Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan páramos*

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Abstract

By means of ordination and classification techniques, the relationships between climate, soils, human activities and vegetation along an altitudinal gradient of the Venezuelan páramos are analyzed and interpreted. The altitudinal gradient chosen is characterized by decrease of temperature, precipitation, soil fertility, soil water-holding capacity, and plant cover as altitude increases. The ordination results suggest vegetation changes to be primarily related to environmental changes occurring with altitude, and secondly to disturbances caused mainly by grazing. Some results point toward a disjunction in the vegetational gradient occurring at ca. 3 500 m.a.s.l. and separating low and high páramo. This disjunction might have been caused by the glacial history of the páramos and the occurrence of frequent night-frosts.

Introduction

Mountains are ideal places for the description and causal study of environmental responses of plant communities because short lineal distances cause large environmental changes. The páramo is a neotropical high mountain biome with a vegetation composed mainly of giant rosette plants, shrubs and grasses (Fig. 1). Latitudinally, it extends from Colombia to northern Peru; altitudinally, it forms a belt between the upper treeline and the perpetual snowfields.

* Nomenclature follows Vareschi (1970).

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The study area is located between 2 900 and 4 100 m.a.s.l. in the Andean Cordillera of Mérida State, Venezuela (8°50′ N and 70°50′ W). Geologically, the páramos are of recent origin and topography has been modelled by glacial action (Schubert, 1980). The soils are mostly acidic, rocky and poorly developed with a low content in inorganic nutrients (Baruch, 1979). In the study area the precipitation is seasonal with rains in the middle of the year. Low evaporation, high cloudiness, and frequent fogs, however, result in relatively humid conditions throughout the whole year. At the highest elevations, there is occasional snow which is of short duration. Air temperatures are low, cold at night and cool during the day with daily oscillations larger than oscillations of monthly averages. Above 3 500 m.a.s.l., night-frosts become frequent.

The páramo vegetation is evergreen with a complete cover at low elevation (Fig. 1) and sparse cover at high altitude. The common life forms are: large and small shrubs, stunted trees, cushion plants, herbs, graminoids, and rosette plants. Many species of rosette plants belong to the subtribe Es-

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(a)

(b)

Fig. 1. Vegetation of (a) low páramo (ca. 3 000 m.a.s.l.) and (b) high páramo (ca. 4 000 m.a.s.l.). Photos by the author.

peletiinae, Compositae (Cuatrecasas, 1976) which is endemic and characteristic of the páramos (these plants are locally called 'frailejones'). The type of vegetation studied here includes two or three strata. The tallest (up to 300 cm) is composed by caulescent rosettes of the subtribe Espeletiinae and large shrubs, mainly *Hypericum laricifolium*. The second stratum, 10–50 cm in height, is composed of herbs, graminoids, several species of *Senecio* and *Castilleja* and seedlings of *H. laricifolium* and Espeletiinae. The third stratum is close to the soil and is formed by acaulescent rosettes, cushion plants, mosses and lichens.

Many of the páramo plants show xeromorphic characters in the leaves (small size, heavy cutinization, and dense pubescence). The adaptive significance of these characters in the páramo environment has been suggested by Baruch, (1979) and Baruch & Smith (1979). Vareschi (1970) cites ca. 420 species of higher plants. This flora is thought to be of mixed origin: neotropical and extratropical (Cuatrecasas, 1968; Vuilleumier, 1971).

Most of the Venezuelan páramos are disturbed by human use. In the low páramo, agricultural activity occurs, while the high páramo is used as pasture. Some of the woody species are used for fuel and parts of the páramo are frequently burned. All this resulted in a lowering of the timberline and an increase of the width of the páramo belt. Building of roads and dams and the increasing tourism also have negative effects on the existence and dynamics of páramo communities.

The purpose of this work is to study páramo vegetation and its relation to climate, soils, and human disturbance by means of ordination and classification. It is important to do this while it is still possible to find areas with little alteration by traditional and modern technologies.

Methods

Ten sites were established from 2 900 to 4 100 m.a.s.l. along the road Santo Domingo-Mucubaji-Apartaderos-El Aguila-Piñango, the first seven at 100 to 250 m difference in increasing altitude, the last three at 4 100 m.a.s.l. They differ in the dominant rosette species: Piedras Blancas – *Espeletia schultzii*, Piedras Blancas – *Coespeletia lutescens*, and Piedras Blancas – *E. schultzii* and *C. lutescens*. Site location and altitude are shown in Figure 2.

Sampling was done in the giant rosette–shrub vegetation, in areas slightly inclined and with apparent good drainage. A transect of 200 m perpendicular to the slope was established and 10 points were selected randomly. At each, a 2 × 2 m quadrat was sampled. This result in 100 samples for the entire study. Species density in each quadrat was obtained by counting the individuals. For *E. schultzii* and *H. laricifolium* two categories were considered: individuals above and below 20 cm in height. Each cushion or tussock was considered as one individual for species with such life forms. For those species with abundant and small individuals, two semi-quantitative categories were employed: 10 and 20 individuals per quadrat. Only vascular plants were counted. Voucher samples are deposited in the Herbarium of Universidad Simón Bolivar. For each site, disturbance was estimated qualitatively on a scale from 1 to 3.

