

Palaeovegetational and palaeoenvironmental trends in the summit of the Guaiquinima massif (Venezuelan Guayana) during the Holocene

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ABSTRACT: The summits of the table mountains (*tepui*) from the Neotropical Guayana region are remote environments suitable for palaeoecological studies with evolutionary, biogeographical and palaeoclimatic implications. Here, using palynological analyses of two radiocarbon-dated peat bogs from a *tepui* summit, the Holocene palaeovegetational trends are reconstructed, and related to possible forcing factors. Because of the pristine character of the Guaiquinima summit, the recorded palaeoenvironmental changes are probably due to natural causes, which makes them valuable archives of the natural component of climatic change at a millennial time scale. The sequence begins with pioneer communities or meadows similar to present-day ones, between about 8.4 and 4.5 kyr BP. After this date, and until about 2 kyr BP the expansion of gallery forests suggests an increase in precipitation, documented also at regional (Neotropical) level. Between ca. 2 kyr BP and the last century, gallery forests are replaced by forests characteristic of the upper Guaiquinima altitudes, coinciding with a regional phase of reduced moisture. The present-day meadows, established relatively quickly during the last century, substituted the former upland forests. In the locality studied, the main controlling factor of the vegetation during the Holocene seems to have been the moisture balance. In contrast to other *tepui* summits, there is no clear evidence for changes linked to temperature oscillations. This could be due to the elevation of the site, far from any characteristic ecological boundary, that makes it insensitive to this parameter. Copyright © 2005 John Wiley & Sons, Ltd.



KEYWORDS: Guayana Highlands; palynology; palaeosuccession; palaeoclimates; Holocene

Introduction

The Venezuelan Guayana is a region of considerable and broad biogeographical, evolutionary and palaeoclimatic interest (Rull, 2004a and 2004c). Among others, the disputed origin of the flora from the remote flat tops of its sandstone table mountains or *tepuis*, and the potential for the *Pantepui* as refuge during the Last Glacial Maximum (LGM), have been the object of intense debate. The flora of the *tepui* summits shows a high degree of specialisation and endemism which has been explained by assuming a long evolutionary process in isolation, due to topographical barriers in the form of huge vertical cliffs that separate these summits from the lowlands (Maguire, 1970; Brewer-Carías, 1980). In contrast, Steyermark and Dunsterville (1980) and Huber (1988) claim the existence of potential migrational pathways that could have promoted the merging and dispersal of high-*tepuian* floras in lowland

regions during the glaciations, when the vegetation was displaced downward owing to cold climates. Similarly, the concept of a *Pantepui* refuge (Mayr and Phelps, 1967) as a biogeographical entity embracing all the *tepui* summits above 1500 m, was created to explain the survival of summit floras during glaciations, when climates were purportedly unfavourable for their development in adjacent areas (Steyermark, 1979). Its existence has been questioned, however, arguing that these *tepui* summits were also arid or semi-arid and devoid of vegetation, during the LGM. This hypothesis is based on the apparent absence of peat of Pleistocene age on the *tepuis* (Schubert and Fritz, 1985; Schubert *et al.*, 1986). Nevertheless, these hypotheses are largely based on present-day phytogeographical observations and need appropriate palaeoecological data to be tested. Furthermore, the *tepui* summits are particularly suitable to record natural climatic trends and corresponding ecosystem responses, because they are practically pristine. Indeed, indigenous communities living in surrounding lowlands do not climb the *tepui* summits, which are practically unknown to them (Huber, 1987). Scientific exploration carried out over more than one century (Huber, 1995b) has produced a great amount of data with negligible disturbance and, fortunately, lucrative activities have not been well developed so far.

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Previous palynological studies of the *tepuis* provided mostly inconclusive evidence for palaeoecological trends, partly because of the lack of ecological knowledge of this remote area, and partly because of problems with pollen identification and interpretation (Rull, 1991; Rull *et al.*, 1988). However, in recent years, new pollen-morphological studies have increased the reliability of pollen identification and the number of pollen types identified (Rull, 2003). Also, the interpretative capacity has been enhanced with abundant ecological and biogeographical information of the taxa involved (Berry *et al.*, 1995; Marchant *et al.*, 2002; Rull, 2003). Palaeoecological studies, thus, have documented vertical displacements of vegetation linked to temperature and moisture oscillations during the Holocene, which, together with physiographical analysis, has suggested that both isolation and floral mixing from the lowlands are needed to explain the origin of the *tepuian* flora (Rull, 2004a, 2004b). Also, millennial-scale vegetation cycles, possibly linked to periodic climate oscillations, have been found (Rull, in preparation). Another study on a low sandstone tableau from Colombian Guayana allowed reconstruction of the ecological succession during the last century (Berrío *et al.*, 2003). However, palynological and, in general, palaeoecological studies, are still too scarce in the Guayana highlands to adequately substantiate evolutionary, biogeographical and palaeoclimatic hypotheses. This paper presents new palynological reconstructions of Holocene vegetation and palaeoenvironments on top of the Guaiquinima tableau, that Steyermark and Dunsterville (1980) studied, which led them to propose the hypothesis of vertical migration.

Study area

Physiography and climate

The landscape of the Venezuelan Guayana is one of the most diversified of South America, owing to the presence of wide plains, deep valleys and impressive rock massifs (Huber, 1995a). It is developed on the Precambrian sandstones and quartzites of the Roraima Group overlying the Guiana Shield (Gibbs and Barron, 1983) (Fig. 1). From a geomorphological point of view, six planation surfaces or peneplains have been described, from the lowermost, the Orinoco floodplain (0–50 m), to the uppermost, the Auyán-tepui surface (2000–2900 m), represented by the summits of the higher *tepuis* or table mountains (Schubert, 1987; Briceño and Schubert, 1990). Physiographically, the region has been subdivided into lowlands (0–500 m), uplands (500–1500 m) and highlands (1500–3000 m), each with particular environmental and ecological conditions (Huber, 1995a).

The Cerro Guaiquinima or *Waikin-ima tepui* is one of the largest and least explored sandstone table mountains of the Guayana region. It is situated between about 5° 35'–6° 05' N latitude and 63° 20'–63° 45' W longitude (Fig. 1), covering an extension of 1096 km². The summit proper has an area of 680 km², and is a NW–SE inclined plain, ranging from 720 m (Fig. 1) to 1650 m elevation (Steyermark and Dunsterville, 1980; Huber, 1995a). This table mountain is part of the Kamarata or Wonkén erosion surface (Schubert, 1987; Briceño and Schubert, 1990), and most of it belongs to the uplands rather than the highlands, except for the northernmost part, which can be considered true highland. Topographically, the Guaiquinima summit is not isolated from the surrounding lowlands (about 300 m elevation), but connected to them through the valleys of their two major drainage systems (Steyermark and

