

A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela

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ABSTRACT: Fire has been considered one of the most important factors in the expansion of savannas in the Gran Sabana region. In Urué, an important fire event that occurred before 1.6 kyr BP led to the replacement of 'primary' forests by savannas and *morichales* (monospecific communities of the palm *Mauritia*). In the present work, the secondary succession after fire is reconstructed by palynological analysis of a previously dated clay core, and the results are compared with those from studies based on present-day ecosystems. Charcoal analysis is used to infer fire incidence and surface samples are used as modern analogues. The secondary succession is subdivided into seven seral stages: open secondary forests, *helechal* or dense fern community, transitional savanna, wet savanna with *morichales*, treeless savanna, wet savanna with *morichales*, and treeless savanna. Fires were common at the beginning, but climate constituted the main successional control from the transitional savanna stage onwards. The process is characterised by a continuous impoverishment of taxa, but there was a steady increase in *Mauritia*, due to its ability to colonise new habitats created by disturbances. The conclusions of this palynological reconstruction show good correspondence with present-day studies on fire ecology. Copyright © 1999 John Wiley & Sons, Ltd.

KEYWORDS: deforestation; forest degradation; forest–savanna mosaic; neotropics; palaeoecological succession.



Introduction

Fire has been considered to be one of the most important forcing factors in the development of the savanna–forest mosaic in the Gran Sabana of southeast Venezuela, where, under the present tropical pluvial climate, extensive rain forests might otherwise be expected to exist. Alternative explanations relate to the hydrological and acidic characteristics of soils, or the savanna patches are considered as relics of a more widespread extension of this vegetation during the Last Glaciation. Finally, some workers view this mosaic as a natural stage in the vegetation dynamics (see review by Fölster and Dezzeo, 1994).

At present, marked deforestation by anthropogenic fires is taking place in the Gran Sabana, which favours the expansion of savannas. This process has been well documented over recent centuries (Galán, 1984), and has been especially effective during dry climatic phases (Rohl, 1948). The recovery of former 'primary' forests has not been observed on a

human time-scale, or in palaeoecological or palaeoclimatic studies extending back several thousands of years (Rull, 1991). In some cases, the establishment of secondary forested communities has been recorded, but these are rapidly degraded to shrub and more open communities, due mainly to hydrological and chemical soil stress (Fölster and Dezzeo, 1994). Therefore, a combination of several factors seems to be necessary to explain the anomalously large extents of savanna, but fire is undoubtedly an important triggering factor, similar in both effects and intensity to the Holocene dry climatic phases (Rull, 1992).

Palaeoecological evidence of fire in the Gran Sabana includes radiocarbon-dated charcoal layers (Dezzeo, 1994) and Holocene vegetational changes (Rull, 1992). In the Urué valley, a fire event that occurred at about 1.4 k ¹⁴C yr BP has been inferred from a spectacular increase in fern spores (Rull, 1991, 1992). This event led to the replacement of gallery forest by treeless savanna, and was followed by the establishment of a *morichal* (monospecific gallery forest of the palm *Mauritia*). Further radiocarbon dates, however, suggest that fires in Urué could be older. Indeed, the charcoal found in a sharp contact between two soil layers indicating the replacement of forest by savanna was dated at 1.8 k ¹⁴C yr BP (Fölster, 1992). The available palynological data however, are mainly palaeoclimatically oriented, and a

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detailed reconstruction of secondary vegetational trends that can be compared with the results from present-day studies is not available. For this reason, using the palynological raw data of Rull (1991) as a starting point, identification and counts have been enhanced and charcoal particles have been counted, in order to provide the basis for a more detailed palaeoecological reconstruction. The same procedures were applied to previously analysed surface samples from the Gran Sabana, in order to obtain suitable modern analogues for comparison. The palaeoecological results in the present paper not only contribute to the knowledge of Gran Sabana vegetation development, but also have potential management applications.

The Gran Sabana region

Geography, geology, soils and vegetation

The Gran Sabana is located between 4°45'–5°30'N and 60°34'–62°50'W, in the River Caroní headwaters of south-east Venezuela (Fig. 1). Its altitude ranges from 800 to 1500 m a.s.l. and represents an erosion surface developed on the Precambrian Roraima sandstones and quartzites (Briceño and Schubert, 1990). Remnants of higher and older erosion surfaces remain in the Gran Sabana as table mountains (*tepuis*), up to 2700 m altitude.

Climate is tropical, with small variations in the monthly average temperatures (around 3°C between the warmer and the cooler month), but with wide daily oscillations (up to 15°C between day maxima and night minima). The annual average temperature is 17°C to 24°C, depending on the altitudinal level (Galán, 1984).

