15,000-yr pollen record of vegetation change in the high altitude tropical Andes at Laguna Verde Alta, Venezuela ☆

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Abstract

Pollen analysis of sediments from a high-altitude (4215 m), Neotropical (9°N) Andean lake was conducted in order to reconstruct local and regional vegetation dynamics since deglaciation. Although deglaciation commenced ~15,500 cal yr B.P., the area around the Laguna Verde Alta (LVA) remained a periglacial desert, practically unvegetated, until about 11,000 cal yr B.P. At this time, a lycopod assemblage bearing no modern analog colonized the superpáramo. Although this community persisted until ~6000 cal yr B.P., it began to decline somewhat earlier, in synchrony with cooling following the Holocene thermal maximum of the Northern Hemisphere. At this time, the pioneer assemblage was replaced by a low-diversity superpáramo community that became established ~9000 cal yr B.P. This replacement coincides with regional declines in temperature and/or available moisture. Modern, more diverse superpáramo assemblages were not established until ~4600 cal yr B.P., and were accompanied by a dramatic decline in *Alnus*, probably the result of factors associated with climate, humans, or both. Pollen influx from upper Andean forests is remarkably higher than expected during the Late Glacial and early to middle Holocene, especially between 14,000 and 12,600 cal yr B.P., when unparalleled high values are recorded. We propose that intensification of upslope orographic winds transported lower elevation forest pollen to the superpáramo, causing the apparent increase in tree pollen at high altitude. The association between increased forest pollen and summer insolation at this time suggests a causal link; however, further work is needed to clarify this relationship.
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Keywords: Palynology; Paleoecology; Paleoclimatology; Holocene; Neotropics; South America; Andes; Venezuela

Introduction

Most palynological studies in the Venezuelan Andes have focused on peat bogs and fluvioglacial sediments. The majority of these studies are paleoecological reconstructions of time slices providing a discontinuous vegetation and climate history since the Late Glacial. The most noteworthy events identified by these records are the 'El Caballo' stadial (~19,500 cal yr B.P.), the 'Mucubají III' cold phase (tentatively correlated with

the Younger Dryas), the 'Miranda' warm phase (3500–4000 cal yr B.P.), the 'Piedras Blancas I' warm phase (correlated with the Medieval Warm Period) and the 'Piedras Blancas II' cold oscillation (correlated with the Little Ice Age) (Salgado-Labouriau, 1989; Rull, 1996, 1999; Rull et al., 1999). The first coordinated lake coring effort in the Venezuelan Andes produced continuous records for the last 17,000 cal yr B.P. (Bradley et al., 1985). Pollen analyses focused on cores from Laguna Los Lirios and Mucubají. Laguna Los Lirios (2300 m) is a closed-basin lake located below both the glacial limit and upper forest line or tree line. The record from Laguna Mucubají spans the period from 9300 cal yr B.P. to present and contains relatively complacent vegetation changes, probably because the

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intermediate elevation (3540 m) of the lake within the páramo belt makes it relatively insensitive to altitudinal vegetation shifts (Salgado-Labouriau et al., 1992).

The causes of climatic changes across the tropics of South America remain uncertain, but may include orbital forcing, solar variability, coupled ocean/atmospheric circulation and human impacts. Here, we present the results of pollen analysis of a sediment core obtained from a high-altitude lake situated at 4215 m, which has a continuous record since the Late Glacial. The objective is to reconstruct the vegetation dynamics at a centennial-scale, and provide insights concerning the ecological sensitivity of Andean biomes to past climate forcings.

Study area

Laguna Verde Alta (N 8° 51.165′, W 70° 52.449′) is located at 4215 m in the Cordillera de Mérida in the upper elevation zone of the páramo, the highest biome of the northern Andes. The páramo is situated between upper forest line and the snow line, which in Venezuela are at 2800–3000 and 4700–4800 m altitude, coinciding approximately with mean annual temperatures of 10 and 0°C, respectively (Monasterio, 1980). Mean annual precipitation ranges from 1800 to 600 mm from southeast to northwest across the rainshadow of the Andes, with the driest conditions between December and March (Monasterio and Reyes, 1980). The result is a downward displacement of the páramo boundary by 100 to 500 m on southeast oriented slopes located on the wet side of the rainshadow. Páramo vegetation is open with three strata. The lower consists of cushion and rosette plants, the intermediate is dominated by graminoid herbs and shrubs, and the upper is characterized by Espeletia (Asteraceae) columnar rosettes, which are the most conspicuous element of the páramos. At present, the study site is located in the superpáramo, which defines the transition from the páramo to the nival stage (Luteyn, 1999).