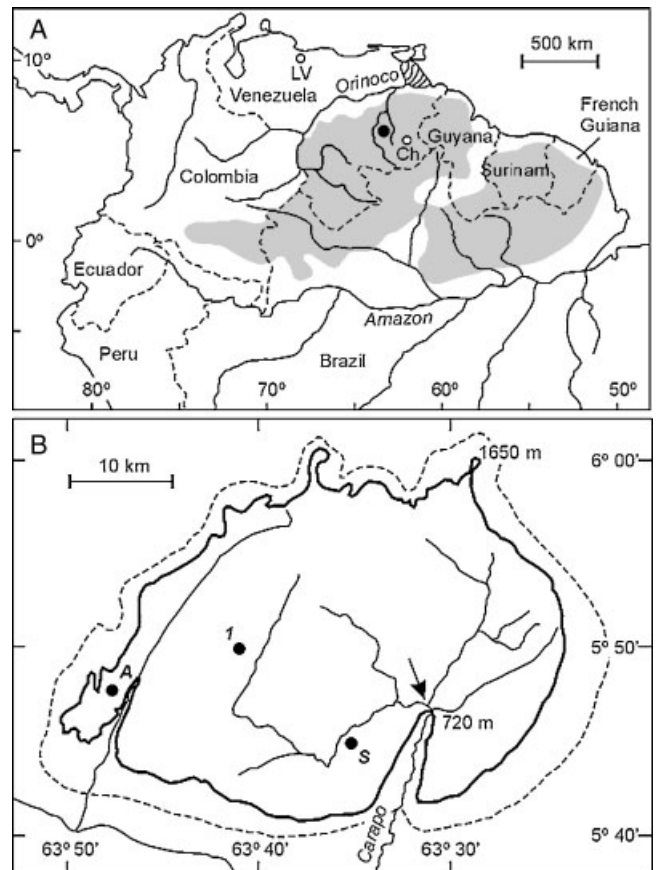


Figure 1 Location map. (A) Map of northern South America, showing the extension of the Guayana Shield (grey area), and the Guaiquinima massif (black dot). LV = Lake Valencia, Ch = Chimantá massif. (B) The Guaiquinima massif, showing the three localities sampled in this study (black dots). The arrow indicates the area represented in Fig. 2(B). Solid contour indicates the summit area, and dashed line indicates the base of the slope. Redrawn from Steyermark and Dunsterville (1980) and Huber (1995a)

Dunsterville, 1980). The climate is sub-mesothermic ombrophilous (SmO) in the uplands, and mesothermic ombrophilous (MO) in the highlands, above 1500 m elevation (Huber, 1995a). Although no climatic data are available, SmO climate is defined as humid submontane, with annual average temperatures from 18 to 24 °C, high precipitation and no dry season (Huber, 1995a). In the MO climate, the average temperatures are lower (12 to 18 °C), and the average annual precipitation is high (2500 mm) to very high (3500 mm). There is some reduction in precipitation from December to March, owing to the seasonal northward migration of the Intertropical Convergence Zone (ITCZ), but it does not represent a true dry season. The formation of dense mists is common, and winds and thunderstorms are frequent. In general, the temperature lapse rate for the Guayana region is 0.6 °C per 100 m altitude (Huber, 1995a).

Flora and vegetation

The flora of Guaiquinima is composed of lowland, upland and highland elements. The degree of endemism is low (9.5%). According to Steyermark and Dunsterville (1980), the lowland component is noteworthy. These authors state that 97 of the 449 known species of the Guaiquinima summit (21.6%) are characteristic of lower elevations (50–500 m). According to

them, this is the result of the migration and interchange with the adjacent plains due to vertical shifts linked to Pleistocene glacial–interglacial alternation. The main migrational route proposed by these authors is the valley of the Carapo river (Fig. 1). Huber (1995c) agrees with this hypothesis, but points out that the occurrence of lowland elements in the Guaiquinima summit merely confirms the transitional character of its flora.

The vegetation cover of the summit of Cerro Guaiquinima is dense and almost continuous, but largely unexplored. On the basis of aerial photographs, a first tentative subdivision into five categories was established by Steyermark and Dunsterville (1980). The more extensive type (covering about 40% of the summit area) are undifferentiated forests, which grow roughly above 1000 m elevation and reach the higher altitudes. They form a belt surrounding the central sector of the summit. Scrubs, either with or without patches of savanna, cover about 30% of the area, mainly in the south-central portion. Savannas with patches of forest occupy 15% of the summit, being especially well developed in the highest parts of the northern and western sectors. The rest of the area (15%) is covered by open rock with scrub or very open woods, which predominate in the eastern sector of the summit. Further exploration clarified the composition and altitudinal arrangement of some of these vegetation types, which at present are broadly classified into three main types: forests, scrubs and meadows (Huber, 1995c).

Forests still remain largely unknown. They belong to the general type of montane cloud forests, present on slopes and summits of the tepuis, roughly between 800 and 1500 m elevation. Although no studies are available for the Guaiquinima massif, surveys from other mountains have shown that these forests used to be low to medium in height (up to 25 m tall), dense, ombrophilous and evergreen, with flattened crowns and coriaceous leaves, with abundant epiphytic mosses, ferns and orchids, and with a well developed understorey of shrubs and herbs (Huber, 1995c). Scrubs develop mainly in the southern sector, between 800 and 1200 m. In locality S (Fig. 1), situated at about 900 m elevation, a tall scrub or low forest of this type was recognised in this study (Figs 1, 2). It is dominated by *Platycarpum rhododactylum* (Rubiaceae) and *Terminalia quintalata* (Combretaceae), other components being *Myrcia* and other Myrtaceae, *Bonyiunya minor* (Loganiaceae), *Calliandra* (Fabaceae), *Gongylolepis* and *Stomatochaeta* (Asteraceae), Sapotaceae, *Poecilandra* (Ochnaceae), and *Aldina* (Fabaceae). The shrub *Bonnetia lanceifolia* (Theaceae), common in the scrubs of other Guayana mountains (Huber, 1995c) and in the highermost meadows (see below), was scarce at this locality, owing possibly to its low elevation (Huber, personal communication, 1987). A well-developed understorey with shrubs such as *Meriania urceolata* (Melastomataceae), and herbs such as *Neurolepis* (Poaceae), Cyperaceae, *Xyris*, (Xyridaceae), *Axonopus* and *Trachipogon* (Poaceae) and small unknown palms, was present. Ferns (represented by *Lindsaea*), and epiphytes were scarce. Forest clearances were occupied by herbaceous communities of aquatic or semi-aquatic vegetation, which formed incipient peat accumulations surrounded by shrubs of *Bonnetia sessilis*, *Meriania urceolata* and *Blepharandra fimbriata*. Along rivers, monospecific stands of *Pacaraimea* (Dipterocarpaceae) were common. Changing river courses and flooding remove shore vegetation and peat from time to time, and the exposed bare rock is re-colonised by *Clusia* (Clusiaceae) and *Stegolepis* (Rapateaceae) (Huber and Rull, field observations).

