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Late-glacial and Holocene vegetational history from two sites in the western Cordillera of southwestern Ecuador

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Abstract

The deciphering of the late-glacial and Holocene vegetation, glacial-geological, and climatic history of Cajas National Park in southwestern Ecuador is undertaken focusing on close-interval sampling of sediment cores from two high elevations lakes, Lagunas Chorreras (3700 m) and Pallcacocha (4060 m). This study involves extensive dating (both accelerator mass spectrometry and tephra), palynological, and sediment analyses of lakes and bogs. Basal dates for the two cores analyzed for pollen range from about 17 000 to about 15 500 cal. yr BP. Vegetation surveys and surface sample pollen and spore analyses were accomplished for two transects in the western Cordillera. One began east of the main divide near Cuenca, Ecuador and the other began at the crest of the western Cordillera, descending towards the Pacific Ocean. These vegetation surveys coupled with pollen analyses of surface samples were used to establish pollen analogues to help in the interpretation of the fossil pollen records. The results of the pollen analyses from the two lake cores indicate two major climatic periods. (1) The late-glacial pollen record, beginning about 17 000 yr BP and ending near 11 000, is characterized by an herb paramo dominated by pteridophytes (primarily *Huperzia* spp.) with Asteraceae (assumed to be woody species) and *Puya* spp. The climate inferred from these pollen records was cooler and moister than today. The sediments for this time period are characterized by low loss-on-ignition percentages, and high magnetic susceptibility values (with secondary peaks between 12 000 and 13 000 yr BP). Low concentrations of charcoal fragments indicate a low incidence of fire, and several pronounced fluctuations in pollen assemblages could be interpreted as changes in the prevailing wind direction and/or climate. (2) The beginning of the Holocene, as represented in the pollen record, is characterized by the disappearance of *Puya* pollen, vastly diminished *Huperzia* representation, high charcoal concentrations, and the expansion of moist montane forest pollen. Asteraceae (possibly *Gynoxys*) are replaced as dominant timberline taxa by *Polylepis*-dominated timberline forest. The charcoal record suggests that fires were much more prevalent during the early to middle Holocene than during the late-glacial. Changes in *Isoëtes* concentrations and trends in upland vegetation may be related to fluctuations in lake levels and precipitation.

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1. Introduction

Attempts to correlate short-term climatic events between South America and the Northern Hemisphere have met with varying degrees of success and little consensus, in part because so few well-dated proxy records exist for the tropical Andes. For Ecuador and Peru, most palynological records (Colinvaux et al., 1997, 1988; Graf, 1992; Hansen, 1995; Hansen et al., 1994; Hansen and Rodbell, 1995) have too few dates, or the dates may be questionable, and do not allow comprehensive comparisons on a regional scale. Our sites lie in the Cajas National Park in southwestern Ecuador (Figs. 1 and 2). This area was chosen for its numerous moraine-dammed lakes and prevalent tephra deposits (Rodbell et al., 2002). A rich pteridophyte flora, a little-studied timberline forest, and an extensive paramo region also contributed to the choice of this area for vegetational and climatic research.

In this study, close-interval sampling and dating of the sediments were a priority. Accelerator mass spectrometer (AMS) dates of macrofossils, as well as tephra layer identification, allowed cross-correlation among several sites. Vegetational studies were coupled with the analysis of surface samples to establish analogues for the fossil pollen and spore records. Charcoal analyses are also included to examine fire frequency as related to climate change, its effect on vegetation communities, and as possible evidence of human disturbance (Markgraf, 1985; MacDonald et al., 1991).

Some basic questions also needed to be addressed regarding how fossil pollen fluctuations relate to treeline movement. During the late-glacial and Holocene, changes in percentages of *Podocarpus* sp. pollen (a moist montane forest component) in fossil records have been attributed to climate fluctuations (Colinvaux et al., 1997; Hansen et al., 1994; Hansen and Rodbell, 1995). But this may be too simplistic due to several factors. One problem is the widespread dispersal of montane forest pollen to elevations above their natural distribution (Grabandt, 1980; Hansen et al., 1994; Hansen and Rodbell, 1995). Another problem is determining what genera or species of South American conifer are actually present at a particular elevation. Conifer stomata (lignified guard cells in leaves) are sometimes found in fossil pollen samples and may be used as proxies for macrofossils. Conifer stomata, like the leaves in which they occur, are not usually transported far from their origin and are thus more indicative of local conifer presence. Conifer stomate analyses have been used in Europe for some time to identify treeline fluctuations in the Alps (Trautmann, 1953; Ammann and Wick, 1993) and recently to clarify the arrival time of conifers following deglaciation in the Hudson Bay Lowlands (Hansen, 1995; Hansen et al., 1996) and in southeastern Alaska (Hansen and Engstrom, 1996). By including stomate analyses in our palynological research, it was hoped that actual conifer presence could be determined and genus and/or species identification might be possible for the late-glacial and Holocene.

Today the prevailing winds in Ecuador are from the east, which is mirrored by the decreasing importance of wet montane forest pollen at palynological sites in Andean Peru at increasing distance to the west (Hansen et al., 1984, 1994). In the past, however, this may not not have been the case. Ash produced by volcanoes in northeastern Ecuador forms a thick mantle in the Amazon Basin, in contrast to a thin deposit at the same latitude in the inter-Andean Corridor. Iriondo (1994) speculates that the thicker ash layers in the Amazon Basin are due to prevailing winds from the west in the early Holocene. Shifting wind patterns in the Ecuadorian Andes over the past 2000 years are also suggested as possible reasons for the absence of some tephras from lake and bog cores in the Cajas area (Rodbell et al., 2002). Laguna Pallcacocha (4060 m), the farthest west of the Cajas pollen sites (Figs. 2 and 10), could as easily be influenced by westerly winds

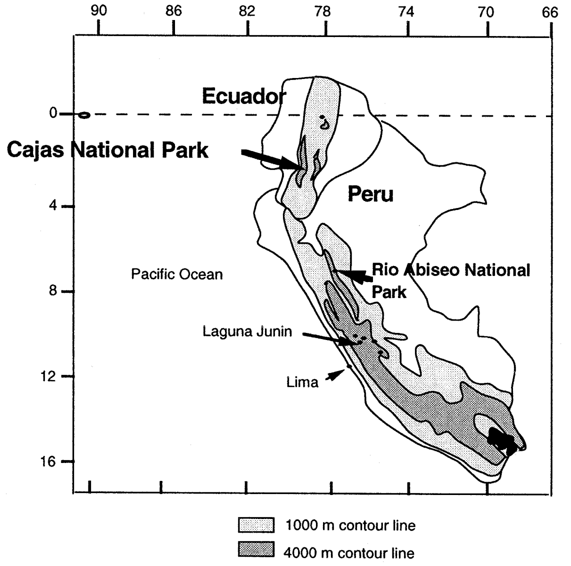

Fig. 1. Map of Ecuador showing the location of the Cajas National Park, Rio Abiseo National Park and Laguna Junin.

as by winds from the east. Surface sample pollen analyses from both the east and west side of the main divide of the western Cordillera in the Cajas National Park could shed light on this issue.

The broad adaptations of tropical timberline forest to wide fluctuations in temperature and moisture over altitudinal differences and diurnal cycles present another challenge for the interpretation of the fossil pollen data. Temperature fluctuations are as large diurnally as annually. These adaptations may mute vegetational response to short-term or minor climatic oscillations.

Thus, the results of these several sorts of investigation are combined with high resolution dating and sedimentological analyses to see if patterns emerge consistent with worldwide short-term and long-term climatic events.

2. Study area

The study area is located on the eastern side of the western Cordillera of southern Ecuador at 2°45′S 79°10′W (Fig. 1). Landscapes above 3500 m and near the divide have been conspicuously modified by glacial action, which has left behind pronounced U-shaped valleys, numerous lakes, lateral and terminal moraines, and other glacial features (Goodman, 1996). The gradient to the west of the divide increases sharply down to the Pacific lowlands, about 50 km distant from the study area. The elevational gradient to the east is less steep, descending to the large inter-Andean valley where the city of Cuenca is situated at 2700 m (about 20 km east of the study area).

Laguna Chorreras (3700 m) is positioned in a narrow valley branching off the Tomebamba River Valley, which is the main drainage of the eastern side of the divide. The lake was formed by a terminal moraine with an outlet on the west side. The lake is bordered to the north and south by patches of forest dominated by *Polylepis*, *Clethra*, *Gynoxys* (Asteraceae) and *Miconia* sp. To the east lies a wetland area with bog plants such as *Azorella*, *Hypericum* sp., and Cyperaceae. Tussock grass paramo, where unoccupied by forest patches, dominates the landscape. Fire-scorched areas of paramo give evidence of recent and older burns.

Laguna Pallcacocha occupies a cirque at about 4060 m at the head of the Tomebamba River Valley. The vegetation cover is less dense at this higher elevation characterized by intermittent grass clumps, and herbs such as *Gentiana*, *Bartsia*, and *Huperzia* sp. Patches of forest are far less numerous here, and those that exist are dominated by *Polylepis* rather than *Clethra* (Young et al., in preparation).

Although Cuenca's annual precipitation is approximately 1000 mm/yr, there is less rainfall than would be expected in this location which is exposed to air masses uplifted from the Amazon basin (Jørgensen and Ulloa Ullva, 1994). Fog and rain are frequent above about 3000 m in the Cajas area, and annual precipitation is at least 2000 mm/yr. Mean annual precipitation at the higher elevations west of the divide is probably similar; however, below an elevation of 3600 m on the western side there is a persistent fog belt. Rainfall on the western side of the divide is much more seasonal, and can amount to as little as 500 mm/year. Temperatures show little seasonal variation but strong diurnal variation, with average night time temperatures of −8°C and average daily temperatures of 12–18°C.

