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Vegetation and environmental constancy in the Neotropical Guayana Highlands during the last 6000 years?

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Abstract

The aim of this paper is to document the Holocene (6000 years BP to the present) vegetation trends on the summit of three tepuis (table mountains), from one of the largest and highest tepuian massifs of the Neotropical Guayana region, the Chimantá, situated in Venezuela. The tepui summits are almost pristine and unique sites to record natural forcings and ecosystem responses. Here, pollen analysis and radiocarbon dating of four peat sequences obtained with a manual Hiller borer are presented, and compared with modern analogues from surface samples, for interpretation. Highland tepuian meadows have been the dominant vegetation type throughout the time interval studied. The sequences studied exhibited different minor vegetation patterns in time, recording primarily local vegetation dynamics, such as lateral variations in the forest–meadow ecotones, and quantitative shifts in the dominant meadow taxa. Moderate climatic shifts formerly reported for other localities were not recorded here, probably because the intermediate altitude and the geomorphological characteristics of the sites studied made them insensitive to subtle regional changes in temperature and moisture, which are hidden by local vegetation shifts. The results of the present study allowed estimation of the magnitude of formerly reported vegetation shifts in the same massif. In the studied sites, the constancy in the vegetation through time cannot be considered only as the result of a high degree of climatic stability, but also the consequence of site insensitivity.

Keywords: vegetation change; Holocene; palynology; palaeoecology; palaeoclimatology; South America; tropics

1. Introduction

In spite of its great biogeographical and evolutionary interest, the Neotropical Guayana Highlands are virtually unknown from a palaeoecological point of view (Rull, 2004c). Physiographically, the region is a complex of extensive erosion surfaces developed on Precambrian sandstones/quartzites, spiked by spectacular table mountains called *tepuis*, or 'stone buds', by indigenous people. Most of the tepuis are in the Venezuelan territory (Steyermark, 1986), having more or less flat summits that can reach up to about 1000 km^2 and 3000 m elevation, and being separated from the surrounding lowlands by vertical cliffs up to 1000

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m high (Huber, 1987, 1995a). The scientific explorations done so far on such remote, totally uninhabited, tepui summits have documented the striking degree of specialization and endemism of their flora, whose origin and evolutionary trends have been the object of debate. Maguire (1970) believed that the flora of the tepui summits was the result of evolution in isolation for millions of years since the Jurassic/Cretaceous, while Steyermark and Dunsterville (1980) claimed that interchange by vertical migration would have been possible during Quaternary glaciations. Another controversial matter is the existence or not of the *Pantepui* refuge during the Last Glacial Maximum (LGM), about 20,000 years before present (20 ky BP). The term Pantepui refers to the ensemble of all the tepui summits, which constitutes a biogeographical province (Berry et al., 1995). The existence of the Pantepui glacial refuge was originally proposed by Mayr and Phelps (1967), based on the present-day distribution of birds, and was further adopted by some botanists to explain the endemism patterns of the flora (Steyermark, 1979). This idea was further questioned by Schubert and Fritz (1985) and Schubert et al. (1986), who proposed the absence of LGM sediments due to aridity. However, this evidence is based on less than 10 point surveys, which is insignificant compared with the total Pantepui surface, of around 5000 km^2 (Huber, 1995a).

The almost-pristine nature of the tepui summits make them unique environments to record the natural environmental variability, and hence to test hypotheses about climatic or non-climatic forcing, and the corresponding ecosystems responses. At present, there is a reasonable amount of botanical and biogeographical information, gathered during more than a century of scientific exploration (Huber, 1995b), but palaeoecological studies are practically non-existent. Preliminary pollen analyses in several tepui summits were mostly inconclusive due to severe constraints imposed by the lack of knowledge of this remote area, mainly in relation to pollen identification and interpretative capacity (Rull, 1991). However, in the last decades, the situation has changed markedly. New pollen-morphological studies have increased the reliability of pollen identification and the number of pollen types identified (Rull, 2003). Furthermore, our ability to interpret observed changes in the pollen record has been enhanced by the recent publication of detailed ecological and biogeographical information of parent taxa (Huber, 1995c; Marchant et al., 2002). Now, accurate vegetation reconstructions based on pollen analysis are possible. Using this information, Rull (2004a,b) documented vertical displacements of vegetation in a relatively high tepui locality (~2250 m altitude) from the Chimantá massif during the Holocene (~6.5 ka BP to present), and estimated that roughly the half of the tepui summits would have been biogeographically connected during the Last Glacial Maximum (LGM), while the other half would not. This suggested that many elements have been isolated for a long time, while others have had the opportunity for vertical migration and interchange through the surrounding lowlands. Such a scenario is consistent with the present-day endemism patterns (Rull, 2004c). During the LGM, a downward displacement of about 1100 m altitude in the vegetation patterns is expected to have occurred, due to a general cooling of around 5 °C in the Neotropical region (Bush et al., 2001; Farrera et al., 1999). A more recent study on the summit of a lower tepui locality (~1400 m altitude) from the Guaiquinima massif, however, seems to account only for millennial-scale moisture changes during the last 8.5 ka BP (Rull, 2005). It was suggested that small temperature-driven vertical shifts of regional extent could not be discarded, but the Guaiquinima locality was insensitive to them, because of the absence of significant ecological boundaries at that altitude (Rull, 2005). Some of the Holocene palaeoclimatic events recorded in the Chimantá and Guaiquinima massifs could be correlated to similar shifts possibly of neotropical extent (Rull, 2004a, 2005).

This paper records the vegetation trends of the last 6000 years BP on three other tepui summits from the Chimantá massif, and discusses their possible causes. The localities studied, although on the same massif where vertical vegetation shifts were recorded previously (Rull, 2004a,b), lie on lower altitudinal levels (1950–2150 m), and are covered by a different plant formation. In order to identify the possible role of altitude on the development of tepui summit vegetation in response to regional climate change, the main objective of the study is to determine to what extent previous evidence of regional temperature and moisture variation is reflected in Holocene pollen records from lower altitudinal sites of the Chimantá massif.

2. Study area

2.1. General characteristics

The Chimantá is one of the largest tepuian massifs of the Guayana region, with a total area of 1530 km^2 (615 km^2 of summit and 915 km^2 of slopes). The summit ranges between 1700 m and 2700 m elevation (Fig. 1) (Huber, 1992, 1995a). Like the other tepuis and tepui massifs, the Chimantá is developed on Precambrian sandstones and quartzites of the Roraima Group overlying the Guiana Shield (Gibbs and Barron, 1983), and is part of the discontinuous Auyán-tepui erosion surface, the highest of the six such surfaces in the Guayana region (Briceño and Schubert, 1990; Schubert, 1987).

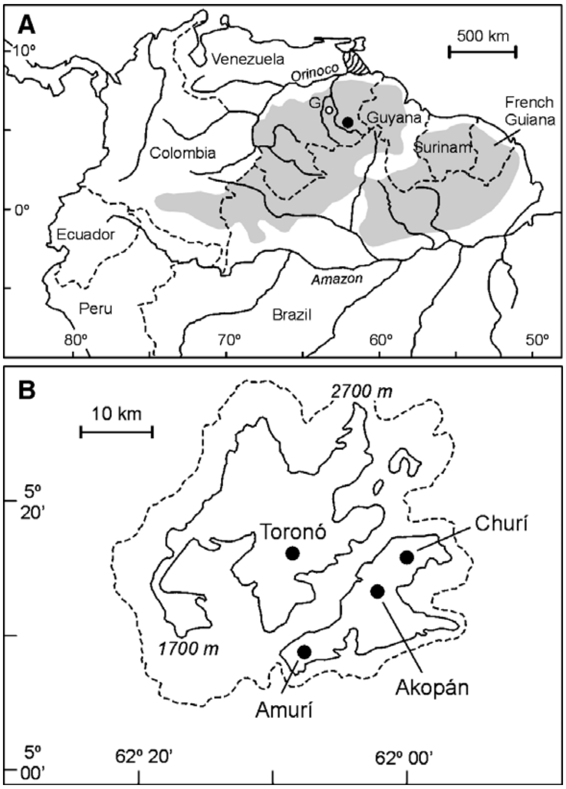

Fig. 1. Location map. A) Relative position of the Chimantá massif (black dot) with respect to northern South America and the Guayana Shield (grey area). G = Guaiquinima massif. B) Location of the three localities studied (black dots), and another locality (Churí-tepui) previously studied (Rull, 2004a). The solid line is the summit complex, and the dashed line indicates the extension of the slopes, vertical cliffs are in between.