Three soil samples were taken from 5 to 20 cm in depth. Water retention properties were determined using a pressure membrane apparatus (Richards, 1949). The water retention capacity was calculated as water % under 0.03 MPa – water % under 1.5 MPa. Soil texture was determined by the Bouyoucos (1936) method. Phosphorus and total nitrates were determined by colorimetric methods while potassium and calcium were determined by atomic absorption. Total nutrient content (ppm NO_3 + ppm P + ppm Ca) was calculated as an index of fertility. From climatic data available from three stations located along the altitudinal gradient, the decrease in precipitation and air temperature with each 100 m of altitude was calculated.

The ordination of samples and species was performed using detrended correspondence analysis (DECORANA Program, Hill, 1979b). The classification of samples and species was performed using TWINSPAN (Hill, 1979a). Species with less than two entries were eliminated from the calculations.

The non-parametric Spearman correlation analysis was performed for the main environmental variables and the location of the sites along each of the two axes generated by the ordination using the Statistical Package for the Social Science (Nie *et al.* 1975). Alpha diversity for each site was calculated with the Shannon-Wiener (H') index (Peet, 1974), on the basis of average density per species per site. Beta diversity was calculated using the method of Whittaker & Niering (1965). The degree of continuity among sites along the altitudinal gradient was estimated by a method similar to Beals' (1969) which considers % dissimilarity of adjacent sites and compares these values with the average among all sites. Values higher than average indicate a possible discontinuity in the gradient. The Sørensen index (Mueller-Dombois & Ellenberg, 1974, p. 277) was used to calculate percentages of similarity (*PS*) and dissimilarity (*PD*) employed in beta diversity and continuity estimations.

