* 1980). In highly humid areas such as the eastern slopes of the Andes, soil development proceeds quite rapidly, leading to acid, highly weathered soils. However, in the Andes even at undisturbed slopes landslides are a common phenomenon (*Frei* 1958). This natural disturbance destroys the highly developed soils and exposes fresh rock material to the soil surface where pedogenetic processes start again. Hence, in addition to altitudinal gradients soil development and nutrient status at Andean slopes may be affected by disturbance gradients caused by landslides.

The aims of the present investigation were (i) to identify soil parameters that are affected by the altitudinal gradient and to assess the direction and extent of these variations with altitude, and (ii) to study whether and how landslides change the soil nutrient status. We approached this by establishing an altitudinal soil transect at the experimental site of the research centre Estación Científica San Francisco, province of Zamora/Chinchipe, south Ecuador.

2. Materials and methods

2.1 Study area

The investigations were carried out near the Podocarpus National Park in south Ecuador. The study area is located at the research centre Estación Científica San Francisco (ECSF), half way between Loja and Zamora, in the province Zamora/Chinchipe in south Ecuador (4°00´ S, 79°05´ W). The research centre is situated at the eastern slope of the Cordillera del Consuelo, that is the eastern chain of the south Ecuadorian Andes and reaches maximum altitudes of about 3500 m asl. The chain is formed by paleozoic rocks of the Loja Terrane containing mainly phyllites, partly metamorphic sandstones as well as quartzites (*Litherland* et al. 1994). The slopes are generally very steep (on average around 30° with maxima >60°), and landslides can be frequently observed even in natural forests. The experimental site covers a slope in NNW to NE position and represents altitudes from 1800 m asl (River San Francisco) to 3150 m asl at the top of the highest peak within the study area.

Because the experimental site is located at the eastern slope of the Cordillera del Consuelo, the study area receives a pronounced orographic precipitation. Estimated yearly precipitation at 1950 m asl is 2000 mm and increases to about 3500 mm at 2850 m asl. Likewise, the number of foggy days increase with increasing elevation. Average yearly temperature is 16°C at 1950 m asl and 10°C at 2850 m asl.

According to *Beard* (1955), the forest of the study area can be divided into the lower montane rain forest (up to 1900 m asl), the upper montane rain forest or cloud forest (up to 2200 m asl) and the elfin woodland which gradually changes to a dry variation of the páramo vegetation. The latter occupies the area above 2900 m asl.

2.2 Soil transect

Fourteen sites were selected along an altitudinal gradient from 1850 m to 3050 m asl (ECSF transect 1). The transect follows a mountain ridge, and about every 150 altimetric m a site was chosen. The vegetation zones cover the upper montane rain forest belt, the elfin forest belt, and the lower part of the páramo. Bedrock at the slope consists primarily of phyllites, metamorphic sandstones, and quartzites with minor contributions of loam stones, silt stones, and schists. In the lower part of the transect (1850-2000 m asl), the slopes partly exceeded 50°. The soils in this part developed in landslide material that is rich in rocks. At higher elevations, the inclination varied between 20 and 40°, and the soils developed in recently undisturbed material. However, the layered

Tab. 1 Main data of representative soils along the altitudinal gradient / *Wesentliche Eigenschaften repräsentativer Böden entlang des Höhentransektes*

Profile No. Location Altitude, aspect,	Classification (*Soil Survey Staff* 1998) Parent material Vegetation type	Horizon	Depth (cm)	Color (moist)	pH (0.01 M $CaCl_2$)	OC $(g\ kg^{-1})$	N_t $(g\ kg^{-1})$	ECEC (cmol(+)/kg)	Particle size distribution (%)		
									Sand	Silt	Clay
Profile No. 1											
Zamorra	*Oxyaquic Palehumult,*	Oi	3.5-1.5	n.d.	5.2	414	18.5	n.d.	n.d.		
Central slope	Granitic debris	Oe	1 5-1	n.d.	4 7	327	17 3	31 5	n.d		
1010 m, 38°, S	Lower montane	Oa	1-0	n.d	3.7	170	8.0	9 4	59	19	22
	rain forest	ABw	0-38	10YR 3/3	4.8	29	2.0	4.2	45	20	35
		Bt	38-48	10YR 5/3	4.9	12	0.9	2.4	39	17	44
		BCr	48-145+	10YR 6/6	5 0	5	0.5	1.4	51	13	36
				10YR 5/4	4.8	25	1.8	2 8	41	21	38
Profile No 3											
ECSF	*Terric Haplosaprist,*	Oi	43-41	n.d.	5.7	442	13.0	n.d.	n.d.		
Central slope	Landslide material	Oe	41-39	n.d.	5.4	421	19 2	65.9	n d		
1850 m, 50°, NNO	(phyllite)	Root layer	39-0	n.d.	3.1	428	21.3	24.4	n.d		
	Upper montane	AC	0-39	n.d.	3.6	85	5 5	11.1	n.d.		
	rain forest	2AC	39-62	10YR 4/2	4.7	56	3 3	6.0	31	60	9
		2BC	62-101	10YR 4/3	5.0	34	2.1	3.0	45	47	8
		3C	101-132+	10YR 5/4	5.2	12	1 1	1.9	40	54	6
Profile No 4											
ECSF	*Aquic Dystrudept,*	Oi	38-37	n d	5.0	432	17 0	n.d	n.d.		
Central slope	Landslide material	Oe	37-36	n.d.	4 8	424	18 1	49.9	n.d		
1950 m, 46°, N	(phyllite)	Root layer	36-0	n.d.	2 8	419	23.5	27 8	n d.		
	Upper montane	A	0-8	10R 2.5/1	3.4	82	4.4	16.7	23	57	20
	rain forest	ABw1	8-20	10R 3/2	4.6	57	2.6	9.2	23	61	16
		ABw2	20-30	10R 2.5/2	4.4	64	2 7	6.6	28	58	14
		BwA	30-60	2 5YR 3/2	4 8	33	1.8	2 3	28	63	9
		Cr	60-90 +	5YR 4/2	4 9	19	0 9	1 8	31	64	5
Profile No 6											
ECSF	*Terric Haplosaprist,*	Oi	50-48	n d	4 4	460	12 3	n.d.	n d.		
Upper slope	Schisted sandstone	Oe	48-47	n.d	3.1	434	16.4	27.4	n d.		
2070 m, 10°, N	over phyllite	Root layer	47-30	n.d	2.5	430	19.0	34 5	n.d		
	Upper montane	Oa	30-0	10R 2 5/1	2 4	434	20 4	18 4	n d		
	rain forest	A	0-20	7 5YR 3/2	3.1	22	1 1	10 6	32	59	9
		2BwA	20-48	7 5YR 5/6	3 9	5	0,5	8.3	19	52	29
				10YR 6/4	4 0	28	1 3	9 7	23	57	20
		2Cr	48-74+	5YR 5/8	4.4	8	0 7	3.0	28	52	20
Profile No. 10											
ECSF	*Histic Placic*	Oi	28-26	n.d	3 3	485	7 8	n.d	n d.		
Central slope	*Petraquept,*	Oe	26-25	n d	2 9	474	10.1	26.1	n.d.		
2510 m, 40°, N	Phyllite	Root layer	25-0	n d	2.5	425	17.2	27.8	n.d.		
	(quartz intrusions)	A	0-16	10YR 2,5/1	2.9	92	3 2	8 5	40	59	1
	Transition upper	Bsm	16-17	7 5YR 5/4	n d	25	0 6	n d	n d		
	montane rain	2Bw1	17-19	10YR 4/3	3.5	26	1.2	8 0	29	58	13
	forest to elfin		2Bw2	19-45	2 5Y 5/6	4 2	4	0 3	1 6	5	77
	forest	2Cr	45-85+	5Y 5/3	4 5	2	0 3	1 2	20	72	8
Profile No 13											
ECSF	*Humaqueptic*	Oi	9-8	n d	3.3	286	6 1	n.d.	n.d		
Upper slope	*Epiaquent,*	Oa	8-0	n d	2 9	328	9 0	18 8	n.d.		
2850 m, 20°, N	Schisted sandstone	A	0-12	5YR 2 5/1	3 2	52	2 9	5 1	48	43	9
	over phyllite	AB	12-15	10YR 4/1	3.7	11	0 7	2 5	67	23	10
	Transition elfin forest	B	15-45	7 5YR 5/6	3 9	3	0.3	1.8	71	17	12
	to páramo	2Cr	45-65	n d	4 2	3	0 3	1 7	24	66	10
Profile No 15											
ECSF	*Humaqueptic*	Oi	27-17	n d.	3 6	404	6.9	n d	n.d		
Upper slope	*Epiaquent*	Root layer	17-0	n d	2.8	396	9.0	29.9	n d		
3050 m, 20°, N	Sandstone	Ag1-3	0-18	10R 2 5/1	3 3	72	3 4	n d.	27	61	12
	Páramo	C(Ag)	18-25+	n d	n.d	27	1 3	n.d	n d		