Precipitation ranges from around 1200 to 3000 mm yr⁻¹; its seasonal distribution being controlled by topography and dominant winds, which, in turn, depend on the position of the Intertropical Convergence Zone (ITCZ). The more humid

phase extends from April to August (reaching values of 500 mm month⁻¹), whereas another less humid but not dry (a few months with less than 60 mm of total precipitation) season occurs usually from January to March. Relative humidity is between 75% and 85% throughout the year, with little variation (Hernández, 1994a).

Soils are developed mainly on the Roraima sandstones and quartzites, and locally on intrusive diabase outcrops, and organic bogs. The sandstones are highly leached and are dominated by quartz, kaolinite, iron and aluminium oxides, falling in the Oxisol or Ultisol categories. Other important types are Entisols, developed mainly in flooded river margins; Inceptisols, on diabase intrusions; and Histosols, in the bogs (Fölster and Dezzee, 1994). It is common for the soils developed on igneous rocks also to be highly leached, and covered by a ferruginous hard layer (Schubert and Huber, 1989). Soil characteristics and vegetation are intimately associated. Soils under forested vegetation are commonly clay-rich, acidic, and covered by a more or less thick layer of humus, whereas savanna soils have low organic content and slightly higher pH, together with diminished nutrient availability. It is assumed that most savanna soils are in fact degraded soils that developed under forest vegetation (Dezzee and Fölster, 1994). On the other hand, shrub communities commonly grow on well-drained, sandy soils.

The main vegetational feature of the Gran Sabana is the savanna, but other important vegetation types are forests, *morichales*, shrubs, bogs and secondary communities. Forests are submesothermic, and can be differentiated from a physiognomic point of view into: (i) tall, well-structured, with a clear stratification pattern, and a mean altitude of 18 m in the higher stratum; (ii) small, poorly structured, up to 14 m tall; and (iii) gallery forests (Hernández, 1994b). Floristically, the Gran Sabana forests can be classified into montane forests and gallery forests. Montane forests are of several types, according to the different altitudinal levels. The classical study of Steyermark (1966) shows at least four altitudinal belts: (i) dense forests, 15–30 m tall (1000–1200 m altitude),

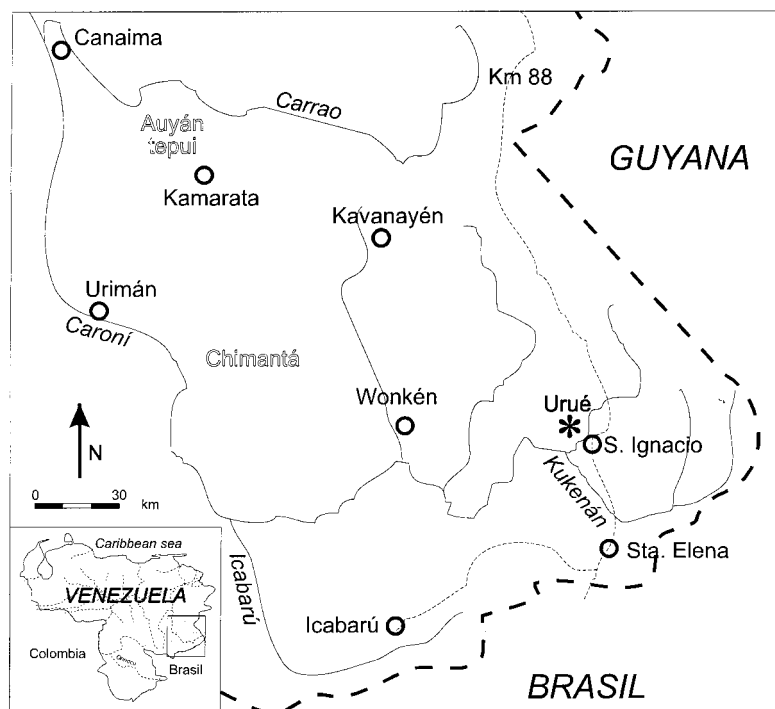


Figure 1 Map of the Gran Sabana region, southeast Venezuela.