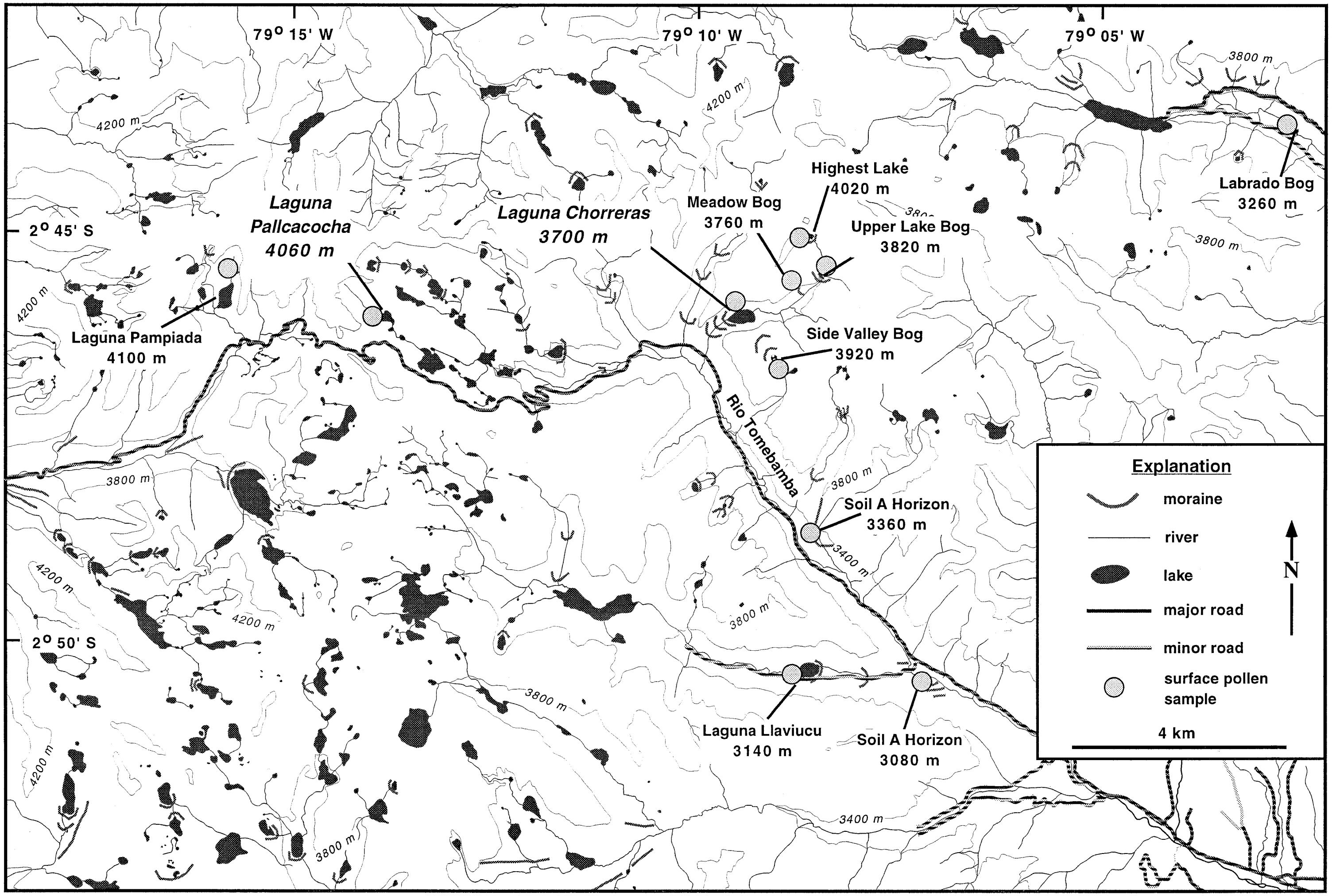

Fig. 2. Contour map showing the locations of palynological sites: A. Laguna Pallcacocha; B. Laguna Chorreras; C. Laguna Llaviucu (Colinvaux et al., 1997); pollen surface samples collected from lake and bog core tops: a. Laguna Pampiada, elevation 4100 m; b. Highest Lake Bog, 4020 m; c. Side Valley Bog 3920 m; d. Upper Lake Bog, elevation 3820 m; e. Chorreras Valley at 3760 m; f. Tomebamba Valley at 3360 m; g. Labrado Bog, 3260 m; h. Laguna Llaviucu, 3140 m; i. Tomebamba Valley at 3080 m.

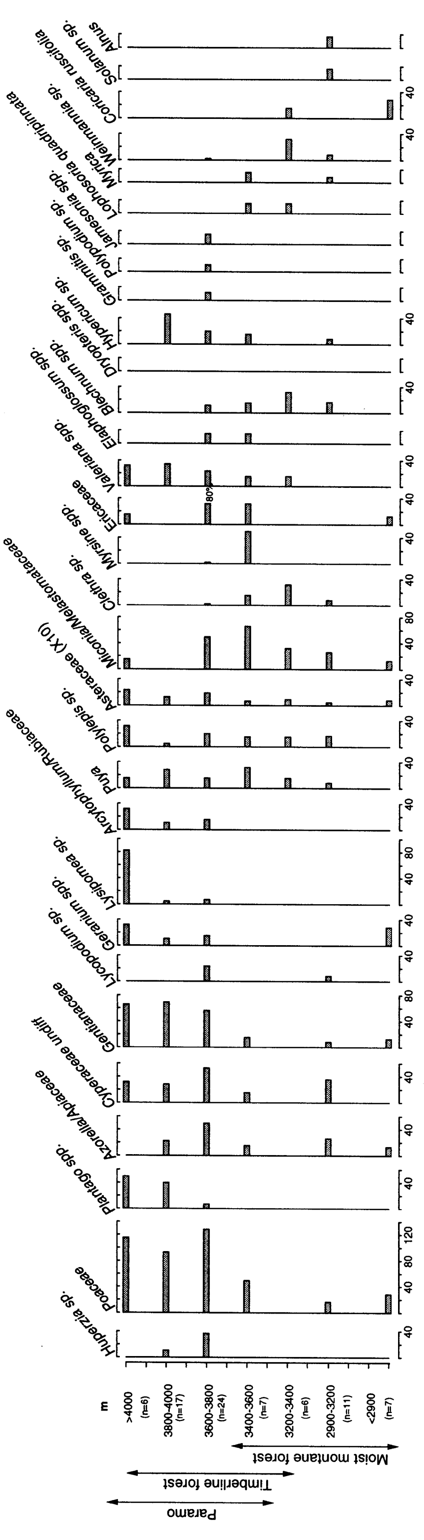

Fig. 3. Vegetational survey of taxa importance expressed as percent frequency of survey plots found within specified elevation ranges, Cajas National Park, eastern slope of the western Cordillera (n = number of survey plots within a particular elevational range).

Our vegetational studies were carried out on sites accessible by foot anywhere from < 1 to 6 km off the main east–west road connecting Cuenca to the Pacific coast (Fig. 2). Much of this land is within or adjacent to the Cajas National Recreation Area, which was established in 1979 to conserve natural landscapes and to offer activities such as fishing and hiking (Cajas National Recreation Area is now Cajas National Park). In addition, communities surrounding the protected area use the high elevations for grazing cattle; although it is technically forbidden, these people continue to burn the paramo in order to increase subsequent regrowth of grasses for forage, as they have done traditionally here and elsewhere (e.g. Young, 1993).

3. Modern vegetation

The principal modern vegetational types at a given elevation are a function of (1) temperature lapse rates and moisture, (2) topographic position, which determines the depth and moisture status of the soil, (3) exposure to regional wind patterns, and (4) the historical and present land use. The tropical alpine formations, known regionally as paramos, are found mostly above 3500 m and reach to the highest peaks at 4300 m. Moist tropical montane forest types are found below 3400 m, although most of these have long been logged, degraded, or converted to farm or grazing land.

The tropical alpine vegetation at or above 4100 m is dominated by low-growing cushion plants such as *Azorella* (Apiaceae) and *Werneria* (Asteraceae) and forbs such as *Chrysactinium*, *Draba*, *Gentiana*, *Halenia*, *Lysipomia* and *Oritrophium*. Also important are pteridophytes, including *Asplenium*, *Huperzia*, *Lycopodium*, and *Thelypteris*, and a variety of terrestrial bryophyte species.

From 3500 to 4100 m, most well-drained sites are dominated by bunch grasses of the genera *Calamagrostis* and *Festuca*, associated with a variety of smaller herbaceous plants in the families Asteraceae (e.g. *Bidens*, *Werneria*), Alstroemeriaceae (*Bomarea*), Scrophulariaceae (*Bartsia*), Apiaceae (*Eryngium*), and Gentianaceae (*Gentiana*, *Gentianella*, *Halenia*). Also common are *Huperzia* spp., *Lycopodium* spp., *Valeriana*, and *Puya* spp. (*P. hamata*, *P. pygmaea*, *P.* cf. *trianae*). Small woody plants are occasionally present, such as *Arcytophyllum*, *Baccharis*, *Berberis*, *Brachyotum*, *Diplostephium*, *Disterigma*, *Loricaria*, *Monnina*, *Muehlenbeckia*, *Pernettya*, *Ribes*, and *Satureja* (Young et al., in preparation). Poorly drained sites have bog and wetland species, including *Azorella*, *Carex*, *Gentiana*, *Hypericum*, *Huperzia*, *Isoëtes*, *Lysipomia*, *Plantago* and *Xyris*. The numerous lakes at these same elevations contain *Myriophyllum quitense* and *Potamogeton paramoanus*. Human impact is most conspicuous in areas near the road.

Also present in the tropical alpine zone are isolated timberline forest patches ranging in size from 100 m^2 to 2 ha. Below 3800 m elevation, these forest patches are dominated by canopy-forming *Clethra* sp. and *Polylepis* spp. (5–7 m tall), along with *Gynoxys* spp., *Miconia*, and Ericaceae; above 3800 m these forest patches are dominated by *Polylepis* spp. and *Gynoxys* spp. (Young et al., in preparation).

The upper limit of the moist montane forest begins at about 3500 m. These forests are 8–12 m tall and contain *Hedyosmum scabrum*, *Miconia pustulata*, *Piper andreanum*, and *Verbesina latisquamata* in the canopy and sub-canopy. *Aegiphila* sp., *Boehmeria* sp., *Cestrum peruvianum*, and *Solanum* spp. are present as trees or shrubs (Young et al., in preparation). Forest edges can include *Baccharis*, *Berberis*, *Bomarea*, *Brachyotum*, *Gaultheria*, *Gynoxys*, *Hesperomeles*, *Hypericum*, *Mutisia*, *Myrica*, *Myrsine*, and *Passiflora*.

Slightly lower, at about 2900–3300 m, near Laguna Llaviucu (Fig. 2) in the southernmost portion of the Cajas National Park region, large stands of montane forests reach heights of 15–20 m, and include *Cornus peruviana*, *Meliosma* sp., *Myrcianthes* cf. *rhopaloides*, *Ocotea* sp., *Oreopanax* sp., *Prumnopitys montana*, *Symplocos blancae*, *Urtica* sp., *Vallea stipularis*, and others. From Cuenca at 2700 m to the highest point in the western Cordillera, most of the original forests are gone, being replaced by agricultural areas and by pine and eucalyptus plantations.

The montane forests on the western side of the divide are even more altered by human impact, with a few small patches of *Baccharis* spp., *Escallonia myrtilloides*, *Gaiadendron punctatum*, *Myrica parvifolia*, *Myrsine* sp., *Podocarpus sprucei*, *Vallea stipularis*, and *Weinmannia* sp. at about 3500–3600 m. Below are agropastoral systems and scrub with woody elements such as *Baccharis*, *Miconia*, and *Oreocallis*.

4. Methods

Two sets of surface samples were analyzed for the eastern side of the western Cordillera in Cajas National Park. The larger set consisted of duff (loose plant detritus) or moss polsters collected from vegetation plots or surveys up the main valley from the outskirts of the town of Cuenca at 2700 m to Laguna Pallcacocha at 4060 m (Fig. 2). Duff surface sample collections to the west of the main divide extended our transect down to 3200 m, and to within about 40 km of the Pacific Ocean. Duff sample collections were made at elevational intervals of 200 m. Locations were determined with a GPS instrument.