The upland meadows grow on the highest parts of the Guaiquinima summit, above 1200 m. The endemic *Stegolepis squarrosa* (Rapateaceae) dominates these broad-leaved meadows growing on peat, which correspond to the so-called

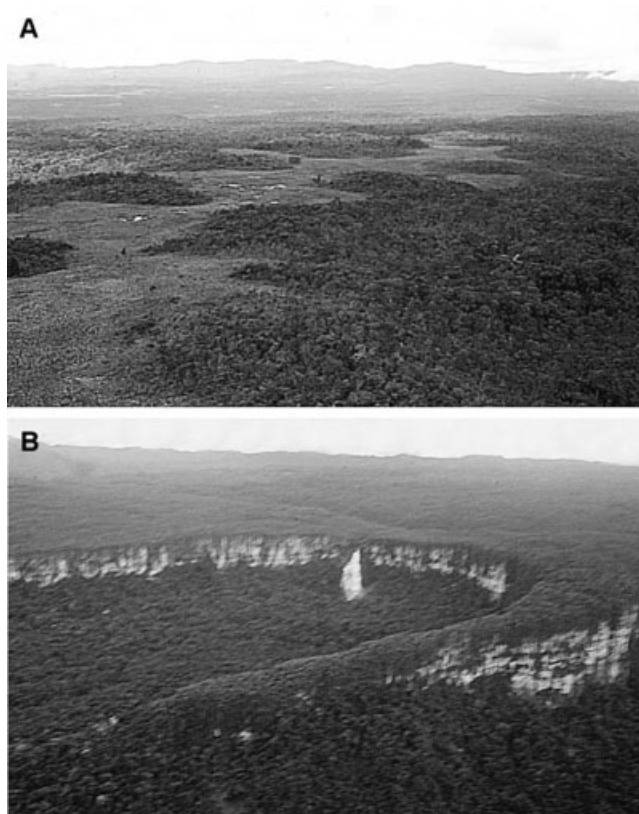


Figure 2 Aerial views of the sampling sites; see Fig. 1 for location. (A) Locality 1 (1350 m elevation), where the two peat cores were obtained. Note the marshy *Stegolepis* meadows at the top, surrounded by high forests and gallery forests dominated by *Archytaea*, at the flanks. (B) The Szczerbanari falls, close to locality S. The vegetation is dominated by *Platycarpum-Terminalia* low forests. Note the absence of herbaceous communities

‘savannas’ by Steyermark and Dunsterville (1980), based on aerial photographs. Typical herbs are *Navia ovoidea* and *Brocchinia acuminata* (Bromeliaceae), *Xyris* and *Abolboda* (Xyridaceae), *Everardia* and *Lagenocarpus* (Cyperaceae), and *Panicum chnoodes* (Poaceae). Low shrubs are also present, such as *Bonnetia lanceifolia*, *Blepharandra fimbriata* (Malpighiaceae), *Terminalia quintalata* (Combretaceae), and *Stomatochaeta condensata* (Asteraceae). In locality A, situated at about 1400 m elevation, an area of meadows with patches of forest was surveyed here. The meadows were composed of the typical elements mentioned above with the addition of *Sauvagesia* (Ochnaceae), *Panicum* (Poaceae) and *Lycopodium* (Lycopodiaceae). Microtopographical variations determine the existence of small, inundated depressions, dominated by *Xyris*, and hummocks, dominated by *Bonnetia lanceifolia* and *Cyrella racemiflora* (Cyrillaceae). In the forest islands, the more common species are *Schefflera* (Araliaceae), *Clusia* (Clusiaceae), *Aspidosperma* (Apocynaceae), *Chrysophyllum* (Sapotaceae), *Ochthocosmus* (Linaceae) and tree ferns (probably Cyatheaceae). The understorey is dominated by *Myriocladus* (Poaceae) and giant (up to about 1 m diameter) rosettes of *Brocchinia tatei* (Bromeliaceae). Characteristic components of the forest-meadow shrubby ecotone are *Bonnetia lanceifolia*, *Poecilandra retusa*, *Terminalia quintalata*, *Pouteria* sp. (Sapotaceae) and *Gongylolepis* (Asteraceae). In locality 1, at about the same elevation as locality A, the vegetation is similar, with the addition of riverine forests along watercourses, dominated by *Archytaea multiflora* (Theaceae) (Fig. 2). In summary, there is a gradient in the altitudinal arrangement of the three main vegetation types from the Guaiquinima summit.

The *Platycarpum*–*Terminalia* scrubs or forests occupy the lowest elevations (720 to about 1000 m elevation), while the *Stegolepis* meadows, with or without patches of forest, grew in the highest terrains (1200 to 1650 m). The montane cloud forests proper are at intermediate elevations. These altitudinal boundaries can show local differences due to microtopographical and microclimatic conditions, but in general the altitudinal sequence is consistent.

Materials and methods

The palynological study was performed on three localities of the Guaiquinima summit (Fig. 1). Two 160 cm long cores of homogeneous peat (GUAIQ-1 and GUAIQ-2, situated about 200 m apart) were obtained at locality 1 (5° 50' N–63° 41' W, 1350 m elevation), using a Hiller borer. Coring was stopped when bedrock was encountered. The vegetation of this locality is a typical meadow of *Stegolepis squarrosa* surrounded by forests, characteristic of the higher altitudes, on the top of a small hill flanked by forested scarps and slopes (Fig. 2). Gallery forests dominated by *Archytaea multiflora* are present in the vicinity, along watercourses. Three surface samples representing the forest-meadow ecotone (1B) and the meadows (1C and 1CB) were also taken. Sample 1C was from the centre of the meadow, while sample 1CB was intermediate between it and that of the ecotone (1B). At the other localities, only surface samples were collected. In locality A (5° 46' N–63° 49' W, 1400 m elevation), the samples correspond to the interior of the forest (A3), and to the meadows, at distances of about 100 m (A2) and 500 m (A1) of the forest-meadow ecotone. At this site, the *Stegolepis* meadows were dominant, and the forests were represented by small patches. Locality S (5° 42' N–63° 36' W, 900 m elevation) was surrounded by *Platycarpum*–*Terminalia* low forests close to an affluent of the Carapo river; herbaceous formations were not present at all in the area (Fig. 2). Surface samples correspond to three different settings: inside the forest (SIII and SV), within a flooded clearance (SI), and mostly bare rocks near the river shore (SII and SIV).

In both peat cores, samples for pollen analysis were taken at a 10 cm interval. The samples were spiked with exotic pollen of *Kochia scoparia* by weight (Salgado-Labouriau and Rull, 1986), and pretreated with HCl and HF and acetolysis (Faegri *et al.*, 1989). Slides were mounted in silicone oil. Pollen identification followed mainly the specific works of Salgado-Labouriau and Villar (1992) and 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). Plant taxonomy follows Berry *et al.* (1995). A minimum of 200 pollen grains were counted, but counts were continued until the diversity did not change significantly (Rull, 1987). The pollen sum includes only pollen types; spores are excluded. Pollen diagrams were plotted and zoned with Psimpoll 4.10 (Bennett, 1994, 2002). Zonation was carried out after optimal splitting by information content (OSIC), and compared with the broken-stick model for significance (Bennett, 1996). Principal

component analysis (PCA) was done on the covariance matrix, using untransformed percentages. Only pollen types over 1% were considered for zonation and PCA. The package MVSP 3.1 was used. Radiocarbon dates, taken from earlier work on the same cores (Schubert and Fritz, 1985; Rull, 1991), were calibrated with CALIB 4.3 (Stuiver *et al.*, 1998a, 1998b) (Table 1). Interpretation of pollen diagrams was based on modern analogues, derived from surface samples, and the known ecological requirements of the taxa found (Berry *et al.*, 1995; Marchant *et al.*, 2002; Rull, 2003).

Results and interpretation

Modern analogues

Figure 3 shows the palynological results for the three localities studied. Modern pollen sample localities 1 (samples 1B, 1C and 1CB) and A (samples A1, A2 and A3) are merged into one single diagram, because they represent similar vegetational features, representative of the upper altitudinal levels. This diagram (localities 1 and A) is ordered in a downward sense with forest samples at the top and the more distant meadow samples at the bottom. The diagram of locality S represent the lower altitudinal levels and has been ordered equally, from forest samples to samples from peat islands on bare rocks, along the river shore.