Table 1 Main differential characteristics of surface pollen assemblages in the Gran Sabana (Rull, 1991)

	Treeless savanna	<i>Morichal</i>	Mixed forest	Gallery forest
Tree pollen	< 1%	1–4%	15–25%	> 40%
Herb pollen	> 95%	60–95%	60–70%	< 45%
Algae	+	+	–	r
Fungi (concentration)	30 000	30 000–90 000	30 000–90 000	> 150 000
<i>Mauritia</i>	–	10–30%	1–4%	r
<i>Schefflera</i>	–	r	5%	5–35%
Sapotaceae	r	r	3–7%	8–40%
<i>Ilex</i>	–	–	+	+
Myrtaceae	–	–	+	+
Compositae	–	–	+	+
Gramineae	80%	55–90%	30–35%	10%
Bromeliaceae	–	–	+	+
<i>Xyris</i>	+	+	–	–

+ = present, – = absent, r = rare.

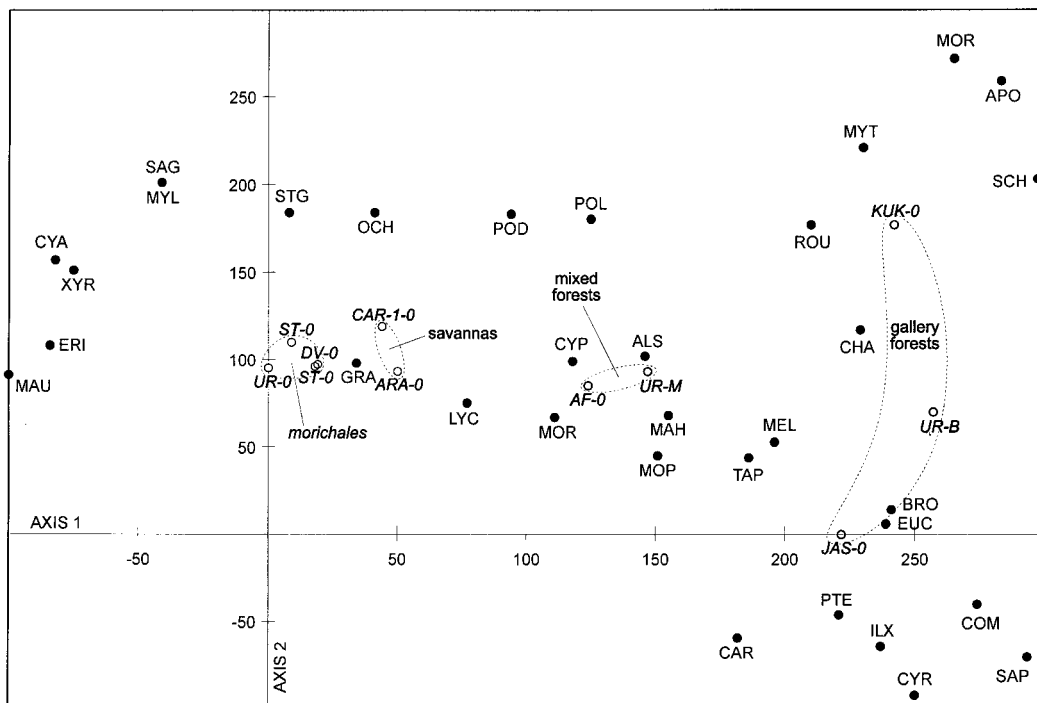


Figure 2 Results of the detrended correspondence analysis (DCA), showing the position of surface samples and taxa with respect to the first two axes. GRA = Gramineae, CYP = Cyperaceae, MAU = *Mauritia*, ERI = Eriocaulaceae, POD = *Podocarpus*, URT = Urticales, OCH = *Ochnaceae*, STG = *Stegolepis*, SCH = *Schefflera*, XYR = *Xyris*, MEL = *Melastomataceae*, SAG = *Sagittaria*, CHA = *Chaetocarpus*, MYL = *Myriophyllum*, ROU = *Roupala*, SAP = *Sapotaceae*, MAH = *Mahurea*, BRO = *Bromeliaceae*, CYR = *Cyrilla*, ILX = *Ilex*, MYT = *Myrtaceae*, EUC = *Euceraea*, COM = *Compositae*, APO = *Apocynaceae*, CAR = *Caraipa*, TAP = *Tapura*, POL = *Polypodium*, ALS = *Alsophila*, PTE = *Pteridium*, LYC = *Lycopodium cernuum*, MOP = *Monoletes* (psilate), MOR = *Monoletes* (reticulate), CYA = *Cyathea*.

with *Pouroma*, *Anaxagorea*, *Alexa*, *Henrietta*, *Byrsonima*, *Qualea*, *Minquartia* and *Pouteria*; (ii) humid forests, 15–25 m for tall (1200–1500 m altitude), with *Virola*, *Simaruba*, *Protium*, *Licania*, *Micropholis*, *Sclerolobium*, *Alchornea*, *Sloanea*, *Matayba*, *Oenocarpus* and *Euterpe*; (iii) high and dense forests (1500–1600 m altitude), with *Dimorphandra*, *Sloanea*, *Caryocar*, *Chrysophyllum*, *Podocarpus*, *Licania*, *Sterigmatalum*, *Moronobea* and *Euterpe*; and (iv) medium, humid forests on rocky substrates with abundant palms and ferns, characterised by *Podocarpus*, *Hyeronima*, *Drimys*, *Magnolia*, *Euterpe* and *Cyathea*.

