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The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands

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Abstract

The impact of extensive livestock farming on the physical and chemical characteristics of the volcanic soils and on the nutrient status of green plant tissues of neotropical alpine grasslands (páramo) is studied. Soil and plant samples were taken over a one-year period at five sites with different agricultural (grazing and burning) management. In the undisturbed páramo ecosystem, soil moisture (50–250%) and organic matter content are high (7–27%) and decomposition ($11\text{--}35\% \text{ yr}^{-1}$) and element concentrations are low. Low temperatures ($\text{max} < 10^\circ\text{C}$) and phosphorus fixation by the soil ($5 \text{ mg P g}^{-1} \text{ soil}$) determine the low mineralization and turn-over rates.

Multivariate analysis of laboratory results indicates that the season of sampling and the agricultural practice are the most important explanatory factors for variation of soil characteristics. After long-term heavy grazing, soils have a higher bulk density and a lower moisture content. The outcome of a litterbag experiment confirms the hypothesis of higher decomposition rates at grazed sites. In the intermediate (wet-dry) season, conditions were somewhat better for plant growth but the system remained nutrient limited.

Surprisingly, no relation between soil density, moisture or carbon content and concentrations of available nutrients in the soil is found. This is supported by the rather uniform nutrient concentrations in green plant tissue among the sites. It is concluded therefore that the effect of burning and grazing on páramo soils is principally restricted to physical characteristics, and that differences in chemical characteristics of the soil do not cause differences in vegetation structure between grazed, burned and undisturbed sites.

Introduction

The páramo ecosystem

Páramos are climax neotropical alpine grasslands, covering extensive areas between the forestline (3000–3800 m above sea level) and the snow line (4400–4800 m a.s.l.) in the Northern Andes. They are found from Ecuador to Venezuela and Costa Rica, having their main extension in Colombia. Páramos are considered an important ecosystem, both ecologically and economically. Their ecological value is the unique floristic composition with a high degree of endemism; their economical importance concerns the function

as a water resource for the large human population in inter Andean valleys (Guhl, 1968; Luteyn, 1992; Monasterio, 1980). In terms of abiotic conditions and adaptations of the vegetation, there are many similarities between páramos and other wet tropical alpine grasslands in the world (Cleef, 1981; Hedberg, 1992; Monasterio and Vuilleumier, 1986; Smith and Young, 1987). In addition, many authors have emphasized the similarities between alpine and arctic ecosystems, with reference to the cold conditions, the retarded decomposition and the resulting vegetative structure (e.g. Billings, 1973; Smith and Young, 1987).

Páramos are subject to extreme, but constant climatic conditions with low average temperatures and a high humidity as the net result of a moderate precip-

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itation (1000–2500 mm) and a limited evapotranspiration (500–1000 mm, Monasterio, 1980; Salamanca, 1991; Sarmiento, 1986; Troll, 1968). As a result of the combination of a cold and wet climate, the rate of decomposition of organic matter is low (Cleef, 1981; Luteyn, 1992; Monasterio and Sarmiento, 1991). The soils are young and slightly weathered and most nutrients are present in forms, unavailable to plants. Phosphorus fixation capacity can be high, especially when the soils are derived from volcanic ash (Andosols, Van Reeuwijk, 1989; Wada, 1980) as in many, though not all páramo areas. Particularly in Andosols, decomposition is seriously retarded because of the protection of soil organic matter against bio-degradation by the formation of organo-metallic complexes (Van Reeuwijk, 1989; Wada, 1980). Consequently, the total stock of nutrients may be high, but the amount of nutrients available for the plants is low. In general, the soils are wet, black coloured (high carbon content) and have a low bulk density (Thouret, 1989).

The vegetation has adapted in various ways to these extreme conditions, resulting in a tall-structured grassland with a relative high above ground biomass, but with low turn over rates and low foliar nutrient concentrations (Beck et al., 1982; Hofstede et al., 1995b; Monasterio and Sarmiento, 1991; Smith and Young, 1987). In these conditions, it might be expected that either phosphorus (due to fixation) or mineral nitrogen (low mineralization) are growth limiting (Chapin, 1980; Chapin et al., 1978; Vitousek, 1982; Vitousek and Howarth, 1991). Dead material is retained within the structure of growth forms, such as the dominant tussock grasses and stem rosettes (Cardozo and Schnetter, 1976; Monasterio and Sarmiento, 1991; Smith, 1979). The tall structure of the vegetation may be important for above ground water and nutrient retention (Chapin et al., 1979; Monasterio and Sarmiento, 1991; Smith, 1979). Besides the stem rosettes and tussock grass, other short growing species and dwarf shrubs can be present (Cleef, 1981; Salamanca, 1991; Sturm and Rangel, 1985).

Grazing and burning practices

A common and widespread agricultural practice in the páramo zone is extensive grazing by cattle, often combined with burning of natural vegetation to provide fresh, palatable grasses to the grazers (Luteyn, 1992; Parsons, 1982; Verweij and Budde, 1992). The natural páramo vegetation is to a certain extent tolerant to these management practices (Chapin et al., 1979;

Fig. 1. Hypothesis on the effect of grazing and burning on soil and plant characteristics in the páramo ecosystem. Thin arrows indicate causal relations between characteristics; bold arrows indicate an increase or decrease in a characteristic as a result of a change in a related characteristic.

Leagaard, 1992; Ramsay, 1993). However, when the burning frequency and grazing intensity increase, the grass tussocks will remain short or will be replaced by short growing grasses and herbs which are more tolerant to disturbance (Fetcher et al., 1984; Milchunas et al., 1988; Pastrana et al., 1990; Salamanca, 1991; Verweij and Budde, 1992). This change in vegetation results in a lower above ground biomass and more exposure of bare ground (Hofstede et al., 1995a; Hofstede et al., 1995b; Salamanca, 1991).

Although the underlying causes for vegetation change after grazing and burning in páramo have not been studied until now, they can be hypothesized (Fig. 1). Fire might be an important factor, as it consumes the vegetation and triggers a fast recycling of nutrients (Rundel, 1981; Vogl, 1974). The grazers also consume the vegetation and compress the soil by trampling (Dormaar et al., 1989; McNaughton et al., 1988). The net result of less vegetation cover and higher soil density are higher maximum temperatures in the top soil as a result of less isolation by vegetation and more decomposition of organic material as a result of these higher temperatures and less acidic conditions. Probably, soil moisture content also will be lower (less C, compression, evaporation, Dormaar et al., 1989; Johnston et al., 1971; Moorhead and Reynolds, 1993; Nadelhoffer et al., 1991; Swift et al., 1979; Seastedt et al., 1991).

