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Behling, H.; Hooghiemstra, H.; Negret, A.J.

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Late Quaternary vegetational and climatic change in the Popayán region, southern Colombian Andes

HERMANN BEHLING1,*, ALVARO JOSÉ NEGRET2 and HENRY HOOGHIEMSTRA1

1University of Amsterdam, Hugo de Vries-Laboratory, Dept. of Palynology and Paleo/Actuo-ecology, Kruislaan 318, 1098 SM Amsterdam (The Netherlands Centre for Geo-ecological Research, ICG)
2Museo De Historia Natural, Universidad Del Cauca, Carrera 2a 1A-25, Popayán, Colombia


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ABSTRACT: Late Pleistocene and Holocene vegetational and climatic change have been studied palynologically at a site at 1750 m elevation in the subandean vegetation belt near Popayán, in the southern Colombian Andes. Time control on the pollen record is based on six AMS 14C ages, ranging from possibly Middle Pleniglacial time (around 50 000 yr BP) to 1092 ± 44 yr BP. Because of the presence of two hiatuses only the Middle Pleniglacial and Late Holocene periods (the last 2300 yr BP) are represented.

Pollen data indicate the presence of closed subandean forest during glacial time. Changes in the contribution of pollen originating from the uppermost and lowermost subandean forest belts, changes in the contribution of a number of other subandean forest taxa, and changes in species composition between the three pollen zones, suggest that the climate during the Middle Pleniglacial was markedly colder, and perhaps also wetter, than during the Late Holocene. Pollen assemblages from the Late Holocene indicate that the landscape has been affected by deforestation and agriculture since at least 2300 yr BP, but that human impact decreased in the last 780 yr BP.

KEYWORDS: subandean vegetation belt; lower montane belt; pollen analysis; palaeovegetation; palaeoclimate; Late Quaternary; pre-Columbian culture; Colombia.

Introduction

Late Quaternary palaeoenvironmental change at low elevations (lower montane forest belt and lowlands) in the Andean mountains is poorly understood. The most significant questions in palaeoclimatology concern past environmental and climatic conditions at low elevations, e.g. the conditions during the Last Glacial Maximum (LGM) (e.g. Anderson and Webb, 1994; Van der Hammen and Absy, 1994; Colinvaux, 1989; Colinvaux et al., 1996; Kerr, 1996). Although a number of palynological investigations have been carried out in Colombia in recent years, little is known about environmental and climatic change in the lowlands (0–1000 m altitude) and in the subandean (= lower montane) vegetation zone (1000–2300 m altitude).

Palaeoecological data from the subandean forest belt form an important contribution to the understanding of the composition and historical development of the present-day eco-systems, as well as their stability and response to climate change. Pollen records from elevations between 1000 and 2300 m may provide estimates of past temperature change. In addition, palynological records may provide critical information for forest management, including aspects of reforestation. This is of particular importance in the inter-Andean valleys, where the original subandean forest has been almost completely destroyed. Finally, palynological records include evidence of the presence of food crops, such as corn and manihot, providing new insights into the pre-Columbian habitation of southern Colombia.

There are no palynological records from the valley of the Río Cauca, the Popayán plains, and the valley of the Río Patía (Fig. 1), with the exception of a single pollen sample from the archeological site San Isidro (10 km north of Popayán). Other pollen records from southern Colombia are from the Central and Eastern Cordilleras: Cabaña San Nicolás (Espejo and Rangel, 1989), Meremberg (Pñeros-Soler, 1988), Pitalito at about 40 km east of Popayán (Bakker, 1990), and Laguna La Cocha (Hooghiemstra et al., in preparation).
Study area

Location

The study area is situated in southern Colombia on the Popayán plain, which forms a saddle connecting the dry valley of the Río Patía (1000–1500 mm annual precipitation) in the south and the more humid valley of the Río Cauca (1000–2000 mm annual precipitation) in the north. The studied swamp ‘Pantano de Genagra’ (2°28′N, 76°37′W, 1750 m altitude) is located on the Hacienda Genagra, 5 km north of the city of Popayán (Fig. 1). The swamp is found in a steep-
sided, U-shaped valley, ca. 200 m long and ca. 50 m wide. The valley has an outlet to the small river Quebrada Piedras, which flows into the Río Cauca.