Gallery forests (*sensu lato*) are associated with water currents, and can be differentiated into riverine forests and

gallery forests proper. According to Huber (1982), the former are surrounded by other types of forests, whereas the latter are isolated within open communities. In the Gran Sabana, both types are present. The riverine forests are dense, evergreen, mesothermic and rarely more than 15 m high. Characteristic trees are from the genera *Pera*, *Symphonia*, *Caraipa*, *Mahurea*, *Tapura* and *Euceraea* (Huber, 1986). A particularly conspicuous gallery forest of the Gran Sabana is the *morichal*, dominated by the palm *Mauritia flexuosa*, which forms almost monospecific associations along flat river courses, on poorly drained soils with a high clay content. They are especially common in the bottom of river valleys and flooded depressions in the southern part of the Gran Sabana. Huber

URUÉ. Gran Sabana surface samples

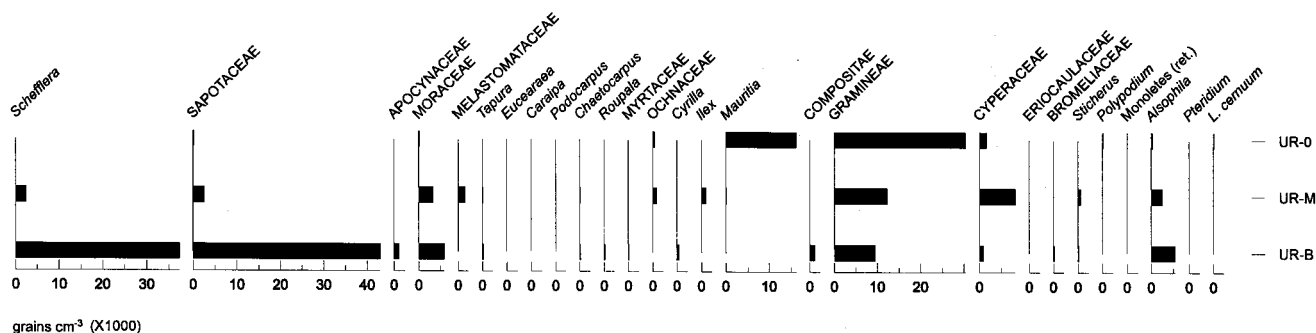


Figure 3 Concentration diagram of the surface samples taken at Urué.

(1994b) considers that the *morichales* are a special type of savanna (savanna with palms), because the herbaceous stratum is ecologically dominant, and the occurrence of palms has a marginal influence. Based on the present spatial arrangement of communities, González (1987) interpreted the *morichales* as intermediate seral stages of an ecological succession culminating in a mixed swamp forest, a gallery forest formed by species typical of riverine forests together

with *M. flexuosa*. Secondary forests commonly follow burning and felling activities, and are characterised by *Hyptis*, *Casearia*, *Cecropia*, *Vismia* and *Miconia* (Huber, 1986).

Among shrub communities, three main types can be distinguished, depending on the substrate (Huber, 1994a). The first one grows on sandstones and is the more extensive, being floristically connected to the *tepui* summits, to some extent (Huber, 1986). Dominant taxa are *Ternstroemia*, *Bon-*