The climate of the Chimantá summit is mild and perhumid. The estimated mean annual temperature is 14.1 °C, with a maximum difference of 2 °C in average between the warmest and the coldest month. The estimated average total annual precipitation is 3351 mm, with 8 months (April to November) over 200 mm (up to 500 mm in June). Potential evapotranspiration rates (Holdridge, 1959) are below 70 mm/month on average, reaching 819 mm/year. Strong winds and sudden changes in most climatic parameters are frequent (Huber, 1992).

2.2. Vegetation

The summit vegetation of the Chimantá massif is arranged in a heterogeneous mosaic pattern, related to the great diversity of environments and altitudes. According to Huber (1992), four main vegetation types are present: pioneer communities, herbaceous communities, shrublands and forests.

2.2.1. Pioneer communities

The pioneer communities grow on rocky substrates, previously weathered with the aid of the blue algae *Stigonema panniforme*, and lichens like *Cladonia*, *Cladina* and *Siphula*. These early communities provide the substrate for the establishment of vascular plants such as *Brocchinia reducta* and *Lindmania* spp. (Bromeliaceae), *Stegolepis ligulata* (Rapateaceae), *Tepuia venusta* and *Ledothamnus decumbens* (Ericaceae), *Cyrilla racemiflora* (Cyrillaceae), and *Stomatochaeta cymbifolia*, *Chimantaea huberi* and *Achnopogon virgatus* (Asteraceae). These taxa are usually dwarf forms of the same species that can be found in other tepuian communities.

2.2.2. Herbaceous communities

Two different types of herbaceous communities are present on the Chimantá summits: grasslands and meadows. The grasslands occur on wide, flooded plains, mainly from the centre of the massif (around 2200 m elevation), where woody plants used to be absent. This formation is 0.5 to 1 m high, and covers 90–100% of the soil. It is dominated by several species of Poaceae (*Cortaderia roraimensis*, *Aulonemia* sp.) and Cyperaceae (*Cladium costatum*, *Rhyncocladium steyermakii*, *Rhyncospora* spp.). Other relevant accompanying species are *Xyris* *chimantae* (Xyridaceae), *Leiotrix flavescens* and *Syngonanthus* sp. (Eriocaulaceae), *Trimezia chimantensis* (Iridaceae), *Thesium tepuiense* (Santalaceae), *Juncus densiflorus* (Juncaceae), and some club mosses (*Lycopodium*) and fungi (*Sphagnum*). The meadows, growing on less flooded, peaty soils, are 0.3 to 1 m high and dense broad-leaved communities, dominated by *Stegolepis ligulata*, which is endemic to this massif. Several species of *Xyris* are also very frequent, accompanied by *Everardia erecto-laxa* and *Lagenocarpus rigidus* (Cyperaceae), *Lindmania* sp., *Brocchinia acuminata*, *Brocchinia reducta*, *Heliamphora minor* (Sarraceniaceae), and *Syngonanthus obtusifolius* and *S. acopanensis* (Eriocaulaceae). The only Poaceae present, *Panicum eligulatum*, is rare. Shrubs occur isolated or in small clusters up to 2 m high. Among them, *Maguireothamnus speciosus* (Rubiaceae), *Digomphia laurifolia* (Bignoniaceae), *Macairea cardonae* (Melastomataceae), *Stomatochaeta condensata* (Asteraceae) and *Cyrilla racemiflora* (Cyrillaceae) are the more frequent. These meadows occur between 1800 and 2300 m elevation, which is the upper limit of distribution of *S. ligulata* (Huber, 1992). According to Givnish et al. (2000), fire may have played a major role in the evolution of *Stegolepis, Brocchinia* and *Heliamphora*. This is based on the existence of massive, tightly packed rhizomes that could facilitate survival under moderate ground fires. However, fire events seem to be unusual on the tepui summits (Huber, 1995d).

2.2.3. Shrublands

Shrublands, the more well-developed and diversified tepuian communities, are two types: tepuian shrublands and ‘paramoid’ shrublands. The first occur in all the tepuian summits of the Venezuelan Guayana, while the second are restricted to the Chimantá massif. The tepuian shrublands occur on sandstone and peat substrates. They are dense communities up to 2 m high, with numerous associations and physiognomic variability, impossible to enumerate here. On sandstone, the families Theaceae, Asteraceae, Ochnaceae, Ericaceae, Myrsinaceae and Rubiaceae are important, while on peat, the most frequent elements are *Bonnetia multinervia*, *Mallophyton chimantense* (Melastomataceae), *Aphanocarpus* sp. (Rubiaceae), *Adenanthe bicarpellata* (Ochnaceae) and *Maguireothamnus* sp.). The paramoid shrublands are so named because of their outstanding physiognomic analogies with the Andean páramos, situated above the treeline (Luteyn, 1999). In both, the caulirossulate growth form (stem rosettes) predominates and characterizes the landscape. In the Andes, the caulirossulae plants are of the genus *Espeletia*, while in the Chimantá they belong to *Chimantaea*, both from the family Asteraceae (Huber, 1995c). Only three species of *Chimantaea* form these types of shrublands: *Ch. mirabilis*, *Ch. lanocaulis* and *Ch. humilis*. These communities grow on water-saturated but non-flooded deep peats and can attain up to 1.5 m (*Ch. humilis*), 3 m (*Ch. mirabilis*) or 9 m high (*Ch. lanocaulis*). Other frequent shrubs belong to Ericaceae, Cunoniaceae, Aquifoliaceae, Winteraceae, Cyrillaceae, Asteraceae, Rubiaceae, Melastomataceae, Sarraceniaceae and Bromeliaceae. In the dense herbaceous stratum, the most important elements are the bambusoid *Myriocladus steyermarkii* (Poaceae), *Lindmania* sp., *Everardia* sp., *Heliamphora minor*, and several Xyridaceae, Cyperaceae and Eriocaulaceae. The paramoid shrublands can reach the highermost parts of the massif (Huber, 1992).

2.2.4. Forests

The forests of the Chimantá summit are reduced formations of two types: gallery forests and low tepuian forests. The first are situated along rivers and creeks, and their development is dependent on a regular availability of water and nutrients throughout the year. These forests are very uniform and relatively poor in species, being characterized by two strata: a tree layer and an herbaceous understory. The tree stratum is usually between 4 and 8 m high and is almost monospecific because of the absolute dominance of *Bonnetia roraimae*. Other, less important components of this layer are *Bonnetia tepuiensis*, *B. wurdackii*, *Schefflera chimantensis* and *Sch. umbellata* (Araliaceae), *Spathelia chimantensis* (Rutaceae), *Stenopadus chimantensis* (Asteraceae), *Malanea mycrophylla* (Rubiaceae) and the palm *Geonoma appuniana*. The high canopy density creates an internal microclimate with poor light availability and high humidity, where epiphytes are rare and lichens and musci abound. Where light can penetrate, a low-diversity understory develops in which the large rosettes (up to 1 m diameter) of *Brocchinia tatei* dominate and *B. hechtioides*, *Stegolepis vivipara* and *S. maguireana* can occur. Other herbs are *Celianthus* *imthurniana* (Gentianaceae), *Psychotria crassa* (Rubiaceae), *Baccharis* sp. (Asteraceae), *Viburnum tinoides* (Caprifoliaceae), and several Poaceae, Cyperaceae and Eriocaulaceae.