According to Torres et al. (1992) and Torres (1997) the underlying geological structure of the study area is formed of volcanic–sedimentary deposits which are several hundreds of metres thick. This so-called Popayán Formation forms the rolling Popayán plain, which is located between the inter-Andean valleys of the Río Cauca and Río Patía in the central part of the Cauca Province. The Popayán Formation, which ranges in age from Pliocene to Holocene, overlies Palaeozoic and Tertiary rocks.

Vegetation

The natural vegetation of the study area has been almost destroyed by pastoral farming, cultivation of coffee and commercial forestry. Small relics of forest, ‘probably secondary’, remain along the rivers and are indicative of the composition of the original vegetation: species-rich, humid subandean forests with trees up to 25 m wide in height. In some areas homogeneous stands of Quercus humboldtii occur. The subandean forest belt of this region, and in other parts of Colombia, has been little studied (Cuatrecasas, 1989; Pinto-Escobar, 1993), but two altitudinal zones are recognised: the uppermost part from 1800 to 2300 m altitude and the lowermost part from 1000 to 1800 m altitude. Several species and genera occur across the full range and are not diagnostic of these altitudinal zones. The Andean forest is found in this region between 2300 and 3000/3400 m altitude, whereas in other regions of Colombia this belt occurs between 2400/2500 m and 3600 m elevation. Páramo vegetation is found as low as 3000 m altitude in the southern Colombian Andes (Becking et al., 1997).

Climate

The climate station nearest to the study site is at Popayán airport, only 2 km distant from the swamp of Genagra and at a similar altitude. Climate records from 1982 to 1995 show annual rainfall of between 1580 and 3160 mm (annual average 2142 mm) (Climate station Airport ‘Guillermo Leon Valencia’, unpublished data). Lower precipitation rates occur in the months from June to August. The mean annual temperature is about 18°C. The average annual minimum temperature is between 12.2 and 13.9°C and the maximum annual temperature is between 23 and 25.1°C. The average annual relative humidity varies from 67.7 to 75.2%.

Methods

Modern vegetation studies

The most frequent plant species in the Popayán region, and in the direct vicinity of Pantano de Genagra, are known from field observations and herbarium collections of the Museo de Historia Natural and the Universidad del Cauca, both in Popayán. The altitudinal distribution has been obtained from herbarium data and field observations. Little is known of ecological relationships, however, because of the almost complete deforestation of the Popayán plain.

Sampling and pollen analysis

Sediments were cored in the central part of the U-shaped valley. The 825-cm-long core was collected in 25 cm length increments, using a Dachnowsky sampler. Samples were wrapped in plastic foil and protected during transportation by PVC guttering. The core was stored in the laboratory under dark and cold (4°C) conditions.

Six, small, 1-cm-thick, bulk sediment samples were taken for radiocarbon dating. All samples were dated by Accelerator Mass Spectrometry (AMS) at the University of Utrecht (Van der Borg et al., 1987).

For pollen analysis, samples of 0.5 cm³ were taken at 5 cm or 10 cm intervals along the profile. Samples were prepared using the standard treatment of sodium pyrophosphate, acetolysis method, and heavy liquid separation by bromoform (Faegri and Iversen, 1989). Pollen preparation included addition of exotic Lycopodium spores to determine the pollen concentration (grains cm⁻³). Most of the samples were counted up to a minimum of 300 grains, excluding aquatic pollen and spores. Some intervals of the core contain no, or badly preserved, pollen grains and spores. In general, pollen and spores were less well preserved in the lower part of the sequence. Samples below 700 cm core depth are devoid of pollen and spores.

About 140 different pollen and spore taxa were identified. Another 20 palynomorphs could not be identified. For identification, the following pollen morphological studies were used: Behling (1993), Hooghiemstra (1984), Roubik & Moreno (1991), and the pollen and spores reference collection at the Hugo de Vries-Laboratory.