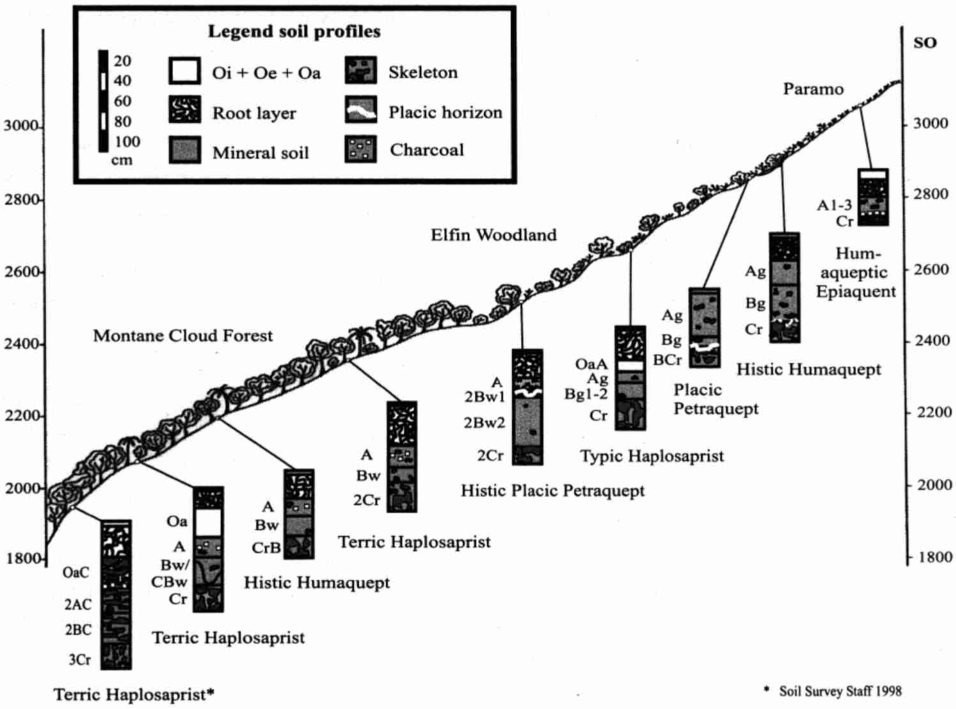

Fig. 1 Composition of soil profiles and soil classification according to Soil Survey Staff (1998) along the altitudinal transect / *Aufbau der Bodenprofile und Klassifizierung der Böden nach Soil Survey Staff (1998) entlang des Höhentransekts*

composition of many pedons suggests that the soils have been developed at least partly in solifluction covers. In order to include a soil from the lower montane forest belt, an additional site at the Podocarpus National Park near Zamora at an altitude of 1010 m was chosen. Despite differences in climatic conditions due to the lower altitude, other abiotic soil forming factors were comparable to those at the ECSF sites. More detailed information on the locations is given in *table 1.*

At each site identified, a pit of about 1x1x1 m was dug by hand. Horizon designation and soil classification were made in accordance with the US Soil Taxonomy (Soil Survey Staff 1998), with Munsell colors given for moist soil. For laboratory analyses, samples were taken by horizon from three sides of the wall.

2.3 Laboratory analyses

The analysis of the mineral soil material was carried out on air dried samples of the fraction < 2 mm. Soil pH was determined using 0.1 M $CaCl_2$ at a soil : solution ratio of 1 (m) : 2.5 (v). Total carbon (C_t) and nitrogen (N_t) contents were analyzed on ball-milled samples on a total element analyser (Elementar Vario EL). Owing to the low pH, C_t was equivalent to organic C (OC). Element stocks were calculated by multiplication of the concentrations with the bulk density for each horizon and were reported for a depth of 1 m or to a lithic or paralithic contact. Bulk density of each horizon was determined from 3 undisturbed cores with a volume of 100 cm^3. Exchangeable cations were extracted by unbuffered 0.5 M NH_4Cl solution (*Trüby* and *Aldinger* 1985) and analyzed by atomic ab-sorption (Varian SpectrAA 400). The exchange acidity was calculated according to *Ulrich* (1966). The effective cation exchange capacity (ECEC) was given as the sum of the extracted cations and the exchangeable acidity.