Estimates of plant cover at duff collection sites were made for an area of about 10 m^2, and results are recorded as percent plant frequency within survey plots in a particular elevation range (Fig. 3). Four surface samples (ca. 1 teaspoon each) were collected randomly from within each survey plot and combined in whirl packs. Forty of the 83 duff samples were prepared and analyzed for pollen.

The second set of surface samples (nine samples) were tops of short cores collected by Rodbell, Seltzer, and Abbott from lakes, bogs and A horizon depressions in Cajas National Park beginning with the sample at 3080 m in the Tomebamba valley as the easternmost site and ending with a surface sample from Laguna Pampiada at 4100 m on the western side of the divide (Fig. 2). This series of samples follows the main glacial valleys in Cajas and duplicates the area covered by the duff surface samples.

A ∼4.4-m-long sediment core from Laguna Chorreras and an ∼9.5-m-long core from Laguna Pallcacocha (Fig. 2) were obtained for fossil pollen analysis with a square rod piston corer

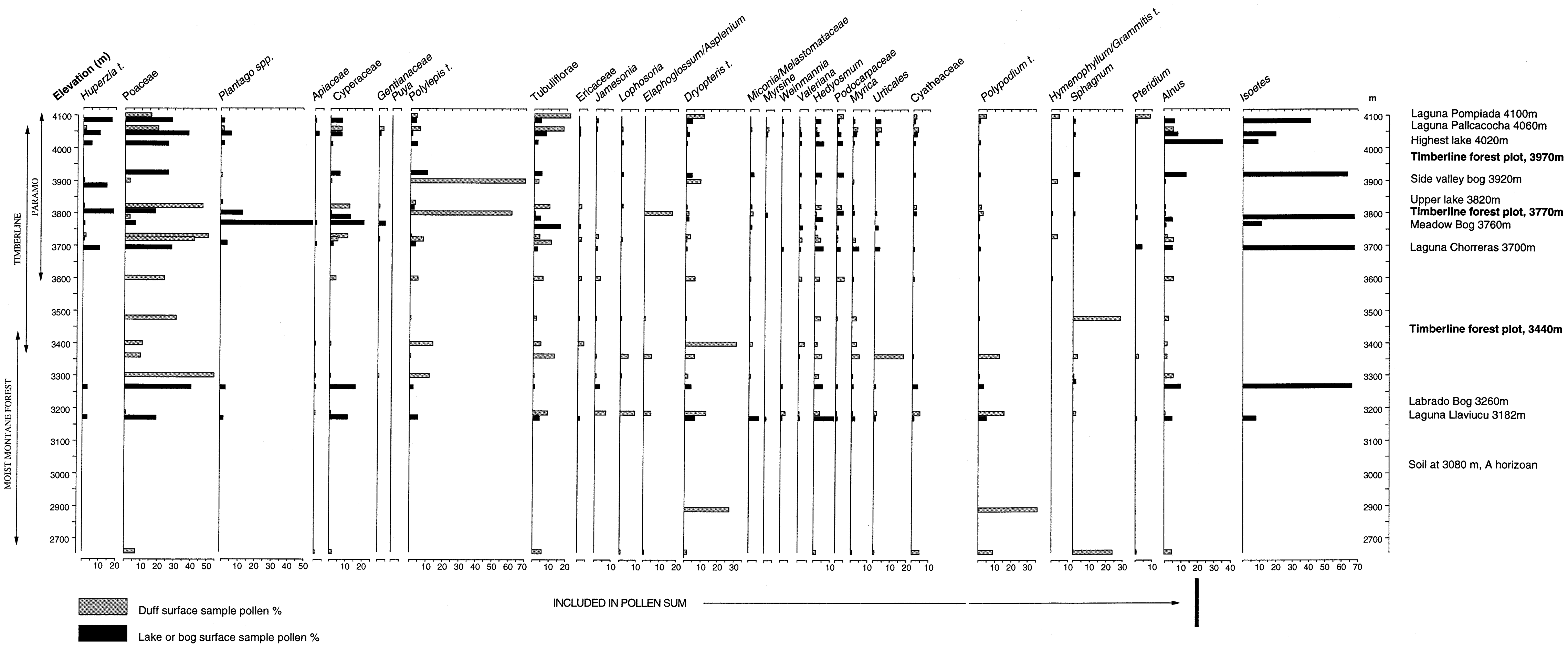

Fig. 4. Surface sample pollen results from lake, bog, and duff samples on the eastern side of the western Cordillera, Cajas National Park. Results plotted as percentage of total pollen and spores according to altitude from west to east.

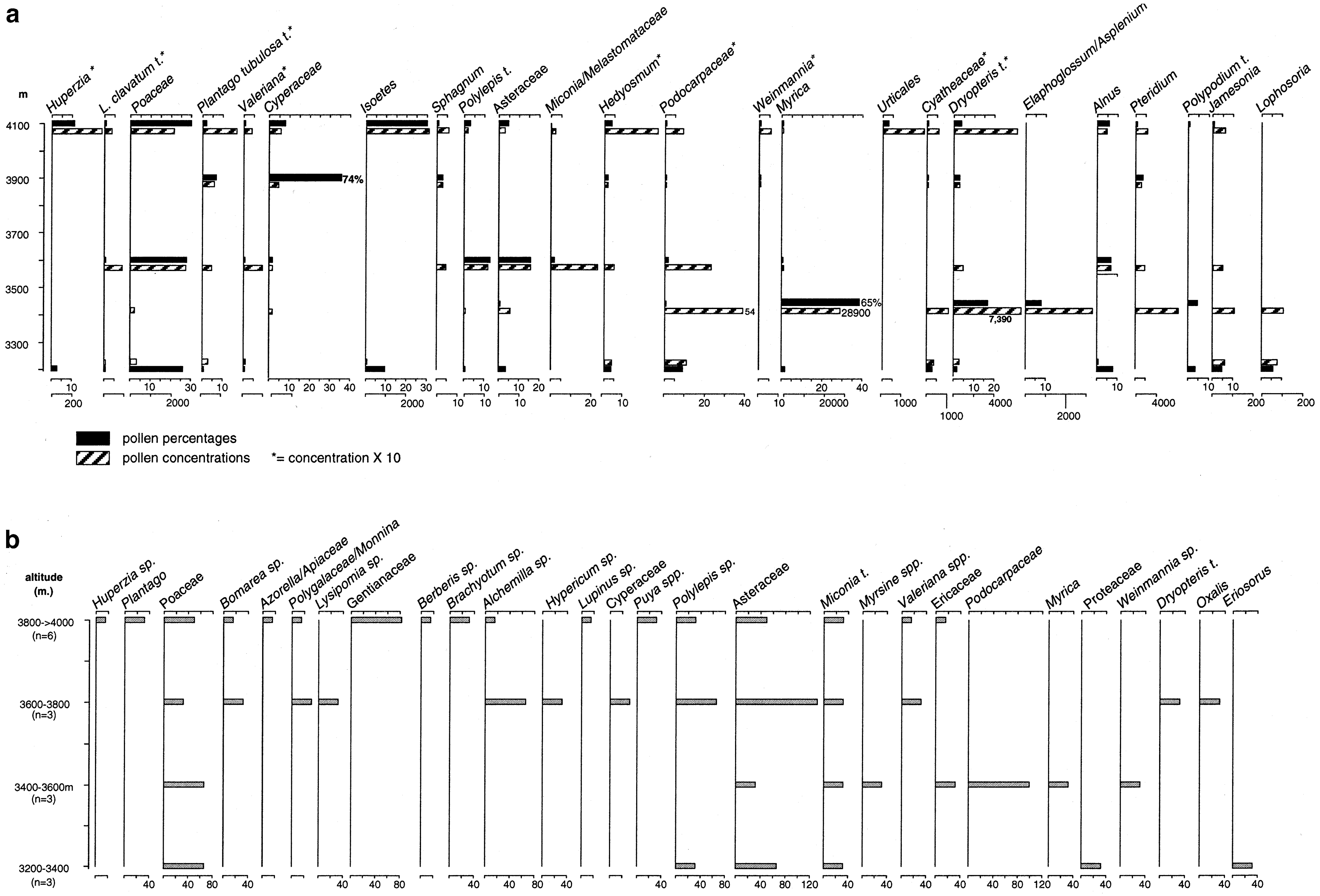

Fig. 5. (a) Surface sample pollen data from duff samples collected from the western side of the divide, Cajas National Park, western Cordillera. Results plotted against altitude as percent of total pollen and spores and as concentration per gram weight of sediment. Note different concentration scales. (b) Plant frequency diagram for the western slope surface sample plots as percentage of total plots within an elevation range.

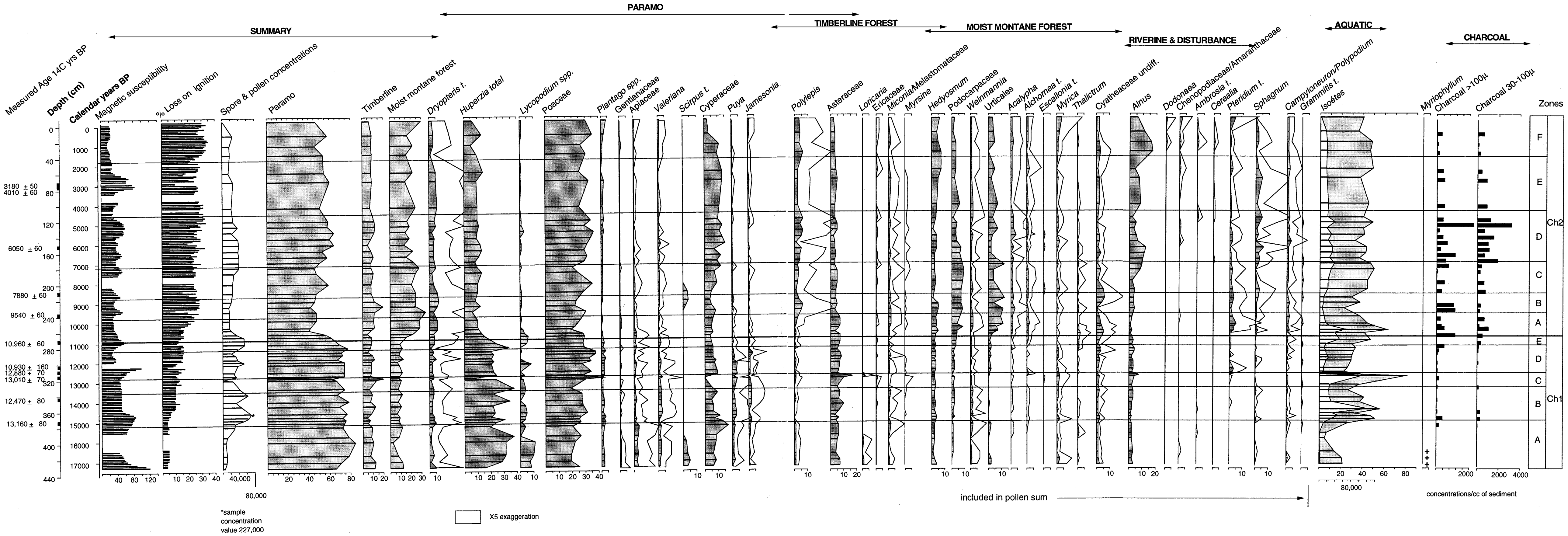

Fig. 6. Laguna Chorreras Holocene and late-glacial pollen and spore percentage diagram with % LOI and MS; site elevation 3700 m; vertical scale in calendar years.