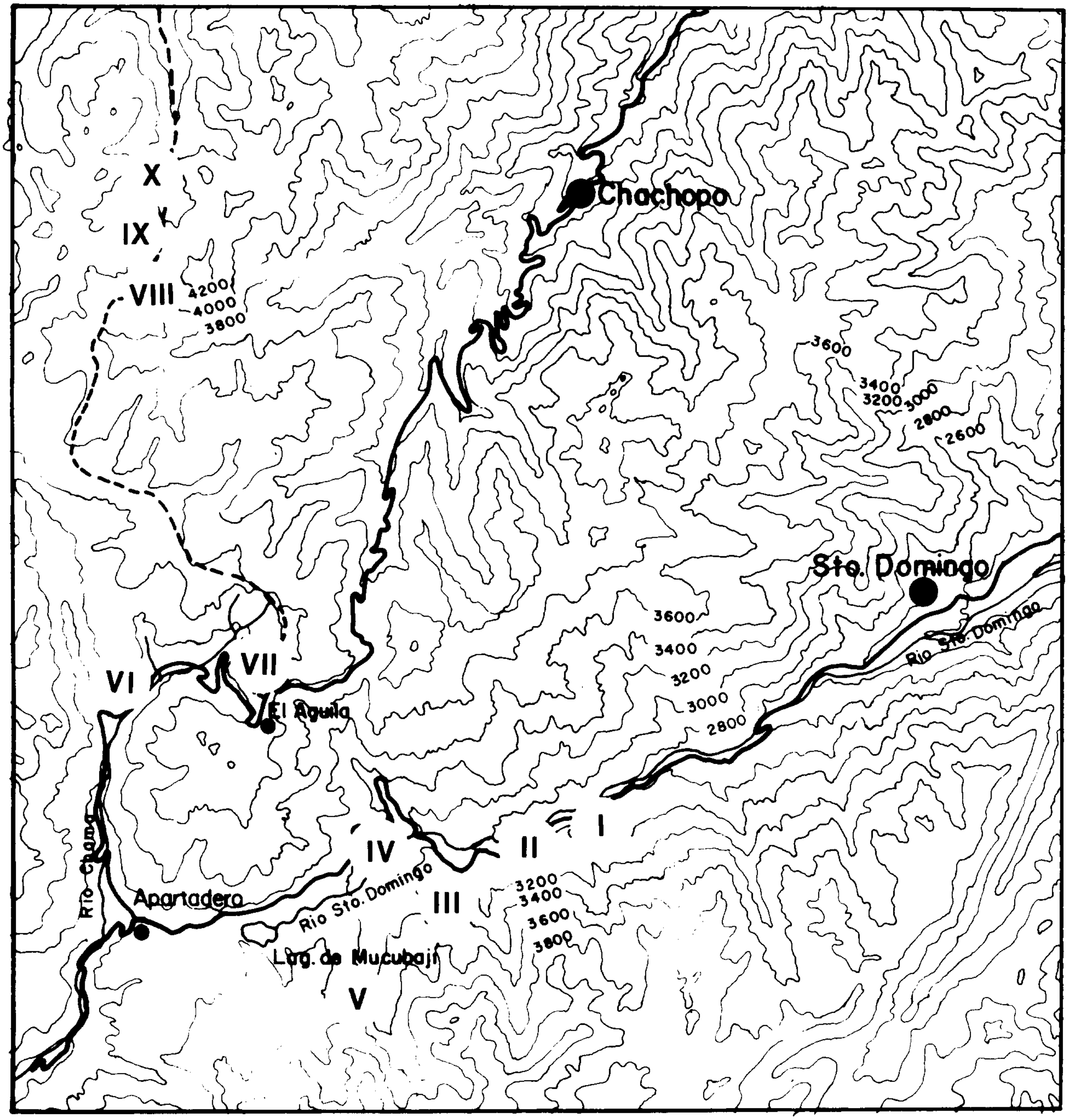

Fig. 2. Map of the study area showing the sampling sites: I-Parra (2900 m.a.s.l.), II-Zerpa (3000 m.a.s.l.), III-Zerpa + 150 (3150 m.a.s.l.), IV-Zerpa + 300 (3300 m.a.s.l.), V-Mucubají (3550 m.a.s.l.), VI-Mucubají + 250 (3800 m.a.s.l.), VII-Mucubají + 400 (3950 m.a.s.l.), VIII-P. Blancas - *E. schultzii* (4100 m.a.s.l.), IX-P. Blancas - *E. schultzii* + *C. lutescens* (4100 m.a.s.l.), X-P. Blancas - *C. lutescens* (4100 m.a.s.l.). Scale 1:100 000. Map #6042, 1976. Ministry of Public Works, Venezuela.

Results

Above 3 000 m.a.s.l. annual precipitation decreases (Fig. 3) at a rate of 15–20 mm/100 m. The precipitation pattern is unimodal with rains especially from April to October. Evaporation values are similar for the three stations: Los Plantios, 887 mm (1970–1979); Mucubají, 907 mm (1970– 1979); El Aguila, 850 mm (1969–1974). There is a positive water balance along the whole altitudinal gradient.

Associated with the tropical location, photoperiod seems to be of little importance in controlling the amount of solar radiation received. Cloudiness and exposure seem to be the important factors determining the radiation received at ground level. The decrease of air temperature with altitude occurs at an approximate rate of 0.5 °C/100 m altitude (Fig. 4). The lowest temperatures, most frequent frosts and largest diurnal variations in temperature are at the beginning of the year, during the dry season.

Soils are of a sandy-loam type with increasing clay content at higher altitudes (Table 1). The pH is in the moderately acid range. The macronutrient

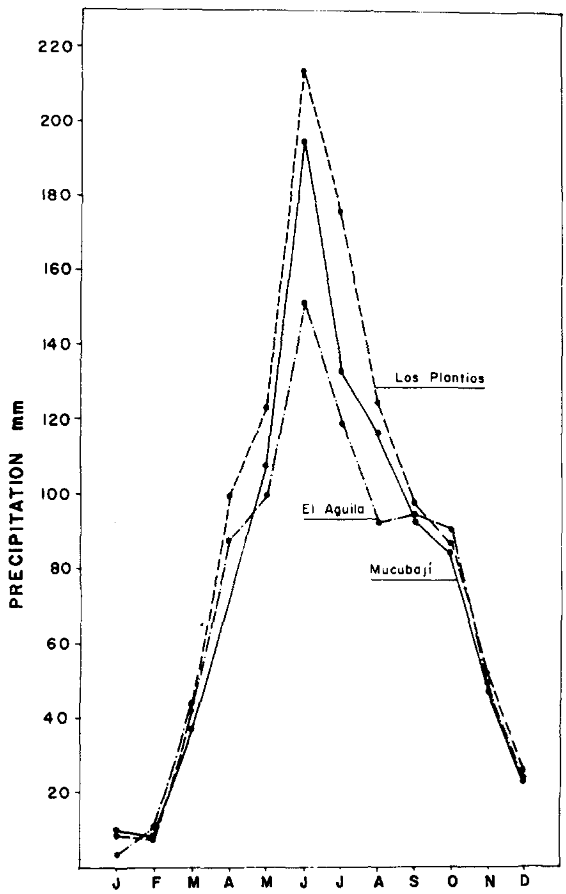

Fig. 3. Monthly averages of precipitation from the three climatological stations in the study area. Annual averages: Los Plantios (3000 m.a.s.l.) = 1061 mm (1969–1979); Mucubají (3550 m.a.s.l.) = 980 mm (1969–1979); El Aguila (4020 m.a.s.l.) = 867 mm (1973–1979). Data from the Ministry of Public Works, Venezuela.