The low tepuian forests are reduced to some patches on intrusive diabase, from which weathering releases more nutrients and develops richer soils than the surrounding sandstones that constitute the main body of the massif. Floristically, these forests are not very different from the gallery forests, but *Bonnetia roraimae* is not so dominant, while *Stenopadus chimantensis*, *Spathelia chimantensis* and *Podocarpus buchholzii* (Podocarpaceae) are more abundant. Another difference is that canopy density is lower and light penetration higher, thus favouring the development of a shrub and an herbaceous strata. Among the shrubs, *Psychotria* (Rubiaceae), *Clusia* (Clusiaceae), *Poecilandra sclerophylla* (Ochnaceae) and *Miconia acutifolia* (Melastomataceae) are worth mentioning, whereas the main herbs are Poaceae (*Panicum eligulatum*) and Cyperaceae (*Lagenocarpus*, *Everardia* and *Rhynchospora*).

3. Materials and methods

3.1. Sampling

This study was carried out on three tepui summits from the Chimantá massif: the Akopán-tepui, the Amurí-tepui and the Toronó-tepui (Fig. 1). Surface samples representing modern pollen sedimentation were peat scraps, similar in nature to the core peats, taken in transects from the interior of gallery forests to open meadows, up to 300 m from the forest–meadow ecotone. Four peat cores ranging from ~1.5 to 3 m depth were obtained using a Hiller borer (Table 1). The cores were obtained within tepuian meadows, several hundreds of meters from gallery forests, and sampled in the field at 10 cm-depth intervals.

Table 2
Radiocarbon dating of samples, according to Schubert and Fritz (1985) and Rull (1991)

Core	Sample	Depth (cm)	14C years BP	Cal years BP
ACO-1	3	20–30	modern	–
	15–19	150–190	3120 ± 80	3360 (3220–3440)
ACO-2	2–3	10–30	1150 ± 60	1060 (970–1170)
	10–14	90–140	4380 ± 60	4910 (4860–5040)
AMU-1	I	50–100	880 ± 40	780 (730–890)
	II	250–300	5260 ± 40	5990 (5940–6170)
TOR-1	1–2	10–20	− 4 ± 70	–
	16–20	160–200	4040 ± 60	4460 (4420–4780)

One sigma confidence interval for calibrated dates is given in brackets.

3.2. Sample processing, identification and counting

From both modern and core samples, 3 to 4 g were used for pollen analysis after spiking with exotic pollen of *Kochia scoparia* by weight (Salgado-Labouriau and Rull, 1986). The samples were then submitted to HCl and HF digestion and acetolysis, and the slides were mounted in silicone oil without sealing. Identification followed Rull (2003), as well as other more general literature (Roubik and Moreno, 1991; Tryon and Lugardon, 1991; Herrera and Urrego, 1996; Colinvaux et al., 1999). A minimum of 300 pollen grains and spores per sample were counted, but counting sizes were usually higher (commonly 350–450), because counts were continued until a diversity asymptote was reached (Rull, 1987).

3.3. Diagrams and interpretation

Pollen diagrams were plotted and zoned with Psimpoll version 4.10. The pollen sum includes all

Table 1
Sampling information

Tepui	Locality	Coordinates	Elevation (m)	Core	Depth (cm)
Akopán-tepui	XIII	5° 12′ N–62° 05′ W	1950	ACO-1	190
				ACO-2	140
Amurí-tepui	XV	5° 08′ N–62° 07′ W	2150	AMU-1	300
Toronó-tepui	XIV	5° 16′ N–62° 09′ W	2100	TOR-1	200

Localities follow the nomenclature of Huber (1992).

pollen types (fern and allied spores are excluded), and was always above 200 grains, in order to produce statistically significant percentages (Rull, 1987). Zonation was carried out after Optimal Splitting by Information Content (OSIC), and their significance tested with the broken-stick model as used by Bennett (1996). Only pollen types over 1% were considered for zonation. Radiocarbon dates, taken from earlier works on the same cores (Schubert and Fritz, 1985; Rull, 1991), were calibrated with CALIB 4.3 (Stuiver et al., 1998a,b). The interpretation of pollen diagrams was based on modern analogues, derived from the mentioned surface samples, and the known ecological requirements of the taxa found (Huber, 1995c; Marchant et al., 2002; Rull, 2003) (Table 2).

4. Results and interpretation

4.1. Modern pollen record

In general, there is a higher abundance of tree and shrub pollen in the forest sample, and a notable decline in the ecotone and meadows (Fig. 2). Hence the pollen from these taxa has low dispersal power and can be considered indicators of forest vegetation. The most indicative taxa are *Bonnetia roraimae* and *Schefflera* (two of the main components of the tree layer), and the shrubs *Maguireothamnus*, *Ilex* and *Terminalia*-type. The dominant species of these forests, *Bonnetia roraimae*, is especially indicative, because its pollen decreases in an exponential fashion with respect to the distance to the forest and ecotone (Fig. 3). Its dispersal power is extremely low, with falling abruptly from around 10% to less than 1% in a distance of only 100 m. Therefore, values around 10% of this pollen are indicative of in situ gallery forests dominated by this tree. Most of the herbs show no characteristic variations with respect to this gradient, except for *Brocchinia*, *Drosera* and especially *Xyris*. All of them are known to be typical of the herbaceous communities from the tepui summits. The case of *Xyris* is remarkable, due to its nearly linear increase with increasing distance to the forest. It is below 1% in the forest sample, between 10% and 15% in the ecotone, and 20% on average (13–27%) in the meadow samples. Among the spores, *Alsophila*-t is superabundant in the forest sample and decreases notably in the ecotone and the meadows. It is also noticeable that the reticulate monoletes, the verrucate *Polypodium*, the verrucate *Cyathea*, *Pteridium* and *Lycopodium contextum* follow a common pattern. They are scarce in both the forest and the meadow samples, their maximum being situated around the ecotone. Poaceae are overrepresented, since their pollen is around 20–40%, without variations linked to the vegetation type, although grasses are scarce in the tepuian meadows of the Chimantá massif (Huber, 1992). Therefore, grass pollen must have been mostly long-distance transported by wind or overrepesented locally.

4.2. Holocene pollen records

From a lithostratigraphic point of view, all the sequences consisted of monotonous peat accumulations without perceptible clastic inputs. No significant changes in the fibrous organic matrix, colour and composition were observed in the field, and during laboratory processing. Gross microscopical examination of the processed samples confirmed these observations. Palynologically, the sequences are described as follows:

4.2.1. Acopán-tepui

The diagram of ACO-1 is dominated by *Xyris* (27–60%) and Poaceae (15–47%), which show no noticeable stratigraphic trends, although Poaceae slightly increase upwards. The most variable elements are *Bonnetia roraimae*, Ericaceae and *Lycopodium contextum*. The diagram was subdivided into two pollen zones (Fig. 4):

ACO1-I (190–95 cm, 3950–1880 cal years BP). Characterized by the maximum values of *Bonnetia roraimae* (average 8%) and Ericaceae (average 6%), and the scarcity or absence of *Lycopodium contextum*. The values of *B. roraimae* are close to the ecotone values (Fig. 3), and attain the forest values two times in this zone, one at the beginning and the other at about the middle. The other elements do not show significant differences.

ACO1-II (85–0 cm, 1680–0 cal years BP). *Bonnetia roraimae* and Ericaceae decrease drastically (average 1 and 1.4% respectively), and disappear in some levels. Poaceae experiences some increase