For texture analysis, soil organic matter was destroyed by H_2O_2 according to *Sheldrick* and *Wang* (1993), and samples were dispersed with $Na_2P_2O_7$. Pedogenic oxides were not destroyed, because they are important constituents of the mineral fraction in the soils under study. The sand was separated by wet-sieving and weighed, whereas the silt and clay contents were determined by the pipette method (*Hartge* and *Horn* 1989). Clay mineral analysis was carried out for mineral horizons from selected pedons. The clay was dispersed with $Na_2P_2O_7$ and separated in Atterberg cylinders (*Schlichting* et al. 1995). The identification of the minerals was performed on oriented clay using sediment preparations of the samples after saturation with Mg (air-dried), Mg plus glycerol (heated to 80°C for 16h), K (air dried), and K (heated to 560°C for 2h). A Siemens D5000 X-ray diffractometer PW 1730 (Cu-Kα radiation) with a scanning rate of $2°2\theta$ min^{-1} was used. Semiquantitative calculations of the clay minerals were done according to *Gjems* (1967) and *Laves* and *Jähn* (1972).

3. Results and discussion

3.1 Soil classification and general description

Along the ECSF transect 1, most soils exhibit a huge forest floor with up to 48 cm thickness. Owing to the pronounced organic matter accumulation on the soil surface Histosols (Haplosaprists) could be identified among other soils up to an altitude of 2650 m (*tab. 1, fig. 1*). At higher elevations, the accumulation of organic material on the soil surface decreased. The four lowest profiles situated at 1850 and 1950 m at an inclination of 45 to 50° have been developed in landslide material. The profiles are characterised by high contents of weakly weathered rock material. As long as the soil did not fulfill the criteria of Histosols, they were classified as Dystrudepts. Charcoal was found at the basis of the AC horizon in profile 4; its conventional ^{14}C age is 710 ± 50 years BP. It is likely that the landslide occurred after the vegetation had been destroyed by fire and the soil surface was bare. Based on this assumption, the ^{14}C age of the charcoal provides a first estimation of the age of the soils and the beginning of the vegetation succession in that landslide area.

With increasing elevation, hydromorphic properties (pale colours, redox concentrations) increase and indicate aquic conditions. Hence, Humaquepts can be designated. At higher altitudes, thin iron pans were identified as placic (Bsm) horizons in the pedons 10 and 12. Placic horizons are typical for tropical mountain soils under perhumid climate (*van Wambeke* 1992). This cemented horizon is largely impermeable for plant roots and diagnostic for the classification as Placic Petraquepts. At elevations around 3000 m asl, the soils became more shallow and less developed, leading to the classification of Epiaquents.

In many soil profiles, eluviation of organic matter and/or A horizon soil material in subsoil horizons along root channels took place. Interestingly we frequently found charcoal in the soil profiles along the whole transect, being particularly prominent in the páramo. The conventional ^{14}C age of charcoal obtained from the basis of the A horizons is 710-980 (± 50) years BP. This indicates that vegetation fires in the upper montane rain forest and the páramo are not only a recent phenomenon but have also occurred in the past. However, it is not yet

Tab. 2 Results of the X-ray diffraction analysis of the clay fraction / *Ergebnisse der Röntgendiffraktometrie an der Tonfraktion*

Horizon	Illite	I-V-ml*	Vermiculite	HIV**	Kaolinite
Zamora					
Oxyaquic Palehumult, 1010 m					
Abw	+	(+)	(+)		+ + + + + +
Bt	+	(+)	(+)		+ + + + + +
BCr	+	+ + +	+		+ + + +
ECSF Transect					
Terric Haplosaprist, 1850 m					
OaC	+ + +	+ + + +		+	+ +
2AC	+ + +	+ + + +		+ + +	+ +
2BC	+ +	+ + +		+ + + #	+ + +
3C	+	+ + +		+ + + #	+ + +
Aquic Dystrudept, 1950 m					
A	+	+ + + + +	(+)		+ + +
ABw1	+	+ + + + +	+		+ + +
ABw2	+	+ + + +		+ +	+ + +
BwA	+	+ + + +		+	+ + + +
Cr	+	+ + +		+ +	+ + + +
Terric Haplosaprist, 2070 m					
A		+ + + + +			+ + +
Bw	(+)	+ + + + +			+ + +
Cr	+	+ + + +			+ + + +
Histic Placic Petraquept, 2510 m					
A~	(+)				(+)
2Bw1	+ + +	+ + + +			+ + +
2Bw2	+ + +	+		+ +	+ + + +
2Cr	+ + +	+ + +		+	+ + +
Humaqueptic Epiaquent, 2850 m					
A	+ +	+ + +	+		+ + + +
AB	+ + + + +				+ + +
B	+ + + + +				+ + +
2Cr~	+ + + + + +				+
Humaqueptic Epiaquent, 3050 m					
A1	+ + + + + +				+
A2	+ + + + + +				+
A3	+ + + + + +				+

* I-V-ml: Illite-vermiculite mixed layers

** HIV: Hydroxy interlayered vermiculite or pedogenic chlorite

\# Besides HIV also chlorites occurred, which could not be quantitavely differentiated from the HIV

~ The analyses was not conducted with oriented clay samples but with total soil samples

(+) traces + < 10% + + 10-20% +++ 20-40%

+ + + + 40-60 % + + + + + 60-80 % + + + + + + > 80 %

possible to establish whether the ancient fires had natural or anthropogenic causes.

In contrast to the soils at the ECSF transect, the single soil profile studied in the lower montane rain forest was more deeply weathered and accumulated very little organic material on the soil surface. According to the increase in clay content with soil depth, the pedon was classified as a Palehumult.

3.2 Soil mineralogical composition

Phyllites alternating at small scale with metamorphic sandstones and, to a lesser extent, quartzites, schists, feldspars, chlorites, pyrophyllites, graphites and epidotes are probable constituents of the mineral soil fraction and form the basis for the clay mineral formation and alteration along the ECSF transect.

For seven soil profiles, the clay mineralogy was analysed in detail (*tab. 2*). Kaolinite was the dominant clay mineral in the soil profile under lower montane rain forest. Other clay minerals such as illite-vermiculite interlayered minerals, illites and vermiculites are restricted to deeper soil horizons.