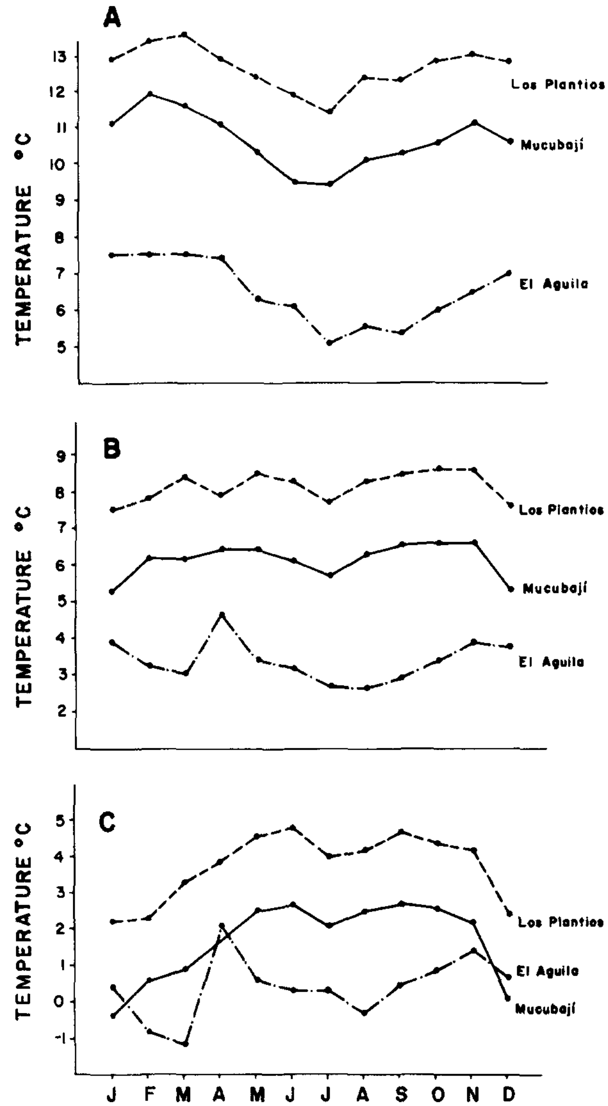

Fig. 4. Monthly averages of maximum (A), medium (B), and minimum (C) air temperatures from the three stations in the study area. Annual averages (non-sequential years): Los Plantios = 7.9 °C; Mucubají = 5.4 °C; El Aguila = 2.8 °C. Data from the Ministry of Public Works, Venezuela.

Table 1. Physiochemical soil analyses and water content under -0.3 and -15.0 bars with the range of water content capacity (ΣNUT = total nutrient content in ppm). These values are the average of three replicates.

Site	%Sand	%Silt	%Clay	ppm P	ppm K	ppm Ca	ppm NO_3	ΣNUT	pH	%H_2O -0.3	%H_2O -15.0	Range △H_2O
I - Parra	66.0	21.3	12.6	12.3	88.0	30.0	42.0	173.3	4.9	33.6	22.2	11.4
II - Zerpa	69.6	21.0	9.3	10.0	72.0	16.6	34.0	132.6	4.3	30.2	16.9	13.3
III - Zerpa + 150	60.0	27.0	13.0	8.0	78.0	26.6	45.6	158.2	4.3	35.0	17.3	17.7
IV - Zerpa + 300	66.0	21.5	12.5	10.3	58.0	15.0	67.5	150.8	4.1	39.6	24.3	15.3
V - Mucubají	75.6	13.6	10.6	5.0	70.6	17.3	62.3	155.2	4.2	35.4	24.3	11.1
VI - Mucubají + 250	69.6	15.6	15.0	11.5	56.0	21.0	42.0	130.5	4.2	23.7	15.0	8.7
VII - Mucubají + 400	63.6	20.6	15.6	5.3	62.6	12.0	32.3	112.2	4.2	34.2	18.3	15.9
VIII - P. Blancas + *E. schultzii*	66.6	19.3	14.0	8.6	89.3	20.0	39.0	156.9	4.6	26.8	15.2	11.6
IX - P. Blancas + *C. lutescens*	73.0	10.3	15.3	10.0	52.0	18.0	18.0	98.0	4.5	16.6	9.7	6.8

content is generally low except for nitrates. Soil fertility decreases with elevation except for site VIII where it is high. The waterholding capacity of the soils is low and tends to decrease with altitude except for site VII.

Figure 5 shows the first two ordination axes generated by the detrended correspondence analysis of samples. The extremes of the x-axis are occupied by samples from the extreme altitudes. There is no evident separation of groups of samples. It is clear