If concentrations of available nutrients are growth limiting, enhanced decomposition and concurrent min-

eralization of nutrients speeds up productivity at for at least a short period (Chapin, 1980; Milchunas et al., 1988; Vitousek, 1982). Higher nutrient availability can result in higher nutrient concentrations in plant tissue (Bryant et al., 1983; Chapin, 1980; Ruess, 1984). Finally, the change in species composition of the vegetation might be explained by the dominance of grazing and burning tolerant species in the competition for the higher soil nutrient levels (Chapin, 1980; Milchunas et al., 1988; Negi et al., 1992). The resulting grassland is likely to consist of a compact and dry soil, with a short growing vegetation which is nevertheless attractive for grazers because of the higher overall palatability (Johnston et al., 1971; McNaughton et al., 1988; Milchunas and Lauenroth, 1993). Seastedt et al. (1991) noted the shift in competition for light to competition for nutrients when burning and grazing are introduced in tall grasslands.

When studying the impact of agricultural management, it should be considered that differences observed in physical and chemical characteristics of soils can also be due to other factors. Firstly, seasonality may cause differences, even though the change in seasons is not so pronounced in the páramo (Smith and Klinger, 1985; Smith and Young, 1987). Secondly, the position on the slope can cause differences in the hydrology and chemistry of the soils. Finally, differences in soil characteristics might be related to vegetation type due to a different organic matter addition by plants (Pérez, 1992). Similar remarks can be made with respect to temporal and spatial variation in plant nutrient concentrations.

The present study was undertaken to test the hypothesis whether the combination of grazing and burning leads to changes in concentrations of nutrients in páramo soils and plant tissues. The following objectives were established: (1) to analyse the impact of extensive livestock farming on physical and chemical characteristics of the volcanic soils of neotropical alpine grasslands (páramo), (2) to test if vegetation growth is limited by P or N availability, and (3) to determine whether the agricultural practice influenced the nutrient status of green plant tissues.

Study area

In the Parque Nacional Natural de los Nevados (Colombian Central Cordillera, 4° 48' N, 75° 24' W), aerial photos and interviews with local inhabitants were used to select five study sites in areas with

different grazing and burning management (Table 1). The management was estimated qualitatively, according to amounts of droppings, trampling indications and fire scars (in close collaboration with P A Verweij and co-workers). As far as could be documented, the present management was constant during at least several decades (this páramo area was first colonized one century ago). The burned sites were burned several times before the last fire, with intervals of 5–10 yr. All sites were situated in the proper tussock grass páramo belt (Cuatrecasas, 1958), they were more or less SW exposed, and had the same climate and soil properties. Witte (in press) reported an average air temperature of 4 °C (absolute range: –3 to 15 °C), and an annual precipitation of 929 mm. Rainfall had a weak bimodal distribution, with peaks in March and November (Fig. 2). The soils were characterized as Cryands (USDA, 1975), formed in ash deposits of nearby (still active) volcanoes. They consisted of two super imposed paleosols (ca. 30 cm thick) and a top layer (5–10 cm) of relatively recent ashes. In every paleosol an inferior layer of small and unweathered gravelsize lapilli was present, grading into fine ashes. The lapilli layer of the oldest paleosol was rather thick and capped by a continuous iron pan (60–70 cm below surface, Thouret, 1989). The roots were highly concentrated in the top layer of the soil (Rossenaar and Hofstede, 1992).

Methods

Soil analysis

The execution of a soil sampling scheme covered the mayor possible conditions that could have had an effect on physical and chemical characteristics. In total, 108 topsoil (0–10 cm) samples were taken from all sites, in the wet season (November) in the dry season (February) and on an intermediate date (December). The samples were from the top, the transition zone and the foot of the slope, and different samples were taken per general vegetation type (two to four per site, Table 2). Each composite sample consisted of five subsamples which were bulked and homogenized; roots were removed carefully by hand.

The physical characteristics of the samples were determined on two volumetric subsamples of each composite soil sample. These samples (60 m were taken with a volume-sampling tube (Eijkkelkamp, Giesbeek, The Netherlands). After oven drying (105 °C, 24 h) and weighing of these samples, both bulk den-

Fig. 2. Walter-climate diagram of the climate station "Laguna del Otún", 4000 masl, based on data from 1983 (Witte, 1995). The lower line indicates temperature; the shaded area represents above this line represents the precipitation; the black shaded area is the precipitation $> 100 \text{ mm month}^{-1}$

sity (mg dry wt cm^{-3} soil volume) and soil moisture content (% of DW, weight difference before and after drying) was established.

The acidity, the C content and the concentrations of readily available (salt-extractable) elements were analysed in field-humid samples, following the laboratory instructions by Allen et al. (1974). The pH was measured immediately after sampling in a 1:5 (dry weight base) water solution (ConsortTM-pH meter). Then, one aliquot of each sample was extracted in 1 N NH_4Ac . After filtration, extractable P (colorimetrically as molybdate-complex; Vogel, 1961), and K, Ca, Mg, Na and Al were estimated, using a Perkin ElmerTM 1100B atomic absorption spectrophotometer. Another aliquot was extracted with 2 N KCl for estimation of concentrations of mineral nitrogen (NH_4^+ and NO_3^-) after distillation and titration with boric acid as indicator. A third aliquot was used for C estimation (oxidation with chromic acid and concentrated H_2SO_4 -heat-of dilution, titration with diphenylamine as indicator).

Total (readily available plus non-available) element concentrations of the soils were determined using the samples that were taken in the wet season. Representative parts of these samples were bulked per site, according to the relative abundance of the vegetation types. The bulked samples (one for each site) were dried (24 h, 105°C), sieved for root removal and ground. To estimate the degree of weathering of the volcanic ash, a separate sample was taken from unweathered lapilli. From all dried samples, one part of each sample was used for C and N detection in a Carlo ErbaTM 1106 ele-

mental analyser. A second part was ignited at 400°C and dissolved in HCl (25%) prior to P, K, Ca, Mg, Na and Al analysis as described above. The mineral ash content of the samples was calculated by comparing the weight before and after ignition.

P-fixation and N-mineralization capacity of the soils were estimated on four soil samples taken in the wet season from every site. These samples consisted of ten randomly selected subsamples, of which the roots were removed by hand. One part of every sample was incubated with a surplus solution of KH_2PO_4 during 24 h, after which the P-fixation capacity (mg P g^{-1} DW) could be established. The other part of every sample was incubated in field-humid condition, in open bags at ca. 10°C , during 14 days. The differences between the concentrations of NO_3^- and NH_4^+ in the soil samples before and after these 20 days represented N-mineralization and nitrification capacity of soil samples. Since incubation was aerobic, loss by denitrification was unlikely.