The lower limit of the superpáramo in the Venezuelan Andes is about 4000 m on the wetter southeast side of the rain shadow, especially on southeast-oriented slopes (average annual precipitation of ~1550 mm), and approximately 4300 m on the dryer northwest side of the rainshadow where northwest-facing slopes received considerably less precipitation (average annual precipitation is <700 mm). Average annual temperatures range from 2.8 to −0.3°C and nightly freezing occurs. The soils are poorly developed and composed of unconsolidated rock fragments derived from periglacial processes (Schubert, 1979). Vegetation cover is sparse and discontinuous with the percentage of bare soil ranging from 50 to 90%. Monasterio (1980) defined two superpáramo vegetation types: the desert páramo and the periglacial desert. The desert páramo is characterized by four dominant Espeletia species, with some altitudinal differentiation: E. semiglobulata (3900 to 4200 m), E. lutescens–E. timotensis (3900 to 4500 m), E. spicata (4100 to 4300 m) and E. moritziana (4200 to 4600 m) (Monasterio, 1979, 1980). The periglacial desert has sparse and discontinuous vegetation cover between 1 and 5%, with patches and

isolated individuals growing on unstable slopes. Characteristic are the almost monospecific cushion-like colonies of Aciachne pulvinata (Poaceae), Draba chionophylla (Brassicaceae)–Calandrinia acaulis (Portulacaceae), Arenaria spp. (Caryophyllaceae), Montia meridensis (Portulacaceae), Azorella julianii (Apiaceae) and Cerastium cephalanthum (Caryophyllaceae). The uppermost part of the periglacial desert from 4700 to 4800 m has only isolated vegetation growing on rock crevasses, including small rosettes (Draba [Brassicaceae], Oritrophium [Asteraceae], Calandrinia [Portulacaceae]), small shrubs (Senecio, Hinterhubera [Asteraceae], Draba [Brassicaceae]) and grasses (Calamagrostis, Agrostis [Poaceae]). The species found at the highest elevations are Draba chionophylla, D. bellardii [Brassicaceae], Calamagrostis coartata, Agrostis hankeana, Helleria fragilis (Poaceae) and Oritrophium paramensis (Asteraceae), which grow around small ice fragments detached from the nearby glaciers. There is only unvegetated rock above 4800 m.

The present superpáramo vegetation in the Venezuelan Andes is the result of a long colonization process beginning at the onset of the Holocene and extending to the present as exemplified by the Miranda sequence (Salgado-Labouriau et al., 1988). The pioneer phase began about 13,000 cal yr B.P. and was characterized by sparse graminoid communities that occupied the site until about 9000 cal yr B.P. At this time a sharp increase in floristic diversity occurred, with the addition of most of the typical superpáramo Asteraceae, as well as Cyperaceae, Gentiana, Cerastium and Arenaria (Salgado-Labouriau, 1988). The colonization process was characterized from this point onwards by gradual, but more or less continual increase of richness. A second less prominent diversification episode occurred between ~7500 and 5500 cal yr B.P. with the addition of Oxylobus, Geranium and Rhizocephalum, among others. Some other important vegetation elements of the present-day vegetation, such as Draba, Jamesonia and Plantago, did not arrive until ~2500 cal yr B.P.

Methods

We collected a sediment core in January, 1999 from Laguna Verde Alta (LVA core A-99), approximately 1200 to 1400 m above the local tree line (Fig. 1). This is the highest of a complex of three moraine-dammed lakes located on the southwest slope of the River Chama valley. The core was obtained from 2.5 m of water in the deepest part of the lake, using a modified square-rod piston corer (Wright et al., 1984). Five plant macrofossil samples were isolated and dated by accelerator mass spectrometry (AMS) ^{14}C. Radiocarbon dates were calibrated according to Stuiver et al. (1998a,b); all the dates discussed in this paper are expressed in calibrated years before present (cal yr B.P.). Organic carbon content was measured with a Carlo Erba 2500 CHNS elemental analyzer. Seventy volumetric samples (1 cm^3) were taken from the core at 5 cm intervals for pollen analyses. Samples were processed at the Limnological Research Center (University of Minnesota), using standard palynological techniques (Bennett and Willis, 2001), after spiking with Kochia scoparia exotic pollen
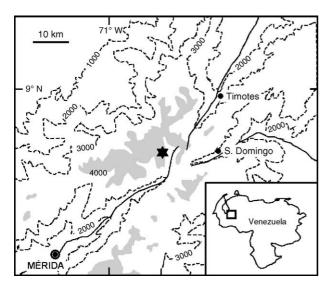
Figure 1. Location map showing the LVA study area (black star). The gray area is the approximate extension of the superpáramo, delimited by the 4000-m altitude line.