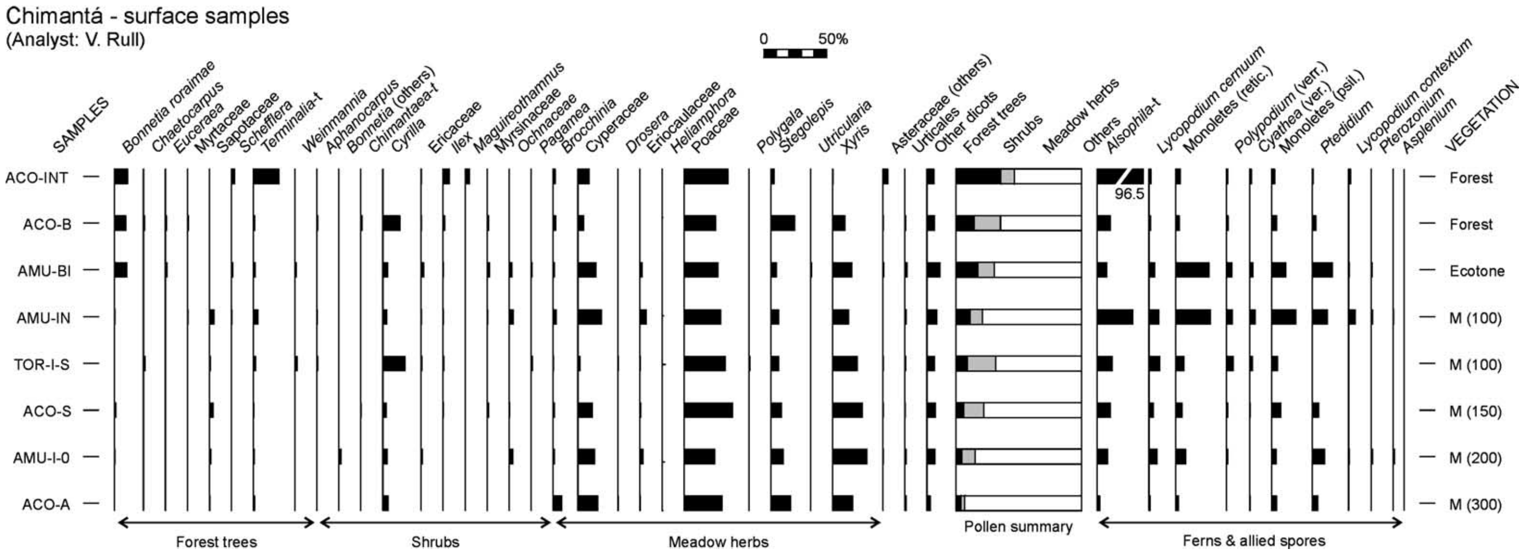

Fig. 2. Percentage pollen diagram for the surface samples taken, ordered according to the distance to the forest (top)–meadow (base) gradient. M = meadows. The number in brackets expresses the distance in m between the sampling point and the forest–meadow ecotone.

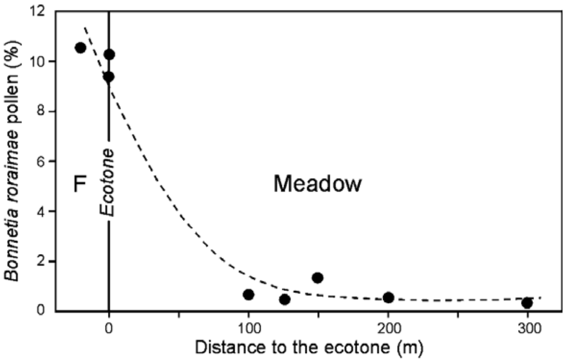

Fig. 3. Decrease of percentages of *Bonnetia roraimae* pollen with the distance to the gallery forest–meadow ecotone. F = Forest.

(average 33%) with respect to the former zone (average 23%). The values of *B. roraimae* are typical for tepuian meadows (Fig. 3). *Lycopodium contextum* increases suddenly.

The transition from zone I to II of this core is interpreted as a vegetation change from a gallery forest to a meadow, which occurred between 1880 and 1680 cal years BP. However, in zone I, alternating maxima and minima of the gallery forest occurred. The maximum forest cover at the site was attained at about 3750 and 2860 cal years BP, when the site was under the canopy. As compared with modern pollen spectra (Fig. 2), the relatively high abundance of shrubs (Ericaceae) and herbs (*Xyris*) suggests a well-developed understory; hence the forest was probably not too dense to totally prevent light penetration. After 1680 cal years BP, the gallery forest abandoned the site, being replaced by a tepuian meadow. The increase of *Lycopodium contextum* is difficult to explain at the present state of knowledge, since the autoecology of the tepuian club mosses is not yet well studied, and no other element of the diagram shows similar trends. Marchant et al. (2002) pointed out that some *Lycopodium* species are indicators of disturbance.

The ACO-2 diagram (Fig. 5) is also dominated by *Xyris* (20–41%) and Poaceae (14–45%), showing similar trends to those recorded in ACO-1; that is, no significant changes in *Xyris* and a subtle increasing trend in Poaceae. The main differences are in *Stegolepis*, with a large peak at the base, and *Bonnetia roraimae*, which in this case is scarce or absent. This diagram was also subdivided into two pollen zones:

ACO2-I (140–125 cm, 5710–5310 cal years BP). This zone is largely dominated by *Stegolepis* (up to 51%), followed by *Xyris* (22–29%) and Poaceae (14–18%), the other elements, including ferns, are under 10%. The abundance of *Stegolepis* is notably higher than that of typical tepuian meadows (maximum 15%), as can be seen in the modern records (Fig. 2), therefore, a meadow with more *Stegolepis* than present is suggested. These types of meadows are not only frequent but also common in the Chimantá massif (Huber, 1992). *Bonnetia roraimae* is very scarce, with values characteristic of the tepuian meadows.

ACO2-II (115–5 cm, 4910–450 cal years BP). A spectacular decrease in *Stegolepis* to values around 10% characterizes this zone. The increasing taxa are *Xyris*, but mainly Poaceae, which reaches 37% at the beginning. The mean assemblage of this zone is almost identical to the present-day assemblages for the site (samples ACO-A and ACO-C in Fig. 2), indicating the same vegetation type. *Bonnetia* disappears, to re-appear later (55 cm, 2480 cal years BP), coinciding with small increases in other trees and shrubs like *Ilex*, *Schefflera*, *Weinmannia*, Myrsinaceae, *Chrysophyllum*, and most spores, mainly *Alsophila*-t, *Polypodium* and *Lycopodium contextum*.

This diagram records the replacement of a meadow dominated by *Stegolepis*, by another in which Poaceae and *Xyris* are the dominants. This occurred between 5310 and 4910 cal years BP A further possible forest expansion is recorded by the coeval small increases of several tree pollen types (probably long-distance transported) around 2480 cal years BP.

4.2.2. Amurí-tepui

Like in Akopán-tepui, the AMU-1 diagram is also dominated by Poaceae (21–36%) and *Xyris* (15–33%), but *Stegolepis* and Cyperaceae are more abundant here. There are no noticeable oscillations in the curves, but some minor trends allowed subdivide the diagram into three zones (Fig. 6):

AMU1-I (300–125 cm, 6510–2080 cal years BP). *Xyris*, Poaceae and *Stegolepis*, followed by Cyperaceae, dominate this zone. *Xyris* and Poaceae oscillate between 18% and 33% without definite trends. *Stegolepis*, however, shows a maximum (18–24%) between 5210 and 4300 cal years BP that, together with a peak of Melastomataceae justifies the