Fertilizer trial

A simplified fertilizer trial was conducted to determine if N or P can be growth limiting (Bowman et al., 1993). At the undisturbed site Agua Leche, four replicate plots of $5.5 \times 5.5 \text{ m}$ were cleaned of vegetation and the topsoil was homogenized. Fences were placed to prevent rabbits to enter the plots. After this, seven subplots of 1 m^2 were selected within each plot, and fertilizer (N and P) was applied in three different dosages (15, 30 and $45 \text{ g element m}^{-2}$). The experimental design was

Table 1. Description of the selected study sites

A. Study sites	Auga Leche	Loma Alta	Loma Baja	Paramillo	La Leona
Agricultural management:	No indication of grazing or fire	Moderately grazed; 6.5 yr after last fire	Heavily grazed; 3.5 yr after last fire	Heavily grazed; no indication of fire (low amount of fuel)	One year after last fire; no actual grazing (moderately grazed/burned before fire)
Size (ha):	12	8	12	15	10
Altitude (m above soil level):	4100	3950	3950	4000	4000
Exposure:	SW	SW	SW	SW	NW
Inclination (°):	20–30	30	30	5–10	25–35
Stem rosette layer: (<i>Espelatia hartwegiana</i> Cuatr.)	1–6 m, dense but individually growing.	1–3 m, less dense as at Auga Leche.	As at Loma Alta.	1–3 m, dense, growing clustered.	As at Loma Alta and Loma Baja.
Tussock grass layer: (<i>Calamagrostis effusa</i> H.B.K.)	0.5–1 m, dense, high cover and low live:dead ratio.	As at Auga Leche, but more live material.	0.1–0.3 m, many fragmented clumps, low cover, mostly live material.	0.5–1 m, large individual tussocks. Very low total cover.	As at Loma Baja, but recovering from fire.
Ground layer:	Acaulous rosettes (<i>Hypochoeris sessiliflora</i> H.B.K., <i>Eryngium humile</i> Cav.), and sedges (<i>Carex</i> spp.). Low cover	Acaulous rosettes and short growing grasses (<i>Calamagrostis</i> ssp., <i>Agrostis</i> ssp.). Higher cover than at Auga Leche	Many short grasses, sedges and acaulous rosettes. Creeping shrubs are present (<i>Pernettya prostrata</i> Cav.) DC.)	Close mat of short grasses (<i>Agrostis haenkeana</i> Hitchc., <i>Aciachne pulvinata</i> Benth.) and rhizome forming herbs (<i>Lachemilla orbiculata</i> R. et P., <i>Lupinus microphyllus</i> Desr.)	Acaulous rosettes, short growing grasses and sedges. Some pionier species (<i>Rumex acetocella</i> L.)
Bare spots	Some	Some	Many	None	Many

not totally randomized, because care was taken that the lowest dosages were applied at the highest position of the plots to avoid bias by leaching from more fertilized subplots. Next, 200 g *Lolium perenne* seeds was sown equally over each parcel. After 3 months, the grass yield was harvested, dried (24 h, 105 °C) and weighed. The non native grass species *Lolium perenne*

was used as a bioassay for practical reasons (Binkley and Vitousek, 1989), since it has a faster and more regular growth than the native *Calamagrostis effusa*. Besides, it is present in the páramo since it is frequently sown in meadows in nearby potato growing areas.

Table 2. Selected environmental variables per study site. A soil sample was taken of most possible combinations of environmental variables (e.g. at Agua Leche, the samples in the wet season were taken on three different positions, and at each of these, soils below five vegetation types sampled)

Site (agricult. management)	Season of sampling	Position on slope	Vegetation type
Agua Leche (undisturbed)	-Wet	-Top	-Tussock grass
	-Wet/Dry	-Trans	-Sedges-shortgrass
	-Dry	-Foot	-Herbs-bare ground
			-Espeletia
Loma Alta (moderately grazing, burned)	-Wet	-Top	-Tussock grass
	-Wet/Dry	-Trans	-Sedges-shortgrass
	-Dry	-Foot	
Loma Baja (heavy grazing, burned)	-Wet	-Top	-Tussock grass
	-Wet/Dry	-Trans	-Shortgrass-mat
	-Dry	-Foot	-Herbs-bare ground
Paramillo (heavy grazing, unburned)	-Wet	-Top	-Tussock grass
	-Wet/Dry	-Trans	-Short grass-mat
	-Dry	-Foot	-Herbs-bare ground
			-Espeletia
La Leona (recently burned)	-Wet	-Trans	-Tussock grass
	-Wet/Dry	-Foot	-Sedges-shortgrass
	-Dry		-Herbs-bare ground

Soil temperature

At every single site, the soil temperature was recorded regularly at 2 cm depth in the soil, during all days in which the fieldwork was executed. This was done between 11.00 and 13.00 h, and care was taken that approx. 100 measurements were available from every site. Temperatures were measured with NiCr-NiAl thermocouple.

Litter disappearance

Differences in disappearance rates of litter from the undisturbed site, Agua Leche, the moderately grazed and burned site, Loma Alta and the heavily grazed and burned site, Loma Baja, were estimated with a litterbag experiment (Wiegert and Evans, 1964). The results of this experiment provided extra information on decomposition. At every site, 75 (100 at Agua Leche) nylon wire bags (25 × 5 cm, mesh 1 mm, with some holes

widened to 1 cm) were filled with about 30 g randomly sampled, freshly fallen litter from that site, with known fresh/dry ratio. These bags were marked and placed randomly within the site, in close contact with the mineral soil. After 3 (only Agua Leche), 6, 9, and 12 months, 25 bags were recovered at each site and their content was dried and weighed.

Plant analysis

To estimate the differences in leaf nutrient concentrations between different growth forms and within these growth forms, samples were taken per growth form from all sites. The samples were from green leaves of tussock grass, short growing grasses, sedges, herbs, shrubs, stem rosettes (both young leaves and green leaves) and taken in the wet season (November), in the dry season (February), and in two intermediate seasons (Wet-dry; December, Dry-wet; First weeks of March). Samples represented a mixture of ten randomly select-

ed subsamples. Analytical methods used were the same as described above for total element analysis of the soil samples.