by weight (Salgado-Labouriau and Rull, 1986). Slides were mounted in silicone oil without sealing. Pollen and spore identification was made according to Van der Hammen and González (1960), Murillo and Bless (1974, 1978), Hooghiemstra (1984), and Tryon and Lugardon (1991). Counts were conducted until a minimum of 300 pollen and spores were tabulated, but counting continued until the saturation of diversity was reached (Rull, 1987). Final counts range between 310 and 451 grains, with an average of 395. The pollen sum ranges from 252 to 407 (average 329) and includes only pollen types, excluding aquatic and semi-aquatic elements such as Cyperaceae, Oenothera and Myriophyllum.

Pollen taxa are grouped in the figures according to the vegetation composition (e.g. Salgado-Labouriau, 1979; Cleef, 1980; Monasterio, 1980; Marchant et al. 2002a). Pollen diagrams were plotted with PSIMPOLL 4.10 (Bennett, 2002). Only pollen types with over 0.5% considered for

zonation. Splitting (OSIC, Optimal Splitting by Information Content) and agglomerative (CONIIC, Constrained Cluster Analysis by Information Content) methods were combined with the broken-stick model to determine the number of significant zones and a zonation modeling test applied with 100 iterations (Bennett, 1996, 2002). Both percentage and influx diagrams are presented. Percentage diagrams are primarily used to estimate the composition of past vegetation. However, the importance of a given taxon in terms of density and/or vegetation cover cannot be fully understood by percentage data alone, and absolute quantification by concentration or influx is necessary. Pollen influx has been particularly valuable for interpreting pollen diagrams from sites located above the tree line where low local pollen production leads to overrepresentation of distant taxa (Birks and Birks, 1980). This is the case in our present study, therefore we use influx values for interpretations. The trends of influx values are nearly identical to those of concentration because of the relatively constant sedimentation rate in LVA (see below). Interpretation of the percentage and influx diagrams is based on comparison with modern analogs from the northern Andes (Salgado-Labouriau, 1979; Grabandt, 1980; Grabandt and Nieuwland, 1985). Especially useful is the percentage of arboreal pollen from upper Andean forests (mainly *Podocarpus, Hedyosmum* and *Alnus*), which in the Venezuelan páramos, has an altitudinal dependence allowing estimation of the vertical distance from the tree line (Salgado-Labouriau, 1979, 1984).

Results

Core stratigraphy and chronology

The LVA A-99 core is almost entirely composed of fine-grained, organic-rich sediments (Fig. 2). The base (328–335 cm) contains a high density (~1 g cm^{-3}), inorganic silty-clay of glacial origin. Immediately above the glacial sediments (308.5–328 cm) is a horizon of organic-rich greenish clay,
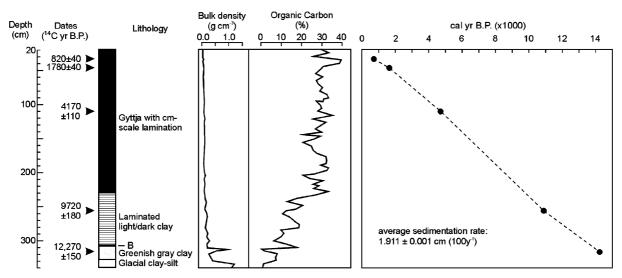

Figure 2. Core stratigraphy, dry bulk density, organic carbon content and age vs. depth. B=thin band of glacial clay.

Table 1
AMS radiocarbon results for core LVA A-99

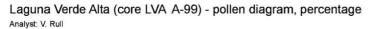| Lab #	Depth (cm)	Material	^{14}C yr B.P.	cal yr B.P.(1σ)
CAMS-73090	33	Macrofossils	820±40	710 (690–760)
CAMS-73091	46	Macrofossils	1780±40	1640 (1610–1810)
AA-35201	110	Macrofossils	4170±110	4700 (4550–4830)
CAMS-96816	256	Macrofossils	9720±180	10,890 (10,750–11,250)
AA-35203	316	Macrofossils	12,270±150	14,240 (14,070–15,120)

overlain by a thin band (about 3 cm thick) of dense, inorganic clay, also of glacial origin. The interval from 230 to 307.5 cm contains cm-scale bands of alternating dark–light laminations, characterized by a progressive decrease in density and an increase in organic carbon content. The uppermost section of the core (0–230 cm) consists of a thick interval of organic-rich sediments, with low density and high organic content. Radiocarbon dates are shown in Table 1. The ages of pollen samples and pollen zone boundaries are interpolated after calibration, assuming a constant sedimentation rate between adjacent radiocarbon dates. The sediment accumulation rate is relatively constant (average 0.19 mm yr^{-1}). Thus, each pollen sample integrates about 50 years and the average spacing between samples is approximately 250 years.

