

Modern pollen deposition in the Venezuelan Andes

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With best regards
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Salgado-Labouriau, M. L.: Modern pollen deposition in the Venezuelan Andes. — Grana 18: 53-58, 1979. Uppsala 7 February 1979. ISSN 0017-3134.

The modern pollen deposition in high tropical mountains was studied by the pollen analysis of 18 surface samples collected between 3 100-4 340 m elevation. The relative value among the pollen types as well as the absolute value of the main types were estimated for each sample. Pollen and spore assemblages reflect well the vegetation types, and their distribution. Each type of páramo studied has a characteristic assemblage. The dispersion power and the quantity of deposition for the montane plants was evaluated by counting the number of grains per mg of sediment. The long-distance type are: *Podocarpus*, *Hedyosmum*, and psilate *Cyathea* (moderate dispersion power); *Alnus* (high dispersion power). The main adjacent source of pollen deposition is provided by Gramineae and Compositae. Other pollen types have low or very low dispersion power, among them the characteristic páramo herbs. *Polylepis sericea*, a tree which grows high above the common tree line, has very low pollen dispersion power, and low pollen deposition; its presence can be detected only if the trees grow near the deposition site.

Key words: Pollen deposition, Andean palynology, modern pollen, páramo, tropical high mountains

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The discovery of old moraines and other glacial features in the Venezuelan Andes at elevations about 2 000 m below the present snow line (4 700 m; Royo y Gómez 1959) indicates the occurrence of a Late Pleistocene glaciation which was recently defined as the Mérida Glaciation (Schubert 1974a). It was also found that the existing glaciers have undergone a rapid retreat, particularly during the last 60 years (Schubert 1972). Evidence from the Cordillera Oriental of Colombia (van der Hammen 1974) shows that the latest major upheaval of that mountain range took place during Middle to Late Pliocene time, and that by the end of the Pliocene it had essentially reached its present elevation. The Venezuelan Andes are the northeastern continuation of the Cordillera Oriental and, therefore, it is probable that they too may have reached their present elevation before the beginning of the Quaternary. Although up to the present no evidence of glaciation older than the Mérida Glaciation has been found in the Venezuelan Andes, they may still be found in view of Herd & Naeser's (1974) recent discovery of glacial deposits older than 100 000 years B.P. in the Cordillera Central of Colombia.

Fluvio-glacial terraces were initially chosen to

study the succession of post-glacial vegetation, and possible paleoclimatic changes by means of pollen analysis. These analyses were begun at La Culata (Salgado-Labouriau & Schubert 1974, 1976), followed by Mucubají (Salgado-Labouriau & Schubert 1975, Salgado-Labouriau et al. 1977), both in the Central Venezuelan Andes, at elevations between 2 600 m and 2 800 m. At present, borings of peat bogs by means of a Hiller Sampler are under study. In order to improve the interpretation of the data from the old sediments it was thought necessary to make a survey of the modern pollen deposition in these mountains.

The site

The northern part of the Eastern Cordillera of Colombia (the eastern branch of the Andes) is divided into two branches, separated by the Maracaibo Basin (Fig. 1, inset). The northeastern branch (designated as the Venezuelan Andes) is an elongated series of mountain ranges separated by deep valleys. They rise abruptly from low elevation plains (llanos: 200 m elevation) to heights up to 5 000 m, in a horizontal distance of less than 60 km. The Central part of the Venezuelan Andes, where these mountains reach their highest elevation, was chosen for the palynological studies (Fig. 1).

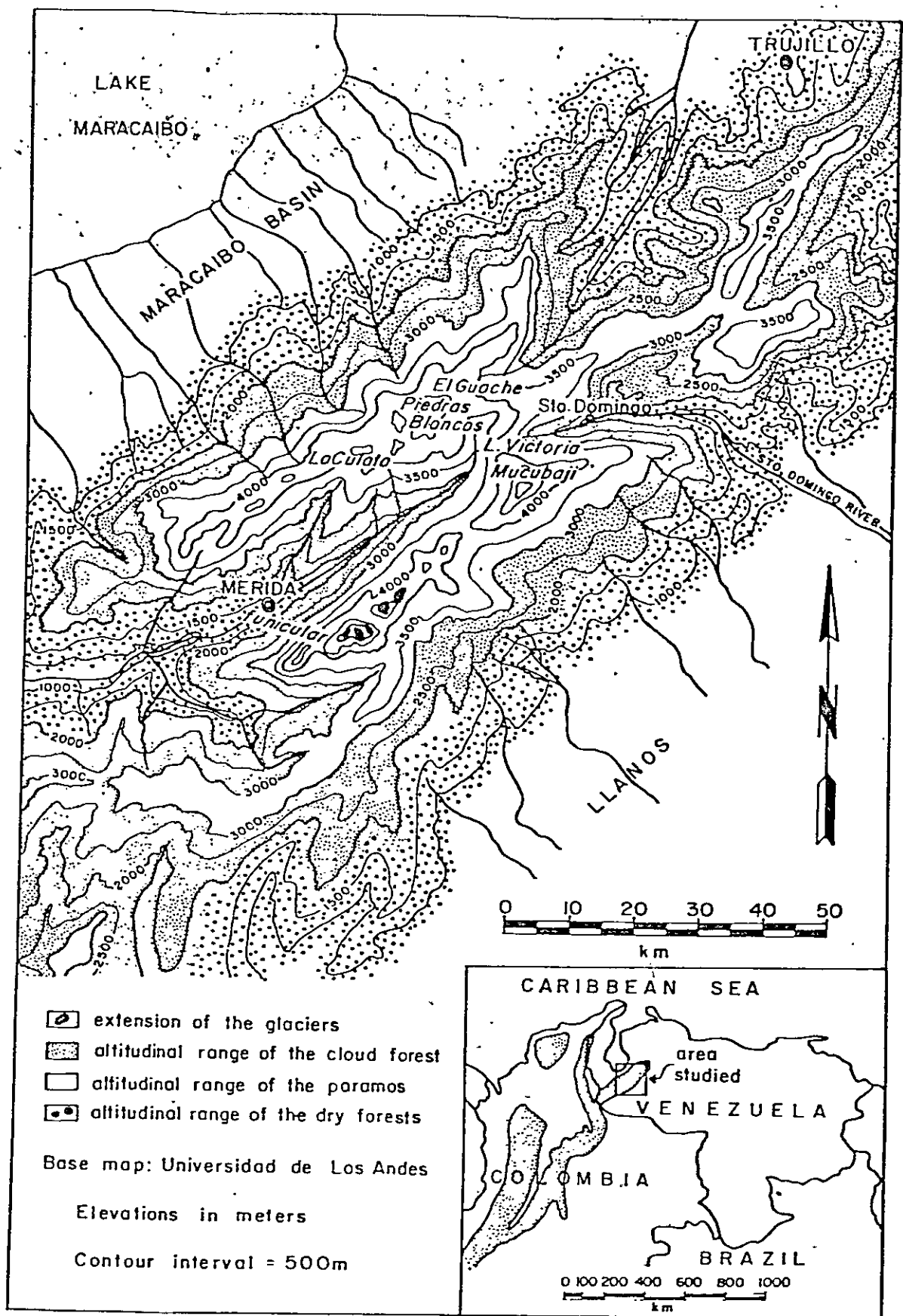




Fig. 2. Páramo landscape: the Mifafi valley at 4000 m elevation.

The vegetation

The Venezuelan Andes have two distinctly defined vegetation belts: the páramos and the montane forest.

In tropical America the word "páramo" is used with two different meanings, for the region between tree line and the zone of permanent snow; and for the open plant formation occupying it (Fig. 2).