URUÉ. Gran Sabana charcoal

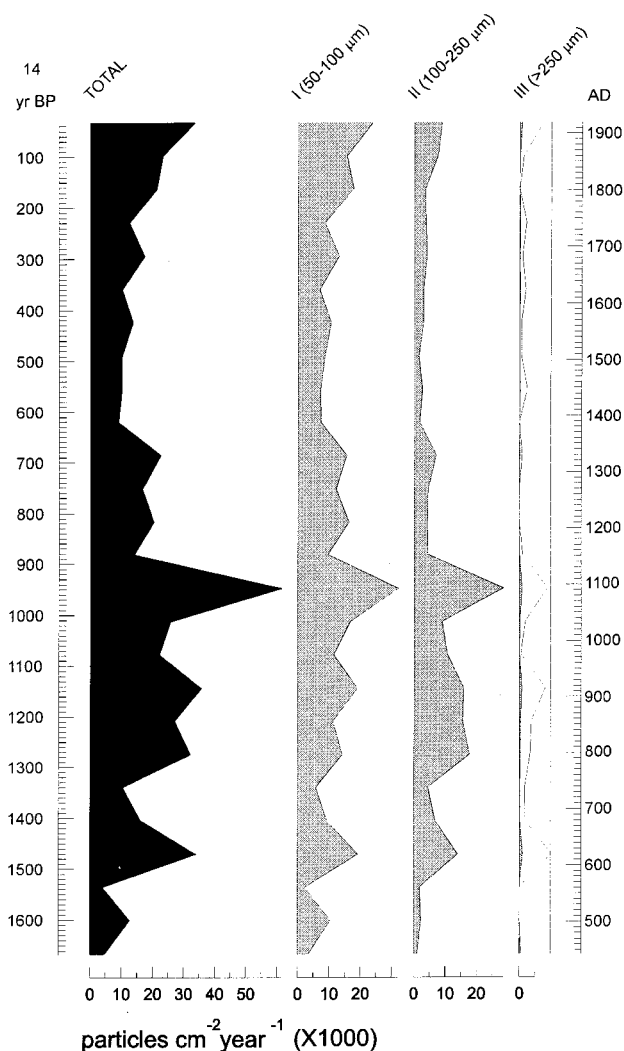


Figure 4 Influx of charcoal particles.

URUÉ. Gran Sabana general categories

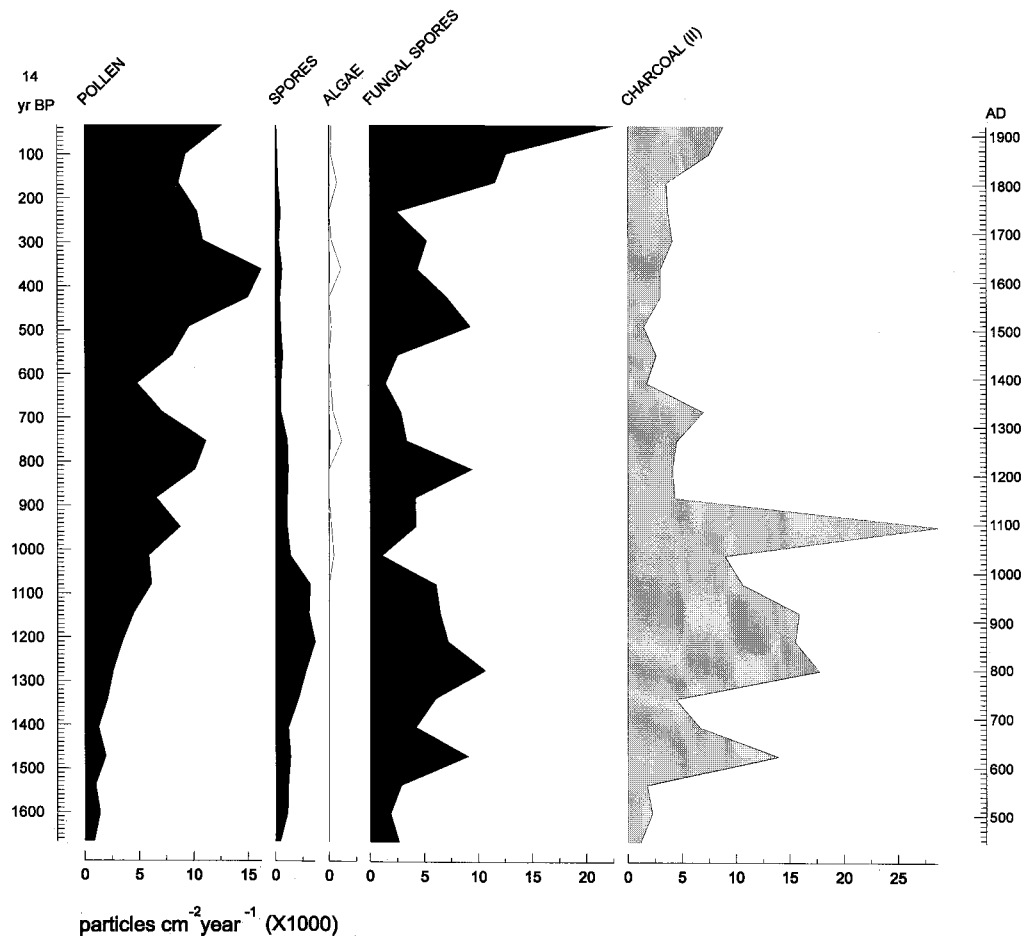


Figure 5 Influx of main categories of palynomorphs found and class II charcoal particles. Solid line for algae is 10× exaggeration.