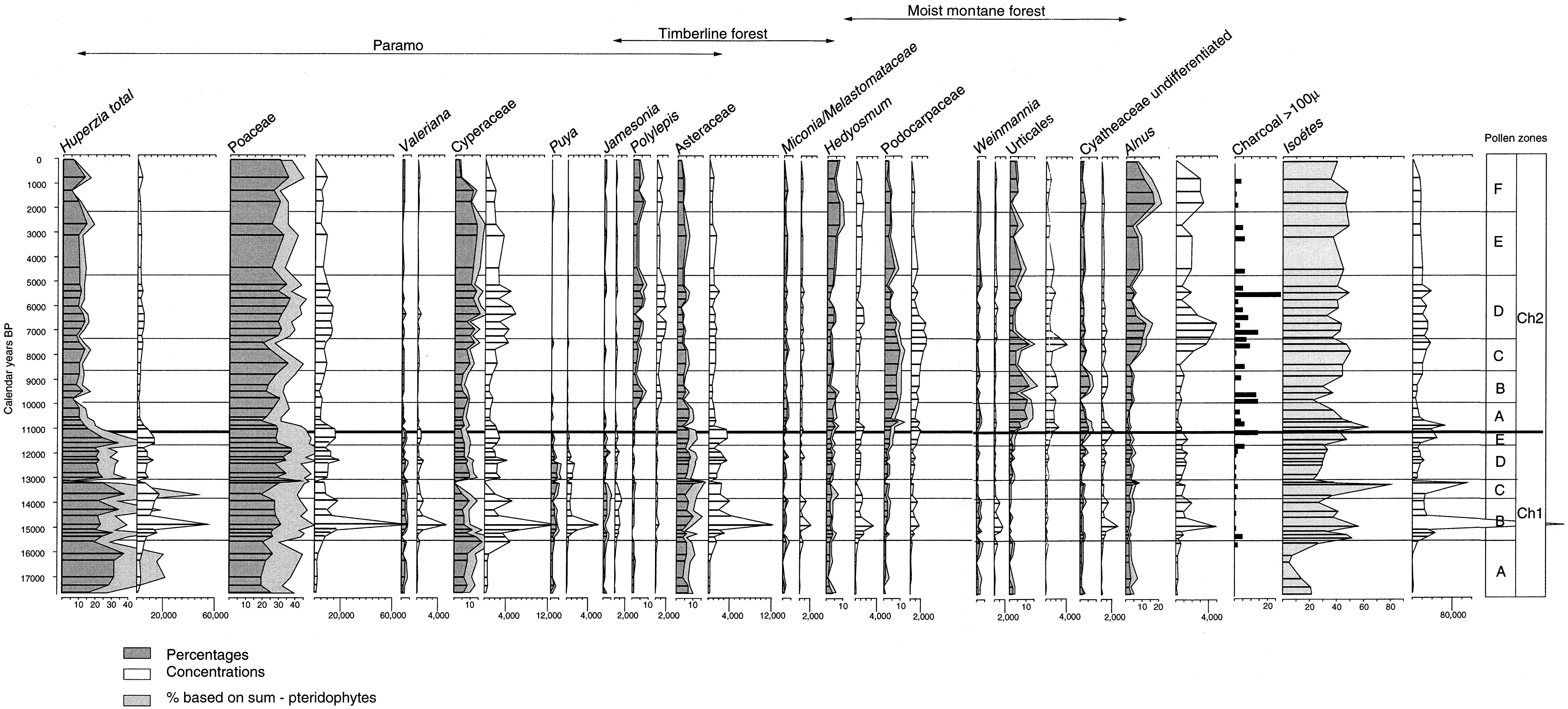

Fig. 7. Laguna Chorreras late-glacial and Holocene selected pollen and spore percentage and concentration curves; also presented are pollen percentages of major taxa based on a pollen sum excluding pteridophytes.

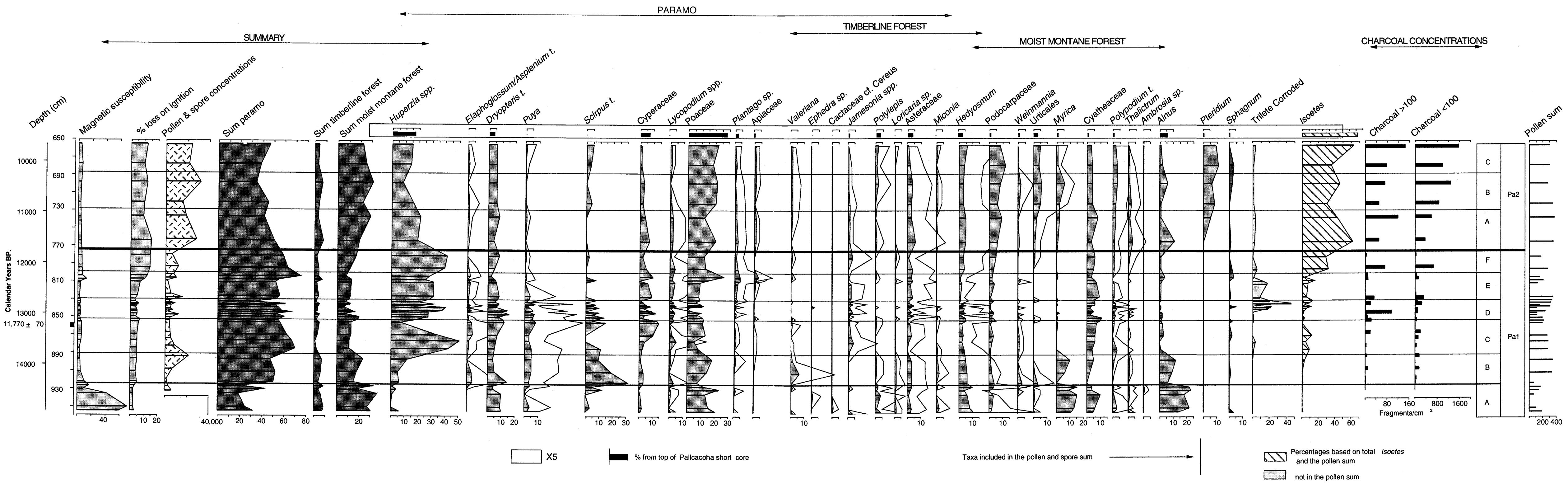

Fig. 8. Laguna Pallcacocha late-glacial/early Holocene pollen and spore percentage diagram; site altitude is 4060 m. Vertical scale is in calendar years BP; bar graph is pollen and spore data from the top 2 cm of the lake core from Pallcacocha.

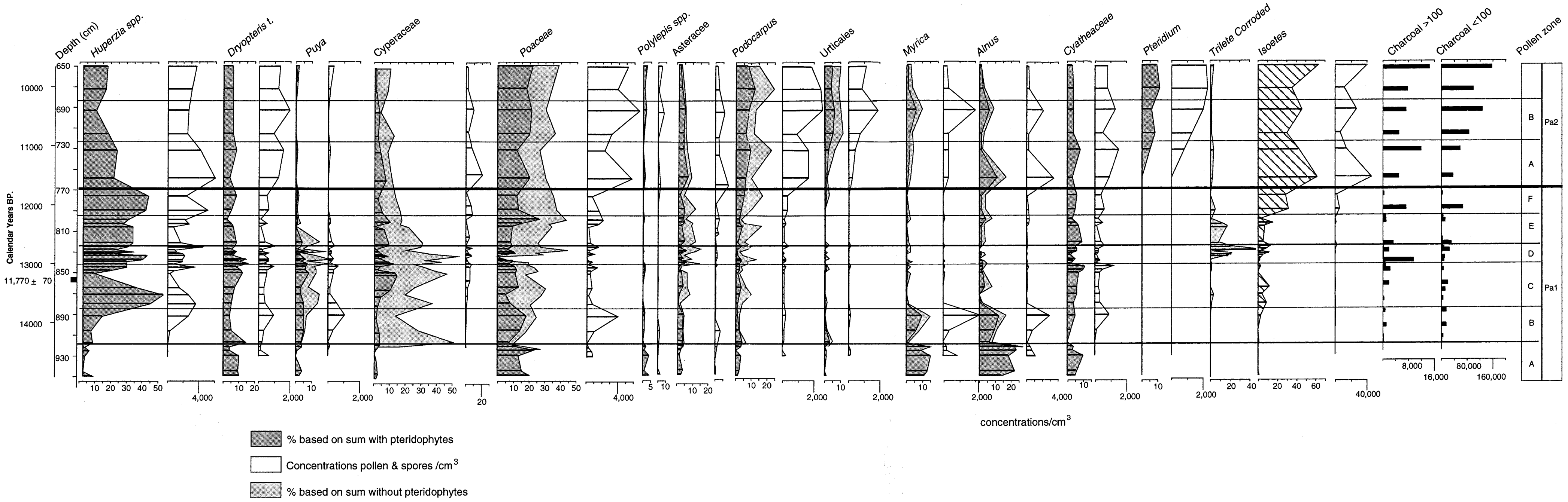

Fig. 9. Laguna Pallcacocha late-glacial/early Holocene selected pollen and spore percentage and concentration curves; also presented are pollen percentages of major taxa based on a pollen sum excluding pteridophytes.

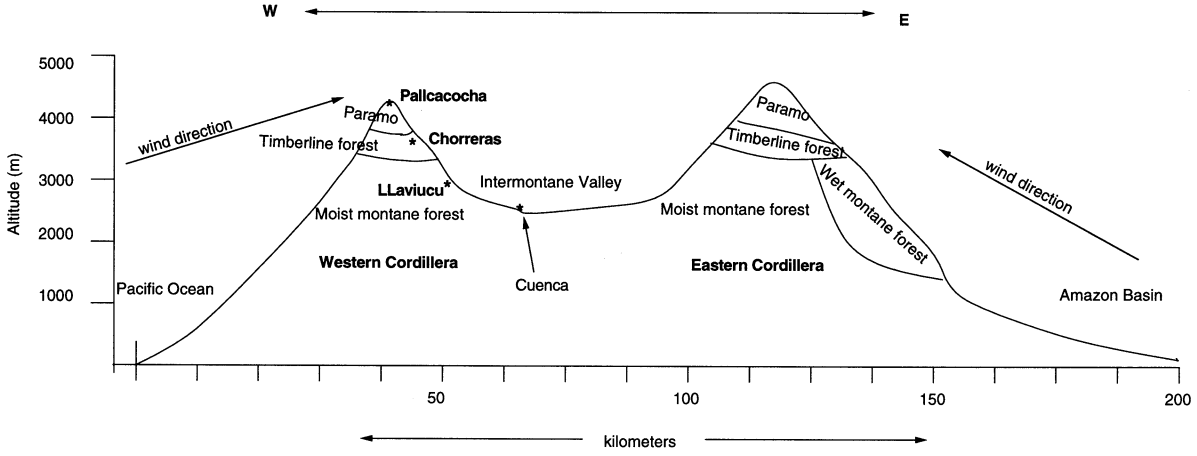

Fig. 10. Diagrammatic cross-section of the eastern and western Cordillera with prevailing wind patterns shown at about the latitude of Cuenca, Ecuador.