The páramo vegetation has been extensively studied by Cuatrecasas (1968), Vareschi (1970), Sarmiento et al. (1971), Azocar (1974), Fariñas (1975), and Monasterio (in preparation). In Venezuela it is found from 2800 to 4700 m elevation, and therefore the páramo is a complex displaying a number of different climatic and edaphic conditions. Its vegetation is an open type of high mountain plant formation, generally formed by a low stratum of cushion-, rosette- and tussock-form herbs, mainly Gramineae, Compositae, Rosaceae, species of the genera *Geranium*, *Lupinus*, *Arenaria* and others. Scattered through this low stratum are small shrubs and tall rosettes of Compositae, *Hypericum*, *Hesperomeles*, *Arcytophyllum*, *Aragoa*, and others. These, under some conditions, can cover up to 60% of the soil. The silvery-leaved species of *Espeletia* (Compositae), varying in life-form from large rosette-forming herbs to tree-like plants eight meters high are, to the human eye, the most conspicuous feature of the páramos. Of this latter genus 45 species are known in Venezuela (Aristiguieta 1964).

In the páramo belt, rivers, creeks, and small glacial lakes are usually bordered by bogs. Peat formation is very common. In these damp soils, Gramineae, Cyperaceae, Gentianaceae, Iridaceae, Musci, Hepaticae, and Pteridophytes are found. At elevations higher than 3800 m it is common to find a high altitude desert (called "Páramo desértico" by Sarmiento et al. 1971) in which several species of tall *Espeletia* stand sparsely over bare rocky soil. The páramos can be divided into (Cuatrecasas 1968): 1) Sub-páramo, transition zone between páramo and

montane forest; 2) Páramo proper, which includes all types of páramo up to the line of nightly freezing; 3) Superpáramo, the region between nightly freezing line and snow line, i.e. the periglacial zone.

High above the normal tree line, on rocky slopes of the páramos, a dwarf forest is sometimes found. Its main component is a tree, *Polylepis sericea*, which reaches heights of 4 to 6 m. Sometimes it is the only tree; in other instances, it is associated with small trees of *Gynoxys* sp. Under the trees there are shrubs of *Hypericum*, *Aragoa*, *Hesperomeles*, and of several Compositae. The existence of the *Polylepis* dwarf forest is still a problem to ecologists and physiologists. It seems that it formerly occupied a larger area (van der Hammen 1974), and it has been suggested that its existence above the tree line is mainly due to favorable soil temperatures (Walter & Medina 1969).

The altitudinal limits of the páramos in the Central Venezuelan Andes are shown in Fig. 1. The dwarf *Polylepis* forest cannot be represented on this scale, but its distribution in the páramo de La Culata and the Páramo de Mucubají can be seen in Figs. 4 and 6. These figures illustrate the reduced size of the dwarf forest, and its anomalous distribution (mapped on aerial photographs and verified in the field).

Disturbance by man is still small in the páramo belt. There are small numbers of cattle in its lower parts, and some cultivation, mainly of potatoes, up to 3500 m elevation.

The tropical Montane Forest begins below the lower limit of the páramo (3000 to 3300 m; usually 3200 m), and in Venezuela this limit is sharp (Sarmiento et al. 1971). The upper part (1700 to 3200 m) consists of a belt of Cloud Forest. Some 40 to 60 species of trees, in several strata up to 35–40 m high, many types of epiphytes, lianas, and tree-ferns, characterize this evergreen mesothermic, hydrophytic forest. The dominant trees genera are *Weinmannia jahnii*, *Podocarpus oleifolius* (and *P. rospigliosii*), several species of Lauraceae (*Ocotea*, *Nectandra*, *Beilschmiedia*) and Guttiferaceae (*Clusia*, *Havetia*). The small trees of *Hedyosmum glabratum* occur through all the altitudinal range, and the bamboo *Chusquea* in the under canopy. Along the streams there are gallery forests, sometimes almost exclusively by *Alnus jorullensis*, that can penetrate into the páramos. Studies on the structure and composition of the Cloud Forest were made by Lambrecht (1954), Veillon (1962) and Sarmiento et al. (1971).

Part of the Cloud Forest was recently cleared. The lower part, especially the flat terraces, up to 2200 m is often used for agriculture, mainly corn; and in its upper part potatoes are cultivated and cattle are raised. In many sites a secondary vegetation consisting mainly of *Psidium*, *Dodonaea*, Compositae, Melastomataceae and Ericaceae, has developed. Most of the Cloud Forest, however, is still fairly intact. The upper and lower altitudinal limits of the Cloud Forest belt is shown in Fig. 1.

In a few places the Cloud Forest is replaced in its lower parts by a dry evergreen forest. The latter occurs at elevations between 1400 and 2400 m, and its main trees are *Podocarpus*, *Vallea*, *Rapanea*, *Myrcia*, *Cecropia*, *Weinmannia*, and *Miconia*. There are several ferns and few grasses. This dry evergreen forest and the lowest montane deciduous dry forest (600 to 1700 m) are much

Fig. 1. Map of the Central Venezuelan Andes; inset: the Northern Andes. Vegetational belts are represented by their altitudinal limits.

Table 1. Dependence of annual average temperature on elevation in a transect along the Sierra Nevada de Mérida, Venezuelan Andes

Station	Altitude (meter above sea level)	Δh (m)	Annual average temperature (°C)	ΔT °C	$\Delta T/\Delta h \times 100$ (°C per 100 m)	Total precipita- tion	Average relative humidity (%)
Mérida	1 497		18.9			2 044	81
La Montaña	2 440	943	13.0	5.9	0.6	2 339	86
La Aguada	3 446	1 006	6.6	6.4	0.6	1 811	85
Loma Redonda	4 065	619	2.4	4.2	0.7	1 498	84
Pico Espejo	4 765	700	-0.6	3.0	0.4	1 135	92
		$c\Delta h=3\,268$		$c\Delta T=19.5$			

$$\frac{c\Delta T \times 100}{\epsilon \Delta h} = \frac{19.5 \times 100}{3268} = 0.59 \approx 0.6 = \text{difference in average temperature for each 100 m elevation.}$$

Source of data: Observatorio Meteorológico y de Radioactividad "Alejandro de Humboldt" Servicio de Meteorología, Comando Aerológico, Fuerza Aérea Venezolana.

disturbed. Settlements were established here after the Spanish invasion, and population has been fairly large since then. The forest in many parts has been cut down for agriculture and cattle raising. The main crop plants are maize, tobacco, manihot, coffee and, in the highest parts, wheat and potatoes. The two types of dry montane forest and their altitudinal range are shown in Fig. 1.

The climate

At present, the glaciers are restricted to a small area on the highest peaks of the Sierra Nevada de Mérida (Fig. 1). Below it is the Superpáramo or periglacial region where temperature variations produce nightly freezing and daily thawing almost every twenty-four hours.

The páramos have a cold and humid climate. Their average temperatures is between 0° and 10°C, depending on the elevation. There is practically no seasonal temperature distinction, and the monthly average throughout the year varies by a little over one degree. However the difference in temperature between day and night is great. In Mucubají (elevations between 3 500 and 3 750 m), where the average yearly temperature is 5.3°C, the daily oscillations are between 6°C and 11.4°C (Azocar 1974). The precipitation varies from 600 to 1 800 mm per year in the páramos, with a dry season of four months (December to March); these values, however, are not connected with altitudinal gradients (Monasterio & Reyes 1974). There is frost almost every night.

The Cloud Forest is defined by the isotherms of 10°C and 18°C. It has a very small daily thermal oscillation. Precipitation is high (between 1000 and 2300 mm per year) with only two months of dry season (January and February). Fog is a constant feature from sunset to sunrise.

The areas of the two dry montane forests have average temperatures between 18° and 23°C. Precipitation varies from 600 up to 1700 mm per year, and dry conditions prevail through most part of the year (6 to 9 months).