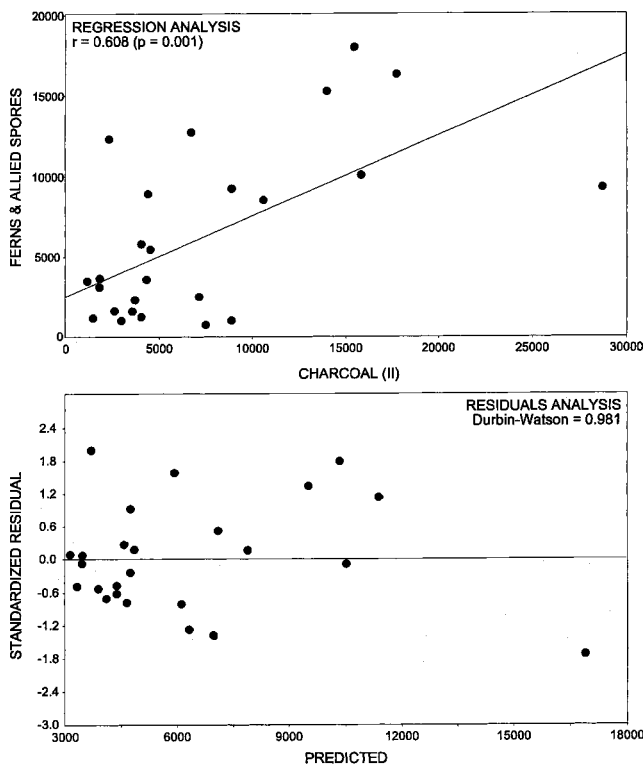


Figure 6 Graphical expression of the correlation between class II charcoal particles and the influx values of fern and allied spores.

netia, Bonyunia, Notopora, Befaria, Macairea, Humiria, Vantanea, Poecilandra, Ouratea and Stomatochaeta, as well as some small trees such as Spathelia and Simaba. The other two types of shrub communities develop on ferruginous soils and peats. They are scattered in localised islands, although they tend to be conspicuous in the general monotonous landscape.

The more important open herbaceous community is the treeless savanna (*sabana lisa*), which gives the Gran Sabana both its character and name. It consists of a continuous herbaceous stratum formed by perennial graminiform plants up to 1.5 m high, dominated by Gramineae and Cyperaceae, with several scattered Rubiaceae, Compositae, Convolvulaceae and others (Huber, 1990, 1994b). It is possible to distinguish two types of savannas based on the dominant species: the Trachypogonnetum, dominated by *Trachypogon plumosus* and the Axonopetum, dominated by *Axonopus pruinosus*. There are no significant differences in floristic composition between these two savanna types, but their elements may vary in their relative abundances. A special type of herbaceous vegetation, localised in small and isolated peat bogs, is dominated by species of the genera *Brocchinia*, *Stegolepis* and *Orectanthe*, which are typical of the *herbazales* (herbaceous communities) on the summits of surrounding tepuis (Huber, 1986).

Present-day fires and secondary successions

According to Hernández and Fölster (1994) most of the Gran Sabana areas are burnt every 1–3 yr. As a consequence,

regrowth of secondary forests, brushwoods (*matorrales*), dense fern communities (*helechales*), and treeless or shrubby savannas are common and are intermingled with burnt trunks of former tall, forest trees. It is well known that many fires are caused by humans for practical reasons, including agriculture, cattle raising, hunting, mining, lumber extraction and tourism. Castro and Gorzula (1986) estimated that ca. 8000–10 000 km² of the savannas of the Caroní basin are secondary. Generally, successional trends are deduced from mosaic patterns apparent in recently burnt areas. It is common to observe areas where patches of the former primary forest merge with extensive areas of secondary forest. Between them, non-forested transitional communities are found. The commonly assumed secondary succession is: primary forest → secondary forest → *matorral-helechal* → shrubby savanna → flat savanna (*sabana lisa*), and is interpreted as a degradation rather than a regeneration process (Fölster, 1986; Hernández and Fölster, 1994; Fölster and Dezzio, 1994). Repeated burning seems to be associated with the transition from *matorral* to savanna, whereas the degradation of secondary forests to *matorrales* is considered a natural process.