Data analysis

To analyse the relations among soil physical and soil chemical characteristics, and between these characteristics and the conditions of sampling, several (multivariate) statistic procedures were used. First, to determine correlations among soil physical and chemical characteristics linear regression analysis was applied to the laboratory results of all soil samples. The factor that was supposed to control changes in other characteristics (following Fig. 1) was used as the independent factor. After this, the patterns of relations between soil characteristics and the conditions of sampling (site, season-of sampling, position on the slope and vegetation type) were studied by ordination analysis, using the conditions of sampling as explanatory factors. Redundancy Analysis (RDA; within the CANOCO computer package, Ter Braak, 1987) was most appropriate, since physical and chemical characteristics of soils were expected to have a linear relation with explanatory factors. With this multivariate analysis technique, the laboratory results are scattered in an ordination diagram. The condition of sampling that corresponds best to one of the dimension-less axes, represents the factor that can explain the largest part of the variation in laboratory results. The soil characteristics were standardized by dividing the difference from the mean by the standard deviation of the data. Since the explanatory factors were at a nominal scale, they entered the ordination as 17 quantitative dummy variables for every value of a nominal factor (Jongman et al., 1987). Finally, the relations between the main explanatory factors and the individual soil characteristics were tested using two-way Analysis of Variance (ANOVA), and a Tukey-Kramer test for pairwise mean comparison. For ANOVA, the original nominal explanatory factors were used.

The effect of the N and P fertilizer and the dosage of fertilizer on the yield of *Lolium perenne* was tested with nested ANOVA. Here, yield was used as dependent variable, and fertilizer type and applied dosage (subordinate) were the independent variables.

Differences in nutrient concentrations among growth forms and within growth forms between sites were analysed for every element using single ANOVA and a Tukey-Kramer test for pairwise mean comparison. Linear regression analysis was executed to deter-

mine inter-element correlations of plant tissue concentrations.

Results

Soil characteristics

The analysis of the numerous soil samples showed that the top soil at all sites had a bulk density that was lower than 1 g cm^{-3} , a moisture content that was around 100%, and a pH in the weakly acid range (4.2–5.5). The organic matter content was high and variable (6.6–26.7%). In all samples, the concentrations of salt-extractable P was limited to $1\text{--}8 \text{ mg kg}^{-1}$ only; mineral N concentrations were moderate ($10\text{--}50$ with outliers up to 300 mg kg^{-1}) and more NH_4 than NO_3 was present. Ca, K, Mg and Al concentrations ranged from 0.1 to 2 mg g^{-1} . Na concentrations were lower than the other cations.

Regression analysis of physical and chemical characteristics of all samples showed some significant correlations among physical characteristics, but relations between physical and chemical characteristics could hardly be detected (Table 3). A strong correlation was found between soil bulk density and moisture content, especially when the samples of the dry season were considered separately (Fig. 3A). Moreover, C content could explain 49% of the variation in the data of soil moisture content, but here no effect of season was distinguished (Fig. 3B). Bulk density and C content also were significantly correlated (Fig. 3C).

Although bulk density, moisture and C content were strongly interrelated, they did not explain much of the variation in concentrations of other elements. One significant relation found was the positive correlation between C and NH_4 , but the correlation coefficient was low, and apparently determined by some high outliers in the ammonium concentrations (Fig. 4A). Also among other physical and chemical characteristics no relations were found, except for pH, which had a weak relation with soil bulk density ($R^2=0.22$, Fig. 4B) and a significant correlation with Al concentration ($R^2=0.30$, Fig. 4C). The latter relation is a functional correlation, since solubility of Al is highly dependent on pH (Wada, 1980). Therefore, Al concentrations were not included in the ordination analysis.

The variance in the soil characteristics was best explained by the factors season-of sampling and site (i.e. the agricultural practice). The quantitative dummy variables wet, wet-dry and dry corresponded best

Fig. 4. Relations of C with NH_4 content (A), of bulk density with pH (B) and of pH with Al content (C) of soil samples, taken at páramo sites with different management, in three different seasons of the year. Correlation coefficients are in Table 3.

with the first RDA-axis (Fig. 5). Accordingly, the first axis represented the season of sampling. The dummy variables representing the undisturbed site, Agua Leche, the heavily grazed, unburned site, Paramillo, the recently burned site, La Leona corresponded strongly to the second axis, so this axis is likely to represent the agricultural management. All other environmental factors were of minor importance. The first axis (seasonality) was more controlled by nutrient concentrations (P, NH_4), the second axis (management) by physical characteristics. Eigenvalues of the first two

RDA axis were similarly low (0.152 and 0.137), other axis had eigenvalues that were smaller than 0.1.

Two-way ANOVA confirmed the significant relation of both site and season-of sampling with all soil characteristics in most cases (F-test, $p < 0.05$). Exceptions were the variables bulk density, having no relation with season-of sampling and NO_3 which was not different among sites. The interaction term was significant for density, moisture content, pH, NH_4 , P and Al. A Tukey-Kramer test of pairwise mean comparison showed that the intermediate (wet-dry) season was different from the other seasons for some important soil characteristics (Table 4). In this season, the soils had an intermediate moisture content and pH, but were significantly lower in extractable P and higher in NH_4 and C. In the dry season, soil moisture content was lower and pH higher but generally the conditions in the dry and in the wet season were similar. Among the sites the soil characteristics of the heavily grazed site Paramillo were different. Here, bulk density was higher and moisture content and Al concentration were lower than all other sites ($p < 0.05$). La Leona had relatively much C. Furthermore, C and Al concentrations were lower than in the intermediate season (all: $p < 0.05$).

The total (available plus non available) element concentrations of the soil were far higher than the concentrations of extractable elements, which indicates that the volcanic ashes and organic matter have low rates of decay (Table 5A). The total stock of P is between 1 and 2 mg g⁻¹, that of the cations between 10 (K) and 60 (Al) mg g⁻¹. Total concentrations of N (organic plus inorganic) were three orders of magnitude higher than the concentrations of available N. If the total stocks are compared with the amounts of extractable elements, it is clear that more than 90% (in most cases over 99%) is non-extractable. Maximal percentages salt-extractable of total N, Ca and Mg appeared somewhat higher at Paramillo than at the other sites. The differences between total element concentrations among the sites were related to the amount of organic material. If the concentrations are transformed to ignited weight, they differed less (Table 5B). These transformed concentrations show high similarity with the concentrations in the unweathered lapilli, confirming the low degree of weathering of the volcanic ashes.