Identified pollen taxa have been grouped according to their presented-day altitudinal and ecological preference, such as uppermost subandean forest (1800–2300 m altitude), lowermost subandean forest (1000–1800 m altitude), other subandean forest taxa without altitudinal preference (1000–2300 m altitude), herbs, aquatics, ferns, tree ferns, mosses and fungal spores. The altitudinal distribution of important species and genera in the area of the Popayán plain and the branches of the San Rafael of the Vulcan Puracé is shown in Fig. 2. Some species, which mostly have an altitudinal distribution below 1500 m, have been recorded in the Cauca valley between Santander de Quilichao and Popayán (Fig. 1). Figure 2 illustrates only the altitudinal distribution of species that have been obtained from the Popayán region. Some species may have a lower and/or higher altitudinal range in other regions of Colombia. A few taxa, which grow in the uppermost subandean and in the Andean forest belt (above 2300 m altitude), such as Podocarpus, have been grouped in the uppermost subandean forest.

For plotting of the palynological data, calculations and cluster analysis, tilia, tiligraph and coniss software was used (Grimm, 1987). The pollen percentage diagram includes records of ecological groups, records of the most frequent individual pollen and spore taxa, a record of the concentration of pollen sum elements, and a cluster analysis dendrogram.
Stratigraphy

The 825-cm-long core from Genagra consists of interbedded organic-rich material, peat, clay and sand. Tephra occur in the form of fine layers in the intervals at 315–337 cm and 625–633 cm depth. The down-core sequence of sediments was as follows:

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–6</td>
<td>living fibrous mat (Cyperaceae)</td>
</tr>
<tr>
<td>6–75</td>
<td>brown organic-rich material, peaty, medium compact and decomposed, plant remains and rootlets</td>
</tr>
<tr>
<td>75–175</td>
<td>dark brown to black organic-rich material, peaty, compact and decomposed, rare plant remains and rootlets</td>
</tr>
<tr>
<td>175–202</td>
<td>dark grey organic-rich clay, somewhat fine sandy, no plant remains and rootlets</td>
</tr>
<tr>
<td>202–275</td>
<td>grey less organic-rich clay, somewhat sandy</td>
</tr>
<tr>
<td>275–315</td>
<td>light grey clay, less sandy</td>
</tr>
<tr>
<td>315–337</td>
<td>grey sand with fine tephra</td>
</tr>
<tr>
<td>337–349</td>
<td>grey-brown organic-rich material in transition to</td>
</tr>
<tr>
<td>349–364</td>
<td>dark brown peat, compact and decomposed</td>
</tr>
<tr>
<td>364–374</td>
<td>black peat, compact and completely decomposed</td>
</tr>
<tr>
<td>374–463</td>
<td>dark brown peat, compact and decomposed</td>
</tr>
<tr>
<td>463–475</td>
<td>grey clay</td>
</tr>
<tr>
<td>475–482</td>
<td>dark brown to black organic-rich material, peaty, compact</td>
</tr>
<tr>
<td>482–538</td>
<td>grey clay</td>
</tr>
<tr>
<td>538–550</td>
<td>transition to</td>
</tr>
<tr>
<td>550–608</td>
<td>grey-brown organic-rich material, clayish with some very fine sand</td>
</tr>
<tr>
<td>592–608</td>
<td>grey-brown organic-rich material, peaty,</td>
</tr>
<tr>
<td>625–633</td>
<td>with tephra and peat fragments</td>
</tr>
<tr>
<td>691–825</td>
<td>yellowish clay, some fine sand</td>
</tr>
<tr>
<td>825–</td>
<td>clay</td>
</tr>
</tbody>
</table>

Chronology and zonation

The AMS radiocarbon dates (Table 1) indicate that the dated organic-rich deposits between 348 and 690 cm depth are older than 50 000 yr BP and therefore beyond the radiocarbon dating range. However, the deposits are probably from the last glacial period (see discussion section). Sediments of the uppermost 315 cm are of Late Holocene age, i.e. representing the period from 2326 ± 45 yr BP to the present. In the pollen percentage diagram (Fig. 3), five zones are recognised (GEN-I to GEN-V), based on significant changes in the pollen assemblages (see below) and results from cluster analysis (see Fig. 3). The interpolated radiocarbon age between zone GEN-IV and GEN-V is 780 BP.