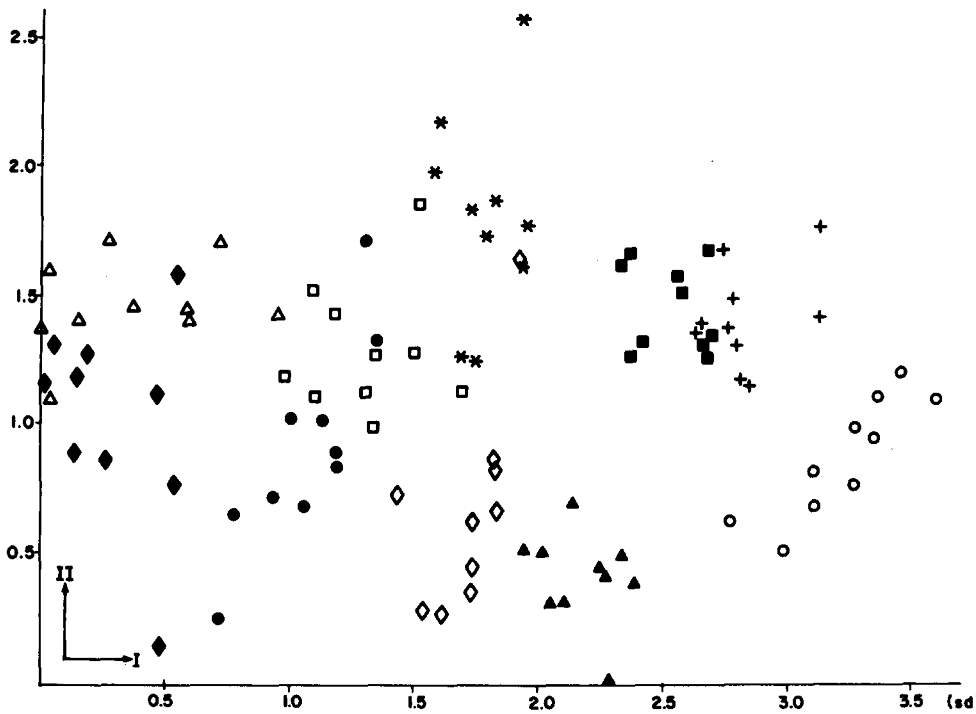

Fig. 5. Graphic representation of the first two axes generated by detrended correspondence analysis of samples. The scale of the axes are standard deviation units. The symbols used are:

Symbol	*Sites*	*Symbol*	*Sites*
○ -	1-10	* -	51- 60
▲ -	11-20	● -	61- 70
+ -	21-30	□ -	71- 80
■ -	31-40	△ -	81- 90
◇ -	41-50	♦ -	91-100

Table 2. Average position of each site along the ordination axes, environmental variables, and species number and diversity used for Spearman's rank correlations.

Variables	Sites									
	I	II	III	IV	V	VI	VII	VIII	IX	X
a –										
x-axis	3.25	2.19	2.84	2.55	1.72	1.80	1.07	1.31	0.38	0.29
y-axis	0.87	0.40	1.40	1.45	0.55	1.80	0.90	1.28	1.45	1.02
b – Elevation (m.a.s.l.)	2900	3000	3250	3400	3550	3800	3950	4100	4110	4120
c – Air temperature (° C)	8.4	7.9	6.7	6.0	5.4	4.1	3.3	2.8	2.7	2.6
d – Precipitation (mm)	1076	1061	1023	1001	980	930	900	867	865	863
e – Disturbance	3.0	1.7	2.2	2.5	1.0	3.0	1.5	2.0	2.0	2.0
f – Species/site	30	29	36	27	34	22	24	31	26	31
g – Species/4 m^2	17.3	12.9	17.8	14.5	16.8	11.7	13.1	17.1	13.0	16.9
h – Shannon-Wiener index (*H'*)	0.801	0.794	0.807	0.827	0.828	0.830	0.808	0.858	0.775	0.849

that this axis is related to some or all of the altitude-associated variables: air temperature, water availability, and fertility. Interpretation of the *y*-axis is more difficult. The samples of site VI (Mucubají + 250) are located at one end while those of site II (Zerpa) and V (Mucubají) occupy the other end. It is possible to interpret tentatively this axis as one related to disturbance which affects species richness. Site VI has only 22 species and shows the clearest symptoms of disturbance. Sites II and V are species rich (29 and 34, resp.) and do not show evidence of heavy disturbance.

The ordination of species (data not shown) have axes with a negative component which are somewhat longer than those of the sample ordination. Along the *x*-axis, the characteristic species of low altitude form a group at the right (*Lepichinia bullata* (8), *Hypoxis* sp. (46), *Viola stipularis* (32), *Aegopogon cenchroides* (57), *Paspalum* sp. (53), *Orthosanthus chimboracensis* (54), etc.). High altitude species are at the other extreme (*Coespeletia lutescens* (3), *Espeletia weddelli* (10), *Lucilia venezuelana* (29), *Calamagrostis mulleri* (52), *Rhizocephallum candollei* (39), *Hypochoeris setosus* (33), etc.). The species common to the whole altitudinal gradient are located toward the center of the axis. Here, the *y*-axis is difficult to interpret.

Table 2 shows the values of the variables used in correlation. The coefficients among these and soil variables and the position along the *y*- and *y*-axes are shown in Table 3. Altitude, precipitation and air temperature are closely related and show statistically significant correlation with the ordination of samples along the *x*-axis. Other variables such as the percentage of clay and potassium, nitrates and total nutrients, are also correlated to this ordination. The only statistically valid correlation of the ordination along the *y*-axis corresponds to the degree of disturbance which supports the tentative interpretation given to this axis.

The number of divisions performed in sample classification (Fig. 6) was that needed to obtain meaningful sample groups whose composition is

Table 3. Spearman's rank coefficients for correlations performed between ordination rankings and environmental variables (* = significant at $p < 0.05$ level).