The capacity of the soils to fix P was highest at the sites Agua Leche, Loma Alta and Loma Baja (5.2 ± 0.35 , 5.6 ± 0.20 and 5.6 ± 0.19 mg g DW⁻¹, resp.; mean ± 1 S.D.; t-test $p < 0.01$; Fig. 6). At the heavily

Table 4. Probability (Tukey-Kramer test of pairwise mean comparison, * $-p < 0.05$, ** $-p < 0.01$, *** $-p < 0.001$) of differences between sites and differences between seasons, for páramo soil characteristics (n=117). When differences are significant, it is indicated whether the factor listed left has a higher or a lower value of that characteristic (+ resp -)

Density	Agua Leche	Loma Alta	Loma Baja	Paramillo	Density		
Loma Baja						n.s.	
Lima Baja							
Paramillo	***(+)	*(+)	***(+)				
La Leona				*** (-)			
Moisture	Agua Leche	Loma Alta	Loma Baja	Paramillo	Moist.	Dry	Dry/wet
Loma Alta					Dry/Wet	***(+)	
Loma Alta					Wet	***(+)	
Paramillo	*** (-)	* (-)	*** (-)				
La Leona				*** (+)			
pH	Agua Leche	Loma Alta	Loma Baja	Paramillo	pH	Dry	Dry/wet
Loma Alta	* (+)				Dry/wet	*** (+)	
Loma Baja		** (-)			Wet	*** (+)	
Paramillo	*** (+)		*** (+)				
La Leona		** (-)		*** (-)			
C	Agua Leche	Loma Alta	Loma Baja	Paramillo	C	Dry	Dry/wet
Loma Alta					Dry/Wet	*** (+)	
Loma Baja					Wet		*** (-)
Paramillo							
La Leona	* (+)			*** (+)			
NH ₄	Agua Leche	Loma Alta	Loma Baja	Paramillo	NH ₄	Dry	Dry/wet
Loma Alta					Dry/wet	*** (+)	
Loma Baja					Wet		*** (-)
Paramillo	** (+)		* (+)				
La Leona				** (-)			
NO ₃					NO ₃	Dry	Dry/Wet
	n.s.				Dry/Wet		
					Wet	* (-)	* (-)
P	Agua Leche	Loma Alta	Loma Baja	Paramillo	P	Dry	Dry/wet
Loma Alta					Dry/Wet	*** (-)	
Loma Baja	* (+)				Wet		*** (+)
Paramillo							
La Leona	* (+)		* (+)				
K	Agua Leche	Loma Alta	Loma Baja	Paramillo	K	Dry	Dry/Wet
Loma Alta					Dry/Wet		
Loma Baja					Wet	* (-)	*** (-)
Paramillo	* (+)						
La Leona							

Table 4. Continued

Ca	Agua Leche	Loma Alta	Loma Baja	Paramillo	Ca	Dry	Dry/Wet
Loma Alta					Dry/Wet		
Loma Baja					Wet		* (-)
Paramillo	*** (+)		*** (+)				
La Leona				*** (-)			
Mg	Agua Leche	Loma Alta	Loma Baja	Paramillo	Mg	Dry	Dry/wet
Loma Alta					Dry/Wet	* (-)	
Loma baja					Wet		
Paramillo	*** (+)		* (+)				
La Leona				** (-)			
Na	Agua Leche	Loma Alta	Loma Baja	Paramillo	Na	Dry	Dry/wet
Loma Alta					Dry/Wet		
Loma Baja					Wet		** (-)
Paramillo	* (-)						
La Leona							
Al	Agua Leche	Loma Alta	Loma Baja	Paramillo	Al	Dry	Dry/wet
Loma Alta					Dry/Wet	*** (+)	
Loma Baja	*** (+)	*** (+)			Wet		*** (-)
Paramillo	*** (+)	* (-)	*** (-)				
La Leona	*** (+)	*** (+)		*** (+)

Fig. 5. RDA ordination diagram of selected characteristics of páramo soil samples. Axis units represent 1 S.D. of data. Eigenvalues (λ) are indicated. Arrows represent the (dummy) environmental variables of the site (i.e. agricultural management), season of sampling and vegetation dominance.

Table 5. Total element concentrations, expressed on basis of dry weight (A) and on basis of ash weight (after ignition, B)

A. Concentrations per dry weight									
Site	N (%)	C (%)	C/N	P	K	Ca	Mg (mg g ⁻¹)	Na	Al
Agua Leche	1.06	16.90	16.18	1.20	9.87	26.69	14.89	18.70	54.86
Loma Alta	0.55	10.37	18.85	1.01	10.03	26.75	15.63	19.62	
Loma Baja	0.78	14.91	19.26	1.01	9.53	25.84	14.12	19.06	
Paramillo	0.83	12.22	15.27	1.67	10.07	27.53	15.65	19.87	60.18
La Leona	1.18	19.80	16.84	1.06	8.46	21.18	12.15	15.51	

B. Concentration per ash weight									
Site	% loss-on-ignition			P	K	Ca	Mg (mg g ⁻¹)	Na	Al
Iapilli ^a	5.80			0.88	18.21	38.18	22.58	28.57	80.99
Agua Leche	24.10			1.58	13.00	35.16	19.62	24.64	72.28
Loma Alta	21.50			1.29	12.78	34.08	19.91	24.99	
Loma Baja	23.30			1.32	12.43	33.69	18.41	24.85	
Paramillo	24.75			2.21	13.38	36.59	20.79	26.40	79.96
La Leona	36.10			1.66	13.24	33.15	19.01	24.27	

^a Unweathered gravelsize volcanic deposit.

Fig. 6. Phosphorus fixation capacity of soil samples, taken at five sites with different management. Bars represent 1 S.D., means sharing a letter were not discriminated by Students t-test ($p < 0.05$, $n=4$).

grazed site Paramillo, P-fixation capacity was significantly lower (4.2 ± 0.28 , t-test $p < 0.01$) and at the

recently burned La Leona it was lowest (3.9 ± 0.09 , $p < 0.01$),

After an incubation period of twenty days, the soil samples from Agua Leche, Paramillo and La Leona had lower concentrations of mineral nitrogen than in the initial situation, indicating N-immobilization instead of N-mineralization (Fig. 7). On the other hand, the samples from Loma Alta and Loma Baja did show a, non-significant, increase in N concentrations.

Fertilizer trial

Phosphorus fertilization had a strong effect on the yield of *Lolium perenne*, while nitrogen had no effect at all (Fig. 8). After 3 months, the average yield (± 1 S.D.) of *L. perenne* in P fertilized parcels was 19.5 ± 10.7 g m⁻², whilst both N fertilized plots and the control plot had only 2.1 ± 1.3 and 2.6 ± 0.8 g m⁻², respectively. Nested ANOVA showed that the effect of the fertilizer was significant (F-test, $p < 0.001$), but that there was no subordinate effect of the dosage applied.