The occurrence of an early phase of dense fern communities (*helechales*) seems to be associated with large amounts of humus in the soil, and plays a significant role in the succession. Indeed, these dense fern communities develop a complex root system that prevents the growth of ligneous plants. Once the soil humus declines, fern communities are replaced by treeless savanna (Todd, in Hernández and Fölster, 1994). In this way, the eventual regeneration of forest vegetation is impeded. The *helechales* can persist over long periods, and some are still present in areas burnt 70 yr ago. The more conspicuous fern in burnt areas is *Pteridium aquilinum* ssp. *arachnoideum*, but *Dichranopteris flexuosa* and *Sticherus* spp. are also common (Huber, 1986).

From a detailed study of recently burnt sites, it has been found that secondary forests are lower (around 15 m tall) than primary ones (average 30 m), and structurally more complicated. Although the taxonomic richness of both is similar, the latter is more diverse. Indeed, whereas primary forests have no clear dominant species, the secondary ones can be dominated by one or few species. *Matorrales* are floristically similar to the secondary forests, but poorer in species. As an example, the more conspicuous species of one of these primary forests (Kako) are *Protium* sp., Melastomataceae, *Dimorphandra macrostachya*, Sapotaceae, Moraceae, *Myrcia* sp. and *Vismia* sp., whereas in the secondary areas *Dimorphandra macrostachya* is clearly dominant. In the *matorrales*, *Myrcia* sp. and *Vismia* sp. are again important, together with species common in the secondary forest, such as *Caraipa tereticaulis* and *Hyptidendron arboreum* (Hernández and Fölster, 1994). The degradation process of the *matorral* begins with gaps in the Forest, which are occupied by ferns or herbs, or are non-vegetated. Other taxa typical of secondary vegetation are *Chaetocarpus stipularis*, *Humiria balsamifera*, *Vantanea minor*, *Clusia* sp., *Miconia* sp., *Clethra guianensis*, *Ilex* sp., *Ochthocosmus roraimae*, *Hyptis arborea*, *Casearia arborea* and *Cecropia* sp. (Hernández and Fölster, 1994; Huber, 1986). Among the causes of the degradation of the Gran Sabana, water stress, loss of nutrients and progressive deterioration of the root system seem to be the more important ones (Fölster, 1986; Fölster and Dezzio, 1994).

Previous palynological and palaeoclimatic studies

Palynological studies carried out so far on surface samples and peat borings in the Gran Sabana have provided (i) a knowledge of the relationship between modern pollen rain and vegetation (Rull, 1991), (ii) evidence for the reconstruction of vegetational and climatic fluctuations over the past 10 kyr (Rinaldi *et al.*, 1990; Rull, 1991) and (iii) the basis for an evaluation of the responses of ecosystems to climatic and fire disturbances (Rull, 1992).

It has been possible to recognise modern pollen assemblages from different vegetation types, as for example treeless savanna, gallery forest, mixed forest and *morichales* (Table 1). Furthermore, Holocene palynological associations can be shown by means of cluster analysis on fossil data to be analogous to those recorded in modern sediments (Rull, 1992), suggesting that, in the Gran Sabana, ecological associations have maintained relative constancy through the Holocene. Therefore, palaeoecological interpretations of past palynological assemblages can be shown to be based on reliable modern analogues.

An arid or semi-arid climate has been suggested for the Late Pleistocene to Early Holocene, at the time when high altitudes in the Northern Andes were glaciated (Schubert and Fritz, 1985; Schubert *et al.*, 1986). From about 5.3 to 4 kyr BP the climate was more humid than today, but a decrease in the precipitation/evaporation ratio (P/E) occurred from about 4 to 2.7 kyr BP, as reflected in the lowering of lake levels and in a significant decrease in plant cover. The most marked climatic change consisted of a moisture increase from around 2.7 kyr BP, correlated with a temperature maximum in the Venezuelan Andes (Salgado-Labouriau *et al.*, 1988). The present climate was established at about 1.7 kyr BP, but two minor moisture shifts occurred between the fourteenth and nineteenth centuries, during the Andean Little Ice Age (Rull *et al.*, 1987; Rull and Schubert, 1989).

From an ecological point of view, it has been found that both climatic droughts and fire have had similar consequences, i.e. the irreversible reduction of forests, reflecting the low resilience of these communities. After these disturbances, successional trends have been towards the establishment of treeless savannas and finally *morichales*, irrespective of the initial community composition (Rull, 1992). Forced substitutions (*sensu* Rull, 1990) seem to have been the rule for these ecosystems during the Holocene, indicating that humidity conditions have played a dominant role in their development and evolution.