At the ECSF transect, the profiles between 1850 and 2070 m had a high content of illite-vermiculite mixed layered minerals and kaolinite in the clay fraction. The soils studied at 1850 and 1950 m had a special position as they developed in young landslide material. These profiles contained considerable amounts of hydroxy interlayered vermiculite (HIV). In profile 4, primary chlorite could be identified in the subsoil horizons, however, it was not possible to quantitatively differentiate the primary chlorite from HIV in the XRD spectra. The occurence of these chlorite minerals, which are not stable under acid soil conditions (*Barnhisel* and *Bertsch* 1992), might be related to the high content of weakly weathered rock material throughout the profile. The relatively young age of the deposits may also explain the high content of illite. With increasing altitude, the proportion of kaolinite minerals decreases and a shift from illite-vermiculite mixed layered minerals to an overall dominance of illites was observed. Illite was by far the dominant phyllosilicate mineral in the clay fraction at the highest profile 15 at 3050 m.

Clay mineralogy suggests that chemical weathering is most advanced in the soil under lower montane rain forest. This concurs with the highly advanced soil development and its classification as Ultisol. However, in contrast to many soils under lowland tropical rain forest (*van Wambeke* 1992), the subsoil horizons of the soil under lower montane rain forest still contain considerable amounts of high activity clays. At the ECSF transect, the decrease of kaolinite with increasing elevation and a shift of a dominance of illite-vermiculite mixed layered minerals at intermediate altitudes to a dominance of illites at high altitudes indicates that the weathering intensity decreases with increasing elevation (*Fanning* and *Keramidas* 1989). In an altitudinal transect of the Bolivian Andes, also *Wilke* and *Zech* (1987) found a dominance of illites at higher altitudes (2600-4800 m asl). However, they did not report a trend of increasing illite contents with increasing elevation. *Wilke* and *Zech* (1987) identified primary chlorites but not, as is the case in the present study, pedogenic chlorites. The much higher precipitation at the ECSF transect in south Ecuador is the reason for the more advanced clay mineral development as compared to the drier Bolivian transect.

The altitudinal gradient of phyllosilicate composition of the soils under study is highly accentuated by periglacial solifluction processes, in particular at higher elevations, and the frequent occurrence of landslides. The

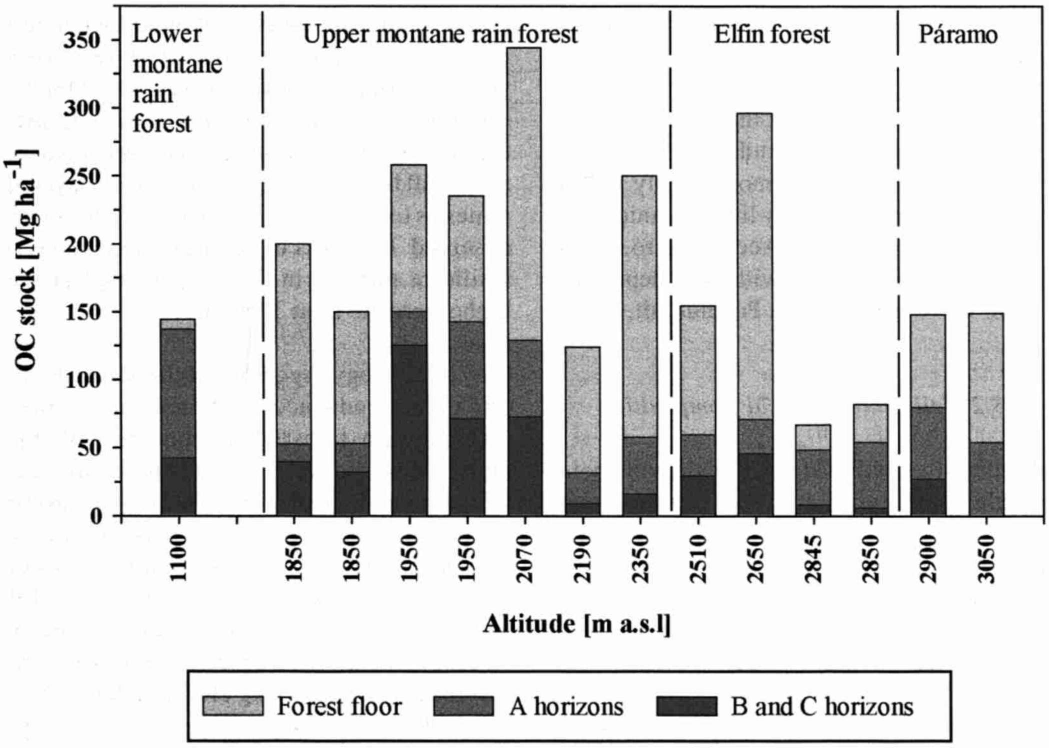

Fig. 2 Organic carbon stocks in the soil profiles along the altitudinal transect / *Vorräte an organischem Kohlenstoff in den Böden des Höhentransektes*

latter is the case in profiles 2-4, where the exposure of relatively unaltered bedrock to the surface results in an enrichment of less weathered phyllosilicates.

3.3 Soil chemical properties

3.3.1 Organic carbon and nitrogen

As previously discussed, the soils under upper montane rain forest are characterised by huge organic layers that have OC concentrations of about 400 mg g^{-1} d.w. Also the mineral soil horizons have considerably high OC contents of up to 80 mg g^{-1} d.w. Organic carbon stocks in the soil profiles vary considerably, but largest stocks of up to 344 Mg ha^{-1} m^{-1} occur between 1850 and 2650 m asl (*fig. 2*). At higher elevations under elfin forest and páramo the OC stocks are lower. This might be related to a decrease in the net primary production and thus of the annual litter input at high elevations. As can be already deduced from the huge forest floor, most OC in soils under upper montane rain forest is located in the forest floor. This is in contrast to lowland tropical forest soils (*Sanchez* 1976) and temperate forest soils (*Ziegler*, 1991), where generally most of OC is found in mineral soil horizons.

According to *Hetsch* (1976), the pattern of the OC stocks within the transect can be explained by the different temperature optima for net primary production (~20-25°C) and the micro-

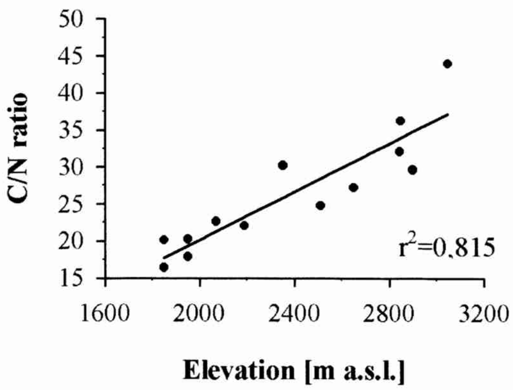

Fig. 3 Changes in the C/N ratio of the root layers of soils along the altitudinal transect / *Änderungen des C/N-Verhältnisses im Wurzelfilz im Höhenverlauf*

bial decomposition of organic matter (~35-40°C). With increasing elevation the decomposition rate is more distinctly reduced than the net primary production. At high elevations the frequently occurring water saturation of the forest floor additionally hampers microbial decomposition and faunal incorporation of organic matter into the mineral soil. Accumulation of huge organic layers under tropical montane rain forest was also observed by *Grubb* and *Tanner* (1967), *Hetsch* (1976), *Fölster* and *Fassbender* (1978), and *Veneklaas* (1991). *Lyford* (1969) reported that earthworms play a major role in the incorporation of OC into the mineral soil horizons and soil development below an elfin forest in Puerto Rico. However, in the ECSF transect we found only very few small earthworms. The role of the soil fauna in organic matter and nutrient cycling in the soils of the transect certainly deserves more attention.