Soil temperature

Highest maximal soil temperatures were recorded at Paramillo (Fig. 9) and the lowest maxima at the undis-

Fig. 7. Mineral nitrogen mineralization or immobilization of soil samples after 2 weeks of incubation (mg N kg^{-1} soil). The samples were taken at five sites with different management. bars represent 1 S.D. means sharing a letter were not discriminated by Students t-test ($p < 0.05$, $n=4$).

Fig. 8. Yield of *Lolium perenne* after 3 months of growth in parcels with N and P fertilizer, in different dosages. Bars represent 1 S.D. ($n=4$).

turbed site Agua Leche and the burned site La Leona. The measured maximal values differed largely: they ranged from 11.9 °C at La Leona to 15.8 °C at Paramillo. The mean temperatures at noon, at 2 cm depth ranged from 9.2 °C at Agua Leche to 11.5 °C at Loma Baja. The means did not differ significantly.

Fig. 9. Average ($n=100$, blocks) and range (bars) in soil temperature measurements at 2 cm depth, at five sites with different management.

Litter disappearance

The disappearance rate of litter was low, but higher at the heavily grazed site Loma Baja than at Loma Alta and Agua Leche (t-test, $p < 0.01$, Fig. 10). After one year, $34.3 \pm 8.03\%$ (mean $\pm$ 1 S.D.) of the initial litter weight had disappeared at Loma Baja, while at Agua Leche and Loma Alta only 11.3 ± 4.64 and $14.4 \pm 7.27\%$ was decomposed. The strong initial disappearance and the constant litterbag values after three months (t-test, $p > 0.1$), indicated that the disappearance is not linear and many years might be needed for total decomposition. At Loma Alta, the disappearance rate was only recorded after 6 and 9 months, and these values were similar to that of Agua Leche (t-test, $p > 0.1$).

Plant analysis

There were significant differences in element concentrations between the various growth forms. (F-test, $p < 0.001$). Generally, tussock grass leaves had lowest concentrations of elements and the short growing growth forms (sedges, herbs and, to less extent, short grasses) had higher element concentrations; herbs were relatively rich in N, P, Ca and K. Shrubs had high concentrations of C and Mg and *Espeletia* leaves had high C, K and Mg concentrations, but were relatively poor in other nutrients. Apart from P and C, element concentrations were higher in green *Espeletia* leaves than in young leaves.

Fig. 10. Litter disappearance at three sites with different management. Bars represent 1 S.D. (n=25).

Table 6. Results of single Analysis of Variance (F-test, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) of elemental concentrations of green plant tissue from sites with different management (A) and taken in different seasons (B)

A. ANOVA sites

	Ash	C	N	C/N	P	Ca	Mg	K	Na	Al
Tussock grass										
Short grass			**	**				*		
Sedges										
Herbs					*			***		
Shrubs								*		**
Espeletia young leaf										
Espeletia green leaf										

B. ANOVA seasons

	Ash	C	N	C/N	P	Ca	Mg	K	Na	Al
Tussock grass										
Short grass							*			
Sedge					*					
Herbs										
Shrubs										
Espeletia young leaf					**					
Espeletia green leaf		*	*	*		*	*			

The presence of differences in green leaf tissue nutrient concentrations among growth forms and the absence of differences within growth forms are shown in Figure 11. The clustered appearance of the average values of a growth form per site reflect that within the individual growth forms, there was little variation (coefficients of variance around 20%). Consequently, there were few significant relations between nutrient concentrations among sites or among seasons, what

was confirmed by ANOVA (F-test, Table 6). Some variation among sites was found for K and N concentrations in short grasses and for K concentrations in shrubs and herbs. In most cases the plants at the heavily grazed and burned site, Loma Baja, had higher concentrations (Tukey-Kramer pairwise mean comparison). Variation among seasons was found for P, which was higher in the intermediate season (wet-dry) in sedges and young leaves of *Espeletia*. Green leaves of *Espele-*

Fig. 11. Average concentrations of elements in green leaf tissue of different growth forms in the páramo vegetation. Samples taken at five sites with different management. Asterisks indicate significant variation of element concentrations within the growth form (F-test, $*=p<0.05$, $**p<0.01$, $***=p<0.001$).

tia had somewhat higher N. Ca and Mg; tussock grass leaves had somewhat higher Mg concentrations in the dry season.

A significant relation could be established for P and N concentrations in plant tissue ($R^2=0.20$, $p<0.05$). In Figure 12, the different growth forms are clearly clustered, showing the high concentrations of both N and P in herbs and the high P concentrations in the young leaves of stem rosettes. Both elements were rather low in tussock grass leaves. There were no significant interrelations among other element concentrations.

Discussion and conclusions

The undisturbed páramo ecosystem

The laboratory results of the present study support the idea of a nutrient poor páramo environment: (1) the observed soil characteristics reflect the classification as Cryand (low bulk density and pH, high moisture content, organic C and Al, USDA, 1975) (2) the similar total element analysis of the ashes and the unweathered lapilli indicate a low degree of weathering of parent material, and (3) the high P-fixation capacity is a typical feature of young volcanic ash derived soils, since they contain large amounts of amorphous material (allophanes) and organo-metallic complexes (Sanchez, 1976; Van Reeuwijk, 1989; Wada, 1980). These factors, in combination with the low average temperatures (ca. 10 °C at noon) and low litter disappearance resulted in a low primary productive ecosystem, with a low turn over time (Hofstede et al., 1995b; Luteyn, 1992; Smith and Young, 1987).

The fertilizer trial clearly showed that P was the limiting element for plant growth. The absence of the effect of the dosage might indicate that 15 g P m⁻² was enough to assure maximal growth. With N there was no effect, indicating that nitrogen is not a single growth limiting element. However, where P was applied this might have influenced N mineralization (Bowman et al., 1993; Vitousek and Howarth, 1991). Care should be taken because only the individual effects of N and P were tested and some bias might have been introduced during soil preparation. Moreover, not the native dominant *Calamagrostis effusa*, but a bioassay was used. Nevertheless, the extreme response indicates that the same effect is to be expected for native species.

In Table 7, a comparison is made between data on soil and plant nutrient concentrations from the present study and from other studies on Colombian páramo

grasslands. The range of data on pH, C, K, Ca and Mg from the present study is similar to the range presented by Sturm and Rangel (1985), based on a set of soil samples from various regions all over the Colombian Andes. The P and Al concentrations are low compared to Sturm and Rangel's study. These concentrations also are low in comparison with the data on P and Al in a previous study in the same National Park (Thouret, 1989). This difference in analysis results can be caused by the sample preparation: both Sturm and Rangel as Thouret air-dried their samples before analysis, which can affect laboratory results, especially the extractable P content, strongly.