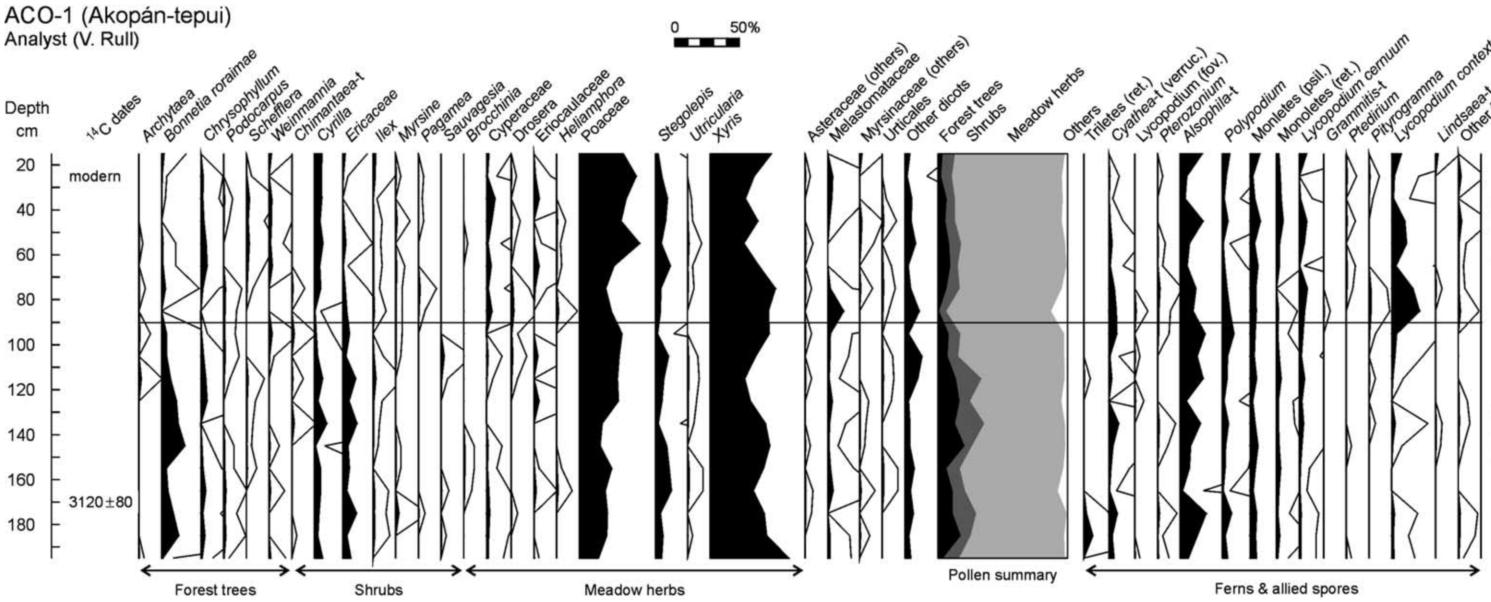

Fig. 4. Percentage pollen diagram for ACO-1. The pollen summary column is based on the elements within the pollen sum.

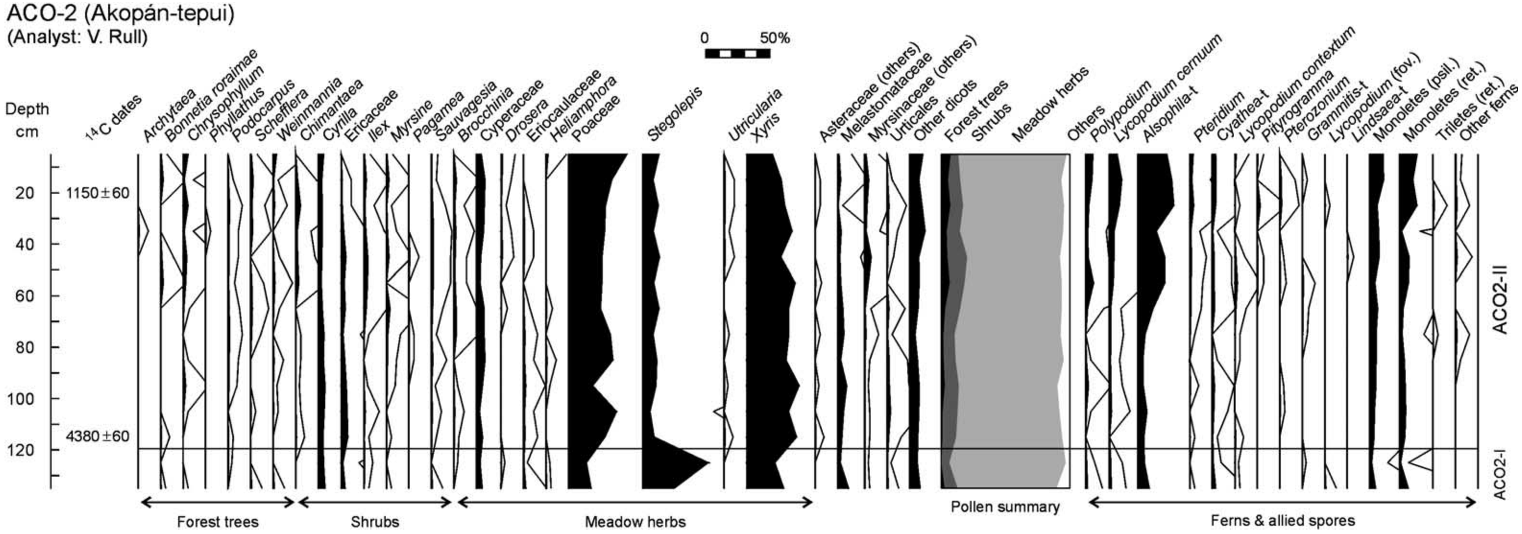

Fig. 5. Percentage pollen diagram for ACO-2. The pollen summary column is based on the elements within the pollen sum.

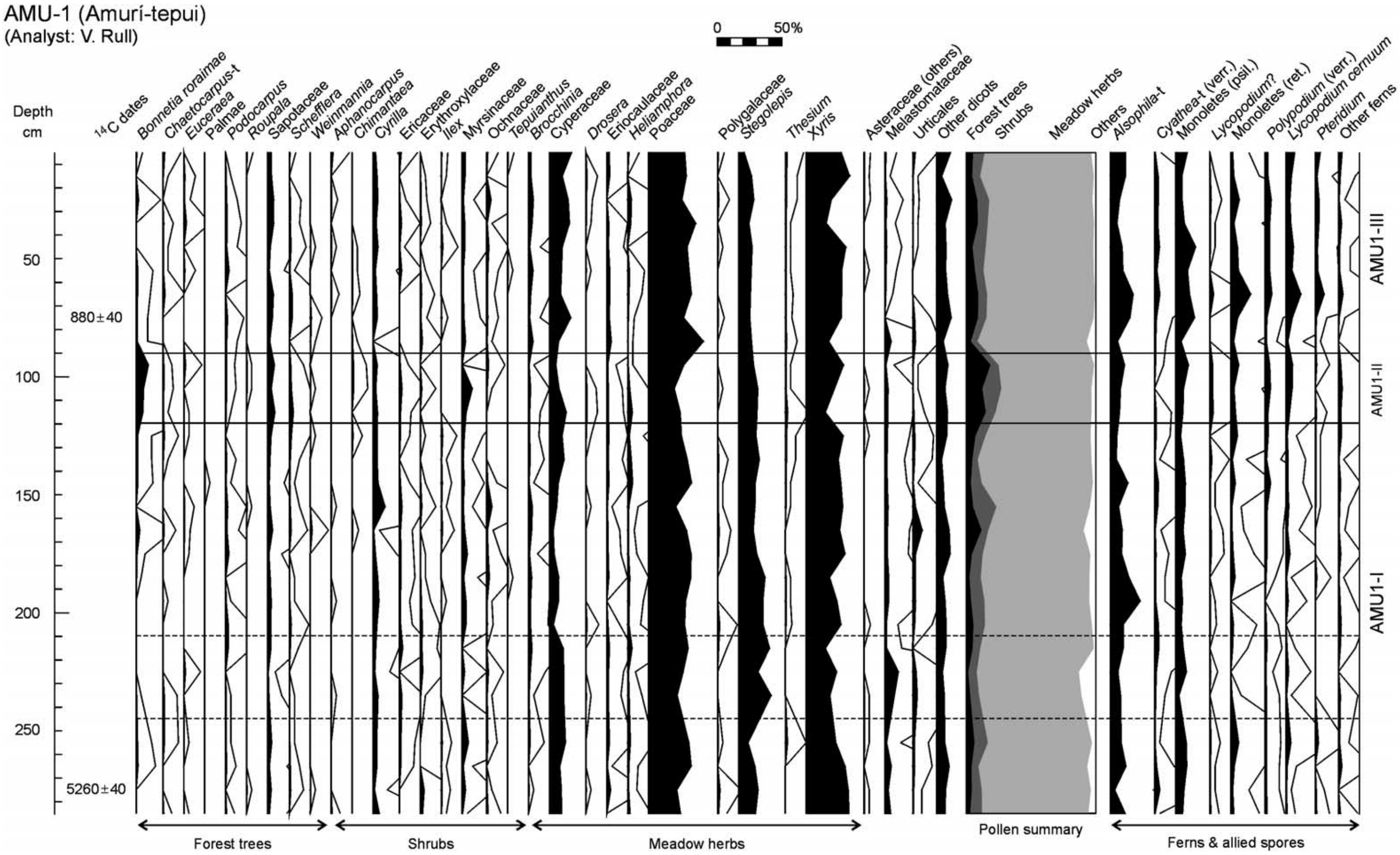

Fig. 6. Percentage pollen diagram for AMU-1. The pollen summary column is based on the elements within the pollen sum.