Variables	*x*-axis	*y*-axis
Elevation	0.94*	0.39
Precipitation	0.94*	0.39
Air temperature	0.94*	0.39
Range H_2O	0.53	0.21
pH	0.04	0.13
Sand	0.52	0.16
Clay	0.66*	0.49
ppm P	0.43	0.27
ppm K	0.59	0.43
ppm Ca	0.38	0.27
ppm NO_3	0.76*	0.02
Total nutrients	0.79*	0.28
Disturbance	0.47	0.60*
Species/site	0.16	0.30
Species/4 m^2	0.30	0.19
Shannon-Wiener index (*H'*)	0.31	0.15

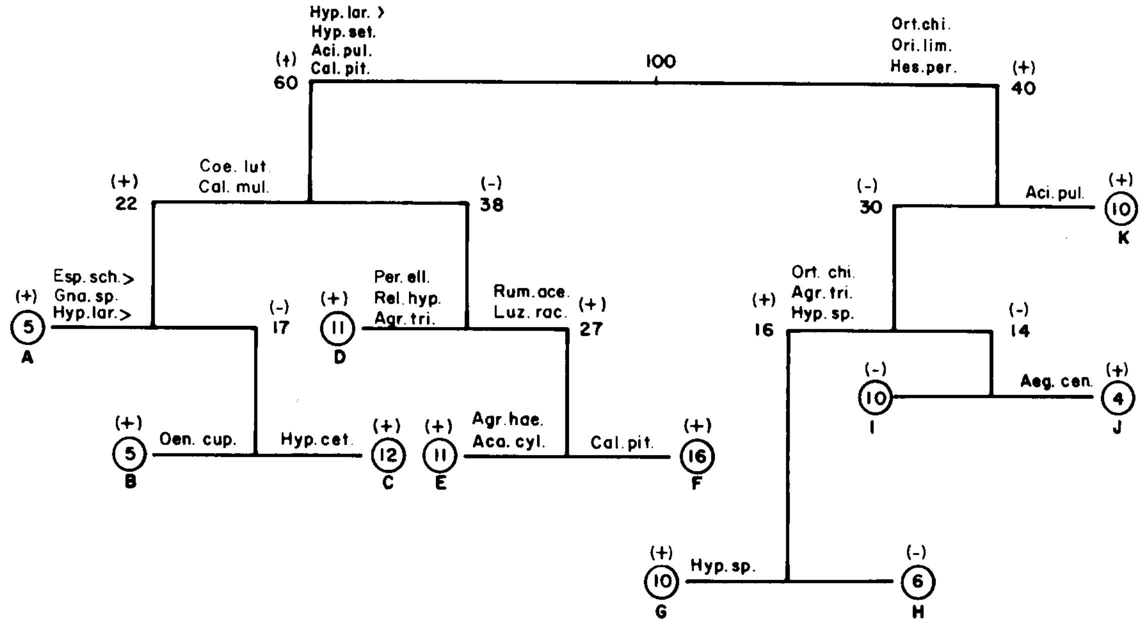

Fig. 6. Sample classification by TWINSPAN. The sample composition of each group is given in Table 4. Abbreviations are formed by the first three letters of the generic and specific names (see Table 5).

Table 4. Key for sample composition of groups generated by TWINSPAN classification.

Group	Number of sample (# of samples in group)
A	78, 95, 96, 97, 99 (5)
B	81, 91, 92, 98, 100 (5)
C	80, 82, 83, 84, 85, 86, 87, 88, 89, 90, 93, 94 (12)
D	41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 71 (11)
E	51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 79 (11)
F	61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 73, 74, 75, 76, 77 (16)
G	1, 2, 3, 4, 5, 6, 7, 8, 9, 10 (10)
H	23, 24, 25, 27, 29, 30 (6)
I	31, 32, 33, 34, 35, 36, 37, 38, 39, 40 (10)
J	21, 22, 26, 28 (4)
K	11, 12, 13, 14, 15, 16, 17, 18, 19, 20 (10)

Location of samples

Number of sample	Site
1- 10	I - Parra
11- 20	II - Zerpa
21- 30	III - Zerpa + 150
31- 40	IV - Zerpa + 300
41- 50	V - Mucubají
51- 60	VI - Mucubají + 250
61- 70	VII - Mucubají + 400
71- 80	VIII - Piedras Blancas - *E. schultzii*
81- 90	IX - Piedras Blancas - *C. lutescens*
91-100	X - Piedras Blancas - *E. schultzii* + *C. lutescens*

shown in Table 4. The first division separates the sites along the Mucubají border using as a criterion high and low elevation species. This separation suggests some degree of discontinuity along the vegetational gradient. In general, this classification generates groups that are closely related to sampling sites.

Five groups were generated by the classification of species (Table 5): (i) high elevation species with greater importance in the Piedras Blancas area (Group A); (ii) high elevation species important in the Mucubají area (Group B); (iii) species abundant along the whole altitudinal gradient (Groups C and E); (iv) species characteristic of the low páramo (Group D).

The lowest diversity is found on site IX (Piedras Blancas - *C. lutescens)* (Table 2). This site, however, is not the poorest in species. The highest diversity is found on site VIII (Piedras Blancas - *E. schultzii)* which is not the richest in species. In general, alpha diversity seems to increase with altitude in the study area. Beta diversity along the gradient was 2.22 half changes which is a moderate value. The average dissimilarity among neighbour sites is 41% with the highest values between sites IV and V (59%), that is at Mucubají (Table 6).