Five meteorological stations in a transect along the funicular of Mérida, at Sierra Nevada de Mérida (1497 to 4765 m elevation; Fig. 1) have provided data showing the dependence of temperature upon elevation. It was calculated (Salgado-Labouriau *et al.* 1977) that for each 100 m increase of elevation there is a decrease of 0.6°C in the annual average temperature. Temperature conditions in the other ranges of the Venezuelan Andes are probably similar to the ones found in this transect. Nevertheless humidity changes with the mountain slope orientation. In Sierra de Santo Domingo (Fig. 3), the Atlantic side

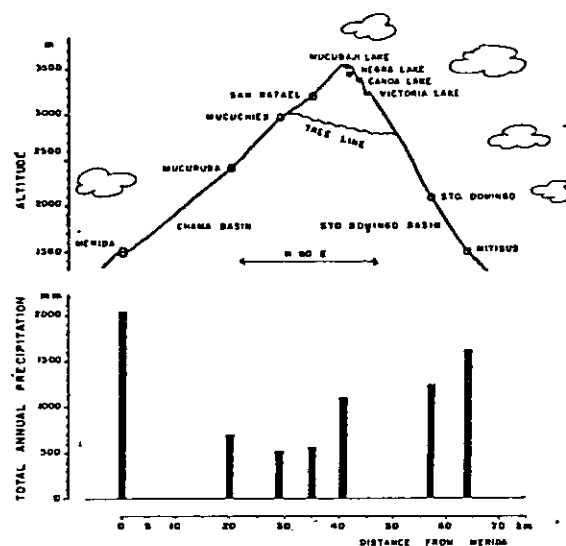
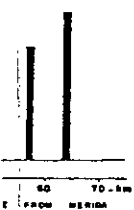
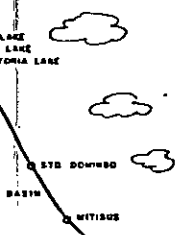


Fig. 3. Diagrammatic profile through Sierra Santo Domingo showing localities and vegetational belts. At bottom the total annual rainfall for each locality (based in Nieto & Arroyo Garcia 1968; Azocar 1974).

Average relative humidity (%)
81
86
85
84
92

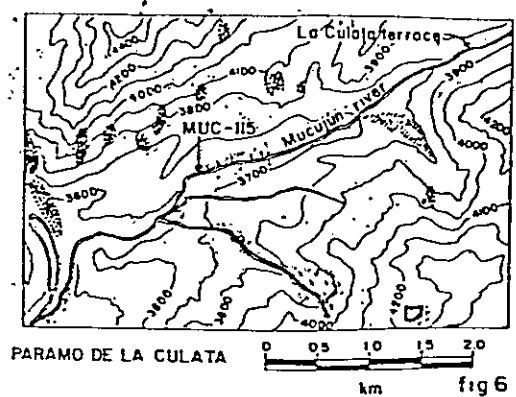
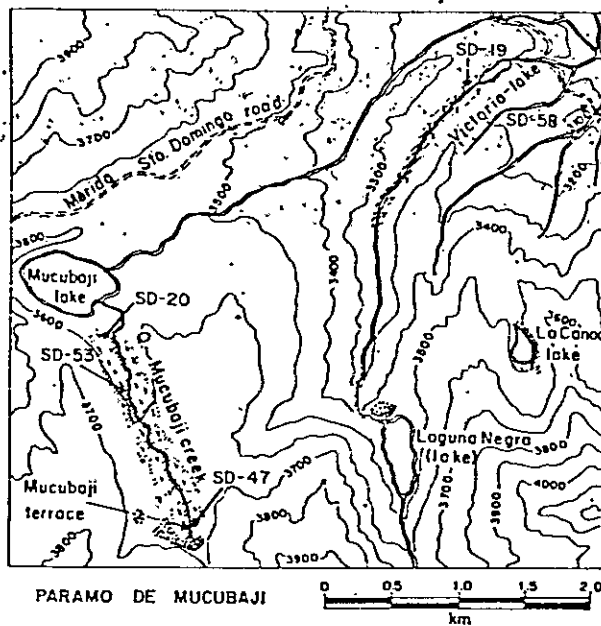
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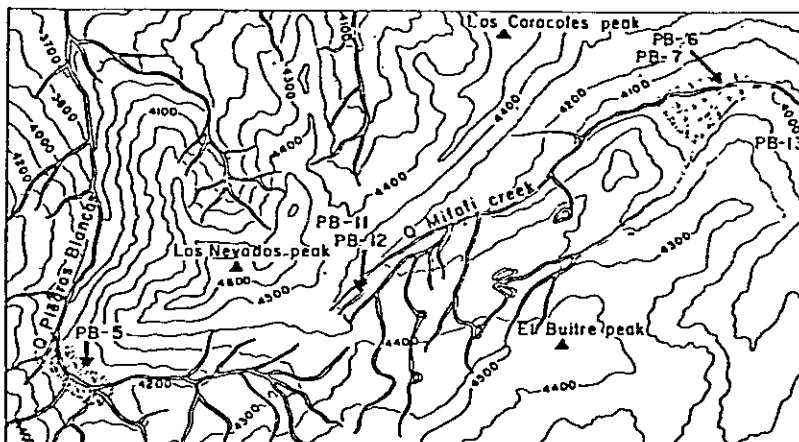


gh Sierra Santo onal belts. At bot- locality (based in 74).

Memorial Volume II



Base maps: C Schubert
Elevations in meters
Contour interval = 100m



Figs. 4-6. 4. Páramo de Mucubaji (Sierra de Santo Domingo) showing sampling sites. Note the small areas occupied by the *Polylepis* dwarf forest which occurrence is marked by aerial photograph, and local verification. Base map: Geologic and Geomorphologic map of Páramo de Mucubaji, Schubert 1970. 5. Páramo de Piedras

Blancas. Base map: Glacial Geomorphologic map of Páramo de Piedras Blancas, Schubert 1975. 6. Páramo de La Culata. *Polylepis* dwarf forest occurrence marked by aerial photograph and local verification. Base map: Geologic and Geomorphologic map of La Culata, Schubert 1974b.

(Mitisus-Santo Domingo-Mucubaji), which includes the Santo Domingo river basin, has a total annual precipitation greater than 1000 mm, whereas in the inner mountain side (San Rafael-Mucuchies-Mucurubá, Chama river basin) it is below 700 mm. Thus, humidity varies with mountain orientation; it plays an important role in the distribution of the different types of páramo (Monasterio & Reyes 1974), and in the altitudinal limits of the vegetation belts. The dryer slopes have the vegetational belts displaced upwards some 100 to 500 m in relation to the wet slopes. The same displacement was observed for the snowline

and periglacial zones by Schubert (1975) in these mountains, both at present and during the Late Pleistocene.

MATERIAL AND METHODS

The method of surface sampling was chosen to study the modern pollen assemblages from the páramo vegetation because it represents an average deposition of several years, and therefore minimizes yearly fluctuations. Furthermore, plant

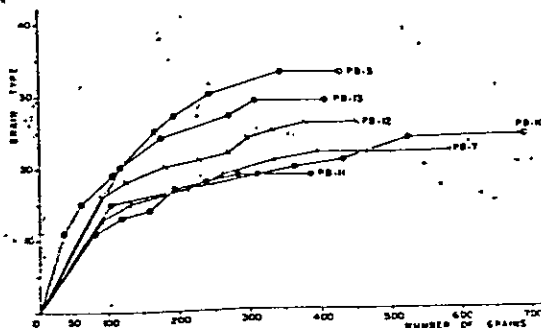


Fig. 7. Saturation curves for the determination of the number of pollen grains and Archegoniatae spores to be counted for the percentage calculation in each sample from Piedras Blancas.

remains found in these samples indicate local conditions which are manytimes very important in the ecological interpretation. Examples are certain algae (as Zygnemataceae) characteristic of warmer water, and also water plants (as *Isoetes*) whose presence in sediments can indicate temperature and/or humidity changes.

All these conditions are also found in post-glacial sediments which make comparable both types of assemblages. Therefore, ecological information taken from the modern surface samples can be used in the paleoecological interpretation of the old sediments.

The modern pollen deposition was studied by sampling the surface of present soils and bogs at the margin of lakes and rivers, or mud in the bottom of lakes. Two transects were studied, Santo Domingo (3100–3600 m elevation) and Piedras Blancas (4000–4340 m elevation). Besides these, samples were also collected in other páramos.

1. Santo Domingo transect

Sierra de Santo Domingo (Fig. 4)

Sub-páramo. The transition zone between páramo and montane forest. Regional vegetation has páramo elements with shrubs and small trees. Cloud forest is at a short distance. Annual rainfall 1100 mm.