(Wright, 1991) from an inflatable rubber raft. Cores were obtained in the deepest basins of the lakes, which are ~8 m deep for Laguna Pallcacocha and 14 m deep for Laguna Chorreras. Cores were taken in 1-m-long, non-overlapping drives. All cores were extruded and described in the field, wrapped in plastic, and returned to the laboratory in PVS tubes.

Cores were split and described prior to sampling. Whole core magnetic susceptibility (MS) was measured with a Bartington MS2 core sensor, and weight loss on ignition (LOI) was measured at 550°C after oven-drying samples at 90°C. Plant microfossils were sampled and dated by AMS. The chronology for the cores from Laguna Chorreras and Laguna Pallcacocha was developed from 21 AMS radiocarbon dates from these two cores and five radiocarbon dates from four other lakes in Las Cajas National Park (Rodbell et al., 2002). All 26 ^{14}C dates provide the basis for a sixfold regional tephrachronology and age models for each of the lake basins (Rodbell et al., 2002).

Standard laboratory procedures were used to prepare both surface and lake core samples for pollen analysis (10% KOH, acetolysis, HF, and sieving with nitex screen; Faegri and Iversen, 1975; Cwynar et al., 1979). One-cm^3 samples were taken from the long lake cores and 2-cm^3 samples from lake and bog core tops. Pollen samples were spiked with 0.2 ml of microspheres to determine pollen concentration. Air-dried duff samples were weighed prior to preparation for determining pollen and spore concentrations. Samples for pollen, charcoal, and stomate analysis were prepared by the Limnological Research Center Core Laboratory. Surface samples 1–6 were combined as were 11 and 12. Samples were mounted in silicone oil and scanned at 400× until a sum of approximately 300 pollen and spores was counted (unless otherwise noted). Pteridophytes are included in the pollen sum because of their importance in the vegetation at Cajas.

Reference pollen and spore material was collected in the field from Cajas National Park and Rio Abiseo National Park, Peru (Fig. 1). Reference pollen and spores were also obtained from the herbarium at the Universidad Católica in Quito (QCA), as well as from herbaria at the Chicago Field Museum and the Missouri Botanical Garden, and from the personal collections of León and Young (deposited at QCA). Reference pollen and spore material was prepared by the Department of Ecology, University of Minnesota under the supervision of E.J. Cushing. Photographs of pollen and spores in Hoogheimstra (1984) were particularly helpful in identifying a number of pteridophyte spores.

Charcoal fragments were counted in pollen preparations and were assigned to two size classes: ca. 30–100 μm and over 100 μm. Charcoal results are plotted as concentrations of fragments per cm^3 of sediment (MacDonald et al., 1991).

Results of surface sample pollen and spore analyses are summarized as percentages of total pollen and spores (Figs. 4 and 5a). Concentrations of pollen and spores from duff samples are based on numbers per weight whereas surface samples from lake cores are based on numbers/cm^3. Both sets of data are plotted according to elevation along an east–west transect (Figs. 4 and 5). Fossil pollen and spore results are summarized as percentage of total pollen and spores (not including *Isoëtes*), and concentration (pollen and spores/cm^3) diagrams plotted against calendar years BP with the depth scale shown at the side (Figs. 6–9, 11 and 12). The pollen plotting program used was Psidium (Cushing, 1993).

5. Results of modern vegetation survey and pollen surface sample analyses

The main objectives of the vegetation-paleoecological part of this study were to: (1) study present-day plant communities in Cajas National Park and nearby areas, focusing on timberline forest composition and the processes affecting vegetation composition; (2) identify differences in plant community composition at various elevations that can be identified in surface pollen samples; these data would provide a framework for interpreting fossil palynological data; (3) document down-core changes in fossil pollen assemblages, relating these changes to climate over the past 18 kcal years; (4) assess pteridophyte ecology and fossil spore value as paleoecological indicators of climatic change; (5) perform charcoal and conifer stomate analysis as additional proxies for vegetation history and climatic change.

5.1. Modern vegetation survey

Two types of vegetational studies were made in the Cajas National Park and adjacent areas. The first was a detailed analysis of *Polylepis* timberline forests, concentrating on arboreal components at three elevations: 3440 m, 3770 m, and 3970 m on the eastern side of the main divide (Young et al., in preparation). The second study was a general survey of both arboreal and non-arboreal plants at the surface sample duff collection sites from 2700 to 4100 m on the eastern side of the main divide and from 4100 to 3200 m on the western side. The results of the vegetation survey are plotted as percent frequency in plots within a prescribed altitudinal range (Figs. 3 and 5b). Percentages above 100 are due to the high number of genera or species found in plant families that are combined for frequency occurrence (e.g. Asteraceae at 4000 m or above include Asteraceae undifferentiated, *Baccharis* spp., *Gynoxys*, *Hypochaeris*, *Loricaria*, and *Oritrophium* spp.).

The results of the vegetational survey on the eastern side of the western Cordillera in Cajas (Fig. 3) indicate that above 4000 m in the high paramo the most commonly found taxa were Poaceae (120%), *Plantago tubulosa* (50%), Cyperaceae (25%), Gentianaceae (includes *Halenia weddelliana* Gilg., *Gentiana sedifolia* Kunth, *Gentianella* spp. (62%), *Lysipomia* sp. (80%), *Acrytophyllum* (30%), *Polylepis* sp. (25%), *Valeriana* spp. (25%), and Asteraceae (ca. 225%) (Fig. 3). In the paramo between 3800 and 4000 m the following taxa were significant: *Huperzia* (15%), Poaceae (90%), *Plantago* (40%), Apiaceae (20%), Cyperaceae (25%), and *Puya* (30%), with Gentianaceae and *Hypericum* between 50 and 60%. The bunch grass paramo (3600–3800 m) was dominated by *Huperzia* (40%), Poaceae (140%), Cyperaceae (50%), *Lycopodium* (20%), Ericaceae (80%), and *Valeriana* spp. (20%). *Jamesonia* and *Lophosoria* were present.

Huperzia and *Plantago* were not noted in survey plots below 3600 m. Between 3400 and 3600 m the taxa most frequently found were *Miconia* (80%), *Clethra* (20%), *Puya* (40%), and *Myrsine* (> 40%). Vegetation surveys below 3400 m indicate that *Myrica*, *Clethra*, *Blechmum*, *Weinmannia* spp., and *Coriaria* were frequent components of roadside forests. *Eucalyptus* spp. and *Pinus* spp., both introduced genera, are now present in plantations at elevations below 3200 m. Many arboreal and non-arboreal plants, such as *Clethra*, Ericaceae, and *Arcytophyllum*, are under-represented in the pollen rain because they are pollinated by animals (e.g. bats, insects) rather than by wind.

5.2. Pollen surface sample results

The first set of surface sample data, combining both duff and lake surface core samples, comes from the eastern side of the western Cordillera, beginning outside Cuenca at 2700 m and continuing to Laguna Pampiada at 4100 m (Fig. 4). The major pollen and spore types found in the upper paramo (> 3800 m) in the Cajas National Park area were *Huperzia* spp. (10–20%), Poaceae (30–50%), *Plantago* (5–25%), Cyperaceae (2–18%), *Polylepis* sp. (3–70%), and Asteraceae (3–25%). Taxa well represented in the paramo surface samples but growing below 3400 m were *Hedyosmum* (1–5%), Podocarpaceae (1–5%), and *Alnus* (5–40%).

The paramo/timberline plant communities between 3400 and 3800 m are dominated by *Polylepis*, Asteraceae, *Clethra*, *Miconia*, *Myrsine*, and Ericaceae (Young et al., in preparation, Fig. 3), but pollen percentage representation of these taxa in the surface samples is low (Fig. 4). *Polylepis* sp. pollen percentages are low in lake and bog surface samples but high in duff from *Polylepis* forests. *Gynoxys* pollen unfortunately cannot be separated from the other 20 or so Asteraceae pollen types. High percentages of Asteraceae pollen in the upper paramo are suspected to represent *Gynoxys*.

The moist montane forest surface samples (2700–3400 m) exhibit slightly higher pollen percentages of *Hedyosmum*, as well as fern spores, *Dryopteris* type, and *Campylomeurum*/*Polypodium* type (Fig. 4). Conspicuous for its absence, in light of plant prevalence on the landscape, was pollen of *Puya* spp. The *Puya* species that grow in Cajas today are thought to be animal-pollinated (e.g. insect, bat), which may account for its absence from surface samples. This is important to note, because pollen of *Puya* sp. is significant in the late-glacial pollen records for Lagunas Chorreras and Pallcacocha but not in Holocene samples. This suggests that another species of *Puya* may have been present in the past.

Some pollen types found in surface samples exhibited a negative or slight correlation to plant presence on the eastern side of the Cordillera; these types were Podocarpaceae, *Alnus*, and *Pteridium* sp. (Fig. 4). Thus the pollen fluctuations of these taxa may be open to various interpretations. *Isoëtes* spores were present in all lake and bog surface samples between 3180 and 4100 m.

On the western side of the western Cordillera four duff surface samples from 3900, 3650, 3400, and 3200 m were analyzed for pollen in addition to the lake sample at 4100 m (Laguna Pampiada, Fig. 5). The 3200-m sample site is about 40–50 km from the Pacific Ocean. The significant thing to note in Fig. 5 is the correlation between the vegetation and the pollen data for Podocarpaceae, *Myrica*, *Polylepis*, *Dryopteris* type, *Elaphoglossum* spp., and *Pteridium* sp.

5.3. Fossil pollen results

5.3.1. Chorreras (Figs. 6, 7, 11, 12)

The Chorreras core is marked by massive laminated gray silt from the base of the core (∼440 cm; ∼17 500 cal. yr BP) to a depth of ∼350 cm (∼14 000 cal. yr BP) (Rodbell et al., 2002). Above this, there is an approximately 20-cm-thick transition to massive brown gyttja with ∼10% LOI, which extends up-core to a depth of ∼250 cm (10 500 cal. yr BP). Above this there is a second 20-cm-thick transition to very dark, massive gyttja with an LOI of >20%, which extends to the core top. There are seven prominent tephra in the Chorreras core (Rodbell et al., 2002).

Zone Ch1-A (439–384 cm; 17 500–15 000 cal. yr BP, Figs. 6 and 7)

Zone Ch1-A core samples are characterized by low LOI values, a peak in MS, and low overall concentrations of pollen and spores (Fig. 6). High elevation paramo pollen and spores dominate; these include *Huperzia* spp. spores (35–40%), *Lycopodium* spp. (10%), Cyperaceae (10–15%), and Apiaceae (3–5%). *Puya* pollen is present. Timberline forest pollen comprise less than 10% of which *Polylepis* accounts for 1.2% and Asteraceae 9%.

Representation of total moist montane forest types ranges from 10% to 5%. *Isoëtes* spores are moderately well represented (20%). Charcoal fragments are present in the top of zone Ch1-A along with *Ambrosia* type.