Pollen zonation

The OSIC and CONIIC methods yield the same pattern of five pollen zones (LVA-1 to LVA-5), with the only difference being the position of the boundary between LVA-3 and LVA-4. This boundary shifted from 212 cm using the OSIC method to 237 cm with the CONIIC method and was placed at the middle point, around 225 cm. The resulting pollen zones are described below and depicted in Figures 3–5.

Zone LVA-1 (340 to 317 cm, 8 samples)

Pollen from forests (~30–55%) and páramo herbs (~25–40%) are the most abundant (Fig. 3). The important forest elements are *Alnus* (~20–30%), *Podocarpus* (~5–10%) and *Hedyosmum* (~2–10%), all from the upper Andean forests. Poaceae (~20–45%) are the dominant herbs and Asteraceae are also noticeable (~10–20%). Trees from the lowland forests (*Chlorophora*, *Clarisia*, *Poulsenia*) and the Andean forests (*Dodonaea*, *Miconia*, *Myrica*) are below 5%. Except for Poaceae and Asteraceae, all páramo elements are scarce (<2%) or absent. The dominant spores (Fig. 4) are those from forest ferns (*Alsophila*, *Cyathea*) and psilate monolete types, while the páramo fern *Jamesonia* is scarce (up to 2%).
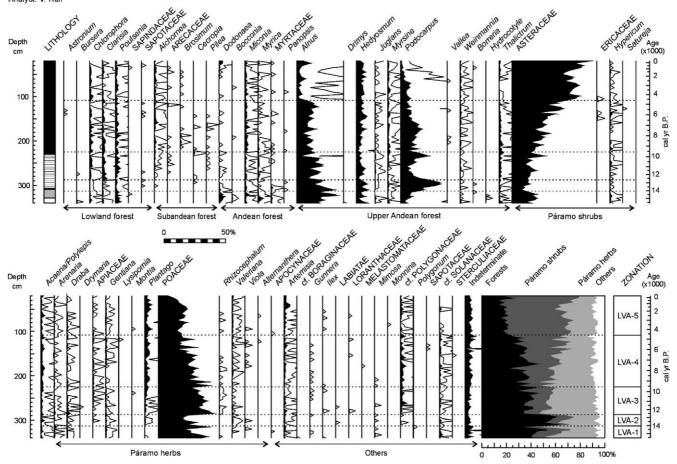

Figure 3. Percentage pollen diagram for core LVA A-99. Solid lines indicate ×10 exaggeration. Ages are in cal yr B.P.
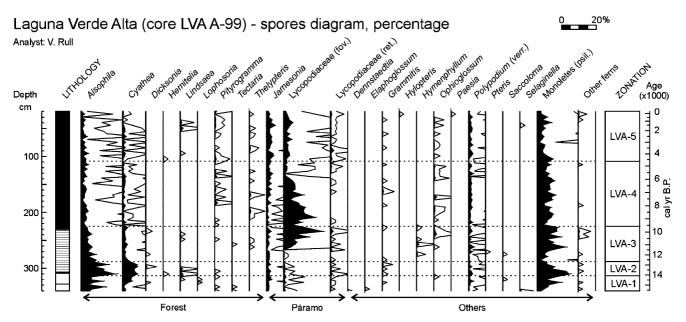
Laguna Verde Alta (core LVA A-99) - spores diagram, percentage
Analyst: V. Rull

Figure 4. Percentage spores diagram for core LVA A-99. Solid lines indicate ×10 exaggeration. Ages are in cal yr B.P.