SD-58: elevation 3100 m; bot at the margin of Santo Domingo river; damp soil.

Páramo. Regional vegetation of grassland páramo in which there are no elements of montane forest. Its upper limits were considered to be the line of nightly freezing. Annual rainfall 1100 mm.

SD-19-1: elevation 3250 m; top of a core from a peat bog behind glacial lake Victoria (pollen analysis of the core in Salgado-Labouriau & Schubert 1977).

SD-20-1: elevation 3600 m; top of a core from a peat bog near the banks of Quebrada Mucubaji (Quebrada = mountain creek), near the first frontal moraine in Páramo de Mucubaji.

SD-53: elevation 3600 m; close to the site of the preceding sample; peat bog covered with shallow water.

SD-47: elevation 3650 m; peat bog close to Quebrada Mucubaji headwaters. Just north of this site there is a river terrace which has been previously analysed (Salgado-Labouriau et al. 1977). This site is close to a *Polylepis* dwarf forest.

2. Piedras Blancas Transect - (Quebrada Mifafi) Páramo de Piedras Blancas (Fig. 5)

Superpáramo. Zone above the line of nightly freezing and below the snow line. Region covered by bare-rocky soil, modified by periglacial processes, with loose stones on the steep slopes; Espeletietum type of páramo: vegetation is dominated by tall rosettes of *Espeletia*; shrubs, grasses and others herbs only on the valley floor, close to the edge of rivers and glacial lakes. Annual rainfall 800–900 mm.

PB-13: elevation 4000 m; peat bog at the margin of the creek.

PB-6: elevation 4100 m; top of a core from the peat bog at the margin of the creek.

PB-7: elevation 4100 m; top of a core from the peat bog at the margin of the creek.

PB-10: elevation 4340 m; clay at the bottom of a small glacial lake.

PB-11: elevation 4340 m; peat bog at the lake edge of the preceding sample.

PB-12: elevation 4340 m; clay at the bottom of another small glacial lake.

3. Other localities

Gallery forest. At Subpáramo. Simón Bolívar National Park, close to the Mérida funicular station of La Aguada (Fig. 1). Regional vegetation is Subpáramo with gallery forests penetrating into it; forest can be seen at short distance. Annual rainfall 1800 mm.

TM-1: elevation 3420 m; dry soil surface at the margin of a creek.

TM-6: elevation 3450 m; dry soil surface at the margin of another creek.

Páramo

MUC-115: elevation 3650 m; peat bog at the edge of the Mucujún river, Páramo de La Culata; close to a river terrace (Fig. 6) which has been previously analysed (Salgado-Labouriau & Schubert 1976). Regional vegetation of a shrub type of páramo with *Polylepis* dwarf forest close by. Annual rainfall 1187 mm.

EG-1: elevation 3840 m; pebbled clay on the bottom of the lower Laguna del Guache, near El Gavilán peak (Fig. 1); Regional vegetation of páramo with very little grasses and *Espeletia*, even at the margin of the lake. Annual rainfall 800 mm.

EG-3: elevation 3860 m; pebbled clay on the bottom of the upper Laguna del Guache, same type of vegetation as EG-1. Annual rainfall 800 mm.

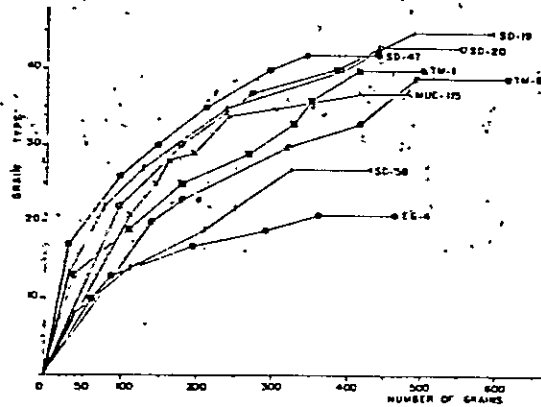


Fig. 8. Saturation curves for the determination of the number of pollen grains and Archegoniatae spores to be counted for the percentage calculation in each sample from Mucubají, La Aguada, La Culata and El Guache.

Superpáramo

PB-5-1: elevation 4 200 m; top of a core from a peat bog at the bottom of a cirque near the headwater of Quebrada Piedras Blancas (Fig. 5), same type of vegetation as samples from Piedras Blancas transect.

Some surface samples were taken at the top of the cores (diameter 2.0 cm). Others were taken by isolating an area of 28.3 cm² by means of a can, open on both sides, which was introduced in the soil. From this area, soil was removed to a depth of 3 cm. All samples were prepared from 2 g of material, and treated by the same procedures used for old sediments (Salgado-Labouriau & Schubert 1976, Salgado-Labouriau et al. 1977), in order to minimize differences in treatment, when compared with the old sediments.

The grain abundance was calculated following the same procedures of pollen analysis: all grains were counted in at least two slides, making a total of 1.0 or more milligrams of sediments; the absolute number of pollen grains, spores and other palynomorphs were estimated separately. The most abundant types were separately estimated in order to observe their dispersion and deposition potentialities. Less frequent types could not be estimated because samples were not large enough.

After the abundance estimation, only pollen grains and Archegoniatae spores were counted. Counting was done on grains embedded in glycerin until no more types appeared among at least 50 consecutive units (Figs. 7, 8, 9). Calculation of frequency of pollen, trilete and monolete spores for the Pollen Diagram was based in these totals.

Because the significance of each type for the interpretation of the Pollen Diagrams was not known, all pollen types with percentages over 1.5% of the total in at least one site were included in the Pollen Sum. An exception was made for Cyperaceae and *Oenothera*, which are surely of local source. Spores of Archegoniatae, pollen grains of Cyperaceae and *Oenothera*, and those below 1.5% are referred as percentage of the Pollen Sum.

The identification of pollen grains and Archegoniatae spores was based on reference slides of pollen and spores of plants from the present day montane vegetation, and on the literature (Salgado-Labouriau & Schubert 1976).

ANALYSIS OF THE DATA

Large quantities of pollen were found in the samples from the Superpáramo, from the grassland and shrub páramos, and from the gallery forest (TM samples) (Fig. 12). The samples from El Guache lakes (EG samples) yielded little pollen, but they have been analysed in order to study the deposition of pollen of long-distance transport when production of local and adjacent vegetation is low.

Nine samples were taken from the Subpáramo, of these, only one (SD-58, Fig. 12) yielded pollen in sufficient quantity for analysis. The remainder contained a few trilete and monolete spores and Compositae pollen and, therefore, were not used. It is possible that the intense use of the land has disturbed the sediments close to the river, where these samples were collected.