Upper-level vegetation

The forest sample (A3) is notably different from the others, being dominated by the pollen of the giant rosettes of *Brocchinia tatei* (>50%), Sapotaceae trees and Poaceae (both around 20%), whereas *Stegolepis* and *Xyris* are absent. Among the spores, the reticulate trilete types reach almost 100% of the pollen sum. All these elements change markedly in the ecotone sample (1B), except for Poaceae. Here, the dominants are *Bonnetia lanceifolia* (28%), *Xyris* and Poaceae (ca. 20% each). In the meadow samples, the percentages of *Xyris* increase roughly with distance from the forest, attaining a maximum of 47% at 500 m; Poaceae is nearly constant at 20%. The dominants within the forest are now either absent (*Brocchinia tatei*) or below 6% (Sapotaceae). Among minor pollen types, *Brocchinia* (others), *Stegolepis*, and Cyperaceae show a small increase in the meadow samples. The spores that increase in the meadows are psilate monolete types, *Cyathea*-type (verrucate), and reticulate monolete types. The reticulate trilete type is absent or present with less than 2%. In summary, the main forest indicators are *Brocchinia tatei*, reticulate trilete types, and Sapotaceae (above 20%), while the main indicator for meadows is *Xyris*. The ecotone is characterised mainly by higher *Bonnetia lanceifolia* proportions. This is in agreement

Table 1 Radiocarbon dating of samples, according to Schubert and Fritz (1985) and Rull (1991). One-sigma confidence interval for calibrated dates are given in brackets

Core	Sample	Depth (cm)	Laboratory number	¹⁴ C yr BP	Cal. yr BP	1σ interval
GUAIQ-1	2–3	20–30	WAT-1162	330 ± 60	380	310–480
	12–16	120–160	WAT-1172	5100 ± 90	5890	5740–5930
GUAIQ-2	2–3	20–30	WAT-1171	350 ± 60	350	310–500
	11–15	110–150	WAT-1161	6000 ± 80	6820	6730–6910

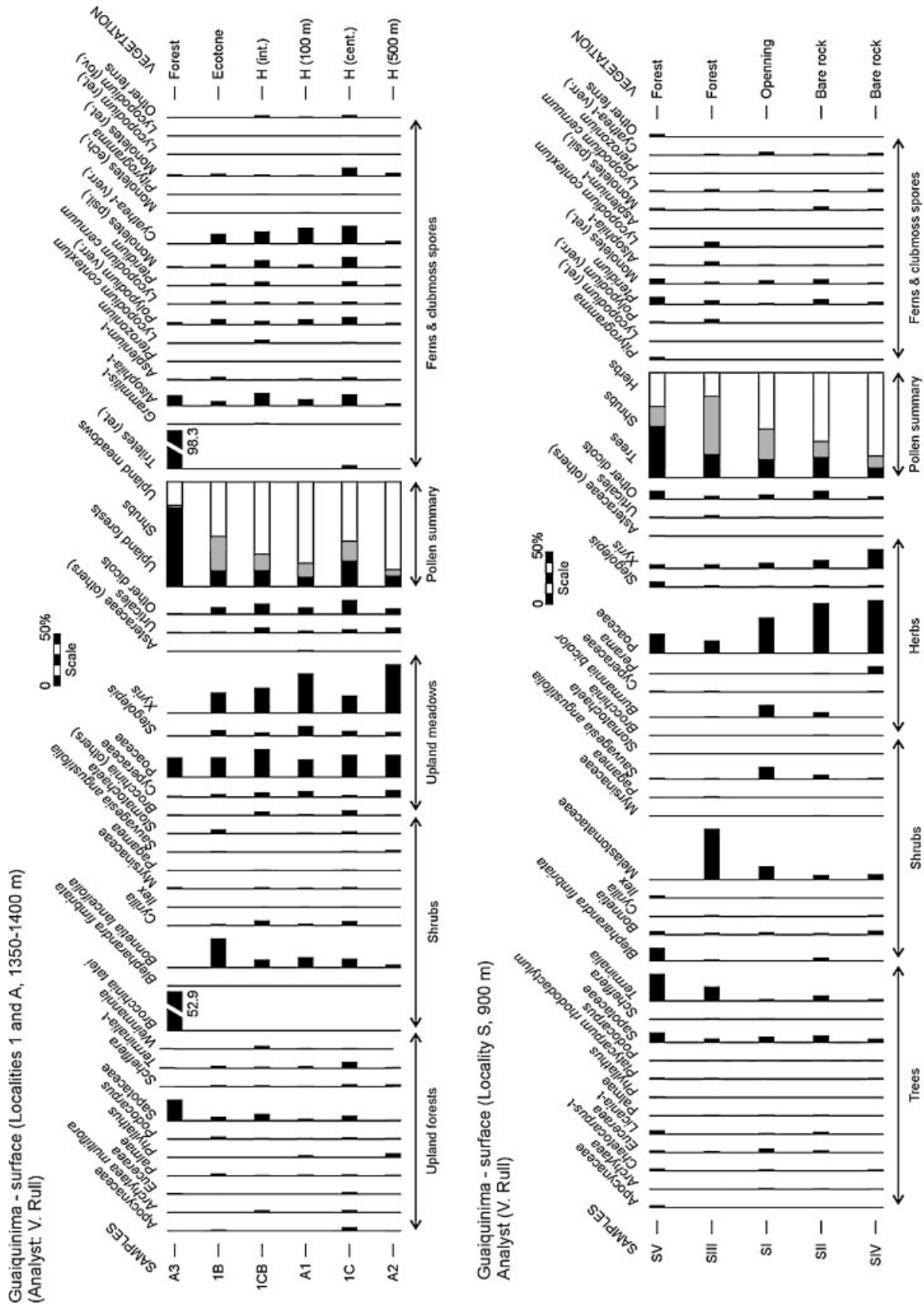


Figure 3 Diagram of percentage pollen and spores of modern surface samples arranged along a forest-meadow (upper diagram, localities 1 and A), and a forest-bare rock (locality S) gradients, from top to bottom. H = meadows, Int. = intermediate

with the major vegetational features observed in the sampling sites (see above). Although the meadows are dominated by *Stegolepis* (see above), its pollen is under-represented in the modern samples.

Lower-level vegetation

The two forest samples (SIII and SV) are different in composition, although their dominant elements are from plants typical of the scrubs or low forests of the locality studied (see above). The dominants are either Melastomataceae (probably from the understorey taxon *Meriania urceolata*), or *Terminalia* (most probably *T. quintalata*) and *Blepharandra fimbriata*. Poaceae and *Xyris* show their minimum values (12–18% and <4%, respectively). The forest opening sample (SI) is dominated by *Xyris* (52%), accompanied by maxima in *Sauvagesia angustifolia* and *Burmanna bicolor* (12%); forest elements are still present but in low amounts. The dominant pollen type in the bare rock peat islands is Poaceae (48–51%), while *Xyris* and *Perama* are slightly higher. Fern and allied spores do not show significant variations along this transect. The data show that forest and non-forest samples can be clearly separated. The former is dominated by *Terminalia*, *Blepharandra fimbriata* and Melastomataceae, and the latter by Poaceae. The strong contrast between the percentages of Poaceae in forest versus non-forest vegetation type is not due to differences in the importance of this family, since they are scarce in all vegetation types (see above). Poaceae abundance in bare rock samples could be due to long-distance dispersal (there are no herbaceous formations at this altitudinal level), combined with the scarcity of local pollen deposition due to the lack of plants in the vicinity. In contrast, the likelihood of Poaceae to appear in the forest samples is lower, and these surface samples are dominated by locally derived tree and shrub pollen. The low dispersion capacity of pollen from forest elements is manifested by their scarcity in the open forest sample.