Zone LVA-2 (317 to 287 cm, 6 samples)

Forest elements dominate this pollen assemblage (~50–60%), with a sharp increase in the relative abundance and influx of *Podocarpus* (up to 45% and 55 grains cm^{-2} yr^{-1}) (Figs. 3 and 5). *Alnus* and *Hedyosmum* do not change similarly in percentage, despite their conspicuous increase in influx (up to 50 grains cm^{-2} yr^{-1}). Other pollen types from forest elements (mainly *Dodonaea* and *Myrica*) decrease slightly. The percentage of Poaceae and Asteraceae also decrease to 20–30% and 10–12%, respectively, but this is a percentage artifact due to the *Podocarpus* increase and their influx values do not change compared with LVA-1. Some forest components in this zone (Sapotaceae, *Alchornea*, *Cecropia* and *Panopsis*) and páramo elements (Apiaceae and *Plantago*) appear for the first time. However, their percentage is so low that they can only be seen in the magnified curve (×10). The same is true for

Labiatae and Polygonaceae. Most páramo elements are still scarce or absent. Forest ferns, mainly *Alsophia* and *Cyathea*, and psilate monolete spores also increased in both percentage and influx values, in a similar way to forest trees (Fig. 4).

Zone LVA-3 (287 to 225 cm, 10 samples)

Forest elements decline and co-dominate the assemblages together with the páramo herbs with almost even percentages (35–50%). The main taxa responsible for this change are *Podocarpus*, which drops to 7–12%, and Poaceae, which reaches 35–45%. *Alnus* and *Hedyosmum* diminish slightly to ~20% and 5%, respectively, because of declining influx values. Lowland forest elements experience a slight influx increase (Fig. 5). Forest elements that appear for the first time, but with very low percentages, are Arecaceae and *Pilea*. Asteraceae (up to 20%) and other páramo elements like

Laguna Verde Alta (core LVA A-99) - selected taxa, influx
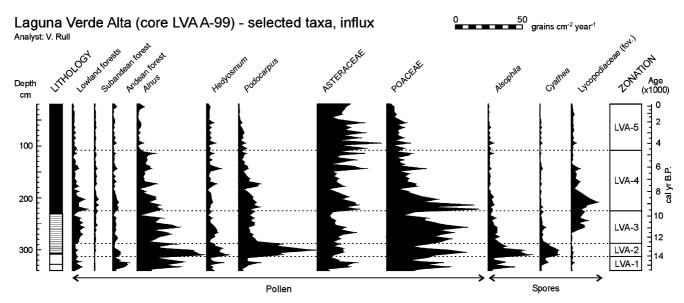Analyst: V. Rull

Figure 5. Influx pollen diagram of selected pollen and spore types (core LVA A-99). Ages are in cal yr B.P.

Apiaceae, *Draba*, *Plantago* and *Rhizocephalum* increase slightly (an artifact of the *Podocarpus* decrease, the influx values are nearly the same in LVA-1, 2 and the base of 3), but remain scarce. The unidentified cf. Polygonaceae shows the same tendency. Spores from forest ferns show the same pattern as that of pollen of forest trees (Fig. 5), dropping to very low percentage and influx values, while psilate monolete spores increase. A prominent increase in both percentage and influx is observed for foveolate Lycopodiaceae starting at the middle of the zone, coinciding approximately with the unidentified cf. Polygonaceae.

Zone LVA-4 (225 to 109 cm, 28 samples)

There is a major change in the abundance of pollen from the different vegetation types in this zone, although it takes place gradually in percentage. This could be considered a 'trend zone' because major components exhibit clear quasi-monotonous tendencies. Forest and páramo herbs start a declining trend from about 35% to 20–25%, whereas páramo shrubs increase from ~15% to 35–40%. The reduction of the forest assemblage is mainly caused by decreasing influx of *Podocarpus* and *Alnus*, but other forest types also diminish. The influx of Poaceae (the dominant páramo herb) decreases along with the forest assemblage, showing a conspicuous sharp decline slightly below the middle of the zone. The increasing percentage of Asteraceae (the dominant superpáramo element) in this zone is an artifact due to the decline of other major components (forest elements and Poaceae), and its influx values do not increase. Forest ferns attain their minima, and foveolate Lycopodiaceae decreases in relative abundance and influx, reaching a minimum, at the end of the zone.

Zone LVA-5 (109 to 20 cm, 18 samples)

Another significant change takes place in the uppermost zone of the diagram. A fairly stable situation is established, in which páramo shrubs dominate (~45–60%), followed by páramo herbs (~20–25%) and forest elements (~15–20%). The decline in forest taxa is due mainly to the sudden drop in *Alnus* percentage and influx values (~5% and less than 3 grains $cm^{-2} yr^{-1}$). Other forest elements also decrease, but to a much lesser degree. However, *Dodonaea* shows a small increase at the end of the zone. The percentages of Asteraceae and Poaceae stabilize around 45–55% and 15–25%, respectively, while the influx of Asteraceae is generally higher than LVA-4. *Artemisia* reaches its maximum at the end of the zone and Solanaceae-type disappears. Most pteridophyte spores are reduced (Fig. 4), but *Jamesonia* slightly increases.