Table 5. Classification of species by TWINSPAN. Numbers in parentheses are the code for species. Groups A (15 species) and B (11 species) are high elevation plants. Groups C (8 species) and E (6 species) are plants abundant along the whole gradient. Group D (18 species) comprises plants characteristic of low elevation páramo.

Code	Species	Group	Code	Species	Group
(1)	*Espeletia schultzii* > 20 Wedd.	E	(30)	*Euphorbia* sp.	D
(2)	*Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatr.	B	(31)	*Oxalis spiralis* R. et P.	D
(3)	*Coespeletia lutescens* (Cuatr. & Aristeg.) Cuatr.	A	(32)	*Viola stipularis* Sw.	D
(4)	*Hypericum laricifolium* > 20 Juess.	B	(33)	*Hypochoeris setosus* Rusb.	A
(5)	*Hesperomeles pernettyoides* Wedd.	D	(34)	*Geranium multiceps* Tourcz.	B
(6)	*Pernettya elliptica* D.C.	E	(35)	*Acaena cylindrostachya* R. et P.	C
(7)	*Valeriana parviflora* Hoeck	B	(36)	*Azorella julianii* Math.	A
(8)	*Lepichinia bullata* (Kunth) Epling	D	(37)	*Arenaria venezuelana* Briq.	C
(9)	*Hypericum laricifolium* < 20 Juess.	C	(38)	*Oenothera cuprea* Schl.	C
(10)	*Espeletia weddelli* Sch. Bip.	A	(39)	*Rhizocephallum candollei* Wedd.	A
(11)	*Hieracium* sp.	E	(40)	*Malvastrum acaule* Gray	B
(12)	*Podocoma baertsifolia* Black.	B	(41)	*Paepalanthus karstenii* Ruhl.	B
(13)	*Senecio formosus* H.B.K.	B	(42)	*Apium leptophyllum* F. Muell.	D
(14)	*Senecio longipenicillatus* Sch. Bip.	D	(43)	*Oritrophium limnophilum* Cuatr.	D
(15)	*Castilleja fissifolia* L.f.	A	(44)	*Peperomia peruviana* Benth.	D
(16)	*Lupinus meridanus* Moritz	D	(45)	*Tofieldia sessiliflora* Hook.	D
(17	*Bartsia laniflora* Benth.	B	(46)	*Hypoxis* sp.	D
(18)	*Stachys venezuelana* Briq.	C	(47)	*Aciachne pulvinata* Benth.	B
(19)	*Hinterhurbera imbricata* Cuatr.	A	(48)	*Agrostis haenkeana* Hitchc.	C
(20)	*Espeletia schultzii* < 20 Wedd.	E	(49)	*Agrostis trichodes* Roem. et Schult.	D
(21)	*Rumex acetostella* L.	C	(50)	*Poa pauciflora* Roem. et Schutt.	B
(22)	*Bidens triplinervia* Sherff.	E	(51)	*Calamagrostis pittieri* Hack.	A
(23)	*Lachemilla hirta* Perry	C	(52)	*Calamagrostis mulleri*	A
(24)	*Gnaphalium* sp.	A	(53)	*Paspalum* sp.	D
(25)	*Relbunium hypocarpicum* Hemsl.	E	(54)	*Orthosanthus chimboracensis* Bak.	D
(26)	*Ranunculus praemorsus* D.C.	D	(55)	*Sisyrinchium bogotense* H.B.K.	D
(27)	*Halenia viridis* Gilg.	A	(56)	*Luzula racemosa* Desv.	A
(28)	*Lobelia tenera* H.B.K.	A	(57)	*Aegopogon cenchroides* Humb. & Bonpl.	D
(29)	*Lucilia venezuelensis* Stmk.	A	(58)	*Jamesonia canescens* Kze.	A

Table 6. Percentages of similarity and dissimilarity (*PS* and *PD*) among sites.

Sites		I	II	III	IV	V	VI	VII	VIII	IX	X	
I		–	61.2	63.3	49.8	25.2	26.8	25.4	25.2	17.5	15.3	
II		38.8	–	69.1	56.7	39.4	38.1	20.8	21.2	18.8	13.1	
III		36.7	30.9	–	65.8	33.3	45.5	33.8	29.2	25.7	23.1	
IV		50.2	43.3	34.2	–	40.3	55.4	31.2	40.9	20.0	19.0	
V	*'PD'*	74.8	60.6	66.7	59.7	–	56.2	51.1	55.4	31.3	36.0	*'PS'*
VI		73.2	61.9	54.5	44.6	43.8	–	48.7	53.9	32.3	32.0	
VII		74.6	79.2	66.2	68.8	48.9	51.3	–	66.5	57.1	54.5	
VIII		74.8	78.8	70.8	59.1	44.6	46.1	33.5	–	54.0	49.4	
IX		82.5	91.2	74.3	80.0	68.7	67.7	42.9	46.0	–	71.1	
X		84.7	86.9	76.9	81.0	64.0	68.0	45.5	50.6	28.9	–	