Description of pollen diagram Genagra (Fig. 3)

Zone GEN-I (691–595 cm, >50 000 yr BP, 11 samples)

Characteristic of zone GEN-I are high percentages of subandean forest taxa (14–28% uppermost zone (average 19%),
3–10% lowermost zone, and 47–62% other) and low values of pollen grains from herbs (4–15%), originating mainly from Asteraceae, Poaceae and Hypericum. Pollen taxa of the uppermost subandean forest group, such as Myrsine, Podocarpus, Hedyosmum, Myrica and Antidaphne are well represented. Alnus, Weinmannia and Ericaceae are less frequent. Viburnum does not occur in this zone. The lowermost subandean forest group is represented by mainly Moraceae/Urticaceae pollen grains. Other taxa, such as Menispermaceae, Acalypha and Vismia are rare. Quercus and Melastomataceae, which belong to the other subandean forest group without a clear altitudinal preference, are frequent. Percentages of Alchornea, Arecaceae, Myrtaceae, Piper, Malpighiaceae and Solanum are moderate, those from Hyeronima, Cecropia and Ilex are low. Ferns and tree ferns have percentages from 27 to 133% and 0.3 to 8%, respectively. Representation of aquatics (1–10%) and fungal spores (1–11) is relatively low in this zone. Moss spores were not found.

Zone GEN-II (475–377 cm, >50,000 yr BP, nine samples)

In zone GEN-II, values of the uppermost subandean forest group are higher (12–35%, average 24%) than in zone GEN-I due to an increase of Myrsine, Myrtaceae, Podocarpus, Hedyosmum, Viburnum and Ericaceae. Percentages of Myrica and Antidaphne are lower. The lowermost subandean forest taxa show values between only 3 and 7%. Percentages of other subandean forest group without altitudinal differentiation (34–74%) are similar to zone GEN-I, but there is an increase at the end of this zone caused by high values of Hyeronima and Arecaceae-type I, followed by Alchornea. Pollen percentages of herb taxa (2–12%), aquatics (1–4%) and fungal spores (1–26%) are low. Ferns (13–1070%) and tree ferns (1–26%), mainly Cyathaea-type I, are very abundant at the beginning of this zone.

Zone GEN-III (377–337 cm, >50,000 yr BP, eight samples)

Zone GEN-III is characterised by high percentages of the uppermost subandean forest group (25–41%, average 33%), primarily the result of an increase of Weinmannia, Podocarpus, Hedyosmum and Ericaceae. Representation of the group of lowermost subandean forest (2–5%), and other subandean forest taxa without clear altitudinal preference (39–48%) are similar to zone GEN-II. Quercus (9–23%) shows its highest percentages in this zone. Pollen grains from herbs show low percentages (6–14%), but values of Hypericum (1–7%) are very high. Only in zone GEN-III are single pollen grains of Valeriana present. Spores of ferns (58–106%) and tree ferns (6–31%) are abundant. Jamesonia shows the highest percentages in this zone.

Zone GEN-IV (205–75 cm, 2326–780 yr BP, 12 samples)

Abundant herb pollen (87–92%), dominated by Poaceae (59–80%), Asteraceae, Spermacoce, Apiaceae and Amanthaceae/Cheronodiscaceae characterise this zone. Zea mais grains appear for the first time between 1 and 9%. The three groups of subandean forest taxa (2–4% uppermost zone, 1–4% lowermost zone, and 1–5% other) show very low pollen sums. Percentages of aquatics (11–21%), primarily Cyperaceae (10–21%), are high. Spores of ferns (8–69%) and tree ferns (0–0.3%) show markedly lower percentages. Spores of Grammitis-type are frequent, of which the record starts from zone GEN-IV onward. Moss spores (0.3–4%) are produced by two different species of Anthoceros and were found from the beginning of this zone. Fungal spores are present in values up to 15%.