Holocene records

The two sediment cores were composed entirely of homogeneous black peat, without differential sedimentary structures. This, together with the absence of clastic sediments, suggests that both sites have been covered by vegetation during the entire time-interval recorded, and no erosive events disrupted the sequences. This is also supported is provided by the calculated sedimentation rates based on radiocarbon dates (0.20–0.24 mm yr⁻¹), which are very similar to other well-dated peat sequences from neighbouring tepui summit cores (Rull, 1991). A constant sedimentation rate is assumed throughout the entire sequences and, as a consequence, the ages of zone boundaries should be considered approximate.

The diagram of GUAIQ-1 shows clear changes in pollen dominance through time. The major taxa are Poaceae, *Archytæa multiflora* and *Bonnetia lanceifolia* (Fig. 4). The respective changes in pollen abundance is the basis for subdivision into three pollen zones:

GUAIQ-1 (160–110 cm, 6.6–4.5 cal. kyr BP)

This zone is dominated by Poaceae (46–68%), with minor contributions of *Xyris* (5–17%) and *Bonnetia lanceifolia* (3–10%);

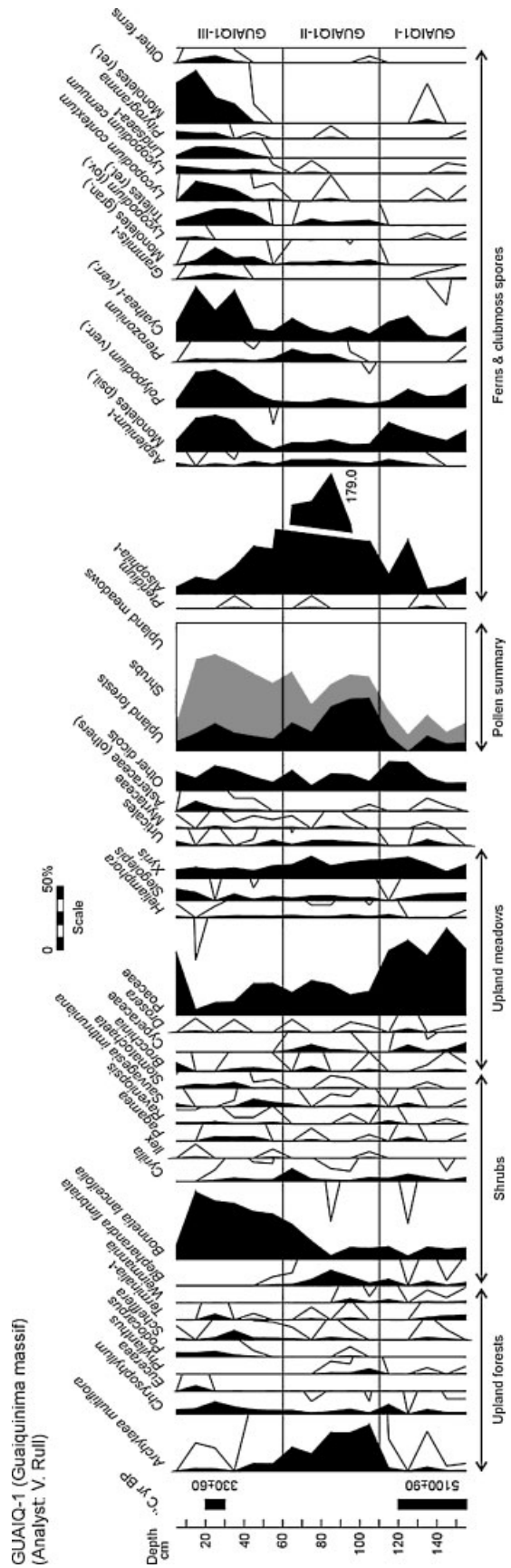


Figure 4 Diagram of percentage pollen and spores of GUAIQ-1 (locality 1) and derived pollen zones. Solid lines represent × 10 exaggeration

Archytaea multiflora is always 3%. The more important spores (always below 40% and frequently less than 20% of the pollen sum) are *Alsophila*-type, reticulate monolete types, verrucate *Polypodium* and verrucate *Cyathea*-type.

This zone has two possible interpretations in terms of the vegetation it represents. On the one hand, comparison with modern pollen assemblages from the same locality (Fig. 3) would suggest the existence of a meadow in the coring site. However, Poaceae are more abundant than in the present-day meadow samples, whereas both *Xyris* and *Stegolepis*, especially the former, were scarcer than in today's samples. The lower values of *Xyris* suggest that the site was probably not flooded. On the other hand, it is important to consider that the lowermost 50 cm of peat were directly overlapping bare rock, thus suggesting the initial phases of colonisation. As it has been noted earlier (Fig. 3), modern assemblages from bare rocks have percentages of Poaceae comparable to those in this zone (around 50%), which are notably higher than modern meadow samples (maximum 27%), and are probably derived from long-distance dispersal.

GUAIQ1-II (110–60 cm, 4.5–2.1 cal. kyr BP)

A spectacular and sudden increase of *Archytaea multiflora* (up to 36%), together with a strong decrease of Poaceae to <19% characterises the beginning of this zone. Coinciding with this change is the increase of *Blepharandra fimbriata*, which reaches its maximum (5%) around the middle of the zone, and the slight decrease of *Cyrilla*. The spores mentioned for the previous zone decrease to less than 10%, except for *Alsophila*-type, which, shows behaviour similar to *Archytaea multiflora*, and reaches 17.9% of the pollen sum. Granulate monolete spore types and reticulate trilete spore types appear for the first time.

There is no close modern analogue for this zone (Fig. 3), but it strongly suggests the replacement of the former meadow by a gallery forest dominated by *Archytaea multiflora*. At present, these forests are close to the coring site, but the pollen of their dominant tree is always less than 3%, indicating a low dispersal capacity. It is thus deduced that values between 14% and 36% indicate that the coring site was covered by gallery forests of this tree type.

GUAIQ1-I (60–0 cm, 2.1 cal. kyr BP to present)

The third zone is characterised by another striking change in dominance: *Archytaea multiflora* returns to values similar to the lowermost zone, while *Bonnetia lanceifolia* increases up to 53%. Poaceae diminish again to their minimum value (4%), but they recover in the uppermost sample (48%). Cyperaceae and *Blepharandra fimbriata* disappear and *Cyrilla* decrease, whereas *Sauvagesia imthurniana*, *Chrysophyllum*, *Pagamea* and *Schefflera* increase slightly. From the middle of the zone, an increase in *Stomatochaeta*, other Asteraceae, *Podocarpus* and *Euceraea* is also observed. All the spore types also show a conspicuous increase, the only exception being *Alsophila*-type, which follows the same decreasing trend as *Archytaea multiflora*.