Zone Ch1-B (380–344 cm; ca. 15 000–13 500 cal. yr BP)

Increasing LOI, a peak in MS, and increased pollen and spore concentrations characterize zone Ch1-B (Fig. 6). *Huperzia* spp. spore percentages decrease from about 40 to 25%, while *Huperzia* spore concentrations increase from about 2000/cm^3 to 8000–60 000/cm^3 (Fig. 7). Poaceae pollen percentages increase only slightly from zone Ch1-A, but concentrations peak midzone along with most paramo taxa (Figs. 6 and 7). Cyperaceae pollen percentages decline from a high of 20% at the Ch1-A/Ch1-B border to <6% at the top of zone Ch1-B. *Puya*, Apiaceae, and *Loricaria* pollen percentages show a pronounced decline relative to the previous zone. *Ambrosia* pollen is present at about 14 500 cal. yr BP. *Isoëtes* percentages increase from 20 to 60% in this zone, and concentrations increase nearly 30-fold. Charcoal concentrations are insignificant.

Zone Ch1-C (345–320 cm; 13 500–13 000 cal. yr BP)

Declining percentages and concentrations of *Huperzia* spp., *Puya*, and Cyperaceae characterize zone Ch1-C (Figs. 6 and 7). Poaceae pollen percentages reach their maximum of 45% at the top of zone Ch1-C, Asteraceae rise to 15%, but pollen concentrations decline for both families. *Isoëtes* spore percentages more than double, and, more importantly, *Isoëtes* concentrations increase fivefold. The small decline in *Miconia*/Melastomataceae type pollen percentages should also be noted.

Zone Ch1-D (320–300 cm; 13 000–12 000 cal. yr BP)

Pollen zone Ch1-D (Fig. 6) shows a midzone decline in LOI with a peak in MS. *Huperzia*

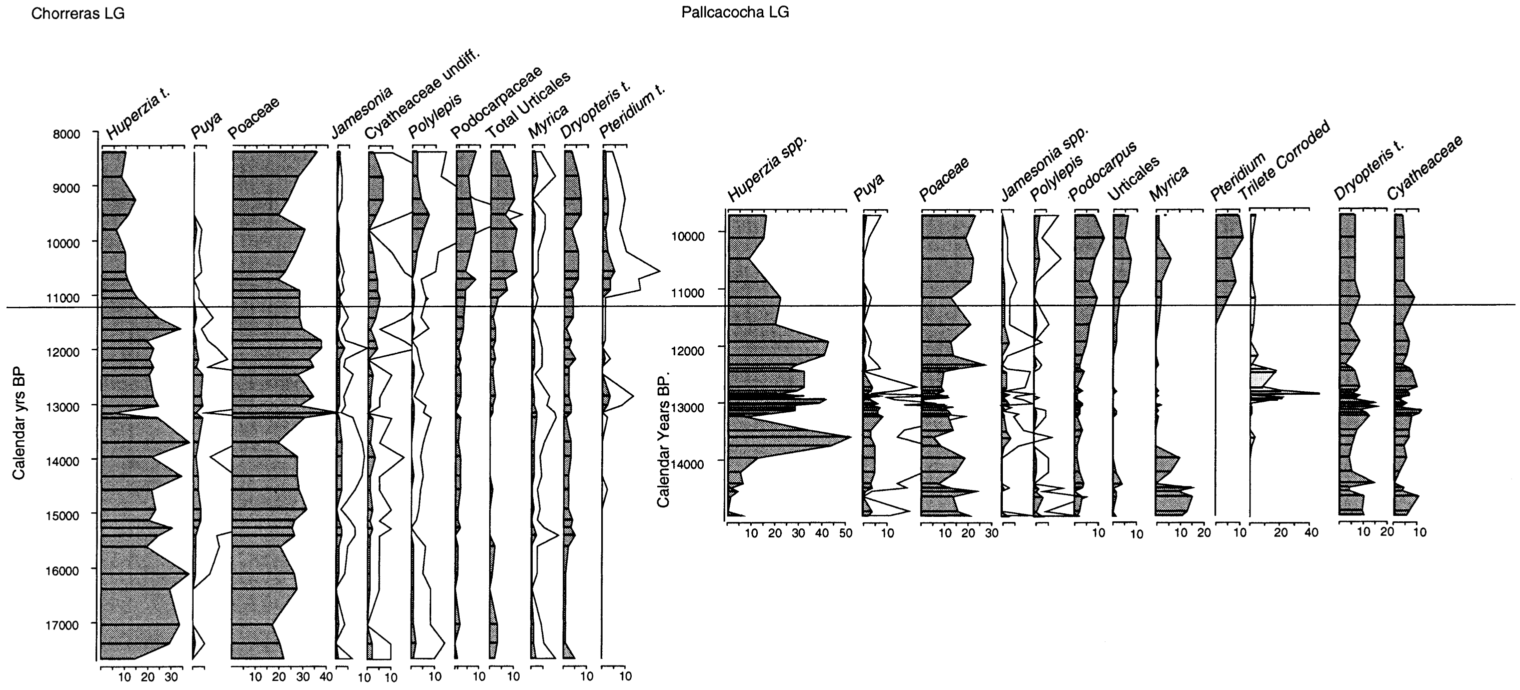

Fig. 11. Summary percentage pollen diagram of major taxa for the late-glacial early Holocene at Lagunas Chorreras and Pallcacocha.

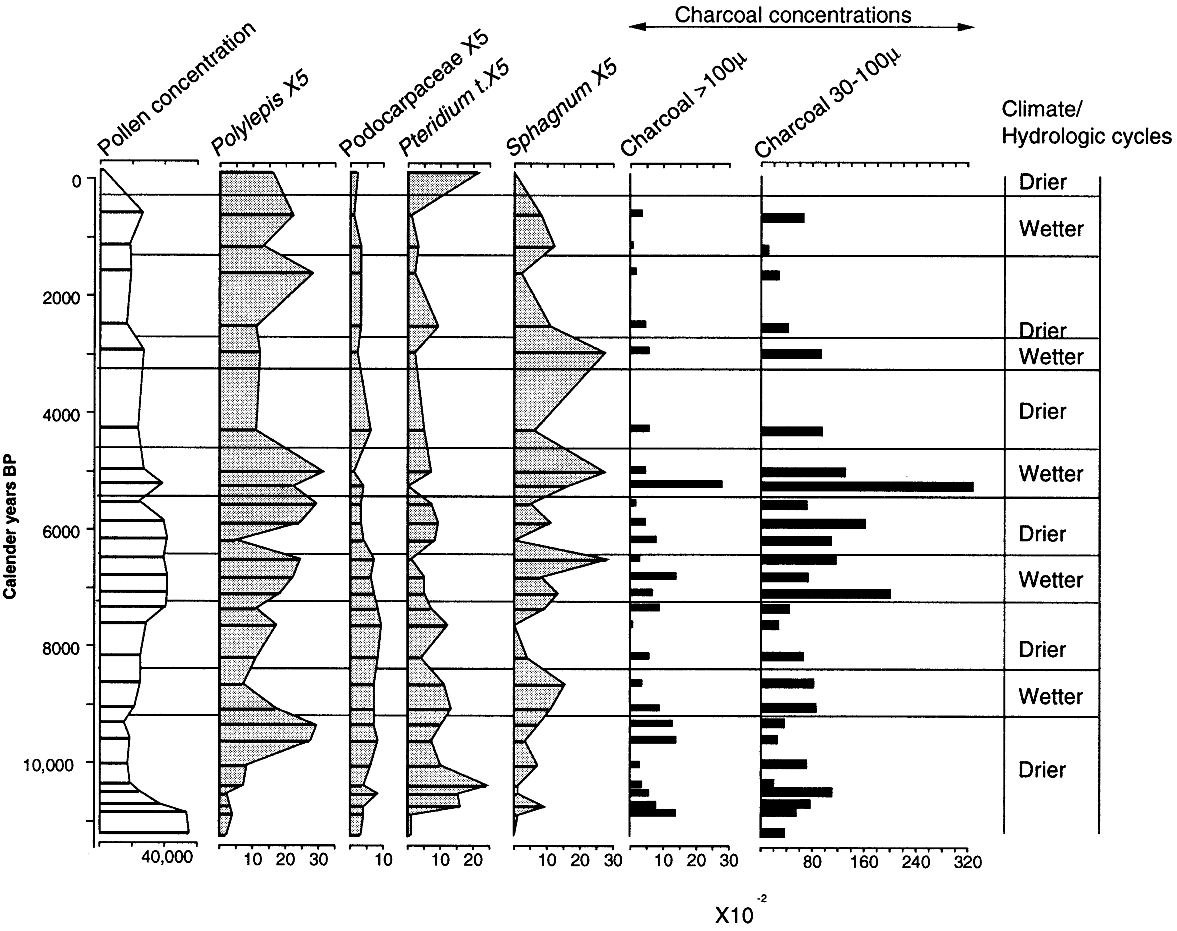

Fig. 12. Selected pollen and spore curves suggesting precipitation fluctuations during the Holocene at Laguna Chorreras.

spp. spore values (25% and 10 000/cm^3) are slightly lower than in the two previous zones. Poaceae (ca. 35%), *Puya* sp. (2–3%), and *Lycopodium* spp. (10%) values remain relatively high and Cyperaceae and *Miconia* pollen increase (Figs. 6 and 7). There is a modest peak in *Pteridium* spore percentages at the bottom of zone Ch1-D, and charcoal concentrations are generally insignificant. *Isoëtes* spore percentages and concentrations drop sharply (Figs. 6 and 7).

Zone Ch1-E (300–270 cm; 12 000–11 000 cal. yr BP)

MS values increase up-core and LOI remains nearly constant as paramo pollen and spores, primarily *Huperzia* spp. spores, decline from 70 to 40% in zone Ch1-E. *Puya* sp. pollen and spores of *Jamesonia*, *Pteridium*, and *Sphagnum* disappear or decline during this period. *Lycopodium* spore presence is significant early in this zone, but drops off at the upper boundary. Increasing charcoal concentrations, together with higher percentages and concentrations of *Isoëtes* spores, mark the transition from Ch-1 to Ch-2.

Zone Ch2-A (11 000–10 000 cal. yr BP)

LOI percentages are relatively higher in zone Ch2-A and MS values are lower; total pollen and spore concentrations decline. Paramo taxa dominance declines from 80 to about 45%, primarily *Huperzia* spp., Poaceae, *Valeriana* sp., and *Puya* sp. At the same time moist montane forest elements (e.g. Urticales, Podocarpaceae, *Hedyosmum* spp., and Cyatheaceae) rise to 30 from about 10% in the early Holocene. *Pteridium* spore percentages increase significantly in Ch2-A, and *Isoëtes* spores reach peak values. High concentrations of charcoal further characterize the early Holocene records (Figs. 6 and 7).