Zone GEN-V (75–0 cm, 780 yr BP–present, seven samples)

In zone GEN-V herbs (62–82%) are less high than in the previous zone, primarily because of decreased percentages of Asteraceae and Spermacoce. Pollen grains of Zea mais are rare (0–1%). Percentages of the subandean forest groups (5–16% uppermost zone, 2–10% lowermost zone, and 9–20% other) are higher, primarily as a result of higher frequency of Myrsine and Hedyosmum (indicative of the uppermost zone), Moraceae/Urticaceae (indicative of the lowermost zone), and Quercus, Alchornea and Cecropia (altitudinally undifferentiated taxa). There is a strong increase in representation of aquatics (54–192%) mainly as a result of an increase of cyperaceous reed swamp. Spores of ferns (8–69%) and tree ferns (0–0.3%) show low values. Fungal spores (22–181%) are abundant in this zone.

Reconstruction of vegetational and climatic change

Interpretation of the pollen record

Almost complete deforestation of the Popayán area means that there are no contemporary analogues in terms of plant sociological or modern pollen data to help interpret the fossil pollen record. Using pollen assemblages of Late Holocene age as a reference for 'modern undisturbed conditions' (0–205 cm core interval) is also problematical because of severe human influence in that part of the pollen record. We have, however, listed modern plant taxa recorded in original and/or secondary patches of forest, which probably

<table>
<thead>
<tr>
<th>Laboratory number</th>
<th>Depth (cm)</th>
<th>¹⁴C yr BP</th>
<th>¹³C/¹²C ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>UtC-5479</td>
<td>100</td>
<td>1092 ± 44</td>
<td>−19.5</td>
</tr>
<tr>
<td>UtC-4959</td>
<td>199</td>
<td>2326 ± 45</td>
<td>−19.6</td>
</tr>
<tr>
<td>UtC-4960</td>
<td>348</td>
<td>53000 −5000/−3000</td>
<td>−30.4</td>
</tr>
<tr>
<td>UtC-4961</td>
<td>463</td>
<td>56000 −9000/−4000</td>
<td>−29.4</td>
</tr>
<tr>
<td>UtC-4962</td>
<td>550</td>
<td>50000 −8000/−4000</td>
<td>−24.6</td>
</tr>
<tr>
<td>UtC-4963</td>
<td>690</td>
<td>&gt;54000</td>
<td>−29.5</td>
</tr>
</tbody>
</table>

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Figure 3. Pollen percentage diagram of Pantano de Genagra at 1750 m altitude, southern Colombia.
reflect remnants of several forest types in the study area (Fig. 2). Apart from more general studies dealing with all of Colombia (e.g. Cuatrecasas, 1989), a short survey of the subandean vegetation belt by Bakker (1990), and a preliminary characterization of the regional paramo vegetation (Becking et al., 1997), Fig. 2 represents the first documentation of the composition and altitudinal distribution of the vegetation in the study area. The pollen record was therefore interpreted in the context of this species list.

The Last Glacial (Pleniglacial): zones GEN-I, GEN-II and GEN-III

The pollen assemblages of zones GEN-I, GEN-II and GEN-III are indicative of different types of subandean forest in the vicinity of the swamp of Genagra. As far as it is possible to compare the fossil pollen spectra with the present-day forest relics, the taxonomic composition and abundance of the subandean forest taxa appear to have been different during the Last Glacial. Some taxa present in the fossil record, such as Podocarpus, Antidaphne, Ilex and Cyathea, are not found in the present-day vegetation of the study area. Podocarpus oleifolius can grow in subandean forests, but is relatively rare in this zone (Torres-Romero, 1988). Other taxa from the uppermost zone of the subandean forest belt, such as Weinmannia, Viburnum and Myrica, are rare today. This arboreal assemblage indicates markedly colder conditions during the time represented by zones GEN-I, II and III, which are most probably of Pleniglacial age, although in the absence of modern pollen rain data precise temperature calculations for the period cannot be made.