The closest modern analogue for this zone is the ecotone sample of the upper elevations (Fig. 3). However, as in the former zone, *Xyris* is less abundant than in the modern sample, suggesting non-flooded conditions. The possibility of a forest-meadow ecotone at this site is reinforced by the simultaneous

Table 2 Eigenvectors and variance explained for principal components 1 and 2, GUAIQ-1

Taxa	PC 1	PC 2
<i>Weinmannia</i>	0.011	−0.018
Cyperaceae	0.049	−0.012
<i>Phyllanthus</i>	0.001	−0.045
<i>Terminalia</i> -t	0.010	0.023
<i>Blepharandra fimbriata</i>	0.026	−0.153
Poaceae	0.776	0.346
<i>Cyrilla</i>	0.010	−0.020
<i>Drosera</i>	0.003	0.003
<i>Xyris</i>	0.043	−0.107
<i>Archytaea multiflora</i>	−0.079	−0.755
Urticales	0.006	−0.046
<i>Stegolepis</i>	0.023	0.035
<i>Heliampora</i>	−0.009	−0.017
<i>Sauvagesia imthurniana</i>	−0.006	0.002
<i>Chrysophyllum</i>	−0.052	0.051
<i>Pagamea</i>	−0.018	0.031
<i>Raveniopsis</i>	−0.007	0.018
<i>Schefflera</i>	−0.029	0.022
Myrtaceae	−0.009	−0.008
<i>Brocchinia</i>	0.009	0.021
<i>Bonnetia lanceifolia</i>	−0.613	0.509
<i>Ilex</i>	−0.007	0.001
<i>Stomatochaeta</i>	−0.040	0.029
Asteraceae (others)	−0.047	0.040
<i>Podocarpus</i>	−0.031	0.035
<i>Euceraea</i>	−0.020	0.015
Cumulative variance	61.14%	92.58%

increase in tree pollen (*Chrysophyllum*, *Schefflera*, *Podocarpus*, *Euceraea*). In the highermost sample, the conspicuous decrease in *Bonnetia lanceifolia* and the trees, coeval with the increase of Poaceae, suggests the return to a meadow similar to the first zone but with less Poaceae, representing the present-day situation. The difference between the two top samples is less than 100 cal. ¹⁴C years.

In the PCA analysis, the first two components are significant, using the broken-stick method (Table 2). Component 1 is positively associated with Poaceae, and negatively correlated with *Bonnetia lanceifolia*, thus expressing the contrast between meadows (positive scores) and upper forests (negative scores). The second component shows a positive relationship with *Bonnetia lanceifolia* and negative correlation with *Archytaea multiflora*, which indicates upper forests (positive scores) versus *Archytaea* gallery forests (negative scores).

Although from the same vegetation type, contrary to GUAIQ-1, the two dominant pollen types throughout the diagram of GUAIQ-2 are Poaceae and *Xyris* (Fig. 5). Other intermediate elements, with lesser percentages—*Blepharandra fimbriata*, *Archytaea multiflora*, *Chrysophyllum*, *Bonnetia lanceifolia* and Cyperaceae—provide the basis for the following zonation:

GUAIQ2-I (160–110 cm, 8.4–4.4 cal. kyr BP)

Zone dominated by Poaceae (with a decreasing trend from 52% to 38%), and *Xyris* (14–31%). *Cyrilla*, *Stegolepis* and *Blepharandra fimbriata* are the most important among the minor elements (up to 6%). Spores, mainly psilate monolete types, *Alsophila*-type and *Polypodium*, show very low values. A subdivision of this zone into two subzones at 110 cm (5.6 cal. ¹⁴C kyr BP) is possible on the basis of a sudden decrease of *Blepharandra fimbriata*, followed by an increase of *Xyris*.

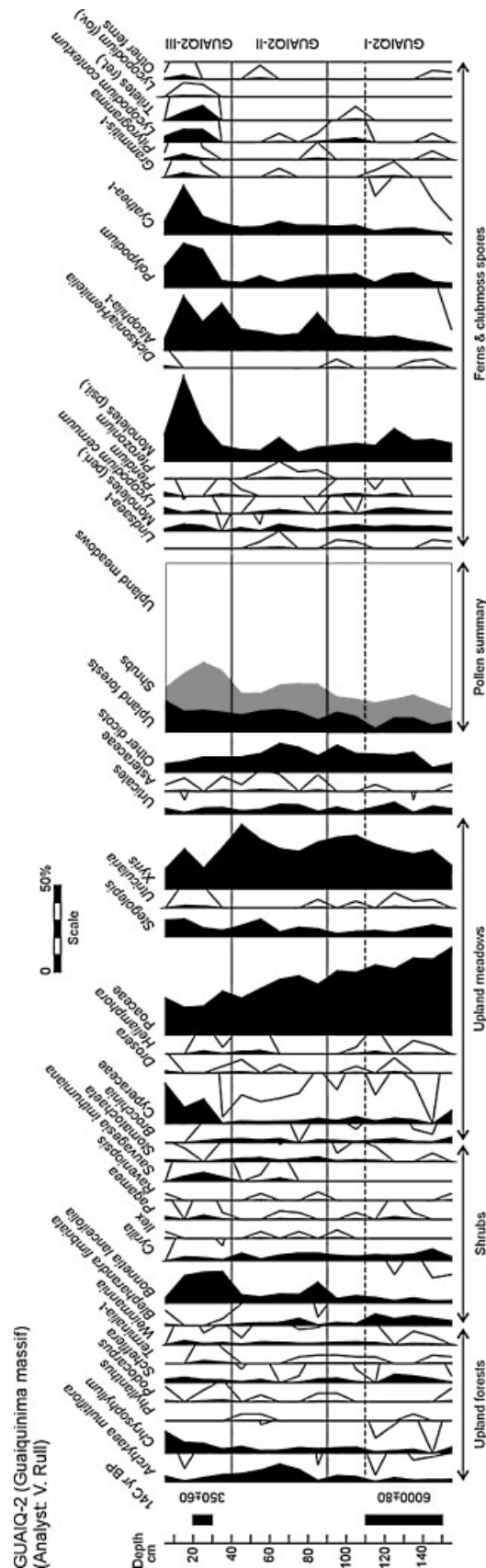


Figure 5 Diagram of percentage pollen and spores of GUAIQ-2 (locality 1) and derived pollen zones. Solid lines represent $\times 10$ exaggeration

Like the lowermost zone in core GUAIQ-1, this zone could indicate either a meadow with more Poaceae than today or pioneer plant stands on bare rock (see above). In the first case, the abundance of Poaceae (always over 27%) suggests that this family was better represented in the ancient meadows than in present ones. However, the percentages of *Xyris* are similar to today, indicating similar flooding conditions as at present.

GUAIQ2-I (110–90 cm, 4.4–1.3 cal. kyr BP)

There are no changes in taxa dominance, although Poaceae pollen decreases (30% to 22%), and *Xyris* increases slightly (22–38%). The differentiating element of this zone is the increase of *Archytaea multiflora*, which peaks (11%) in the middle of this zone. Other significant increases are those of *Bonnetia lanceifolia* at the beginning, and *Stegolepis* at the end. No significant changes are observed in the spore percentages.