Vegetational and environmental reconstruction

The sedimentology and radiocarbon chronology indicate that deglaciation of the LVA basin began prior to 15,500 cal yr B.P., but glacier ice was present near the lake until at least 14,000 cal yr B.P., as indicated by the last occurrence of glacigenic sediments. The organic carbon content of the sediments is <10%, suggesting a combination of low lake productivity and scarce vegetation in the catchment during deglaciation. The increasing organic carbon content through time suggests an increase in the catchment and lake production, coupled to reduced dilution by mineral sediment. Since about 9900 cal yr B.P., the development of organic-rich sediments indicates more stable lake conditions and higher organic matter production within the lake and catchment. The reconstruction of vegetation dynamics through time is based upon pollen zones previously defined, which boundaries are dated by interpolation among adjacent AMS dates.

15,500 to 14,030 cal yr B.P.

The scarcity and low diversity of páramo elements found in zone LVA-1, together with the interpretation of the lithostratigraphy, suggest that during this phase the site was an uppermost periglacial desert close to the receding glaciers, and nearly devoid of vegetation (Fig. 6). Given this environment, the abundance of arboreal pollen is striking and deserves explanation. The modern-analog study used here for interpretation (Salgado-Labouriau, 1979) found three samples with similar numbers, two of them close to the treeline, and one at high altitude. The difference is that, while in the first two cases concentration values are also high, in the third, despite low concentrations, pollen from upper Andean forests is over-represented in percentage due to its ability to be transported by up drafting winds and the scarcity of pollen produced by local vegetation. In zone LVA-1, however, both percentages and influx are high. It is highly unlikely that the tree line was close to the site since it would imply an upward shift of 1000 to 1200 m with respect to the present, or an approximate temperature increase of about 6–7°C using the present lapse rate of −0.6°C 100 m^{-1} (Salgado-Labouriau, 1979). Previous work has shown that during the time interval represented by this zone, the climate in the Venezuelan Andes was notably colder than today
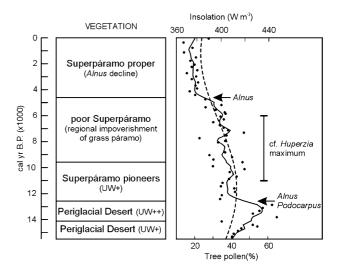

Figure 6. Interpretation of LVA A-99 pollen sequence and comparison between the upper Andean forest (UAF) tree pollen (solid line) and the insolation at the Equator (dashed line). The UAF curve has been smoothed by locally weighted regression, LOESS (Cleveland, 1994). Insolation curve after Berger and Loutre (1991). The taxa responsible for the two UAF pollen declines are indicated by arrows. The extent of the increased cf. *Huperzia* spores is indicated by a bar. UW=Upward orographic winds.

(Rull, 1998; Rull et al., 1999). The high influx values for arboreal pollen, which are greater than anywhere today, suggest that their transport was enhanced, possibly by stronger upslope winds. Among the involved trees, the high values, both in percentage and influx of *Alnus* relative to *Podocarpus* and *Hedyosmum* suggest an increased relative abundance or population density of this tree in the upper Andean forest. Presently, *Alnus* occurs up to ~300 m above tree line, following páramo watercourses as the dominant element within their gallery forests (Monasterio, 1980). Therefore, it is also possible that during this phase, gallery forests were more widespread or that *Alnus* reacted more rapidly than other trees to warming during the Late Glacial. Alternatively, the abundance of *Alnus* could simply be caused by its high pollen output and the dispersal capacity of this anemophilous genus (Grabandt, 1980).

14,030 to 12,600 cal yr B.P.

The appearance of general páramo elements in zone LVA-2, together with the slight increase in organic carbon content and the change in sediment composition, imply an increase in lake productivity and the vegetation cover surrounding the site. However, the dominant vegetation type was still an uppermost periglacial desert (Fig. 6). The assemblages of this zone are similar to LVA-1, except for the high influx of forest components. The quantity of arboreal pollen and spores that reached the site increased sharply, suggesting stronger upslope orographic winds. This inference is supported by a peak in Poaceae, a mostly anemophilous taxon. Among trees, the increase in *Podocarpus* is remarkable, but *Alnus* and *Hedyosmum* remain similar to LVA-1, suggesting changes in upper Andean forest composition. It is possible that the abundance of *Podocarpus* in the upper levels of these forests increased or that enhanced winds resulted in a greater upslope wind transport. The pollen of *Podocarpus* has two sacci that make it notably more buoyant than that of *Alnus* and *Hedyosmum*.