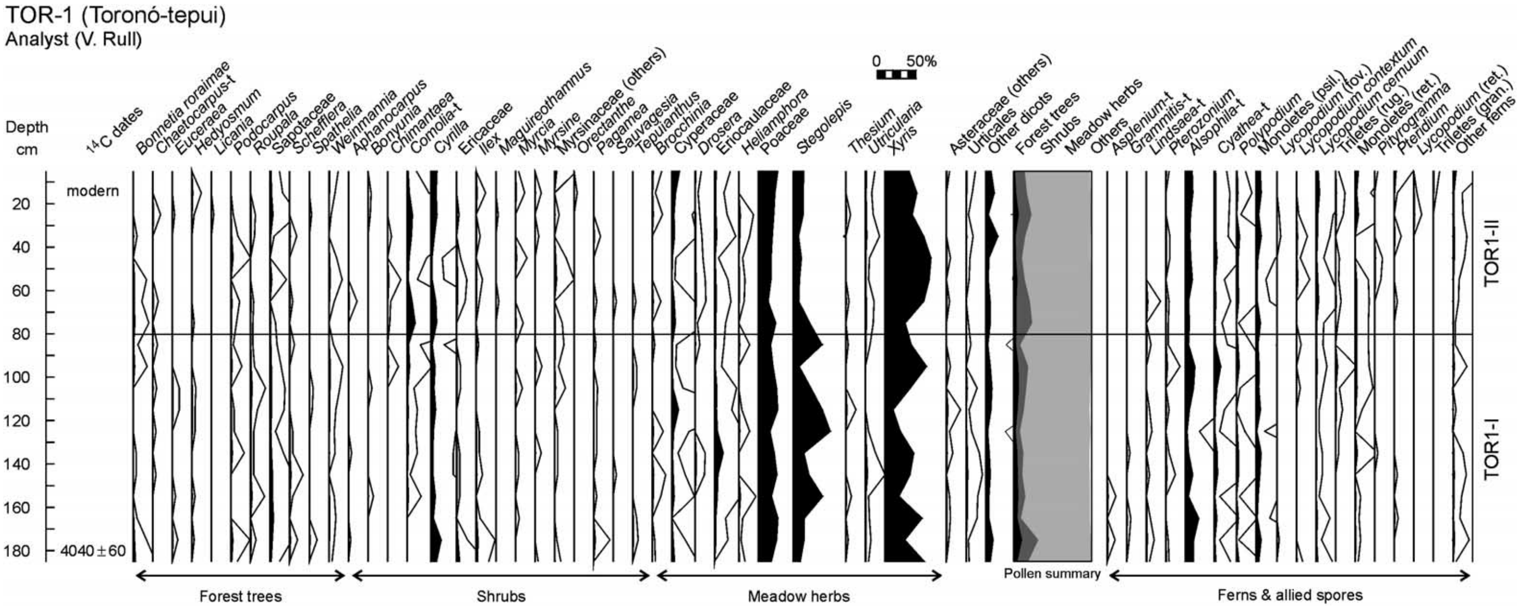

Fig. 7. Percentage pollen diagram for TOR-1. The pollen summary column is based on the elements within the pollen sum.

subdivision into three subzones. The corresponding modern analogue for the zone is sample AMU-1-0 from Fig. 2; hence the vegetation was a tepuian meadow similar to the present, except for the middle subzone, in which *Stegolepis* was codominant. AMU1-II (115–95 cm, 1820–1300 cal years BP). This zone is characterized by the increase of *Bonnetia roraimae* attaining values up to 9.5%, similar to those of the gallery forest and the ecotone (Fig. 3), together with a decreasing trend of *Stegolepis*. Other forest trees and shrubs like Myrsinaceae, *Schefflera* and Sapotaceae also show small increases. Therefore, the forest occupied the site or was very close to it. As in zone ACO1-I, the abundance of herbaceous elements suggests a relatively well-developed understory.

AMU1-III (85–0 cm, 1040–0 cal years BP). This zone is similar to the first one (AMU1-I), but with slightly more *Xyris* (up to 33%), Poaceae (up to 42%) and Cyperaceae (which attains its maximum values in this zone), and less *Stegolepis* (below 12%) and Melastomataceae. In this zone, almost all the spores increase. The vegetation was a typical meadow again.

In general, the sampling site was covered by typical tepuian meadows with variable abundance of *Stegolepis*, except between about 1820 and 1300 cal years BP, when forests reached the site.

4.2.3. Toronó-tepui

The more abundant taxa in the TOR-1 diagram (Fig. 7) are *Xyris* and *Stegolepis*, which experienced important fluctuations (10–58% and 10–47% respectively), followed by Poaceae, less oscillating (15–25%), and *Cyrilla*. Ferns and allied are generally scarce, the most important being *Alsophila*-type. Two zones were defined:

TOR1-I (200–85 cm, 4830–2110 cal years BP). *Xyris* and *Stegolepis*, showing an evident alternating stratigraphic pattern, alternatively dominate this zone. The behaviour of Poaceae is similar to that of *Xyris*, but less pronounced. Eriocaulaceae peaks around the middle of the zone, coinciding with a *Xyris* maximum. On the contrary, a peak of Cyperaceae is found upwards, coinciding with the reverse situation (*Stegolepis* maximum). *Bonnetia roraimae* is present at the beginning and at the end of the zone, while spores are very scarce or absent.

TOR1-II (75–0 cm, 1860–0 cal years BP). This zone is characterized by a strong decrease in *Stegolepis* (13–24%) and a maintained increase of *Xyris* (up to 59%) and *Comolia*-t (up to 10%). *Bonnetia roraimae* is still present but disappears toward the top. The spores increase slightly with respect to the former zone.

The whole diagram reflects a meadow with important dominance variations. In the lower zone, the alternation of *Xyris* and *Stegolepis* is recurrent. The upper zone shows the establishment of a meadow dominated by *Xyris* with no further changes. In general, the stratigraphic patterns of *Cyrilla* and Cyperaceae are similar to that of *Stegolepis*.

5. Discussion and conclusions

The tepuian meadows have been the dominant vegetation of the summits studied for the last 6 ka BP. Only in one locality of Akopán-tepui (ACO-1) and in Amurí-tepui, the gallery forests dominated by *Bonnetia roraimae* have been present, but at different times. *Xyris* and *Stegolepis* have dominated the meadows, with alternating abundances. The most striking fact in the chronostratigraphic correlation of the different vegetation successions is the high degree of asynchronism (Fig. 8). The only more or less synchronous horizon is around 2 ka BP, where vegetation changes occur in all the localities except for ACO-2. However, these changes do not have the same ecological meaning, being inverse in ACO-1 (forest to meadow) and AMU-1 (meadow to forest), and different (*Stegolepis* meadows to *Xyris* meadows) in Toronó-tepui. Another inverse shift occurred around 5 ka BP in ACO-2 and AMU-1, but this time the communities involved are the *Stegolepis*-dominated meadows. On the other hand, the presence of gallery forests in a locality of Akopán-tepui (ACO-1), and its absence in another of the same tepui (ACO-2), separated only by few hundreds of meters, suggest local events such as lateral changes in the drainage patterns or migration of river courses, and the consequent corresponding displacement of the accompanying forests. Therefore, the obvious lack of correlation in the vegetation trends among sites suggests that local vegetation dynamics, rather than