The N_t contents in the soils mirror the OC values (*tab. 1*). Likewise the pattern of the N_t stocks in the soil transect follows that of OC (not shown). Highest N_t stocks of up to 17 Mg ha^{-1} were found in the upper montane rain forest. In this vegetation zone, most N_t is located in the forest floor, whereas the soils under lower montane rain forest, elfin forest, and páramo store the most N_t in the mineral surface soil. In the litter layers, the N_t contents decrease with increasing elevation (*tab. 1*). This results in a linear decrease in the C/N ratio of the litter layer with increasing altitude (*fig. 3*). Decreasing C/N ratios in soils under tropical montane rain forests with increasing elevations were also observed by *Veneklaas* (1991) in Columbia and by *Proctor* et al. (1993) in Sarawak. *Bruijnzeel* et al. (1993) hypothesised that the N_t content of the litter layer is a function of the proportion of scleromorphic leaves. Indeed, the analysis of the vegetation structure along the ECSF transect revealed that the proportion of semisclerophyllic and sclerophyllic plants increases from about 10% at 1800 m asl to about 80% at 2400 m asl (*Müller-Hohenstein* and *Zech*, 1998).

Increasing C/N-ratios with increasing elevation indicate a decreasing decomposition rate (*Yamakura* and *Sahunalu* 1990). At higher elevations of the transect, nitrogen mineralisation rate might be in addition restricted by low temperature and high soil water contents (*Marrs* et al. 1988). Together this indicates a low N_t supply in the soil of the upper part of the transect. *Vareschi* (1980) reported that scleromorphy can be also caused by nutrient limitations besides water stress. Hence, in the transect under study there appears to be a feedback mechanism between low N_t supply of the soil and scleromorphic vegetation.

3.3.2 Soil reaction

Within all soil profiles the soil reaction is acidic or very acidic (*tab. 1*). This has been observed for many tropical montane forest soils (*Tanner* et al. 1998). Lowest pH values

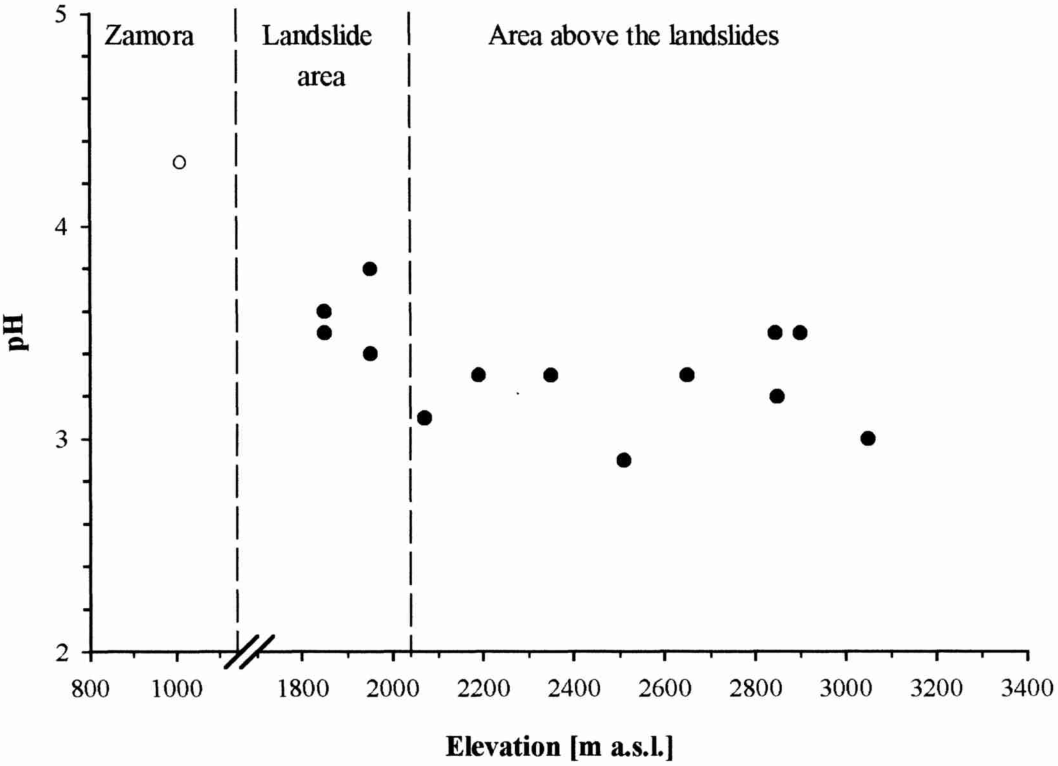

Fig. 4 pH values ($CaCl_2$) of the A horizons of soils along the altitudinal transect / *pH-Werte ($CaCl_2$) der A-Horizonte der Böden im Höhenverlauf*

have been found in the Oa horizon and the root layer. We assume that several processes were responsible for this observation. The pH minima in the root layer may be caused by organic acids with low pK_a-values, which are released into solution during organic matter decomposition and by roots exudation. Also nitrogen and sulphur mineralisation and NH_4^+ nutrition of plants release protons. *Wilcke* et al. (1999) showed that the forest canopy effectively buffers the protons in the precipitation leading to pH values of about 7 in the canopy drip. The buffered protons, however, are released by the roots and contribute to acidification of the root layer.

In the mineral soil, pH values increase owing to chemical buffer processes. The four profiles developed in the landslide material showed slightly higher pH-values compared with the profiles above (*fig. 4*). This might be related to the higher content of unweathered rocks. In the next chapter it is discussed whether the soils developed in landslide material are more favourable with respect to supply with nutrient cations than the soils above the landslide area.