Comparison with modern assemblages (Fig. 3) indicates that the vegetation is still a Poaceae–*Xyris*–*Stegolepis* meadow with increasing similarity to today, because of the progressive decrease of Poaceae. At the end of the zone, the comparable modern assemblage is the meadow sample, which is more distant (500 m) from the forest. The gallery forests dominated by *Archytaea multiflora* were not far from the coring site, although not *in situ*.

GUAIQ2-I (90–0 cm, 1.3 cal. kyr BP to present)

A sudden and notable increase of *Bonnetia lanceifolia* (attaining 19%), together with the return of *Archytaea multiflora* to former values of less than 3%, are the main features of this zone. Other decreasing elements are *Blepharandra fimbriata* (which almost disappear) and Poaceae (similar to present-day values). On the other hand, *Chrysophyllum*, *Cyperaceae* and *Sauvagesia imthurniana* parallel the *Bonnetia lanceifolia* increase, as they do all the spore types. This zone very similar

Table 3 Eigenvectors and variance explained for principal components 1 and 2, GUAIQ-2

Taxa	PC 1	PC 2
<i>Blepharandra fimbriata</i>	0.135	–0.038
<i>Cyrilla</i>	0.079	0.061
Poaceae	0.821	–0.292
<i>Brocchinia</i>	0.025	0.022
Urticales	0.040	–0.028
<i>Schefflera</i>	–0.007	–0.020
<i>Xyris</i>	0.113	0.758
<i>Terminalia-t</i>	–0.013	–0.009
<i>Heliampora</i>	–0.011	0.025
<i>Weinmannia</i>	–0.013	0.044
<i>Stegolepis</i>	–0.112	–0.037
<i>Archytaea multiflora</i>	–0.016	0.100
<i>Utricularia</i>	–0.018	–0.007
<i>Stomatochaeta</i>	–0.018	0.060
<i>Podocarpus</i>	–0.013	–0.016
Asteraceae	–0.012	0.017
<i>Pagamea</i>	–0.030	–0.048
<i>Chrysophyllum</i>	–0.167	–0.170
<i>Drosera</i>	–0.009	–0.006
<i>Bonnetia lanceifolia</i>	–0.367	0.113
Cyperaceae	–0.316	–0.520
<i>Sauvagesia imthurniana</i>	–0.090	–0.010
Cumulative variance	54.21%	80.56%

to GUAIQ1-III, and represents a forest-meadow ecotone. The main difference with the ecotonal sample is the abundance of Cyperaceae. The top sample also represents the modern vegetation.

The first principal component of GUAIQ-2 has the same associated taxa and the same ecological implications as in GUAIQ-1 (Table 3). Component 2 is positively associated to *Xyris* and negatively correlated with Cyperaceae, which emphasises the importance of meadow development at this site. The meaning of this component is difficult to explain because of the lack of auto-ecological studies in the Guaiquinima massif, but the apparent antagonistic nature of these two taxa is reinforced by the significant negative correlation they show ($r=0.683$, $p<0.01$). At present, *Xyris* is more abundant in flooded microdepressions from the uppermost Guaiquinima meadows (Huber and Rull, field observations). However, Cyperaceae could not be identified at generic or specific level due to the homogeneity in their pollen morphology (Rull, 2003), and a definite answer is not possible so far.

Discussion: vegetation succession and palaeoenvironments

The main trends in Holocene succession of vegetation were deduced from the above zonation combined with the stratigraphic variations of PCA scores (Fig. 6). Detailed comparisons with other studies from the Neotropics are not yet possible, owing to insufficient age control of our records, but the main tendencies for these remote summits are presented and compared, at a millennial time scale, as working hypotheses to be tested and complemented with future studies of higher resolution.

Both Guaiquinima sequences show an initial interval between ca. 8 and 4.5 cal. kyr BP in which the diagrams are dominated by

Poaceae, and component 1 has the highest scores, indicating that most of the variance in pollen trends is explained by Poaceae (Tables 2, 3). Therefore, either a meadow different from today (with less importance of Poaceae) or pioneer communities on rocky substrates would have occupied the top of the sampled hill. The latter possibility is supported by the existence of similar modern analogues on bare rocks from lower altitudes (Fig. 3). The similarity, however, is limited to the Poaceae over-representation; the absence of low-altitude markers such as *Platycarpum rhododactylum* and *Burmanna bicolor* does not support an upward displacement of vegetation. In this case, the bottom zones of both sequences might represent the initial phases of colonisation of the hilltop. The other possibility, a meadow different from today, has some support in modern samples from some tepui summits of the Chimantá massif (Fig. 1). There, the surface samples taken within *Stegolepis* meadows are richer in Poaceae pollen, which attain up to 40% of the pollen sum (Rull, 1991). These meadows are dominated by the endemic *Stegolepis ligulata*, and occur from 1800 m upwards (Huber, 1992); hence, their hypothetical occurrence on the uppermost parts of the Guaiquinima summit during the early Holocene would imply a vertical displacement of the vegetation a few hundreds of metres downward. However, this is hard to demonstrate, because of the difficulty in differentiating the pollen of *Stegolepis squarrosa* (endemic to Guaiquinima) from that of *Stegolepis ligulata* (endemic to Chimantá) (Rull, 2003). The fact that at the same time, the vegetation of the Chimantá massif was effectively displaced downward due to a climate cooling (Rull, 2004b) (Fig. 6) is very suggestive, although not conclusive. Other evidence to support this interpretation is that at the end of this zone, nearly 1 m of peat had already accumulated in GUAIQ-2, which is incompatible with the existence of bare rock.

A gallery forest dominated by *Archytaea multiflora* represents the mid-Holocene interval (4.5–2 cal. kyr BP). These forests were *in situ* at site GUAIQ-1 (see component 2 in Fig. 6), and closer than today to site GUAIQ-2, where a meadow is still present. This could be due to an expansion of gallery forests or