Zone Ch2-B (10 000–9000 yr BP)

Between 10 000 and 9000 cal. yr BP, a peak in MS and a drop in LOI accompany a pollen maximum of *Polylepis* (Figs. 6 and 7). Poaceae pollen comprises 35% of the pollen sum, but concentrations diminish from $>16\,000/\text{cm}^3$ to about 4000 grains/cm^3 in zone Ch2-B (Fig. 7). Other shifts in this zone include increases in Urticales, *Miconia* type, and *Weinmannia* concomitant with declines in Podocarpaceae, *Alchornea* type, Cyatheaceae, and *Pteridium* pollen/spore percentages. Concentrations of *Isoëtes* spores are low; charcoal concentrations remain high.

Zone Ch2-C (220–180 cm; 9000–7000 cal. yr BP)

Higher LOI percentages continue into zone Ch2-C as productivity increases. The peak in MS may be related to the higher charcoal concentrations associated with increased fires. Poaceae pollen percentages increase slightly from the base to the top of zone Ch2-C as *Polylepis* pollen percentages decrease. *Weinmannia* pollen and Cyatheaceae and *Sphagnum* spores are notable components of this zone.

Zone Ch2-D (180–100 cm; 7000–4500 cal. yr BP)

The period from 7000 to 4500 cal. yr BP (Figs. 6 and 7) is characterized by steady LOI values and three MS peaks. Percentages and concentrations of Poaceae pollen are higher (ca. 35%) and pollen and spore percentages of moist montane forest elements are lower. Podocarpaceae and *Alnus* pollen percentages and concentrations are higher in the basal portion of this zone and decline upward. *Ambrosia* type and Chenopodiaceae/Amaranthaceae pollen are present. Tantalizingly, a single grain of *Zea mays* (Beug, 1961) was found at the 7000 cal. yr BP level. *Pteridium* and *Sphagnum* spores seem to fluctuate reciprocally (Fig. 12). Charcoal concentrations reach their highest values here.

Zone Ch2-E (100–40 cm; 4500–1800 cal. yr BP, Figs. 6 and 7)

A major peak in MS occurs at mid-zone in Ch2-E; this peak corresponds to the presence of a 1-cm-thick tephra layer. The vesicular glass contains micro-inclusions of magnetite, which are responsible for the high MS. LOI drops substantially over the section of core containing the tephra. Moist montane forest representation increases slightly, with the various taxa fluctuating independently. *Polylepis* pollen percentages decrease significantly from the previous zone. *Sphagnum* spore percentages peak near the upper zone boundary. Charcoal concentrations are low compared to zone Ch2-D.

Zone Ch2-F (40–0 cm; 1800 yr BP to present Figs. 6 and 7)

This zone is characterized by lower MS values, higher LOI percentages, and relatively low pollen and spore concentrations. Poaceae and *Polylepis* pollen values increase (Figs. 6, 7 and 11). Podocarpaceae percentages continue a gradual decline, while *Hedyosmum* pollen percentages increase. Cyatheaceae spore percentages decrease appreciably. *Alnus* pollen peaks at 20%. Urticales, *Myrica*, and *Dodonaea* (a shrub associated with disturbance and dry intermontane valleys) pollen percentages increase at the top of this zone. Charcoal concentrations and *Isoëtes* spore percentages and concentrations remain stable.

5.3.2. *Laguna Pallcacocha (Figs. 8, 9 and 11)*

The Pallcacocha core is marked by a similar sediment stratigraphy to that noted above for the Chorreras core. The base of the core (9.5 m; ~14 500 cal. yr BP) is a gray-pink, finely laminated–massive, inorganic silt (LOI ~5%), which extends up-core to a depth of ~810 cm. At 810 cm there is an ~10-cm-thick transition to massive gyttja with an LOI of ~10%. This, in turn, is overlain by interbeds of organic-rich and organic-poor laminae that extend to the core top; the frequency of occurrence of clastic, inorganic laminae increases up-core, which has been interpreted to reflect an increase in storm-derived clastic sediment to the lake (Rodbell et al., 1999). Finally, there are seven distinct tephra in the Pallcacocha core (Rodbell et al., 2002).

Zone Pa1-A (955–920 cm; 15 000–14 400 cal. yr BP)

The pollen record for Laguna Pallcacocha begins about 15 000 cal. yr BP, or about 2000 years after pollen deposition began at Laguna Chorreras (Figs. 8, 9 and 11). The basal zone is characterized by high MS, low LOI, and low pollen/spore concentrations. Total paramo elements amount to less than 25%, with Poaceae pollen dominating at 15% and *Dryopteris* type increasing to 8%. Timberline forest elements (e.g. *Polylepis*, Asteraceae, and *Miconia*) together comprise about 10%. Moist montane and riverine forest elements dominate the assemblage; these are primarily *Alnus* (>20%), *Myrica* (15%), Cyatheaceae (up to 10%), *Hedyosmum* (5–11%), and Podocarpaceae (up to 3%). Also present are *Ephedra*, Cactaceae (cf. *Cereus* type), and *Ambrosia*. Charcoal concentrations are insignificant, and *Isoëtes* spores are absent.

Zone Pa1-B (920–880 cm; 14 400–13 800 cal. yr BP)

Zone Pa1-B (Figs. 8 and 9) is characterized by a slight increase in LOI, low MS, and rising pollen and spore concentrations. Paramo pollen and spores, in particular Poaceae, *Elaphoglossum* spp., other *Dryopteris* type, and *Puya*, together with moist montane forest pollen and spores (e.g. *Myrica*, Cyatheaceae), and high *Alnus* pollen percentages characterize this zone. Charcoal concentrations are negligible, as are percentages of *Isoëtes* spores.

Zone Pa1-C (890–860 cm; ca. 13 800–13 000 cal. yr BP)

Pollen zone Pa1-C is characterized by a very slight rise in MS and LOI values and high percentages and concentrations of *Huperzia* spp. spores (to 50%; Figs. 8 and 9). There is a modest increase in spore percentages of *Elaphoglossum*, *Dryopteris* type, *Lycopodium* spp., and *Jamesonia* spp. Percentage values for *Puya* sp. and *Huperzia* spp. decrease in the upper part of the zone. *Scirpus* pollen disappears, while pollen of other Cyperaceae increase. Timberline and moist montane forest pollen/spores diminish in importance in this zone, the exception being spore percentages of Cyatheaceae, which remain relatively high (ca. 10%). *Isoëtes* spore percentages are notable for the first time; charcoal concentrations are insignificant.

Zone Pa1-D (840–820 cm; 13 000–12 600 cal. yr BP)

In subzone Pa1-D, MS values remain low, and LOI values diminish slightly. Moist montane forest pollen declines in a series of diminishing peaks. Total timberline forest pollen percentages are unchanged. Individual taxa (e.g. *Huperzia* spp., *Scirpus*, *Dryopteris* type, and *Puya* sp.) appear to fluctuate considerably in this zone. The Poaceae pollen and the Cyatheaceae spore curves have pronounced minima. These curve lows are concurrent with high percentages of corroded trilete fern spores (up to 50%, mostly *Huperzia* type). Charcoal concentrations are low, and *Isoëtes* spores are present.

Zone Pa 1-E (820–780 cm; 12 600–12 200 cal. yr BP)

Zone Pa 1-E is characterized by a slight peak in MS together with increasing LOI values. Paramo pollen and spore percentages increase, in particular Poaceae pollen (to 30%), as do percentages of *Plantago*, *Loricaria* type, and moist montane forest pollen (Figs. 8 and 9). In contrast, timberline forest taxa percentages remain low (less than 3%). *Puya* and *Scirpus* pollen all but disappear, while Cyatheaceae spore percentages increase and corroded trilete spore percentages decline. Charcoal concentrations and *Isoëtes* spore values are low.

Zone Pa1-F (800–780 cm; 12 100–11 800 cal. yr BP)

Higher LOI values, low MS values together with a modest increase in pollen and spore concentrations characterize zone Pa1-F (Figs. 8 and 9). Although *Huperzia* spore percentages and concentrations remain near their maxima (Fig. 9) in this zone, other paramo elements decrease in representation, in particular Poaceae, *Puya*, other Lycopodiaceae, *Plantago*, and Apiaceae. There are commensurate increases in moist montane forest pollen, primarily Podocarpaceae and *Hedyosmum*. Cyatheaceae spore percentages decline. *Isoëtes* spore percentages increase, but concentrations are low (Fig. 9). Charcoal concentrations are relatively high in one sample.

Zone Pa2-A (770–730 cm; 11 800–11 000 cal. yr BP, Figs. 8 and 9)

LOI values remain high in this zone and MS readings are low. Paramo taxa values are declining except for higher concentrations of *Huperzia*, *Dryopteris* type, Cyperaceae, and Poaceae. *Puya* pollen is negligible. Increases in Podocarpaceae, *Isoëtes*, and the appearance of *Pteridium* spores are notable. Charcoal concentrations are somewhat higher.

Zone Pa2-B (730–690 cm; 11 000–10 200 cal. yr BP, Figs. 8 and 9)

Pollen and spores of paramo taxa, in particular *Huperzia* type, continue to decline as pollen and spores of moist montane forest increase in zone Pa2-B (Figs. 8 and 9). MS and LOI values stay relatively unchanged from the previous zone. *Polylepis*, *Miconia*, Podocarpaceae, *Weinmannia*, Urticales, and *Myrica* are the important timberline and moist montane forest components. Percentages and concentrations of *Pteridium* increase significantly. Cyatheaceae and *Isoëtes* spore percentage values are low.

Zone Pa2-C (690–650 cm; 10 200–9000 cal. yr. BP, Figs. 8 and 9)

The uppermost pollen zone from Laguna Pallcacocha exhibits lower percentages of montane and timberline forest elements with a slight increase in paramo taxa, in particular *Huperzia* type, Poaceae, and *Sphagnum*. Podocarpaceae pollen percentages are higher, and those of *Weinmannia* spp. and *Myrica* decline. *Pteridium* spore percentages continue to increase.

5.4. Late-glacial discussion

From about 17 000 to 15 000 cal. yr BP, glaciers retreated up the Tomebamba River Valley, forming lakes behind terminal moraines and in cirques. A paramo dominated by *Huperzia*, other Lycopodiaceae, and Poaceae with Apiaceae, *Plantago*, and Gentianaceae initially occupied the area around Laguna Chorreras. The dominance of *Huperzia* spores, along with high values of other Lycopodiaceae, suggests that the climate between 17 000 and 15 000 cal. yr BP was initially wetter and cooler than today. The highest plant percent frequency of *Huperzia* today is found between 3600 and 3800 m, and the maximum *Huperzia* spp. spore representation occurred in samples above 3800 m (Figs. 3 and 4). High MS values confirm basin disturbance from glacial meltwater, and the low LOI values indicates a cold non-productive environment.

The low pollen percentages and concentrations of *Polylepis* pollen at Laguna Chorreras suggest that *Polylepis* timberline forests, like those existing today, were probably absent in the early late-glacial. Negligible charcoal presence in the early late-glacial Chorreras pollen record indicates few fires and little timberline forest for fuel.

At Laguna Llaviucu 15 km east of Chorreras at 3180 m, paramo taxa also dominate the pollen record (Llav 1) during local glacial retreat; there is minimal pollen evidence for the major timberline forest taxa (Llav 1; Colinvaux et al., 1997).