Discussion

The altitudinal gradient studied here spans 1 200 m, over which the environment becomes more severe for plant life as altitude increases. The analysis of climate and soils confirms a decrease in air temperature and precipitation, increase in solar radiation and night-frost frequency, and decrease in soil water-holding capacity and nutrient content with altitude. These relationships constitute a complex environmental gradient (Whittaker, 1967) as in all mountain regions. The páramos, however, differ from non-tropical mountains because climatic conditions are relatively favourable for plant growth during the whole year. This seems to be fundamental for the particular páramo biota. Other facets of the páramo environment take the place of winter as limiting factors: a relatively dry season, wide thermic oscillations on a daily basis during the whole year, and frequent night-frosts at higher elevations. The vegetation studied here is the result of the integration of the different survival and reproductive 'strategies' of the altitudinal populations (Smith, 1974; Baruch, 1979), the phylogenetic origin of its species (Cuatrecasas, 1968; Vuilleumier, 1971), the modification of climate and soils in the past and present due to glacial influence (van der Hammen, 1968; Vuilleumier, 1971) and human disturbance in historic times.

The detrended correspondence analysis suggests the main floristic variation to be related to the complex altitudinal gradient. It is difficult to establish the most important environmental variable related to vegetational change. The analysis of correlations is of little help because most parameters related to altitude are also statistically associated to the ordination sequence. The interpretation of the *y*-axis of the ordination is even more difficult. One of the extremes of this axis is occupied by samples of site VI which is located above the limit of frequent night-frosts (3 500 m.a.s.l.) and subject to high grazing pressure. This combined influence may be responsible for this site being the poorest in species. On the other hand, sites II and V, which occupy the other extremes of this axis, are located at or below the night-frost line and in areas with relatively low disturbance. It seems possible to interpret this ordination as due to disturbance, mainly grazing, perhaps in combination with frost. This is supported by the statistically significant correlation coefficient between ordination sequence and disturbance index.

The ordination of species shows similarities to that of samples. The species common in the high and low páramo are located at the extreme of the *x*-axis. Those common to the whole altitudinal gradient are located in the center of the axis. Gauch (1977) considers it appropriate to compare species and sample ordinations in order to test the consistency of the interpretations. Here, the general form of the graphs is similar and both ordinations are interpreted ecologically in terms of altitude.

The classification performed separates low and high páramo samples at the Mucubají borderline. Among the high páramo sites, those with *Coespeletia lutescens* as a dominant giant rosette species form a clearly differentiated group. This agrees with the 'superpáramo' name given by Monasterio (1980) to these areas in the páramo of Piedras Blancas. In the low páramo, the samples of site II are separated as a group at the first division; this supports the results obtained in the ordination where they are located at one end of the *y*-axis. In six of ten possible cases, the groups generated by classification correspond exactly to the samples of the sites. This indicates a certain degree of discontinuity. The classification of species also generated ecologically significant results comparable to the ordination results.

Alpha diversity tends to increase with altitude. This agrees with some reports that diversity increases in places with relatively high environmental stress (Peet, 1978; del Moral & Watson, 1979). However, this relationship is complex and the data available do not permit further speculation.

The effectiveness of ordination techniques depends on beta or interhabitat diversity. As it increases, the ecological interpretation of ordinations becomes more difficult (Gauch *et al.*, 1977). The altitudinal gradient studied here shows a moderate beta diversity, due perhaps to the relatively high proportion of species present along the whole gradient. Under these conditions, reciprocal averaging and its derivative, detrended correspondence analysis have been reported as the best ordination techniques available (Gauch *et al.*, 1977; Hill & Gauch, 1980).

The degree of dissimilarity among neighbor sites is moderate (41% as average) with a maximum of 59% between sites IV and V. This result supported by the classification separation of samples along the same borderline, and personal observation, point toward a disjunction in the vegetational gradient. This is not evident, however, in the ordination results. This possible disjunction might represent an interesting situation in regard to the relationship between vegetation, glaciation and, periglacial climate. According to Schubert (1980), the lowest altitude reached by the latest Mérida glaciation was 3 500 m.a.s.l., 10 000 years B.P. Therefore, the vegetation history above and below this line is different. This altitude is also the approximate limit of frequent night-frosts which could have acted as a barrier to the establishment of some species. These combined effects might have caused the disjunction. However, microclimate–flora relationships are probably complex, as illustrated by data from another tropical mountain, Mt. Wilhelm in Papua New Guinea (Smith, 1977).

Due to the scarcity of vegetation studies in the páramos, it is difficult to evaluate and compare the results presented here. Fariñas and Monasterio (1980) and Lozano & Schnetter (1976) agree that drainage and soil water balance are the most important environmental variables affecting vegetation in specific páramos such as Mucubají and Cruz Verde (Colombia). The latter authors add natural and human disturbance as other important factors. Studies on more extensive elevational gradients, similar to that presented here, describe qualitatively the plant formations in Venezuela (Monasterio, 1980). For Colombia, Cleef (1981) presents an extensive phyto-sociological study and relates vegetation diversity to temperature and humidity. In this study, the variations observed in the vegetation are related to altitude as a complex environmental gradient, with human disturbance playing a secondary role.

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