Radiocarbon dates from organic-rich sediments between 348 and 690 cm depth suggest for this core interval a range of early Last Glacial, or early to middle Pleniglacial age. The lowermost deposits may be much older, because the AMS date at 690 cm core depth is >54,000 yr BP and beyond the range of radiocarbon dating. Two tephras layers have been observed between 315 and 337 cm, and between 625 and 633 cm. A tephra-based chronology of the study region is being constructed, but at this time is not available.

Deposition of peaty sediments at Pantano de Genagra was interrupted on at least two occasions by the input of clay, either as a result of significant erosion or temporal contact of the valley with the local river system. These deposits between 595 and 633 cm (between zones GEN-I and GEN-II) and from 337 to 205 cm (zones GEN-III and GEN-IV) contain either very badly preserved pollen grains and spores or are lacking in microfossils. The gap in the pollen record between zones GEN-I and GEN-II is represented in the lithological column by organic-rich clay. Absence of pollen grains may have been caused by intermittent dry conditions in the swamp, or other conditions, resulting in corrosion of microfossils. Very high percentages of fern spores in the lowermost sample of zone GEN-II may indicate vegetation recovery following a hiatus. The time interval represented in the gap between zone GEN-I and GEN-II is unknown.

The gap between zones GEN-III and GEN-IV is represented in the lithological column by about 25 cm of sand, overlain by clay. Absence of pollen in these sediments is probably caused mainly by erosion of organic-rich sediment, followed by burial by volcanic sediments. The presence of grey sand deposits with fine-grained tephra from 315 to 337 cm depth supports this interpretation.

Changes in the proportion of pollen grains from uppermost, lowermost and other subandean forest taxa without altitudinal preference, and changes in the taxonomic compo-
sition may suggest changes in temperature and precipitation during glacial times. The summary pollen diagram (Fig. 3) shows that the highest representation of taxa, characteristic of the uppermost subandean forest belt, occurs in zone GEN-III (average 33%), followed by zone GEN-II (average 24%) and GEN-I (average 19%). This may indicate that the uppermost subandean forest belt shifted further downslope during zone GEN-III, suggesting the lowest temperature at that time. The ferns *Jamesonia bogotensis* and *J. imbricata* (Fig. 2) presently have an altitudinal distribution from 3000 to 3350 m. As spores of *Jamesonia* are only frequent during zone GEN-III, cold climatic conditions are also suggested by this taxon. Also the high frequency of the paramo genus, *Hypericum*, and single grains of *Valeriana*, support the inference that zone GEN-III reflects the coldest interval. *Hypericum* was at that time most probably an element of the swamp vegetation.Highest values of *Weinmannia*, *Podocarpus*, *Hedyosmum* and the tree fern, *Cyathea*, are found during zone GEN-II, and particularly in zone GEN-III. These taxa have a preference for cold and/or humid climatic conditions and may suggest that zone GEN-II, but especially zone GEN-III, is the wettest and/or coldest part of the Last Glacial in the Genagra sequence. The accumulation of peaty deposits during these zones lends further support to this interpretation.

Interestingly, there is a sequence of percentage maxima, which starts with *Moraceae/Urticaceae*, *Hyeronima*, *Arecaceae*, *Alchornea* (at the end of zone GEN-II) and is followed by maxima of *Quercus* and relatively high percentage values of some taxa of the uppermost subandean forest belt, such as *Weinmannia* and *Podocarpus* (zone GEN-III). This may possibly indicate forest development related to a change to colder and wetter climatic conditions.