By way of contrast, the pollen record from Laguna Junin in the central Peruvian Andes suggests that between 18 030 and 16 000 radiocarbon yr BP the Junin plain at 4100 m was sparsely covered by grassland (Hansen et al., 1984). But between 16 000 and 12 000 radiocarbon yr BP, *Polylepis* and Compositae (= Asteraceae in Cajas) timberline forest dominated parts of the Junin plain. Also in contrast, the Junin late-glacial climate favored very few pteridophyte taxa; samples from this time period exhibited less than 10% total pteridophytes as compared to more than 50% pteridophytes at Laguna Chorreras for that time period. These data attest to large vegetation differences between the Junin plain and the Tomebamba River Valley in the late-glacial which are the result of differences in precipitation at that time.

Between ca. 15 000 and 13 500 cal. yr BP, herb paramo continued to dominate the Chorreras area and also to spread to higher elevations around Laguna Pallcacocha (Figs. 6–9). An unknown species of *Puya* became an important component of the paramo at both sites. This is interesting, because no pollen of *Puya* was found in any of the surface samples collected in the Cajas area even though *Puya* spp. were found in up to 40% of the vegetation plots (Fig. 3). Three species of *Puya* are known to grow in Cajas National Park today (Léon, personal communication). These species are assumed to be pollinated by insects, bats or birds, which may partly explain the absence of *Puya* pollen in surface cores, but not the presence of the unknown *Puya* species in the late-glacial.

Low percentages (20–30%) of paramo pollen and spores and high percentages ($>30\%$) of moist montane forest taxa characterize Laguna Pallcacocha (4060 m) in the early late-glacial. This is in contrast to 60–80% paramo pollen/spores and less than 10% moist montane forest pollen/spores at both Laguna Chorreras (3700 m) and Laguna Llaviucu (3180 m; Llav 1 and 2; Colinvaux et al., 1997). In addition, *Myrica* pollen comprised 10–15% at Pallcacocha in the early late-glacial, but $<1\%$ at both Lagunas Chorreras (3700 m) and Llaviucu (3180 m, Colinvaux et al., 1997), sites both east of Pallcacocha and at lower elevations.

The reason for these differences is suggested by the modern vegetation, pollen, and spore data from west of Pallcacocha (Fig. 5). The modern pollen and spore data from the western surface samples exhibit higher percentages and concentrations of Podocarpaceae, *Myrica*, Cyatheaceae, and *Dryopteris* type (Fig. 5) than do surface samples from east of the main divide (Fig. 4). Assuming that existing vegetation on both sides of the divide was similar in the past, it is likely that the montane forest pollen in zone Pa1-A from Laguna Pallcacocha was deposited when local winds were from the west (Figs. 8 and 10). Spot occurrences of *Ephedra*, Cactaceae, and *Ambrosia* pollen may also originate from the western side of the western Cordillera, where Young suggests that seasonality is more pronounced. Based on high spore percentages of *Huperzia* spp., Lycopodiaceae and other pteridophytes at both Cajas sites, a wet, cool environment with local winds from the west is postulated for the late-glacial period 15 500 to 13 500 cal. yr BP.

About 13 000 cal. yr BP (Ch1-C, Fig. 6), a pronounced increase of Poaceae and Asteraceae pollen at Laguna Chorreras is accompanied by a decline in such moist habitat types as *Huperzia*, Cyperaceae, *Lycopodium* spp., and *Sphagnum*. A peak in *Isoëtes* percentages and concentrations occurs at about the same time, suggesting lower water levels in Chorreras. The basis for this interpretation comes from a study of postglacial vegetation and fire history in a paramo in Costa Rica (Horn, 1993). In essence, the argument is that lower lake levels expose larger areas of lake shore for *Isoëtes* habitat; this in turn increases *Isoëtes* spore deposition and concentrations within the lake. Therefore, high concentrations of *Isoëtes* along with the decline in moisture-loving taxa above suggest drier conditions.

At Laguna Pallcacocha, the pollen and spore record at ca. 13 000–12 500 cal. yr BP exhibits very high percentages of corroded spores (20–50%). This is unusual. Cushing (1964) noted in analyzing redeposited pollen from late-Wisconsin cores that “corroded pollen are often redeposited from in-wash of soil from surrounding slopes.” Corroded spores or pollen are easily recognized in our pollen samples from Cajas. The high percentages of corroded spores in the pollen record from Laguna Pallcacocha (Pa1-D and E) was probably due to erosion during periods of enhanced seasonality. During this same time period, Poaceae pollen all but disappears from the Pallcacocha record, and other pollen/spore percentages of paramo and timberline forest taxa fluctuate erratically (Figs. 8 and 9). Also, Cyatheaceae spore percentages from the western moist montane forest decline (Pa1-D) and rebound in the zone above (Pa1-E). The interpretation for the climate for this period is increased seasonality with lengthened dry seasons that affected both the western montane forest (e.g. Cyatheaceae) and the paramo. Overall, the climate was cold and wet with prevailing winds from the west.

At Laguna Baja (3700 m) in Rio Abiseo National Park (Fig. 1), the late-glacial pollen record begins with a moist montane forest ($>12\,000$ radiocarbon yr BP), which is replaced between 12 000 and 10 000 radiocarbon yr by a grass-dominated paramo with *Jamesonia*, a fire-tolerant pteridophyte (Hansen and Rodbell, 1995). High percentages of charcoal accompany this expansion of paramo. Several interpretations are offered for this late-glacial period. One is that relatively warm and moist conditions existed in the early late-glacial, followed by a temperature depression as recorded in the expansion of paramo. Another interpretation presented was that the replacement of forest by paramo reflected unidirectional succession, with the early forest presence being an artifact of long-distance pollen dispersal. The third interpretation was a short-term climate reversal characterized by cooler temperatures and a longer dry season, which would account for both high Poaceae and charcoal percentages (Hansen and Rodbell, 1995).

Leading up to the Holocene, between 12 500 and 11 000 cal. yr BP, climate reverted to cool, wet conditions, and paramo maintained its dominance.

5.5. Holocene discussion

The transition to the Holocene (ca. 11 000–10 000 cal. yr BP) at both Cajas sites is characterized by the pronounced decrease in spores of *Huperzia* spp. (50 to 20%, Pa1–2; and 40 to 15%, Ch1–2) and other Lycopodiaceae as moist montane forest pollen and spores increased (Podocarpaceae, Urticales, Cyatheaceae and *Pteridium*). *Puya* pollen all but drops out of the pollen record and Asteraceae pollen percentages and concentrations remain unchanged. After the initial expansion of pollen/spores of moist montane forest elements, *Polylepis* pollen becomes important, reaching its maximum in the mid-Holocene at Chorreras. In contrast, the highest percentages of *Polylepis* pollen at Laguna Llaviucu occur at the beginning of the Holocene (Colinvaux et al., 1997). High concentrations of charcoal fragments in the early Holocene indicate frequent fires due to both the availability of woody fuel and favorable climatic conditions (i.e. pronounced dry season and warmer temperatures). These conditions in turn may have favored the expansion of *Polylepis* timberline forest at higher elevations and the spread of *Pteridium* in disturbed areas. Frequent fires may have encouraged the demise of the unknown *Puya* sp. as well.

Stable pollen and spore percentages between 10 000 and 7500 cal. yr BP, in particular moist montane forest elements, imply that climatic conditions remained fairly stable. Higher percentages of moist montane forest pollen in the early Holocene than occur in recent fossil samples suggest warmer temperatures with moderate seasonality. Local vegetation changes appear related to the incidence of fire and changes in hydrology.

Between 7500 and 4000 cal. yr BP, a grass paramo expanded around Laguna Chorreras; pollen of Poaceae replaced in importance *Huperzia*, *Plantago*, and Apiaceae, taxa preferring moist habitats. *Polylepis* appears to be the dominating timberline taxon and its prevalence appears to fluctuate with charcoal frequency and fires. One pollen grain of *Zea mays* was identified in zone Ch2-D, and occasional pollen grains of *Ambrosia* and Chenopodiaceae/Amaranthaceae tantalizingly suggest anthropogenic disturbance.

After 4000 cal. yr BP, Podocarpaceae pollen percentages decline as those of other moist montane forest elements increase. High *Sphagnum* spore percentages, and low charcoal values, could be interpreted as indicating moister conditions or cooler weather. *Zea mays*, *Ambrosia*, and Chenopodiaceae pollen become more frequent at this time suggesting forest clearance and the possible beginnings of regional agriculture.

Around 2000 cal. yr BP, Poaceae, *Plantago* spp., and *Valeriana* spp. pollen percentages increase, and Cyperaceae pollen decreases. Pollen of some moist montane forest elements (Podocarpaceae, Cyatheaceae) lessen in importance, while those of other montane forest taxa increase (e.g. *Hedyosmum*, *Myrica*); this would seem to rule out a major climate change. The increased presence of weed/disturbance pollen types, *Ambrosia* sp., Chenopodiaceae/Amaranthaceae, *Dodonaea*, and *Alnus*, suggests forest clearance and farming. No clear climate signal is evident in this zone.

6. Conclusions

The *Huperzia* spp./Lycopodiaceae-dominated paramo of the late-glacial in Cajas is unique in comparison with other late-glacial pollen records from Ecuador and Peru because of the importance of an unknown species of *Puya* and the dominance of *Huperzia* spp.

Total timberline forest percentages varied little between the late-glacial and the Holocene. The pollen of woody timberline taxa did not create a strong climate signal either except for the shift in dominance from Asteraceae in the late-glacial to *Polylepis* in the Holocene.

Emphasis on present-day pteridophyte plant distribution and spore identification aided in the recognition of paleoclimatic conditions. *Huperzia* spp. and *Lycopodium* spp. characterize the upper cold wet paramo (> 3700 m) today whereas grasses dominate the drier areas below 3700 m. *Jamesonia*, *Hymenophyllum* type, and *Lophosoria* type pteridophytes favor timberline forest patches below 3800 m today and their spore presence in the late-glacial confirms the presence of some sort of timberline forest communities. Higher percentages of spores from Cyatheaceae (tree ferns) were useful in recognizing times of higher temperatures and moisture at lower elevations.

Stomate analyses of surface and fossil samples at Cajas were useful in a negative sense for our study in Cajas National Park. No conifer stomata were found in surface samples or in fossil samples suggesting that individual trees of Podocarpaceae never grew near either of the Cajas pollen sites. On the other hand, Podocarpaceae stomata were found in surface samples from Rio Abiseo National Park in northern Peru, where Podocarpaceae trees still exist. Stomata of Podocarpaceae type also occur in the fossil pollen record for Laguna Negra (3200 m) in Rio Abiseo National Park, where these data illuminate the local history of these conifers (unpublished data).

Reciprocal fluctuations in spore percentages between *Pteridium* and *Sphagnum* seem to correlate with possible changes in hydrology or precipitation (Fig. 12).

Shifts in prevailing wind patterns during the late-glacial are suggested by the pollen and spore data from Pallcacocha. These changes did not, however, seem to affect the pollen assemblages from palynological sites further to the east. Additional palynological records from the western side of the western Cordillera might elucidate this phenomenon.

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