3.3.3 Effective cation exchange capacity

The soils of the ECSF transect have low ECEC of < 16 cmol(+) kg soil in their mineral soil horizons (*tab. 1*). The highest values were observed in the soils developed in the landslide material (1850 and 1950 m asl). Above the

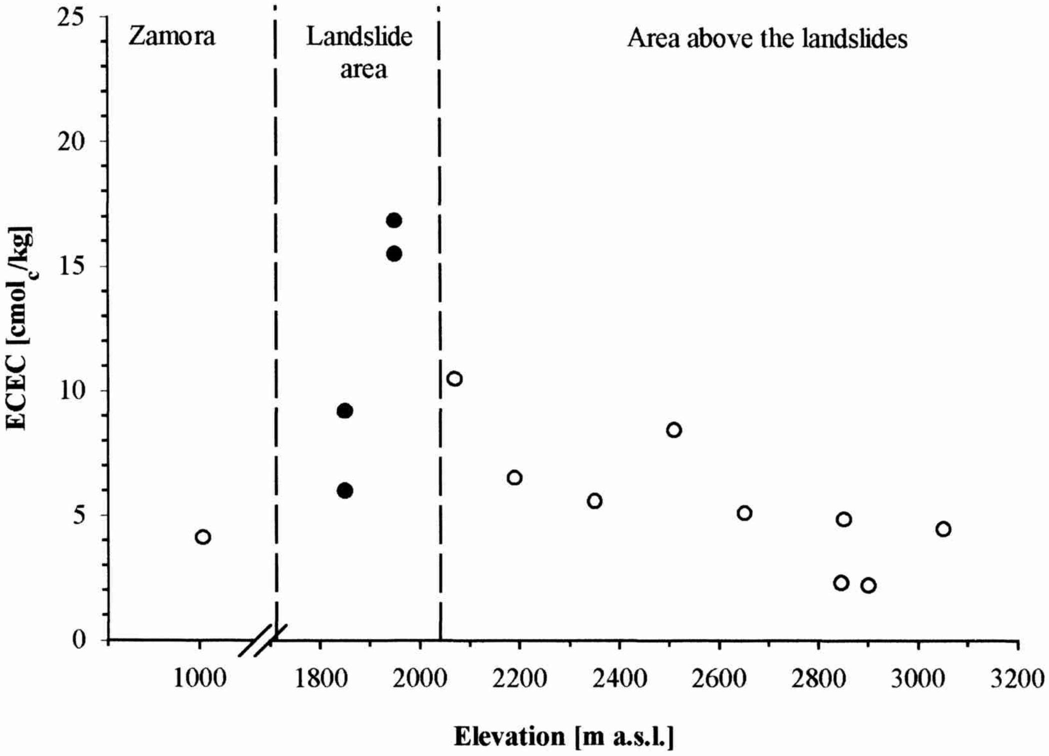

Fig. 5 Effective cation exchange capacity (ECEC) in the A horizons of soils along the altitudinal transect / *Effektive Kationenaustauschkapazität (ECEC) in den A-Horizonten der Böden im Höhenverlauf*

landslide area, the ECEC of the soils decreased with increasing altitude (*fig. 5*).

The acid soil reaction might be one reason for the generally low ECEC values, as it causes a low negative charge of the organic acids and the variable charge minerals. But the pH values show no altitudinal gradient and could, therefore, not be held responsible for the decreasing ECEC with increasing elevation. As the organic matter content did not show an altitudinal dependency either, we assume clay contents and mineralogy are responsible for the decrease of the ECEC above 1950 m asl. In the soils of the ECSF transect the clay content decreases with increasing altitude (*tab. 1*) and clay mineralogy is dominated by minerals of low to intermediate permanent charge, such as kaolinites and illites (*tab. 2*). Expandable phyllosilicates occur primarily at lower elevations. However, the interlayer space of vermiculites, occurring either as part of the illite-vermiculite interlayered minerals or as pure minerals, is occupied by Al-hydroxy-interlayers. The degree to which such interlayers reduce the cation exchange capacity of these minerals is not known. Therefore, it cannot be stated exactly how altitudinal changes of the cation exchange capacity relate to changes in the clay mineral composition.

Only in the forest floor horizons, basic cations contribute to a considerable degree to ECEC. This is caused by the release of basic cations during litter decomposition (ash alkalinity) and subsequent sorption to organic anions. In

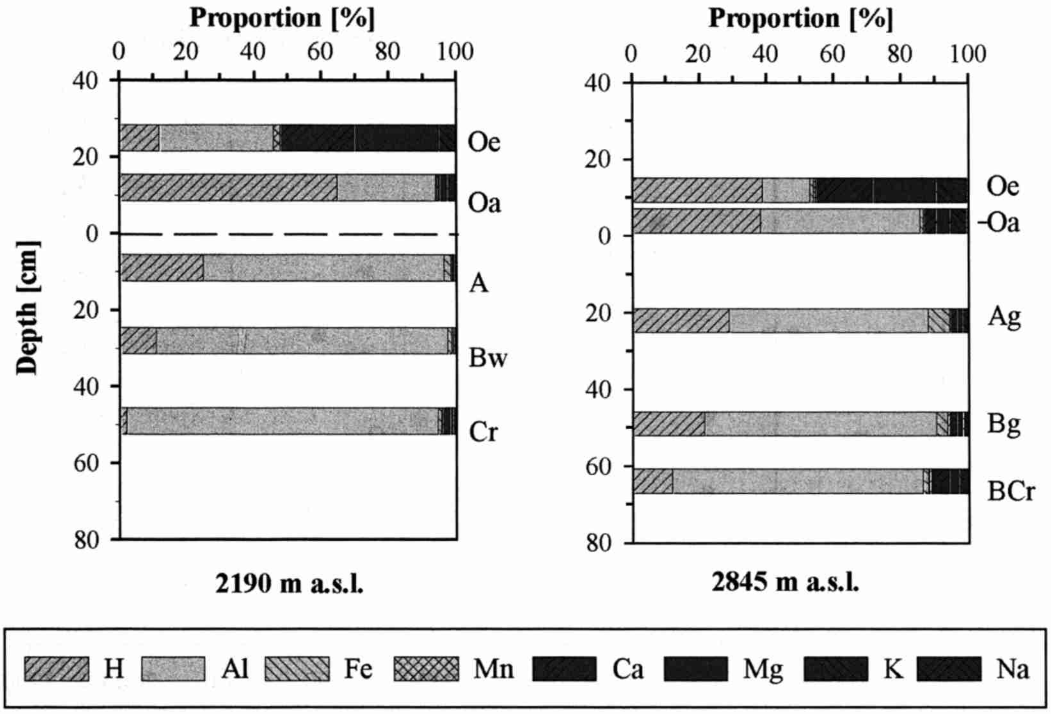

Fig. 6 Contribution of basic cations, Al, H and Fe to the ECEC of profile 7 (2190 m asl) and profile 12 (2845 m asl) / *Relativer Anteil von basisch wirkenden Kationen und von Al, H sowie Fe an der effektiven Kationenaustausch-kapazität der Profile 7 (2190 m) und 12 (2845 m asl)*