12,600 to 9540 cal yr B.P.

The stabilization of the bulk density at low values by ~12,600 cal yr B.P. indicates that the influx of glacial sediments to the lake had ceased. The conspicuous increase of the foveolate spores of Lycopodiaceae ~11,000 cal yr B.P., paralleled by cf. Polygonaceae, *Plantago* and other páramo elements, is outstanding. These spores are typical of modern superpáramo samples in the Venezuelan Andes (Salgado-Labouriau, 1979). The same type of spores occur in the genus *Huperzia* (Lycopodiaceae) which, in the Peruvian Andes, characterize the upper cold and wet páramo environments above 3800 m (Hansen et al., 2003). In LVA, these spores are the first local superpáramo element to show such values, both in percentage and influx, suggesting the initial colonization phases of the site by superpáramo vegetation. The vegetation in this interval consists of a low-diversity, superpáramo-like assemblages dominated by lycopods, which has no modern analog. The transition from a periglacial desert (LVA-2) to a superpáramo environment (LVA-3) suggests an increase in temperature and possibly moisture as well. The dramatic decrease of tree pollen (especially *Podocarpus*) recorded at the beginning of the zone LVA-3 suggests a strong relaxation of upslope wind intensity. The wind, however, was still sufficient to transport regional pollen, as indicated by grasses. Grass páramos, situated immediately below the superpáramo, are the main source of Poaceae pollen in the Venezuelan páramos (Salgado-Labouriau, 1979).

9540 to 4600 cal yr B.P.

The lycopod-dominated superpáramo was gradually replaced by a superpáramo assemblage dominated by Asteraceae that was similar to today, but still less diverse (Fig. 6). This replacement is the major change observed in the diagram after the initial colonization of the site. The major pollen element responsible for this shift is the outstanding decrease in Poaceae after 8000 cal yr B.P., suggesting an impoverishment of this herbaceous páramo element at a regional level. Although there is a slight decrease in the intensity of upward winds as shown by the tree pollen, it is not enough to explain the decrease in grass pollen. This drop is probably due to either a downward migration of the grass páramos (with or without a contraction of their altitudinal range), a regional decrease in herbaceous plant cover, or both. In the first case, a temperature and/or moisture decrease could be involved, while in the second, a drop in available moisture would be the more likely causative variable. In any case, a trend towards drier conditions between ca. 7500 and 4600 yr B.P. seems likely.

4600 cal yr B.P. to present

The zone LVA-5 reflects a typical modern superpáramo assemblage (Salgado-Labouriau, 1979) and suggests that modern vegetation and climate were established at the site about 4600 yr B.P. (Fig. 6). This supports the idea that the colonization of the Venezuelan superpáramo by present-day communities did not occur until around 5000 cal yr B.P., as suggested by the Miranda sequence (Salgado-Labouriau et al., 1988). The later date of superpáramo establishment in LVA is consistent with its higher altitude (around 200 m). In the Miranda record, this event coincides with a temperature/humidity increase suggesting some climatic control probably of regional extent, which favored both weathering (and therefore soil development) and upward migration of superpáramo taxa. In LVA, there is no any clear climatic signal, but the vegetation reacted in the same way, suggesting similar climatic trends. Andean forest tree pollen has values similar to today reflecting upslope winds, which are clearly lower than in earlier periods. The sudden drop in *Alnus* values around 4500 cal yr B.P. is contrary to what would be expected for a climatically driven phenomenon, since no other palynological signal is associated, which suggests a selective cause.

Discussion and conclusions

Immediately following glaciation around 15,500 cal yr B.P., the Laguna Verde Alta basin was a cold periglacial desert close to receding glaciers and almost devoid of vegetation. This situation was maintained until about 12,600 cal yr B.P., coinciding with a warming recorded by changes in sedimentology and geochemistry in the sediments of Laguna Los Lirios, located nearby at 2300 m altitude (Weingarten et al., 1991). The same deglacial period in the lowlands was arid, as indicated by the sediments of Lake Valencia, which contain a sedimentological, geochemical and biological record representative of intermittent lakes and marshes (Bradbury et al., 1981). Similar conditions were also recorded across the circum-Caribbean and the northern lowlands of South American during this interval (Iriondo, 1997; Curtis et al., 1999).