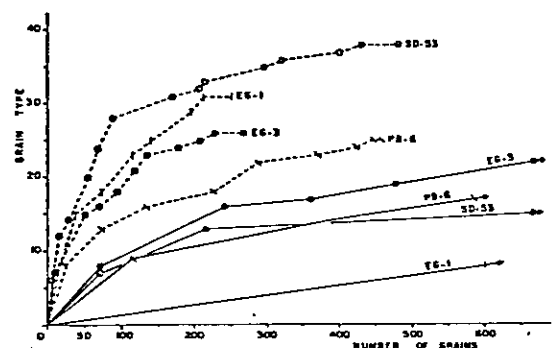
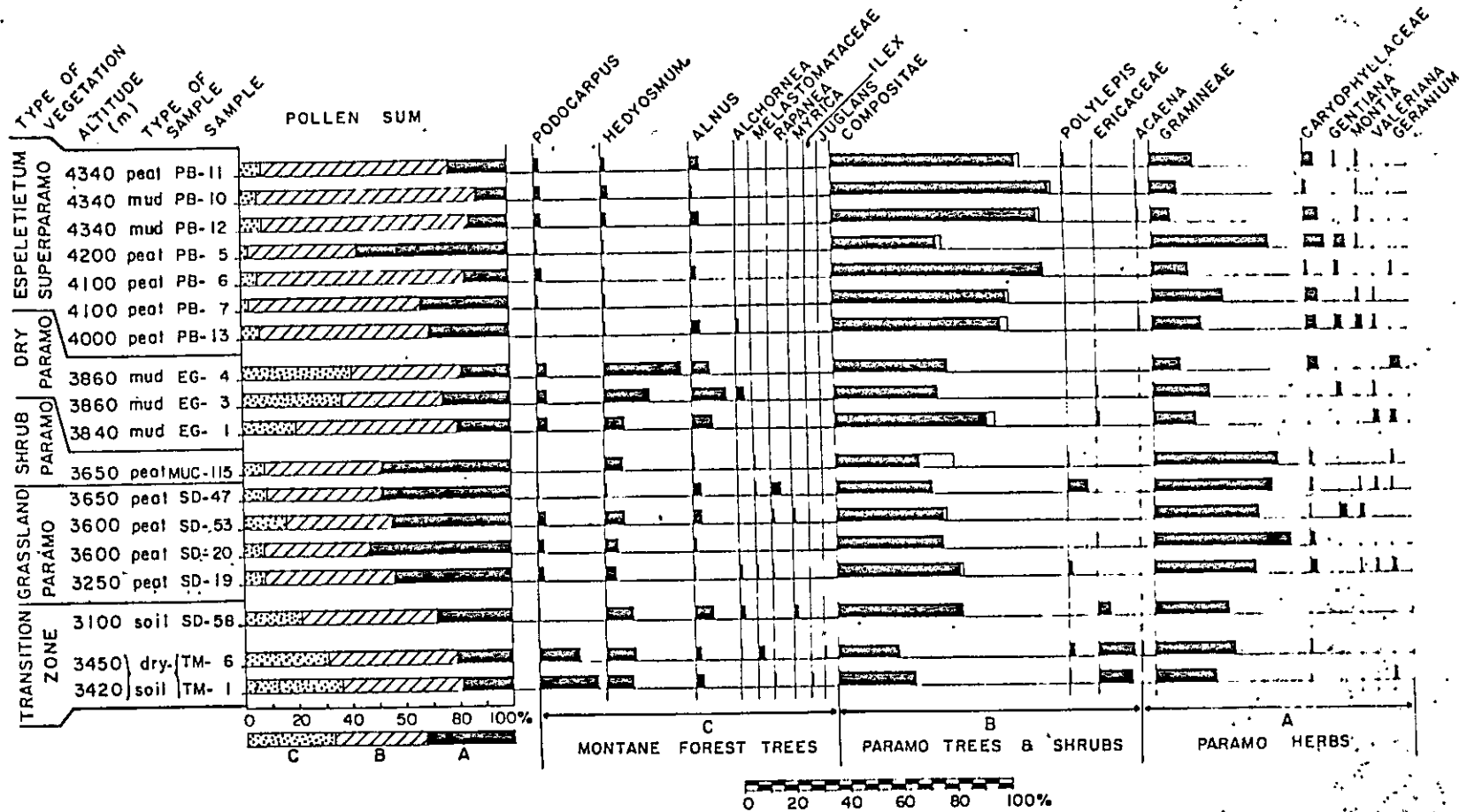


Fig. 9. Saturation curves from samples where one type of spore represents more than 74% of all grains. Continuous line: all grains included; dashed lines: main type excluded.



A. Diversity of types

The number of types of pollen grains and spores is shown in Figs. 7, 8 and 9. The samples which have a large amount of one type of spore are separately shown in Fig. 9. Grains in PB-6 were counted until 1808 units, but even so the curve did not saturate when *Lycopodium* spores (main type) were excluded. *Isoetes* spores are the main type in SD-53, EG-1, -3. In EG-3 saturation was reached with 1602 grains counted. In SD-53 and EG-1, counting including the main type was stopped at 3258 and 2392 grains, respectively, because the amount of other types was still very low (88 and 49, respectively); counting was carried out, excluding *Isoetes* spores, until saturation.

Grassland páramo (SD-19, -20-47, -53) and shrub páramo (MUC-115) show the greatest diversity of types (36 to 45), whereas the Espeletietum Superpáramo (PB samples) and dry páramo (EG samples) show the lowest (16 to 33 types). The values from the transition zone are intermediate, but since only one Subpáramo sample yields pollen, this result has to be considered with caution.

B. Relative pollen frequency

The pollen diagram is divided into two figures. Fig. 10 represents the elements of the Pollen Sum; Fig. 11 represents other pollen types and all the Archegoniatae spores. The pollen Sum used in this work was the basis for the analysis of the old sediments in the Venezuelan Andes, and its division into three groups is similar to that of Colombia (van der Hammen et al. 1973) in order to facilitate comparison of results. The Pollen Sum includes the following elements found in this analysis:

— Montane forest elements: *Podocarpus*, *Hedyosmum*, *Alnus*, *Alchornea*, *Rapanea*, *Myrica*, *Ilex*, *Juglans*, and one type of Melastomataceae.

— Shrubs and trees of the páramos: Compositae, Ericaceae, and *Polylepis*.

— Herbs of the páramo: Gramineae, Caryophyllaceae, *Gentiana*, *Montia*, *Valeriana*, *Geranium* and *Acaena*.

Samples are arranged according to altitudinal type of páramo. The comparison of the relative

grain frequency among the different samples shows that assemblages from the same type of páramo are similar, and can be separated from those of the other types of páramo, as follows:

1. *Transition zone between páramo and montane forest*.—The two samples taken inside the gallery forest (TM-1, -6) show a surprising low percentage of forest pollen (31 to 36%); the assemblages are dominated by pollen from an open type of vegetation. SD-58 (Subpáramo) shows a pollen assemblage similar to the gallery forest. The three samples are characterized by a) dominance of Compositae and Gramineae pollen; b) absence of other páramo herbs; c) presence of Ericaceae pollen. Tree pollen values are high (21 to 36%); nine forest types are present, but only *Podocarpus*, *Hedyosmum* and *Alnus* are found in all samples, and have the highest frequencies. *Polypodium* spores and other monolete spores are the dominant Archegoniatae; foveolate *Lycopodium* spores are absent or in very low frequency whereas reticulate *Lycopodium* spores are frequent; *Pityrogramma* spores, although frequent in one sample, are probably of local source; *Jamesonia* (two types of spores) is present in the gallery forest samples.

2. *Grassland and shrub páramo* (samples MUC-115, SD-19, -20, -47, -53).—Compositae and Gramineae pollen are highly frequent, and in the same proportion; Ericaceae pollen is absent or in low frequency; Caryophyllaceae pollen occur in low percentage (0.7 to 2.6%); other páramo herbs are not always found. Tree pollen is between 8 and 9% (one sample 16%), *Podocarpus*, *Hedyosmum* and *Alnus* are the main components. The frequency of monoletes decreases (except the local spores of *Isoetes*), and trilete spores increase in relation to the transition zone; foveolate *Lycopodium* spores are more frequent than the reticulate type; psilate *Jamesonia* (*J. auriculata* type) occurs in less frequency than verrucate *Jamesonia* (*J. scammanae* type).

3. *Dry páramo* (EG samples).—Compositae pollen percentage is higher than Gramineae pollen; pollen from other páramo elements has a frequency similar to that in the grassland páramo. The high tree pollen and spore frequencies are due to distortion caused by the use of relative values (see sections C and D).

4. *Espeletietum Superpáramo* (PB—samples).—Compositae pollen dominates the assemblages; grass pollen has a lower frequency than in the grass-

Fig. 10. Pollen diagram of modern pollen deposition in the Venezuelan páramos with elements included in the Pollen Sum. In the Compositae representation, black bars represent Tubuliflorae pollen; white bars, Liguliflorae pollen.