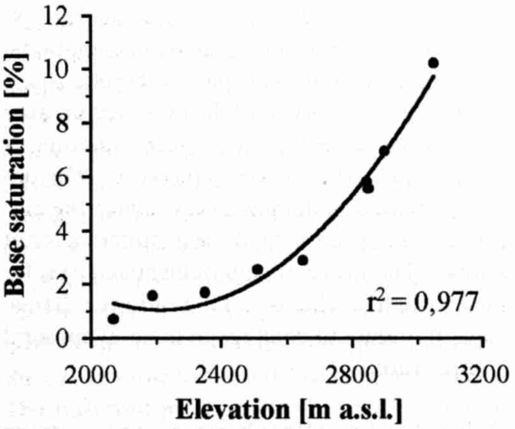

Fig. 7 Base saturation in the A horizons of the soils above the landslide profiles / *Änderung der Basensättung in den A-Horizonten von Böden, die sich oberhalb der Hangrutschungen entwickelt haben*

the mineral horizons of the undisturbed sites the exchange sites are dominated by Al ions, while basic cations represent < 5% of ECEC (*fig. 6*). Low base saturation in the mineral soils have been described for a wide range of tropical montane rain forest sites (*Grimm* and *Fassbender* 1981, *Steinhardt* 1979, *Grieve* et al. 1990). Mineral weathering in these soils is proceeded, due to the high precipitation and fairly high temperatures. The polyvalent Al ions released during destruction of clay minerals and Al-hydroxides occupy the exchange sites thereby desorbing basic cations.

Above the landslides, the soils are less developed and, according to clay mineral analysis, less intensively weathered with increasing elevation. This may explain the increasing base

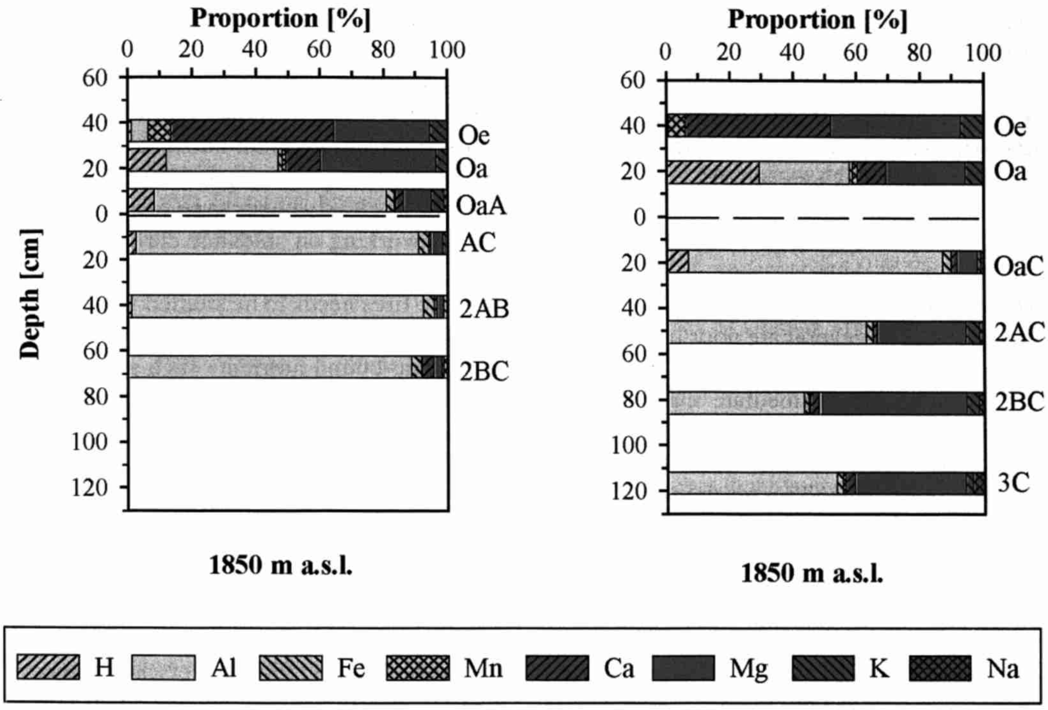

Fig. 8 Contribution of basic cations, Al, H and Fe to the ECEC of profiles 2 and 3 (1850 m asl) / *Relativer Anteil von basisch wirkenden Kationen und von Al, H sowie Fe an der effektiven Kationenaustauschkapazität der Profile 2 und 3 (1850 m)*

saturation at higher altitudes (*fig. 7*). Higher percentages of exchangeable basic cations may be also due to vegetation fires. According to *Lægaard* (1992) the páramo vegetation belt has frequently been burnt in Ecuador. Burning releases cationic nutrients that are otherwise immobilised in the forest floor which decomposes only slowly (see above). The cations can then be leached into the mineral soil horizon and adsorbed to the exchange sites. However, although we found charcoal in the soil profiles under páramo, no indication of high burning frequency or recent fire was identified.

3.3.4 Special position of the profiles developed in landslide material

The soil profiles developed in landslide material differ in many ways from the soils developed in the less disturbed parent material. Compared to the latter, the soils developed in landslide material have higher pH-values and ECEC and are richer in exchangeable cations (*fig. 6* and *8*). This could be explained by the high content of weakly weathered rock material which could have released these cations during weathering. One of the landslide profiles holds a special position as it contains a high amount of exchangeable basic cations, in particular Mg. The reason for the high Mg concentration is probably the occurrence of primary chlorite within this profile. During weathering, this mineral releases Mg (*Barnhisel* and *Bertsch* 1992). The fact that the other soil profile studied at this elevation was situated only 10 meters apart and did not show these high amounts of exchangeable

Mg (*fig. 7*) indicates a high spatial variability within the landslide profiles. Nevertheless, it appears that nutrient supply of soils developed in landslides is superior to that of soils not affected by this natural disturbance.

4. Conclusions

The investigation of the soil transect revealed that the soils in general are poor in exchangeable nutrient cations. In particular, this is true for the sites at intermediate elevations. In these soils, by far the most exchangeable nutrients are located in the forest floor. Thus plants largely depend on nutrients which are released during organic matter mineralisation in the forest floor and respond with the production of a high root biomass that is located on the soil surface (*Jordan* 1985).