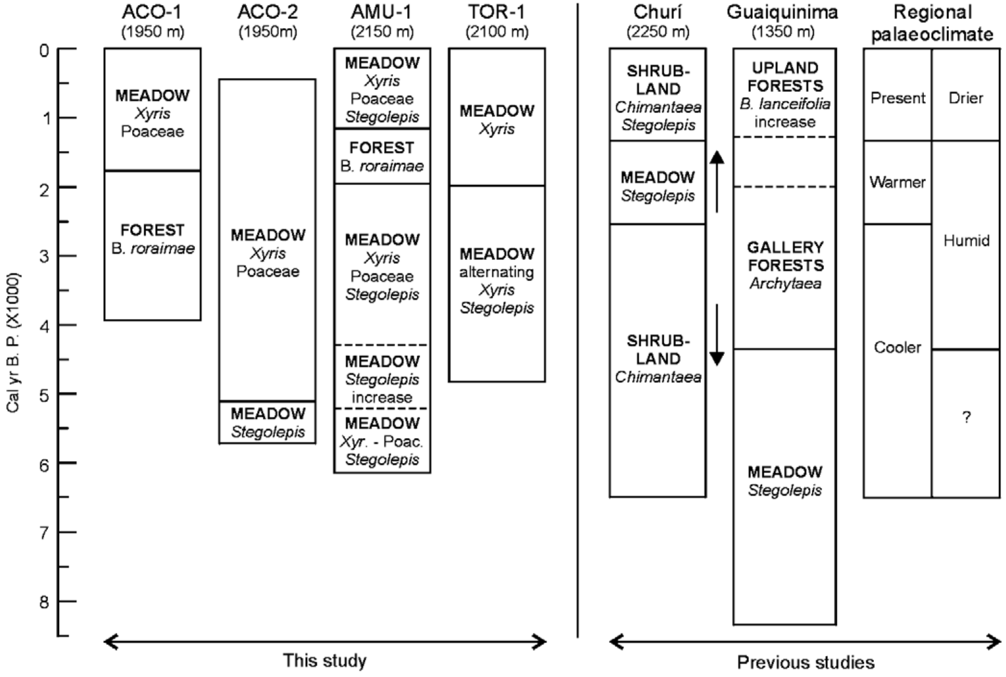

Fig. 8. Chronostratigraphic correlation of the pollen zones defined in the Chimantá diagrams and the vegetation types deduced, compared with former studies and their palaeoclimatic interpretation (Rull, 2004a, 2005). The arrows indicate the upward/downward displacement of sensitive taxa, namely *Stegolepis* and *Chimantaea*, in the Churí section.

climatically induced regional changes, seems to have dominated since the mid-Holocene in the area. Boundaries of pollen zones were estimated by interpolation among radiocarbon dates, hence errors inherent to this procedure should be taken into account; however, chronological disagreement among individual diagrams is of thousands of years, larger than expected under this assumption.

The apparent vegetation constancy on the studied sites might be interpreted in principle as the reflection of climatic stability in the Chimantá tepui summits, during the last 6 ka BP. Similar unchanged trends have been found in other localities of northern South America, especially in wet environments from the Amazon basin and adjacent areas (Bush, 1994, 2002; Colinvaux and de Oliveira, 2001; Colinvaux et al., 2000; and literature therein). Such picture, however, disagrees with previous studies showing some Holocene climatic changes of regional significance, correlated with similar palaeoclimatic events throughout northern South America. For example, temperature-driven vertical migrations of key taxa were reported in another tepui of the same Chimantá massif, situated at higher elevation (Rull, 2004b) (Figs. 1 and 8). The Churí locality is particular because it is situated around the upper limit of distribution of *Stegolepis* (2300 m elevation), and holds extensive paramoid shrublands dominated by *Chimantaea*, typical of the highermost summits of the Chimantá massif (see above). This altitudinal differentiation was the key for the record of climatic trends. The replacement of a *Chimantaea* shrubland by a *Stegolepis* meadow, which nowadays show a clear altitudinal segregation, around 2.5 ka BP, indicated an upward displacement of the vegetation due to a temperature increase, while the augment of *Chimantaea* after 1.3 ka BP was interpreted as a minor temperature decrease (Rull, 2004a) (Fig. 8). Such climatic shifts were in good agreement with records from other neotropical areas, suggesting that they were of sub-continental extent (Rull, 2004a,b). The localities studied in the present paper have been apparently insensitive to these temperature changes, probably because they are not near any altitudinal boundary or feature for which displacement could be a climatic signal. At these altitudes, meadows and forests coexist in a patchy arrangement of *Stegolepis* meadows and *Bonnetia* gallery forests controlled by drainage patterns; therefore the mutual replacement of these communities should be interpreted as lateral changes in local moisture conditions and no vertical displacements. This would allow roughly estimate the vertical displacement recorded at Churí, which should have been of one or few hundreds of meters altitude, since the descending ‘paramoid’ shrublands did not reach the sites studied here, which lie only 100–300 m below the Churí site. A similar situation was reported for the northern Andean páramos, the typical communities above the tree line (Luteyn, 1999), showing physiognomic and taxonomical affinities with the tepuian ‘paramoid’ shrublands (Huber, 1992). In them, climatically triggered vegetational shifts were undoubtedly recorded during the Holocene (review in Salgado-Labouriau, 1989 and Rull, 1999); however, some localities did not show any significant vegetation change after detailed pollen analyses, because of the lower magnitude of the vertical displacement as compared to the distance from the coring site to the closest significant ecological boundary (Salgado-Labouriau et al., 1992).

Concerning humidity changes, the Guaiquinima record is consistent with other results from northern South America showing a moister phase between about 4.5 and 2 ka BP, followed by a drier period extending up to now (Rull, 2005). Such a trend could not be deduced from the records studied here (Fig. 8). A possible explanation is that communities submitted to very high precipitation regimes could have been able to absorb comparatively small moisture changes. This is supported by other palaeoecological data from northern South America, which show that areas receiving above 2500 mm/year and with less pronounced dry seasons, have been able to accommodate Pleistocene and Holocene climatic changes, without substantial vegetation change (Bush, 1996, 2002). However, the Guaiquinima summit has a precipitation regime similar to that of Chimantá. The basic difference is that in the Guaiquinima site, which is at the top of a hill, the only source of moisture is rain, so any change in the water balance is a climatic signal, whereas in the Chimantá localities, usually on alluvial plains, water currents can migrate laterally (and the gallery forests with them) thus obscuring eventual minor climate shifts.

Another intriguing observation is that, although the meadows were dominated by *Xyris* and *Stegolepis*, these taxa show an inverse and alternating behaviour in the diagrams. At the present state of knowledge, it is not possible to attribute these shifts to the action of some environmental factor (climate, fire, etc.) that affected *Stegolepis* and *Xyris* in an opposite manner, or to internal ecosystem dynamics. Neither detailed field surveys nor ecophysiological studies are available to explain this fact. Previous vegetational studies showed that flooding is a major factor determining the composition of herbaceous communities in the tepuian summits (Huber, 1992). Therefore, it is possible that the edaphic water regime could have played some role. If this is governed by climate or not is a remaining question. Another possibility to explain the observed recurrence is fire incidence. As previously stated, *Stegolepis* might resist fires of moderate intensity and duration, due to special morphological adaptations (Givnish et al., 2000), while *Xyris* do not. Therefore, their alternating abundances could be theoretically due to the existence of recurrent fire events. However, the low present-day incidence of fires on the tepui summits (Huber, 1995d) and the scarcity/absence of charcoal in the studied sediments seem to argue against this hypothesis.

In summary, eventual environmental shifts, if occurred, were not strong enough to modify the plant communities of the studied sites to an extent that can be recorded through vegetation changes. Therefore, the observed vegetation constancy cannot be considered only the reflection of a high degree of climatic stability, but also the consequence of site insensitivity. Therefore, biotic constancy through time does not necessarily indicate environmental stability in the tepui summits. This situation contrasts with the above-mentioned Holocene temperature and humidity shifts at higher altitudes (Rull, 2004a), and also with moisture variations that caused significant lake-level oscillations and conspicuous community replacements in the adjacent lowlands and midlands (Rull, 1992, 2005). These differential responses to the environmental shifts notably enhance the heterogeneity in space and time, thus creating more long-term opportunities for biotic differentiation, and contributing to the generation and maintenance of the high biodiversity of the Guayana region. From a methodological point of view, the recorded heterogeneity clearly shows the unsuitability of generalisations based on one or few palaeoecological records in the Guayana region, and in the Neotropics, in general.

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References

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytol. 132, 155–170.

Berry, P.E., Huber, O., Holst, B.K., 1995. Floristic analysis and phytogeography. In: Berry, P.E., Holst, B.K., Yatskievych, K. (Eds.), Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden Press, St. Louis, pp. 161–191.

Briceño, H.O., Schubert, C., 1990. Geomorphology of the Gran Sabana, Guayana Shield, southeastern Venezuela. Geomorphology 3, 125–141.