In comparison to the results of the studies on Eastern Cordillera páramo soils (Bekker and Cleef, 1985; Tol and Cleef, 1992), the soils of the present study were relatively dry and less organic, though within the presented range. In addition, the maximum values of cation concentrations exceed those reported for the Eastern Cordillera sites. Soil bulk density was higher in the Central Cordillera sites. It should be considered though, that grazed sites were excluded and that volcanic influence was less in the studies by Bekker and Cleef and by Tol and Cleef. Except for Al, the chemical composition of *Calamagrostis effusa* leaves from the Eastern Cordillera (Tol and Cleef, 1992) was very similar to the composition of the leaves from the Los Nevados National Park. This general similarity in data from different páramo regions may support the representative value of the present study for other (non-volcanic) páramo areas. The higher macromineral composition of (non-native) forage species in the Eastern Cordillera, show the generally low concentrations in the native tussock grass. Nevertheless, Pastana et al. (1990) mentioned that even the higher element concentrations in these exotic species were deficient if related to the requirements of sheep.

Although at equatorial latitudes seasonality is very limited, and restricted to some differences in precipitation volume only, the season-of sampling was the most important explanatory factor in the ordination of soil characteristics. The RDA-biplot shows that the seasonality axis is mostly related to differences in nutrient concentrations. In the wet-dry season, P concentrations are lower and NH₄ is higher than in other seasons. This accords to the higher concentrations of P in sedges and young *Espeletia* leaves in that season. It is likely that in the shift between seasons there is some positive effect on decomposition and plant growth: some extra P uptake by plants can occur and therefore lower soil P concentrations are present. However, the availability

Fig. 12. Relation of phosphorus and nitrogen concentration of green leaves of different growth forms in the páramo vegetation ($R^2=0.20$, $p<0.05$, $n=124$).

of P remains low and limiting and therefore there is a surplus of other mineralized elements which are not absorbed. Pastrana et al. (1990) also mentioned low influence of seasonality, but found highest concentrations in the rainy season.

The effect of grazing and burning on soil characteristics

The characteristics of the soils were to certain extent determined by grazing and burning. Although the effect of the agricultural management was clear in the ordination of the data on soil bulk density, moisture content pH C, Ca and M concentrations, this effect explained only 14% all variation in the data, the rest was explained by other factors (season-of sampling, vegetation type, position on the slope). Although the RDA-ordination and two-way ANOVA showed that soil bulk density and moisture content were strongly dependent on the site (i.e. the management), only the heavily grazed site Paramillo could be discriminated individually from the other sites, mostly because of higher pH and concentrations of Mg and Ca (Tukey-Kramer).

The inter-relation between soil bulk density, moisture and C content was evident. Soil samples with a higher bulk density had a lower moisture content. It is likely that higher density is caused by trampling and that a lesser volume and lower C content after compression of the soil caused a lower moisture content (Dor Maar et al., 1989; Johnston et al., 1971). The relation between density and moisture content was absent in the

dry season, indicating that the soils were not saturated then. Where the soils were drier, the C content was lower. This might indicate that soils at trampled sites were denser, drier and that decomposition was higher. The latter was confirmed by a higher litter disappearance rate at grazed sites. Ruíz and Bustamante (1988) mentioned a low decomposition rate for *Stipa ichu* bunchgrass in Bolivian puna, based on C-content of litter samples. They also found a strong initial decomposition in the first two months, followed by an almost absent decomposition after this initial period.

A faster decomposition can be caused by a lower soil moisture content or by higher soil temperatures, due to the lack of a thick insulating vegetation layer at grazed sites (Marion and Miller, 1982; Moorhead and Reynolds, 1993; Swift et al., 1979). Studies on soil respiration in Andean ecosystems showed a strong relation of day temperature and microbial activity (Medina, 1968; Valencia, 1983). Although soil temperature measurements did not provide enough information to show significant differences between the sites, the indication of higher maximal temperatures attained at grazed sites are indicative for a higher decomposer activity here. Another reason for a higher decomposition rate at grazed sites is the possible higher nutrient content of the litter here (Enriquez et al., 1993; Vitousek and Howarth, 1991). This higher litter quality might be caused directly by consumption and trampling, which shortens the life-span of leaves.

In contrast to the hypothesis from the introduction to this article (Fig. 1), the enhanced decomposition did not seem to result in differences in soil nutrient

Table 7. Laboratory analysis data of samples from the topsoil (A) and from green leaves of *Calamagrostis effusa* (B). Results from studies on páramo grasslands in different regions of the Colombian Andes. Figures represent range (min/max) or mean value

A. Top soil

Reference		pH	C (%)	N (%)	P (mg kg ⁻¹)	K	Ca	Mg (mg g ⁻¹)	Na	Al	Density (g cm ⁻³)	Humidity (%)
Various: EC, CC, WC ^a (Shrum Rangel, 1985)	min	3.9	4.90		3	0.04	0.08	0.05	0.01	0.16		
	max	5.4	29.20		34	0.86	3.21	1.26	0.02	3.62		
Laguna Verde, E C (Bekker and Cleef, 1985)	min	4.3	11.30	0.78	1	0.08	0.04	0.02	0.05	0.22	0.36	113.8
	max	4.8	34.60	1.78	5	0.23	0.10	0.06	0.11	1.59	0.61	225.7
Chingaza, EC (Tol and Cleef 1992)	mean	5.2	34.60	3.00	5.8	0.15	1.39	0.05	0.03	0.01	0.19	
Los Nevados, CC (Thouret, 1989)	min	5.3	7.43	0.41	1.5	0.08	0.04	0.02	0.02	0.17		
	max	5.9	22.47	1.00	110	0.78	0.96	0.45	0.07	1.57		
Los Nevados, CC (This study)	min	4.2	6.60	0.55	1	0.04	0.14	0.09	0.02	0.00	0.37	40.4
	max	5.5	26.70	1.18	9	1.02	2.71	0.69	0.21	0.49	0.81	246.2

B. Green leaf tissue

Reference		ash (%)	N (%)	P	K	Ca	Mg (mg g ⁻¹)	Na	Al
Chingaza, EC (Tol and Cleef, 1992)	mean	7.6	0.9	0.95	9.77	1.75	0.75	0.05	0.24 (<i>Calamagrostis effusa</i>)
Los Nevados, CC (This study)	mean	7.0	0.9	0.81	10.09	1.10	0.51	0.15	0.12 (<i>Calamagrostis effusa</i>)
Sheep farms, EC (Pastrana et al., 1990)	mean ^b			2.7	28.9	3.7	1.7	0.4	(various forage species)

^aEC = Eastern Cordillera, CC = Central Cordillera, WC = Western Cordillera.