**The Holocene: zones GEN-IV and GEN-V**

High percentages of grass pollen and very low percentages of subandean forest taxa are indicative of forest disturbance and deforestation, related to human presence in the area of Popayán during the period represented by zone GEN-IV. High percentages of pollen grains of *Zea mais* are indicative of corn plantations, suggesting important agricultural activities next to the swamp. Also the presence of pollen grains of *Spermacoce*, *Amaranthaceae/Chenopodiaceae* and spores of *Grammitis*-type and *Anthoceros* are indicative of human disturbance. Climate changes may have occurred during the recorded Holocene period, but they would be masked by the marked human influence on the vegetation.

It is not clear if the beginning of the Holocene part of the pollen record around 2300 yr BP has any relationship to the significant climatic change, possibly at a global scale, at ca. 2650 yr BP (Van Geel et al., 1996). The gap between zone GEN-III and GEN-IV was probably caused primarily by volcanic activity followed by a period of human disturbance of the swamp vegetation. Deforestation and related land use by pre-Columbian communities over the past 2300 yr may have caused erosion on the steep slopes surrounding the valley.

The uppermost zone GEN-V shows a marked decrease of human impact on the surroundings of Pantano de Genagra. Representation of the subandean forest taxa are markedly higher, suggesting that cultivation had diminished. The increase in *Cecropia*, a pioneer of regenerating forest is particularly significant. Representation of pollen grains of *Zea mais*, indicative of food production, is lower in zone GEN-V. High values of *Cyperaceae* indicate that environmental conditions resemble the present-day vegetation dominated by cyperaceous reed swamp. Whether climatic conditions during the Late Holocene were wetter or drier than in the Pleistocene is difficult to establish, but absence of tree ferns during the Late Holocene may suggest a drier climate than in the period reflected by zones GEN-I, GEN-II and GEN-III.

**Discussion and comparison with other pollen record of the southern Colombian Andes**

Two pollen records from cores from the intramontane Pitalito Basin (1°52’N, 76°02’W), are located at the other side of the Central Cordillera at 1300 m altitude (Bakker, 1990). These records span the Last Glacial (core Pitalito-II: ca. 20 000 to 68 000 yr BP) and most of the Holocene (core Pitalito-I: ca. 7150 yr BP to the present). Our zones GEN-I to GEN-III are possibly coeval with the zones R (estimated period 61 500–57 500 yr BP), S (estimated period 57 500–55 500 yr BP) and T (estimated period 55 500–52 500 yr BP) in core Pitalito-II. Arboreal taxa with a more or less similar representation in core Pitalito-II as in core Genagra, are *Urticaceae–Moraceae*, *Quercus*, *Hedyosmum*, *Myrica*, and *Antidaphne*. The following taxa are better represented in Pitalito: *Arecaceae*, *Viburnum*, and *Alnus*. Taxa common in Genagra and rare/absent in Pitalito during this interval are, *Hyeronima*, *Ilex* and *Podocarpus*. However, lower representation of *Ilex* and *Podocarpus* in Pitalito might be expected because of the lower elevation. It therefore seems that this does not contradict our interpretation that zone GEN-III represents the coldest part of the Last Glacial in Pantano de Genagra. Higher representation of *Arecaceae* may simply reflect dominance of a different forest type. High values of *Alnus* most probably point to the presence of swamp forest on poorly drained areas in the Pitalito basin, which has no implication for climatic conditions.

Our zones GEN-IV and GEN-V may be coeval with zone 2Y3 (estimated interval 2800–1100 yr BP), and zone 2Z (estimated period 1100 yr BP–recent) in core Pitalito-I, but time control of the upper part of this core is weak. Pollen zone Z shows the presence of *Zea mais*, *Psidium* and *Manihot*, indicative of agriculture, and high representation of *Cecropia*, indicative of forest disturbance and regeneration. Thus human presence is also indicated. In fact, the Pitalito-II record shows evidence of human impact during most of the Holocene (since ca. 6000 yr BP). Taxa characteristic of the lowermost subandean forest belt, such as *Urticaceae–Moraceae*, *Trema* and *Acalypha* are more frequent in core Pitalito-II compared with Genagra. In general the Pitalito basin seems to have been more densely forested, as the percentage of subandean forest elements reach 40–50% in contrast to 5–15% at Genagra.