The interval between about 12,600 and 11,000 cal yr B.P., before the increase in cf. *Huperzia* spores, coincides with a cold phase recorded by the sediments of Laguna Los Lirios (Weingarten et al., 1991) and the Mucubají cold phase (MU-III). It is estimated that temperatures were between 2 and 3°C below present based on pollen changes at these sites (Salgado-Labouriau, 1989). These events occurred at approximately the same time as the Colombian El Abra stadial, which has been correlated with the Younger Dryas (YD) (Van der Hammen and Hooghiemstra, 1995). The YD climatic reversal was also recorded in the Cariaco Basin, where plant biomarkers indicate aridity (Hughen et al., 2004). Despite regional evidence for climatic shifts during the YD, this event is not reflected in the pollen records of tropical Andean localities in Peru and Ecuador (Hansen, 1995; Paduano et al., 2003). The only conspicuous palynological signal associated with the onset of the YD in the LVA A-99 core is the strong decline in forest pollen, but there is no obvious indication of regional vegetation change.

The subsequent onset of the cf. *Huperzia* increase in LVA, suggesting warmer and possibly wetter conditions, occurs after the end of the YD chron, ~11,000 cal yr B.P., coinciding with the onset of the Holocene thermal maximum of the Northern Hemisphere. At the same time, higher lake-levels were recorded in Lake Valencia, which was surrounded by vegetation similar to the present (Leyden, 1985; Salgado-Labouriau, 1980). After 8000 cal yr B.P., a progressive replacement of the lycopod community was initiated, primarily by a low-diversity superpáramo assemblage dominated by Asteraceae, coincident with the impoverishment of lower-elevation grass páramos. This is interpreted as a regional moisture (and possibly temperature) decrease extending until about 4600 cal yr B.P. A coeval mid-Holocene arid period possibly of regional extent was found by Marchant et al. (2002b) in Colombia, and a trend towards drier conditions starting at the peak of the northern hemisphere Holocene thermal maximum is present in the Cariaco record (Haug et al., 2001). The superpáramo replacement in LVA occurs without significant additions of new elements, contrary to the observed colonization patterns of the Miranda sequence (Salgado-Labouriau et al., 1988). This suggests that the LVA area was drier than the Miranda site during the early to middle Holocene, a difference that can be observed today in instrumental records.

A conspicuous and abrupt *Alnus* decline is observed after 4600 cal yr B.P. A similar decrease in the northern Peruvian Andes, accompanied by the increase of pollen from human disturbance indicators (*Ambrosia*, Chenopodiaceae/Amaranthaceae, *Plantago sericea* and *Dodonaea*), around 5000 cal yr B.P., was interpreted as the result of gallery forests clearance for agricultural purposes (Hansen and Rodbell, 1995). Weng et al. (2004) identified a number of sites from the Peruvian and Ecuadorian Andes in which the *Alnus* decline seems to be synchronous at ~4500 cal yr B.P. They suggest that the combination of drought intensification, regional cooling and human activities drove the observed alder shift. In the Venezuelan Andes, the climatic hypothesis is favored because human societies were poorly developed at that time (Wagner, 1979). However, this contrasts with the interpretation of wetter conditions since 4600 yr B.P., which coincides with a regional shift towards increased humidity in tropical South America recently postulated by Marchant and Hooghiemstra (2004). The causes for the alder decline in LVA, remain open to discussion.

Throughout the entire sequence, the abundance of pollen from upper Andean forest trees, most notably *Podocarpus*, *Hedyosmum* and *Alnus*, have almost certainly been controlled by upslope orographic winds. In this way, arboreal pollen can be used as a proxy for the relative strength of these winds in the study area. The maximum strength of these winds is thus inferred for the deglaciation phase, especially between 14,000 and 12,600 cal yr B.P. The general relationship between LVA tree pollen frequencies and insolation (Fig. 6) suggests a causal relationship. It is known that orographic winds are produced from the instability created by differential heating of lowland and upland air masses. The more incoming radiation, the steeper this gradient, and consequently the stronger the resulting winds will be (McGregor and Nieuwolt, 1998). However, at present, it is not possible to decipher if there is a causal link involving local, regional or global factors because of the lack of similar observations. Although no prior records exist of such strong late-glacial upper Andean forest representations, there are too few existing high elevation sites from which to draw comparisons. Therefore, it seems plausible that steep orographic gradients, driven largely by equatorial insolation 5% greater than present, advected forest pollen in great quantities to the highest elevations in adjacent high-mountain environments.

Acknowledgments

comments of Nathan Stansell and two referees (Chengyu Weng and Henry Hooghiemstra) clarified and improved the manuscript.

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