^bMeans of rainy season.

concentrations. No relation was found between physical and chemical characteristics of the soil samples, indicating that differences in soil chemistry were not related to the measured environmental factors. The chemical characteristics were relatively constant, and very little difference was found between the different sites. The constant and low figures of nutrient concentrations can be a result of the general poor conditions for plant growth. In the páramo, the mineral nutrients released during the decomposition process are immediately immobilized. This immobilization can occur in various ways: (1) by the soil matrix, (2) by micro-organisms and (3) by plant biomass (Chapin, 1980; Sanchez, 1976; Vitousek, 1982; Wada, 1980). The first two factors are most likely to occur, for the third

factor there is less support since differences in plant nutrient content was very constant among sites and seasons. Especially the strong P-fixation capacity in these volcanic soils seems to be an important factor but also immobilization by micro-organisms is high in cold climate ecosystems with high C/N and C/P ratios of organic matter (Enriquez et al., 1993; Moorhead and Reynolds, 1993). In general, micro-organisms have a high nutrient demand (Swift et al., 1979), and the decomposer subsystem is mentioned to be able to buffer the nutrient concentrations in some grassland ecosystems (Chapin et al., 1978; Nadelhoffer et al., 1991; Seeling and Zasoski, 1993).

Fire alone did not seem to have much effect on the soil characteristics. The results from the recent-

ly burned site La Leona were not very different from the results from other sites. Here, soil C and moisture content were relatively high, although these were expected to be lower due to the fire and subsequent increased decomposition. This unexpected result can indicate that the natural situation at the site was somewhat different from the other sites (more peaty) and that the effects of this fire are not so dramatic that large differences were caused. When it is considered that the management history at La Leona before the fire was comparable to Loma Alta (moderately grazed, several years after a previous fire), it might be concluded that the fire did not have much effect on the soil, since no large differences were found between these two sites. Plant nutrient concentrations at La Leona also lacked any effect of the recent fire.

Effects of grazing and burning on plant tissue composition and ecosystem stability

The leaves of the plants had a fairly constant nutrient status among the sites and among the seasons. Although at some sites (Loma Baja, Paramillo) and in the some seasons, tissues (short grass, *Espeletia* green leaf sedges) had somewhat higher element concentrations, no clear trend was discovered. The short grasses showed variation, but this can be explained by the composition of the samples: many species were represented in samples of this growth form and it was difficult to sample exact replicas. However, constant leaf nutrient concentrations are in accordance with the constant nutrient availability in the soils: if no differences in nutrient availability are detected, differences in plant nutrient contents will be very unlikely.

The relative amount of nutrients that is stored in the above-ground vegetation is high and influenced only to certain extent by fire and grazing. It is evident that every growth form had its own particular composition of elements, with the short growing growth forms (sedges and herbs) being richer than the tussock grass leaves. The short species have an increased relative cover and biomass at the grazed sites (Salamanca, 1991; Verweij and Budde, 1992). This can signify that at the grazed sites, the overall nutrient content of the vegetation is not as low as the decrease in vegetation biomass indicates. Moreover, a higher contribution of species with relatively high nutrient concentrations also increases litter quality, and so influences decomposition rates (Enriquez et al., 1993). Finally, the amount of nutrients lost by consumption (by fire

or by cattle) seems to be low in relation to the amount present in the vegetation.

The low impact of the agricultural management on soil and plant nutrient concentrations are in contrast to what is found in many grasslands. Many authors mention an enhanced turn-over rates in when grazing is introduced, leading to an exhaustion of soils (e.g Chapin, 1980; McNaughton et al., 1988; Vitousek and Howarth, 1991). However, generalizations can not be made: Milchunas and Lauenroth (1993) compared many large and complete data sets from various grazed and ungrazed grasslands, and they found as many positive as negative effects of grazing on soil nutrient status. Shaver and Chapin (1991) mentioned strikingly little difference among nutrient and carbon turn-over rates, when comparing several physiognomically very different arctic vegetation types. They explained these constant processes in their tundra sites by the allocation of elements and energy into long-living plant organs. This allocation pattern was mentioned to be an adaptation to the extreme circumstances: both low nutrient availability and low temperatures limit plant growth in the arctic environment (Billings, 1973; Chapin et al., 1979). The small amount of extra nutrients liberated by grazing is not likely to cause measurable changes in the limited ecosystem. The tussock growth form, also dominant in páramo, is well adapted to these extreme conditions, since it possesses a good internal nutrient cycling capacity, and can alter internal temperature and pH (Caldwell et al., 1981; Chapin et al., 1979). The similarity of arctic tussock tundra and alpine vegetation, in terms of low temperatures and high moisture content, allows to apply this nutrient allocation-theory to the páramo ecosystem.

The results from this study show that nutrient mineralization (decomposition) and phosphorus dynamics (fixation, limitation) play a key role in the ecology of the páramo. The effects of relatively long-term extensive livestock management on the páramo soils are restricted to physical characteristics only. Temperature does influence decomposition, but is not likely to stimulate growth with present low P availability at the sites. P is low and remains growth limiting for both plants and decomposers at all sites and in all seasons. The observed difference in vegetation structure between the grazed, burned and undisturbed grassland sites must be caused by factors other than soil nutrient availability. The lower soil moisture content at heavily grazed páramo sites can indicate drought stress and a deteriorated hydrology. However, in the dry season, the moisture content of the top soil was generally at the

same level as at the other sites. More possible reasons for vegetation change are the strategies of plants to tolerate the extreme climatic conditions on one hand, and strategies to tolerate grazing and burning on the other.

For the conservation of these ecosystems it should be considered that grazing can have negative effects, since it can result in a lower soil moisture content and hereby in a deterioration of the hydrology: the main ecological and economical function of páramos. At the present highest level of grazing intensity (Paramillo), the soils in the wet season were as dry as in the dry season. This indicates that during wet periods no extra water could be retained. No additional negative impacts of fire on the soils were found, but no positive impact either: it provided no lasting enhanced nutrient levels, nor higher productivity of the grasses. Care should be taken while applying this management tool since after a fire the soils are very vulnerable to destruction and drying (Rundel, 1981; Vogl, 1974).

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