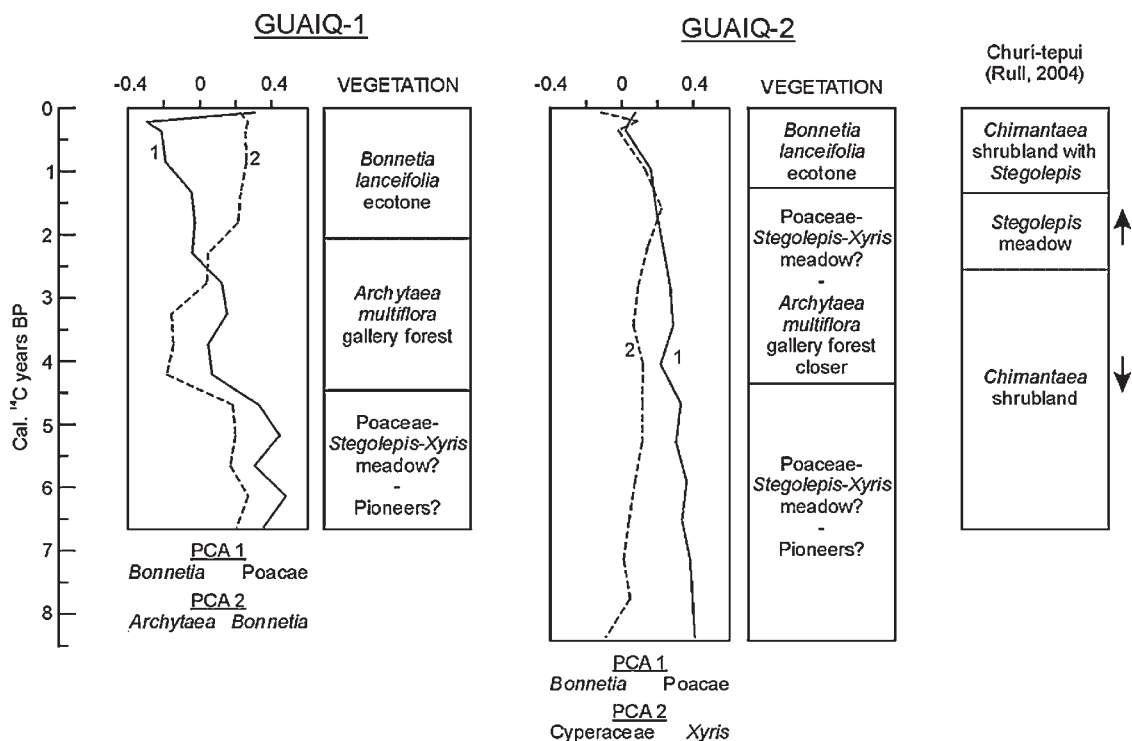


Figure 6 Chronostratigraphic correlation of pollen zones and PC scores from GUAIQ-1 and GUAIQ-2, and comparison with the zones defined previously in Churi-tepui, on the Chimantá massif (Rull, 2004b). The arrows indicate the relative position of the vegetation types of Churi-tepui with respect to today

to a lateral shift of the associated watercourse. The only running waters at the sampling locality are those descending from the top of the hill, which is part of the headwaters of both drainage subsystems present in the Guaiquinima (Fig. 1). These are torrential creeks running within steep sandstone gorges, where lateral shifts are unlikely at the time scale considered; therefore, an expansion of the *Archytaea* gallery forests is the more reasonable explanation. This would be probably due to an enhancement of the drainage system, indicating an increase in the available moisture. At the top of the hill sampled, the only water source is rain; hence, an increase in total precipitation is suggested. A period of general moisture increase is supported by palaeolimnological studies on Lake Valencia (Fig. 1) and its surroundings, where high lake levels and forest expansion was recorded between 5.2 and 2.2 kyr BP (Leyden, 1985; Curtis *et al.*, 1999). Similarly, a phase of high precipitation was recorded in Lake Titicaca between 4 and 2.4 kyr BP (Baker *et al.*, 2001). Behling and Hooghiemstra (2000) also recorded a change from dry early Holocene to wetter mid-Holocene in the Colombian Llanos, and later considered it as the reflection of a general moisture increase in northern South America (Behling and Hooghiemstra, 2001). These changes have been linked to the latitudinal displacement of the Intertropical Convergence Zone (Haug *et al.*, 2001), which plays a major role in the intensity and distribution of precipitation in the Neotropics (McGregor and Nieuwolt, 1998). Around 2.5 cal. ^{14}C kyr BP, an upward shift of vegetation due to a temperature increase was recorded in the Chimantá massif (Rull, 2004b) (Fig. 6). This event is not recorded in the Guaiquinima diagrams, probably because the vegetation of the sampling area is not sensitive to such change. The vertical distance between locality 1 and the upper limit of the lower vegetation type, the *Platycarpum-Terminalia* scrubs or low forests, is about 400 m, more than the vertical displacement estimated for the Chimantá (Rull, 2004b).

Both pollen zones and PC scores indicate that a shift towards a forest-meadow ecotone occurred later, roughly around 2 cal. ^{14}C kyr BP in GUAIQ-1, and 1.4 cal. ^{14}C kyr BP in GUAIQ-2 (Fig. 6). This lag is longer than expected for a differential colonisation chronology, since the horizontal distance between the coring sites is ca. 200 metres. Alternatively, the apparent lag may be an artefact of inherent errors in the ^{14}C -based chronology. In terms of vegetation, the interpretation is that forests invaded the hilltop, although they did not cover it entirely. Owing to the lack of ecological studies on the vegetation types involved, it is difficult to explain the replacement of the gallery forests by the upper Guaiquinima forests in environmental terms. It is possible that a decrease in moisture favoured the propagation of *Bonnetia lanceifolia*, which prefers non-flooded terrains (see above). In support of this, a coeval decrease in temperature and humidity was recorded in the Chimantá massif, which, together with other similar shifts observed in the Neotropics, suggests a regional climatic oscillation (Rull, 2004b). It was also reflected in the Lake Valencia Basin by lower lake levels and the expansion of savannas after 2.2 kyr BP (Leyden, 1985). In the Colombian Llanos, the expansion of savannas also began around 2.3 kyr BP (Behling and Hooghiemstra, 2000). Finally, in the last century, a vegetational shift to the present-day conditions, i.e. a meadow dominated by *Stegolepis* surrounded by forests, occurred.

With the available data, the possibility of fire events governing or influencing the observed vegetational changes on the Guaiquinima summit is unlikely. On the one hand, the charcoal content of the sediments studied is almost negligible. In addition, modern observations argue against the frequent occurrence of fires on the *tepuí* summits. After many visits and observations by numerous scientists (especially during the dry season) during

more than a century, there is no reliable report of fire by lightning or other natural causes (Huber, 1995d).

Conclusions

At the locality studied, which is representative of the uppermost parts of the Guaiquinima massif, the Holocene vegetational changes have been characterised by the successive replacement of three vegetation types, namely *Stegolepis* meadows (ca. 8.4 to 4.4 kyr BP), *Archytaea* gallery forests (ca. 4.5 to 2 kyr BP), upland forests (ca. 2 kyr BP to the last century), and ultimately meadows, during the last century. These trends are related to changes in moisture, rather than temperature. A period of gallery forest expansion and increased precipitation is proposed between ca. 4.5 and 2 kyr BP, which coincide with other Neotropical records (Lake Valencia, Lake Titicaca and the Colombian Llanos). After 2 kyr BP the substitution of gallery forests by upland forests agrees with a phase of savanna expansion and aridity in the Lake Valencia catchment and the Colombian Llanos. A clear relationship between the Guaiquinima record and low-range temperature oscillations, as deduced from altitudinal shifts in other *tepuí* summits, is not suggested. It is therefore deduced that the sampling site is not sensitive to small temperature changes because of the absence of ecological boundaries at that elevation.

As on other *tepuí* summits, the Guaiquinima uplands and highlands vegetation is pristine; hence, the environmental changes recorded are of natural origin. This makes these environments unique in evaluating the natural component of climate variability, which is one of the main objectives of the palaeoclimatic research oriented to the study and prediction of present climatic change (Alverson *et al.*, 2003). Palaeoenvironmental records acquired so far on the *tepuí* summits are of Holocene age and record millennial-scale variability (for example Rull, 2004b); higher-resolution studies are not available and should be encouraged, especially for the last millennium. During this time interval, the interactions of natural and anthropogenic forcings have resulted in complex responses, making it difficult to disentangle the effects of both (Bradley *et al.*, 2003; Oldfield and Dearing, 2003). In the *tepuí* summits, the lack of direct human impact, even in recent centuries, would provide a more 'clean' signal of natural trends, thus providing a standard to compare with areas under greater anthropogenic pressure.

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