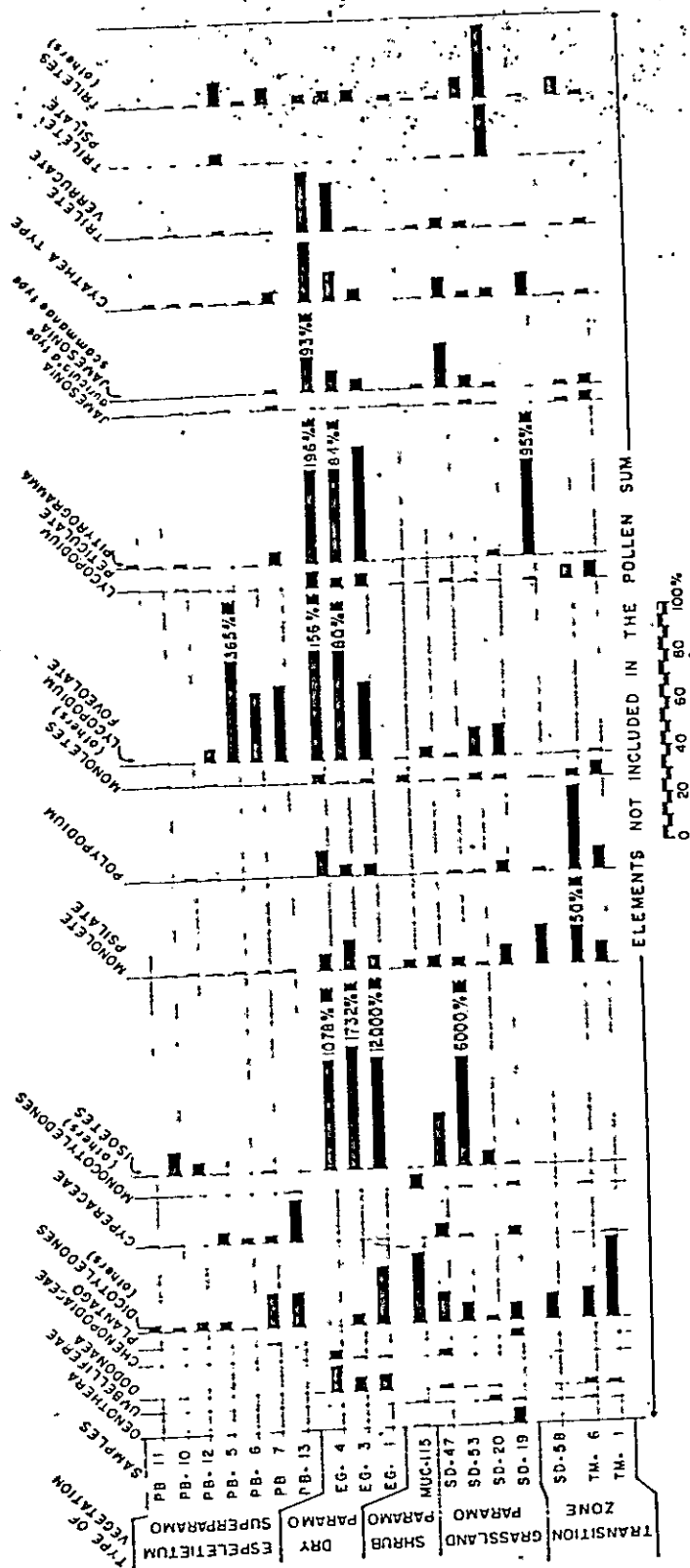


Fig. 11. Pollen diagram of modern pollen deposition in the Venezuelan páramos with elements not included in the Pollen Sum.

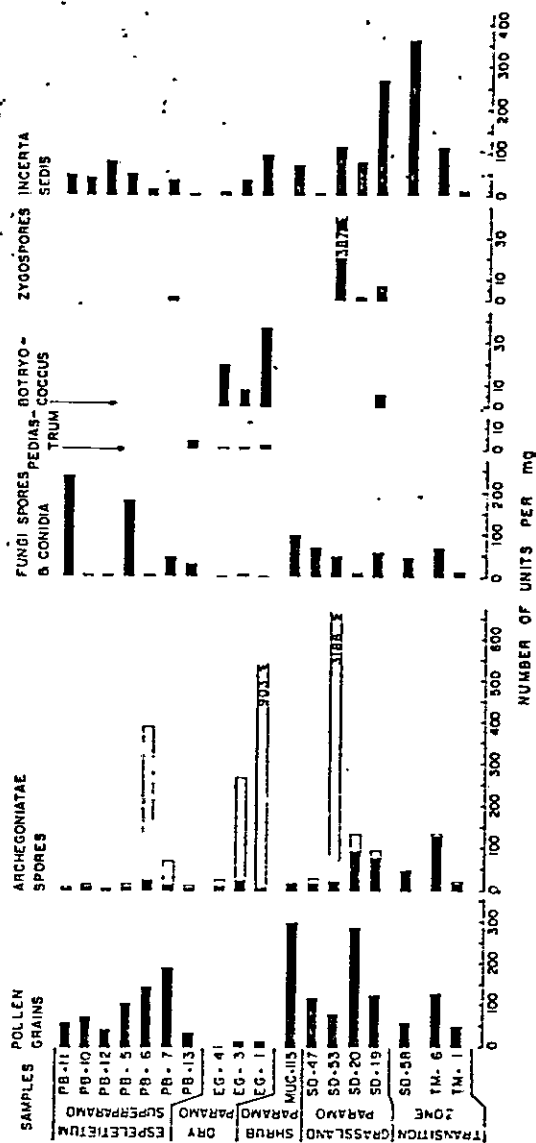


Fig. 12. Abundance of palynomorphs within the modern samples from the páramos. The white bars represents only spores of *Isoetes* plus *Lycopodium*; the black bars include all other types.

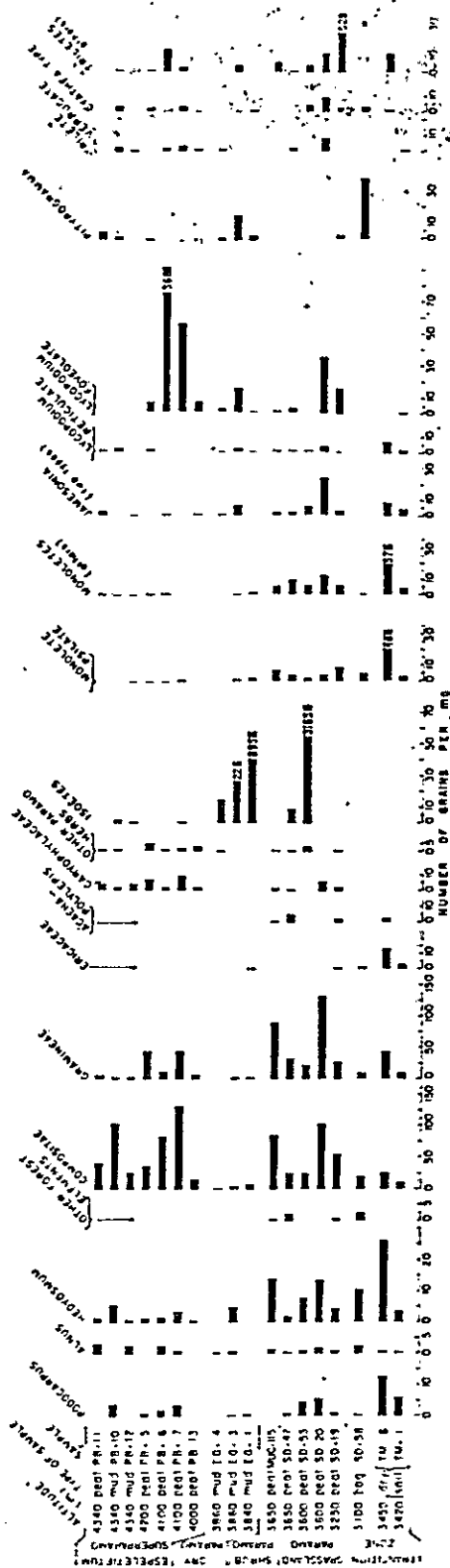


Fig. 13. Histogram of the absolute values for pollen grains and Archegoniatae spores in the modern samples from the Venezuelan páramos. Mud refers to lake bottom sediments.

of modern pollen
Venezuelan páramos with
in the Pollen Sum.

land páramo; Caryophyllaceae (mostly *Arenaria* type) occurs in higher frequency than in the other types of páramos; other páramo herbs are found in low frequency. Tree pollen has a lower percentage than in the preceding assemblages, and only *Podocarpus*, *Hedyosmum* and *Alnus* are present. Trilete spores dominate over monolete ones and the main type is a foveolate *Lycopodium* spores; *Jamesonia* (both types) occurs in low frequency.