Bush, M.B., 1994. Amazonian speciation, a necessarily complex model. J. Biogeogr. 21, 5–17.

Bush, M.B., 1996. Amazonian conservation in a changing world. Biol. Conserv. 76, 219–228.

Bush, M.B., 2002. Distributional change and conservation on the Andean flank, a palaeoecological perspective. Glob. Ecol. Biogeogr. 11, 463–473.

Bush, M., Stute, M., Ledru, M.-P., Behling, H., Colinvaux, P.A., de Oliveira, P.E., Grimm, E.C., Hooghiemstra, H., Haberle, S., Leyden, B.W., Salgado-Labouriau, M.L., Webb, R., 2001. Palaeotemperature estimates for the lowland Americas between 30° S and 30° N at the Last Glacial Maximum. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, San Diego, pp. 293–306.

Colinvaux, P.A., de Oliveira, P.E., 2001. Amazon plant diversity and climate through the Cenozoic. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166, 51–63.

Colinvaux, P.A., de Oliveira, P.E., Moreno, J.E., 1999. Amazon Pollen Manual and Atlas. Harwood Academic Publ., Amsterdam.

Colinvaux, P.A., de Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales, The failure of the aridity and refuge hypotheses. Quat. Sci. Rev. 19, 141–169.

Farrera, I., Harrison, S.P., Prentice, I.C., Ramstein, G., Guiot, J., Bartlein, P.J., Bonnefille, R., Bush, M., Cramer, W., von Grafenstein, U., Holmgreen, K., Hooghiemstra, H., Hope, G., Jolly, D., Lauritzen, S.-E., Ono, Y., Pinot, S., Stute, M., Yu, G., 1999. Tropical climates at the Last Glacial Maximum, a new synthesis of terrestrial paleoclimate data. I. Vegetation, lake-levels and geochemistry. Clim. Dyn. 15, 823–856.

Gibbs, A.K., Barron, C.N., 1983. The Guiana Shield Reviewed. Episodes 2, 7–14.

Givnish, T.J., Evans, T.M., Zjhra, M.L., Patterson, T.B., Berry, P.E., Sytsma, K.J., 2000. Molecular evolution, adaptative radiation, and geographic diversification in the amphiatlantic family Rapateaceae, evidence from ndhF sequences and morphology. Evolution 54, 1915–1937.

Herrera, L.F., Urrego, L.E., 1996. Atlas de Polen de Plantas Útiles y Cultivadas de la Amazonia Colombiana. Tropenbos Colombia, Bogotá.

Holdridge, L.R., 1959. Simple method for determining potential evapotranspiration from temperature data. Science 130, 572.

Huber, O., 1987. Consideraciones sobre el concepto de Pantepui. Pantepui 2, 2–10.

Huber, O., 1992. El maciso del Chimantá: Un Ensayo Ecológico Tepuyano. O. Todtmann, Caracas.

Huber, O., 1995a. Geographical and physical features. In: Berry, P.E., Holst, B.K., Yatskievych, K. (Eds.), Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden Press, St. Louis, pp. 1–61.

Huber, O., 1995b. History of botanical exploration. In: Berry, P.E., Holst, B.K., Yatskievych, K. (Eds.), Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden Press, St. Louis, pp. 63–95.

Huber, O., 1995c. Vegetation. In: Berry, P.E., Holst, B.K., Yatskievych, K. (Eds.), Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden Press, St. Louis, pp. 97–160.

Huber, O., 1995d. Conservation of the Venezuelan Guayana. In: Berry, P.E., Holst, B.K., Yatskievych, K. (Eds.), Flora of the Venezuelan Guayana. Volume 1. Introduction. Missouri Botanical Garden Press, St. Louis, pp. 193–218.

Luteyn, J.L., 1999. Paramos. A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. Missouri Botanical Garden Press, St. Louis.

Maguire, B., 1970. On the flora of the Guayana Highland. Biotropica 2, 85–100.

Marchant, R., Ameida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., Kapelle, M., de Oliveira, P., Teixeira, A., Lozano-García, S., Hooghiemstra, H., Ledru, M.-P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Páez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev. Palaeobot. Palynol. 121, 1–75.

Mayr, E., Phelps, W.H., 1967. The origin of the bird fauna of the southern Venezuelan highlands. B. Am. Mus.. Nat. Hist. 136, 269–328.

Roubik, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden Press, St. Louis.

Rull, V., 1987. A note on pollen counting in palaeoecology. Pollen Spores 29, 471–480.

Rull, V., 1991. Contribución a la paleoecología de Pantepui y la Gran Sabana, clima, biogeografía y ecología. Scientia Guayanae 2, 1–133.

Rull, V., 1992. Successional patterns of the Gran Sabana (South-eastern Venezuela. Vegetation during the last 5,000 years, and its responses to climatic fluctuations and fire). J. Biogeogr. 19, 329–338.

Rull, V., 1999. Palaeoclimatology and sea-level history in Venezuela. New data, land–sea correlations and proposals for future studies in the frame of the IGBP-PAGES Project. Interciencia 24, 92–101.

Rull, V., 2003. An illustrated key for the identification of pollen from Pantepui and the Gran Sabana (eastern Venezuelan Guayana). Palynology 27, 95–129.

Rull, V., 2004a. An evaluation of the Lost World and the Vertical Displacement hypotheses in the Chinmanta massif, Venezuelan Guayana. Glob. Ecol. Biogeogr. 13, 141–148.

Rull, V., 2004b. Is the 'Lost World' really lost? Palaeoecological insights on the origin of the peculiar flora of the Guayana Highlands. Naturwissenschaften 91, 139–142.

Rull, V., 2004c. Biogeography of the 'Lost World', a palaeoecological perspective. Earth-Sci. Rev. 67, 125–137.

Rull, V., 2005. Palaeovegetational and palaeoenvironmental trends in the summit of the Guaiquinima massif (Venezuelan Guayana) during the Holocene. J. Quat. Sci. 20, 135–145.

Salgado-Labouriau, M.L., 1989. Late Quaternary climatic oscillations in the Venezuelan Andes. Biol. Int. 18, 12–14.

Salgado-Labouriau, M.L., Rull, V., 1986. A method of introducing exotic pollen for paleoecological analysis of sediments. Rev. Palaeobot. Palynol. 47, 97–103.

Salgado-Labouriau, M.L., Bradley, R.S., Yuretich, R., Weingarten, B., 1992. Palaeoecological abalysis of the sediments of lake Mucubají, Venezuelan Andes. J. Biogeogr. 19, 317–327.

Schubert, C., 1987. Origen de la topografía tepuyana, Una hipótesis. Pantepui 2, 11–14.

Schubert, C., Fritz, P., 1985. Radiocarbon ages of peat, Guayana Highlands (Venezuela). Naturwissenschaften 72, 427–429.

Schubert, C., Briceño, H.O., Fritz, P., 1986. Paleoenvironmental aspects of the Caroní–Paragua river basin (southeastern Venezuela). Interciencia 11, 278–289.

Steyermark, J.A., 1979. Plant refuge and dispersal centres in Venezuela, their relict and endemic element. In: Larsen, K., Holm-Nielsen, L. (Eds.), Tropical Botany. Academic Press, New York, pp. 185–221.

Steyermark, J.A., 1986. Speciation and endemism in the flora of the Venezuelan tepuis. In: Vuilleumier, F., Monasterio, M. (Eds.), High-altitude Tropical Biogeography. Oxford Univ. Press, New York, pp. 317–373.

Steyermark, J.A., Dunsterville, G.C.K., 1980. The lowland floral element of the summit of Cerro Guaiquinima and other cerros of the Guayana Highlands of Venezuela. J. Biogeogr. 7, 285 – 303.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G., van der Plicht, J., Spurk, M., 1998a. INTCAL98 Radiocarbon age calibration 24,000–0 cal BP. Radiocarbon 40, 1041 – 1083.

Stuiver, M., Reimer, P.J., Braziunas, T.F., 1998b. High-precision radiocarbon age calibration for terrestrial and marine samples. Radiocarbon 40, 1127 – 1151.

Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta. Springer-Verlag, New York.