Several soil parameters follow the altitudinal gradient. At higher elevations, soils are less developed than in the lower parts of the transect but show more pronounced hydromorphic properties owing to increasing precipitation and decreasing soil temperature. The decreasing weathering intensity at higher altitudes is also reflected by the clay mineral composition and the higher proportion of exchangeable nutrient cations to total ECEC. In contrast to the availability of exchangeable cations, the supply of organically-bound nutrients probably decreases with increasing elevation. Increasing C/N ratios and increasing water contents of the forest floor both negatively affect the mineralization of nitrogen. There appears to be a close correlation between the soil chemical properties and the structural composition of the vegetation. However, the cause and effect relationship still needs to be elucidated in detail.

Disturbances are a natural phenomenon at the transect under study. Soils developed in landslide material have enhanced pH values and more exchangeable nutrients. It can be tentatively concluded that landslides are important ecosystem processes that renew the soil's capacity to supply plant nutrients in the otherwise nutrient-poor montane rain forest. This hypothesis clearly needs to be tested in future studies working on landslide chronosequences. Likewise, the effects of natural and anthropogenic fires needs to be studied with respect to nutrient cycling, in particular with reference to organic-bound nutrients such as N, P, and S. This will be realized in the near future, using a water catchment approach.

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Summary: Tropical montane rain forest soils. Development and nutrient status along an altitudinal gradient in the south Ecuadorian Andes

In order to study the impact of elevation on soil properties under humid tropical conditions, fourteen soil profiles were investigated along an altitudinal transect in the south Ecuadorian Andes. The transect followed a steep ridge from the lower montane rain forest belt to the páramo region. The soils were analysed for their clay mineral composition, pH-values, total carbon and nitrogen, effective cation exchange capacity and composition of exchangeable cations. In the soil of the lowest site located at 1010 m asl, the most important phyllosilicate is kaolinite. With increasing elevation, illite-vermiculite interlayer minerals and illites become dominant. The soil reaction is generally very acidic, resulting both in low ECEC and in low base saturation. At higher elevations base saturation increases, which can be attributed to higher concentrations of weatherable clay minerals. In contrast to the availability of exchangeable cations, that of organic-bound nitrogen decreases with altitude as is deduced from high C/N-ratios and frequently occurring water saturation in the forest floor horizons. Soils which have developed in landslide material have distinct properties in comparison to the other soils. Owing to the exposure of less weathered parent material to the surface, the nutrient availability of the landslide profiles was strongly enhanced. Therefore, we conclude that landslides play an important role in the nutrient cycling of this ecosystem.

Zusammenfassung: Böden unter tropischem Bergregenwald. Bodenentwicklung und Nährstoffstatus entlang eines Höhengradienten in den südecuadorianischen Anden

Ziel dieser Studie war die Untersuchung des Einflusses eines Höhengradienten auf Bodeneigenschaften unter humiden tropischen Bedingungen. Hierfür wurde in den südecuadorianischen Anden ein Bodentransekt vom Unteren Bergregenwald bis zur Páramo mittels vierzehn Profilen erkundet. Die Böden wurden untersucht hinsichtlich: Tonmineralgarnitur, pH-Werte, Gesamtkohlenstoff und -Stickstoff, effektive Kationenaustauschkapazität sowie Zusammensetzung der austauschbaren Kationen. Während im Profil des in mit 1010 m ü.N.N am tiefsten gelegenen Standortes Kaolinit dominiert, verschiebt sich die Tonmineralgarnitur mit zunehmender Höhe über eine Dominanz von Illit-Vermiculit-Wechsellagerungsmineralen zur Dominanz von Illit. Die Bodenreaktion ist generell sehr sauer, was niedrige effektive Kationenaustauscherkapazität und geringe Basensättigung zur Folge hat. In größerer Höhe ist eine Zunahme der Basensättigung aufgrund höherer Anteile leicht verwitterbarer Tonminerale zu verzeichnen. Im Gegensatz zur Verfügbarkeit an austauschbaren Kationen sinkt jene von organisch gebundenem Stickstoff mit zunehmender Meereshöhe. Ursache hierfür ist das weite C/N-Verhältnis der Streu und die oftmals auftretende Wassersättigung der organischen Auflage. Böden, die sich in Hangrutschungsmaterial entwickelt haben, nehmen im Transekt eine Sonderstellung ein. Aufgrund des hohen Anteils an wenig verwittertem Skelett ist der Anteil basischer Kationen zum Teil deutlich erhöht. Wir schließen daher, daß die natürlich vorkommenden Hangrutschungen eine bedeutende Rolle im Nährstoffkreislauf dieses Ökosystems spielen.

Resumen: Suelos bajo bosque de montaña tropical húmeda. Desarrollo y estado de nutrientes a lo largo de un gradiente altitudinal en los Andes del sur del Ecuador

El objectivo del presente estudio fue examinar los más importantes procesos del desarrollo de los suelos y el estado de nutrientes en suelos bajo bosque de montaña tropical a lo largo de un transecto altitudinal en los Andes del sur del Ecuador. Como este transecto fue ubicado en sotavento de la cordillera entre 1590 y 3320 msnm no sólo representó un gradiente de temperatura sino también de precipitación. En los suelos fueron analizados: la composición mineral, el contenido total de carbono y nitrógeno, el pH y la concentración de los cationes intercambiables. Varias propiedades del suelo cambiarón sistemáticamente con el incremento de la altitud. Los cambios más pronunciados se observarón entre las cotas 1600 y 2200 msnm. La parte baja del transecto es caracterizada por un clima subhúmedo y restos bajo bosque seco de montaña están conservados. La mineralogía de la arcilla y las fracciones del Fe de los suelos de la parte baja indican alteración sólo moderada. En estos suelos la saturación de los metales básicos es alta y la taza de mineralización de nitrógeno orgánico parece estar suficiente para alimentar la vegetación. En la parte central del transecto, un bosque de montaño perhúmedo se desarrolló. Una lixiviación fuerte causó una alteración avanzada de los minerales, bajos valores del pH en el perfil entero de los suelos y una saturación de metales básicos baja dentro del suelo mineral. La acumulación de una capa orgánica profunda y altas relaciones C/N indican una provisión baja con nutrientes ligados a la materia orgánica. En altitudes sobre los 2700 msnm el bosque montañoso cambia gradualmente al bosque de 'silfos', un bosque de baja densidad con árboles pequeños y finalmente a la ceja andina. Los suelos en esta parte del transecto son caracterizadas por una hidromorfía pronunciada. En la parte central y alta del transecto la mayoría de los nutrientes está ubicada en la capa organica. La nutrición de las plantas depende de la mineralización de nutrientes en la materia orgánica. La presencia de una alta densidad de raíces en la capa orgánica indica ciclos cerrados de nutrientes.

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