C. Absolute number per milligram

Fungi (spores and conidia) occur in all samples (Fig. 12). Their abundance varies greatly from one sample to the other (1.1 to 241.0 units/mg), but the lowest values are found on lake bottom sediments (EG-1, -3, -4; PB-10, -12).

Among the algae, *Pediastrum*, *Botryococcus* and spores of Zygnemataceae were identified in the samples. They do not occur in all assemblages, and are absent in the soil samples from the transition zone (Fig. 12). In the grassland páramo samples, zygospores are the most abundant. *Pediastrum* and *Botryococcus* occur in lake bottom samples from the dry páramo, the latter being the most abundant. In the Superpáramo, these algae, when present, are found in low numbers either in lake bottom sediments or peat samples. These results suggest that *Pediastrum* and *Botryococcus* are more abundant between 3800 and 4000 m elevation whereas zygospores prevail in páramos between 3250 and 3600 m elevation. Because algae were not the subject of this project, these are mere suggestions, but they show that algae remains can be detected after the strong chemical method of pollen separation, and that a careful study of them could probably be helpful in determining water temperatures at the site.

Archegoniatae spores are found in all samples (10.7 to 3 187.8 spores/mg) (Fig. 12). The main maxima are due to a single type of Pteridophyte spore (*Isoetes* in SD-53, EG-1, and -3; *Lycopodium* in PB-6). If these two genera are subtracted from the rest, values are low, usually lower than those for pollen grains (black bars in Fig. 12). The highest values are found at the lowest elevations (3 100–3 600 m).

Abundance of pollen grains varies between 2.5 and 298.5/mg (Fig. 12). Values in the Superpáramo (PB samples) are within the range of the grassland páramo (36.0–298.5/mg). The lowest values are found in the dry páramo (EG samples, 2.5–

15.9/mg), thus in the two El Guache lakes pollen input is low. The deposition potentialities of each type (pollen and spore) are analysed in the following section.

D. Dispersion and deposition of grains

Although the absolute number cannot give information on pollen and spore production by the different plants, it gives direct data on dispersion power and abundance of deposition of the different grain types.

The diagram of absolute values of pollen grains, monolete and trilete spores is shown in Fig. 13.

1. *Tree pollen*.—Pollen grains of the three forest genera, *Podocarpus*, *Hedyosmum* and *Alnus*, are found in all páramo samples up to the highest elevation studied which is approximately 1340 m above the upper limit of the forest. Thus, they experience longdistance transport. *Podocarpus* (several species) shows an average of 9.3 pollen grains/mg at the upper forest limit, and decreases gradually until an average of 1.6/mg at the highest elevations. This shows that it has moderate dispersion power, which decreases with elevation. A rough estimation of the distance between the deposition site and the place where the tree grows can be made by the number of grains deposited. *Alnus jorullensis* pollen shows an average of 1.2 to 1.3 grains/mg in all samples, except El Guache in which it decreases to the average of 0.4/mg; therefore, although it is present in low quantity in the atmosphere, it has a high dispersion power, and the amount of grains deposited cannot help to estimate the distance from the mother plant. *Hedyosmum glabratum* pollen decreases from an average of 14.5 to 2.2/mg as elevation increases, thus although its quantity in the atmosphere near the forest is the highest of all trees, its dispersion power is moderate. On the other side, this genus can give the best estimation of the distance between the forest of origin and the site of deposition.

The following genera have very low dispersion power: *Myrica*, *Ilex*, *Juglans*, *Rapanea*, *Alchornea*, and the family Melastomataceae.

2. *Páramo pollen*.—Deposition of Compositae pollen is slightly higher in the Espeletietum Superpáramo (average 65.0/mg) than in the grassland páramo (average 58.4). The lowest values are found in the dry páramo, thus the Compositae pollen from higher and lower elevations was not transported to El Guache lakes. These data indicate that these grains do not have good dispersion power

either upwards or downwards, and their absolute values are due to abundance or scarcity of the plants around the site of deposition.

Gramineae pollen deposition is lower at higher altitudes (Superpáramo and dry páramo) than in the grassland páramo, which reflects local and adjacent conditions. Therefore, grass pollen probably does not disperse upwards.

The Caryophyllaceae (*Arenaria* type) show a larger pollen deposition in the superpáramo, whereas Ericaceae pollen is more abundant at the transition zone, both indicating local and adjacent conditions.

The *Polylepis-Acaena* type has low values, and is detected only in the samples collected close to the plants. TM-6 was collected under a *Polylepis sericea* tree and it only shows 2.5 grains/mg. Other páramo herbs also show low values.

The results show that the low pollen values from El Guache samples are not due to a decrease of the local pollen deposited, but to the low pollen input from the main páramo source, that is, Gramineae and Compositae.

3. *Monoletes*.—*Isoetes* shows the highest values among the monoletes, nevertheless it is not found in all samples. It occurs in all lake bottom sediments from páramos (which is predictable of an aquatic plant), and in three of the peat bogs. The other monoletes decrease as elevation increases, a psilate monolete being the most abundant.

4. *Triletes*.—Spores of *Lycopodium*, *Pityrogramma* and a highly verrucate type do not show any correlation with elevation or with the type of páramo. Their abundance in the sample is probably due to the presence or absence of the plant around the site. Among the *Lycopodium* spores, the foveolate type is more frequent in the páramo than the reticulate. The latter is more abundant at the lower elevations.

Jamesonia spores (two types) are less abundant in the Espeletietum than in the other types of páramo. The plants are very abundant around the upper El Guache lake (probably *J. canescens*); nevertheless their spores are not abundant in the lake samples (0.8 and 6.4/mg). This indicates that they have a very low dispersion power.

The other trilete spores are more abundant in the lower parts of the páramos. Among them, a psilate type is the most frequent. This type of spore is found among the Cyatheaceae, such as *Cyathea* and *Sphaeropteris*, and was referred in our other works

as *Cyathea* type. If this psilate spore found in the páramos belongs to tree ferns from the forest, it was detected well above the forest belt, and therefore it has long-distance transport, and a moderate dispersion power. Verrucate spores are also found among the Cyatheaceae but the ones found during this work do not show any correlation with altitude, thus suggesting a local source. It is possible that some páramo ferns also have verrucate grains.

E. Absolute and relative values

In the three El Guache samples, long-distance tree pollen increases to 20–41% of the Pollen Sum (Fig. 10), although the forest upper limits are approximately 850 m below the lakes. The absolute values for tree pollen do not increase, and are kept within the range expected for this elevation (Fig. 13). This clearly shows that the increase of relative values is an artifact of the percentage method, and it is due to decrease in pollen input of the main adjacent source, that is, Gramineae and Compositae (see part D). The region of those lakes is covered by sparse vegetation, and most of the soil is bare. Therefore, the absolute numbers reflect the regional distribution whereas percentage values do not.

These results support Hedberg's interpretation that the increase of *Podocarpus* pollen percentage in the highest parts of the East African mountains was caused by small pollen production of the sparse vegetation around the collecting site (Hedberg 1954).

Comparison of relative and absolute values from the Venezuelan páramos show that pollen spectra from sparse vegetation are distorted, and there is an artificial increase in the percentages not only of long-distance pollen and spores, but also of local types. Such are the cases of the long-distance grains of *Podocarpus*, *Alnus*, *Hedyosmum* and psilated Cyatheaceae; as well as the local pollen and spores of *Dodonaea*, *Isoetes* and several triletes of Pteridophyta (Figs. 10, 11). Accordingly, the relative values have to be taken with caution in assemblages with less than 16 pollen grains/mg (main adjacent source lower than 12.5/mg).

When regional pollen input is large (deposition above 35 pollen grains/mg), and the main adjacent source is higher than 24/mg, relative and absolute values are similar, both reflecting the regional vegetation distribution.