The nearest site to Pantano de Genagra is Meremberg at 2500 m altitude in the Valle de La Plata (Alto Rio Magdalena) in the Central Cordillera (Fig. 1). The pollen record has two radiocarbon dates of 12 730 ± 110 yr BP and 7370 ± 110 yr BP. Using pollen density dating (Middeldorp, 1986) the base of the 240-cm core was estimated at 13 700 yr BP (Piñeros-Soler, 1989). The uppermost 50 cm of the core seems to represent the last 2000–3000 yr. The most important trees in zone 3B of the Meremberg pollen record...
are *Hedysosmus*, *Melastomataceae*, *Miconia*, *Urticaceae*, *Alchornea* and *Quercus*. According to Fig. 2 these taxa are beyond their altitudinal range, suggesting either that the zonal vegetation in the Valle de la Plata differs from the Popayán area, and/or that Fig. 2 does not show the full range at the upper limit. The Merembberg site does not show evidence of agriculture, but in another pollen record from Valle de la Plata (Herrera, 1986), *Zea mays* has been recorded since 2700 yr BP. The pollen record from Cabaña San Nicolas, Perfil B (Espejo and Rangel, 1989), close to the volcano Purace, appears to represent the Middle and Late Holocene (Piñeros-Soler, 1988). However, this record lies at 3000 m altitude and, therefore, is difficult to compare with our record at 1750 m.

Archaeological excavations from the San Isidro site, at 1700 m altitude and 40 km north of Popayán (Gnecco, 1995), and La Elvira site, 10 km north of Popayán (Gnecco and Mohammed, 1994), show that the first human occupation dates back to at least the time of the Pleistocene–Holocene boundary. Palaeo-indians were well adapted to hunting and gathering in the tropical montane forests. It is known that plants have been used since about 10,000 yr BP, including fruits of several palms such as *Acrocomia*, seeds of *Persea* and *Virola*, and nuts of *Caryocar*. Interestingly, most of the species of these genera grow in the lowlands (Gnecco, 1995). The first Europeans visited the region in 1535, and during the Spanish Conquest, Don Juan de Amundia and Pedro de Anasco searched for the famous gold treasure ‘El Dorado’ (Arboleda Llorente, 1966). It is known that Indians had settlements in this area before the foundation of Popayán by the Spanish conqueror Don Belalcazar at 1537 (Acosta, 1848).

The pollen assemblages of the uppermost zone may therefore reflect post-Columbian land use after the destruction of the Indian culture in this region. However, the start of zone GEN-V has an interpolated age of 780 yr BP, corresponding to calendar years about AD 1215. This is more than 320 yr before the period of the Spanish Conquest. Therefore, it is suggested that an earlier event may have had an impact on the pre-Columbian culture in this region.

Conclusions

The sedimentary core of Pantano de Genagra spans a part of the Last Glacial and the Late Holocene. The core includes two hiatuses in pollen deposition, which may be erosional hiatuses. Calibration of the pollen record is difficult because there are no modern pollen rain data as a calibration set, although the uppermost Holocene pollen spectra cannot be used as an alternative for calibration because human impact during this period was too strong. However, pollen spectra of glacial age, probably Pleiniglacial, are different from those of the Holocene and indicate the presence of dense subandean forest in the study area at 1750 m elevation. Pollen and spore assemblages during glacial time (zones GEN-I, -II and -III) show changes in the uppermost and lowermost subandean forest belts, suggesting a markedly colder and perhaps wetter climate than during the Late Holocene. Zone GEN-III shows the strongest presence of taxa of the uppermost subandean forest, indicating the coldest period. Before ca. 2300 yr BP, clayey sediments do not contain preserved pollen grains, which may be related to frequent drainage of the swamp, causing oxidation and corrosion of microfossils. The Late Holocene environment has been strongly influenced by deforestation and agriculture at least since the last 2300 yr BP (zone GEN-IV). The expansion of forest in the surroundings of Pantano Genagra, indicate that human impact has been less strong in the last 780 yr BP (zone GEN-V).

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