Table II. Measurements of pollen of *Polylepis sericea* and *Acaena* species from Venezuela (in μm)

Species	Polar diameter ^a	Equatorial diameter ^a	P/E	Oral region (height) ^a
<i>P. sericea</i>	40.9 \pm 1.2	38.0 \pm 1.5	1.08	7.9 \pm 1.8
<i>A. elongata</i>	32.3 \pm 1.8	29.8 \pm 1.8	1.08	5.1 \pm 0.7
<i>A. cylindrostachya</i>	30.4 \pm 1.5	29.2 \pm 1.2	1.04	4.5 \pm 0.7
<i>A. argentea</i>	29.3 \pm 1.5 ^b	28.6 \pm 1.6 ^b	1.02	3.6 \pm 0.6

^a $\bar{X} \pm t 0.95 (24) \cdot s_x = 99\%$ confidence interval of the average, \bar{X} .

^b $n=15$.

Absolute values between 16 and 35 total pollen grains/mg were not found in this analysis.

F. Comparison between modern and old pollen assemblages

The ecological interpretation of the old pollen assemblages is made by comparison with the similar modern ones. The Venezuelan páramo post-glacial sediment which have been analysed (Salgado-Labouriau & Schubert 1976, 1977, Salgado-Labouriau et al. 1977) have pollen assemblages similar to the present-day pollen deposition in the páramo region. Accordingly, there is good indication that páramo vegetation has occupied these high elevations during the last 12 650 radiocarbon years (Salgado-Labouriau et al. 1977). Nevertheless, post-glacial páramo vegetation was not strictly analogous to present-day vegetation.

In the modern páramo assemblages Compositae pollen dominates, and Gramineae pollen is the co-dominant. This is specially true in the Espeletietum Superpáramo and in the dry páramo. In all the old sediments analysed so far, grass pollen dominates whereas Compositae pollen shows low percentage. The large increase of Compositae pollen is discussed elsewhere (Salgado-Labouriau 1979b) and it seems possible that it was caused by the intense use of the land after the arrival of the Spanish in the 16th century.

In modern pollen assemblages, local and long-distance vegetation are known by the study of present-day vegetation distribution. In the old assemblages these facts are not known and, therefore, absolute values are essential to determine the true maxima for the ecological interpretation.

G. Pollen of *Polylepis sericea* and *Acaena*

Pollen grains from the two genera *Polylepis* and *Acaena* are similar. This was shown for the species of Colombia (van der Hammen & González 1960),

Chile (Heusser 1971) and Venezuela (personal observations). Both genera occur along the Andes, and in the Northern Andes they belong to the páramo belt. Although both indicate páramo conditions in Venezuela and in Colombia, a distinction should be attempted, because *Polylepis* species are trees that live high above the common forest belt, forming dwarf forests within the open páramo vegetation, whereas *Acaena* species are herbs and small shrubs of the páramo. Furthermore, the discovery of large quantities of *Acaena-Polylepis* type in Pleistocene sediments (Van der Hammen 1974) suggests that large numbers of these plants lived during certain intervals, the beginning of which were identified as the beginning of glacial periods. If these grains belong to *Polylepis*, large extensions of *Polylepis* forests existed in the past.

The Venezuelan *Polylepis sericea* is a different species from those occurring in other parts of the Andes. Fortunately it can be separated, under the light microscope, from the three *Acaena* species of Venezuela (*A. cylindrostachya*, *A. elongata* and *A. argentea*).

Description of *Acaena-Polylepis* type:

Shape: prolate sphaeroidal with circular amb, and protruding, transparent oral region.

Apertures: grains 3-colporate; colpi not always visible at small magnifications (below 400 \times), thus grains appear to be "3-porate". Os provided with a protruding transparent operculum sided by two pleats of the colpus margo; these pleats do not extend out of the oral region.

Exine: rugulate, sexine visible from 600 \times up; in the oral region sexine is psilate and transparent. Nexine thinner than sexine, stratification not always clear.

Measurements: polar axis 29–41 μm ; equatorial diameter in equatorial view 28–38 μm ; P/E=1.02–1.08.

Distinction among the Venezuelan species:

Apertures: *P. sericea* has colpus with margo, central part of colpus always visible at the border of the oral region; ends of colpus visible from 600 \times up; salient margo with rough surface. *A. argentea*: colpus without margo, whole colpus always visible. *A. cylindrostachya* and *A.*

elongata: colpus without margo, visible from 600 \times up. Oral region: highly protruding in *P. sericea* and *A. elongata*; moderately protruding in *A. cylindrostachya* and *A. argentea*.

Exine: rugulate pattern in *P. sericea* forms \pm rounded ridges; in the three *Acaena* species ridges are narrow and undulated.

Size: all three species of *Acaena* are significantly different from *Polylepis sericea*, but not among themselves (Table II).

Although in Venezuela the two genera can be easily distinguished, their separation in old sedimentary deposits has to wait until the pollen grains of all the South American species are morphologically studied, because other species could have existed.

GENERAL CONCLUSIONS

1. The pollen and spore assemblages of surface samples from the páramos reflect the regional vegetation (type and distribution).

2. In sparse vegetation relative values of pollen and spores of long-distance transport, as well as local pollen and spores, tend to increase due to an artifact of the percentage method. When deposition is lower than 12.5 pollen grains/mg of treated sediment, it indicates sparse vegetation, and relative values have to be counterchecked by absolute values in order to be used in ecological interpretation.

3. When pollen assemblages have more than 36 pollen grains/mg relative and absolute values are comparable.

4. The dispersion power of forest trees is different according to the species. *Alnus jorullensis* has high dispersion power, and its deposition is low but constant throughout the páramos. *Podocarpus* (several species) and *Hedyosmum glabratum* show moderate dispersion power, that is, the absolute number of their grains decrease with the increase of vertical distance from the forest belt. Therefore, the quantity of pollen deposited by these two genera can be used to roughly estimate the distance between the forest upper limits and the site of deposition. Other forest genera have very low dispersion power.

5. Among the páramo elements, Compositae and Gramineae are the main source of deposited pollen. The first shows low upward and downward dispersion power. Grass pollen has low upward dispersion power, and its downward dispersion could not be verified.

6. Grassland páramo shows the greatest diversity of pollen and spores among the different páramo types.

7. The shrub páramo could not be distinguished from the grassland páramo because páramo shrubs (except Compositae) yield little pollen. A better knowledge of the pollen morphology among the páramo Compositae will probably enable the distinction between these two types.

8. Sub-páramo, grassland (and shrub) páramo, and Superpáramo have characteristic pollen and spore assemblages.

9. The *Polylepis* dwarf forest can be detected in the assemblages only when it grows close to the site of deposition.

10. Páramo lake sediments are not easily distinguished from peat sediments, although the first have low quantities of fungus spores and conidia, and more algal remains. *Isoetes* spores are found in all lake sediments, but they can be also found in peat bogs.

11. The indicators of páramo conditions are: *Polylepis*, *Acaena*, *Geranium*, *Gentiana*, *Montia* and *Jamesonia*. Unfortunately none of them have large pollen deposition, and all have low dispersion power. But since they include many species, some of them always occur in páramo sediments.

12. Trilete and monolete spores usually are less abundant than pollen grains. Their highest values (except for local production) are found at lower elevations.

13. Some algae can be detected after the strong chemical method of pollen separation. *Pediastrum* and *Botryococcus* are more frequent between 3 800 and 4 000 m elevation, and spores of Zygnemataceae between 3 250 and 3 600 m.

14. Local sources of pollen and spores for the páramo vegetation are: *Isoetes*, *Pityrogramma*, *Jamesonia*, Cyperaceae, *Polylepis* and *Acaena*. Adjacent sources are: Compositae, Gramineae, and probably Caryophyllaceae and Ericaceae. Long-distance pollen and spores are: *Podocarpus* (moderate dispersion power), *Hedyosmum glabratum* (moderate), *Alnus jorullensis* (high dispersion), psilate Cyatheaceae (moderate dispersion). Other elements found in this analysis could not yet be characterized.

15. Comparison between modern and old pollen assemblages suggests an increase of Compositae in the last centuries.