Materials and methods

The valley of Urué is a small basin in the headwaters of River Kukenán, situated at about 5°10'N and 60°57'W, around 940 m a.s.l. (Fig. 1). It is dominated by flooded savannas and *morichales* in its flat bottom, its gentle slopes being covered by coarse-grained soils with grasses and sedges, except in the main drainage channel, where a dense gallery forest is present. It is worth noting that boundaries between gallery forests and savannas are sharp, a common feature in the Gran Sabana. Recently burnt areas could be observed during the sampling period.

Surface soil samples were taken inside the gallery forest, at the boring site within the *morichal*, and at the transition

URUÉ. Gran Sabana percentage diagram

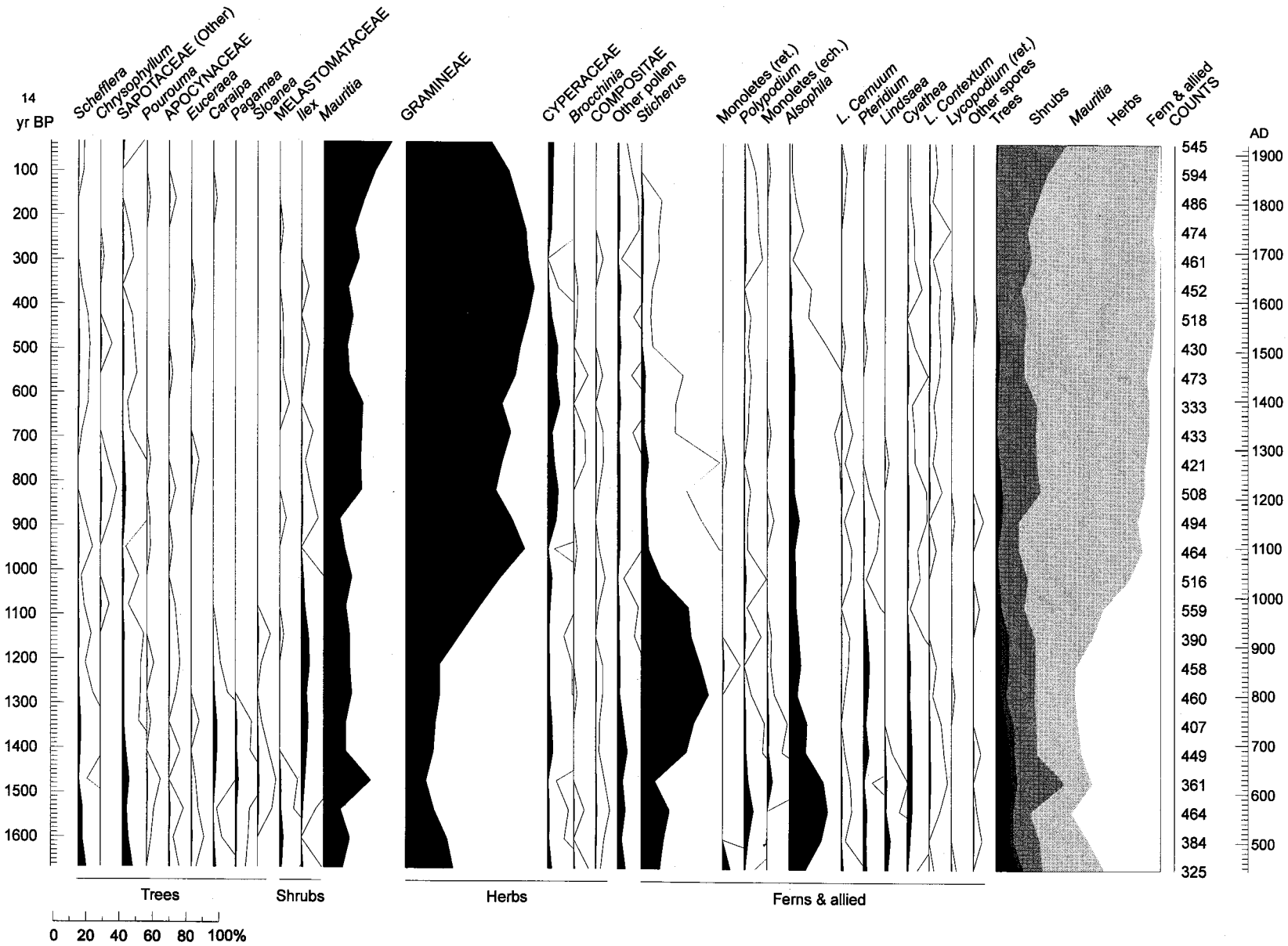


Figure 7 Percentage diagram of Urué, including all the pollen and spores found. Solid lines are 10× exaggeration.

URUÉ. Gran Sabana pollen succession

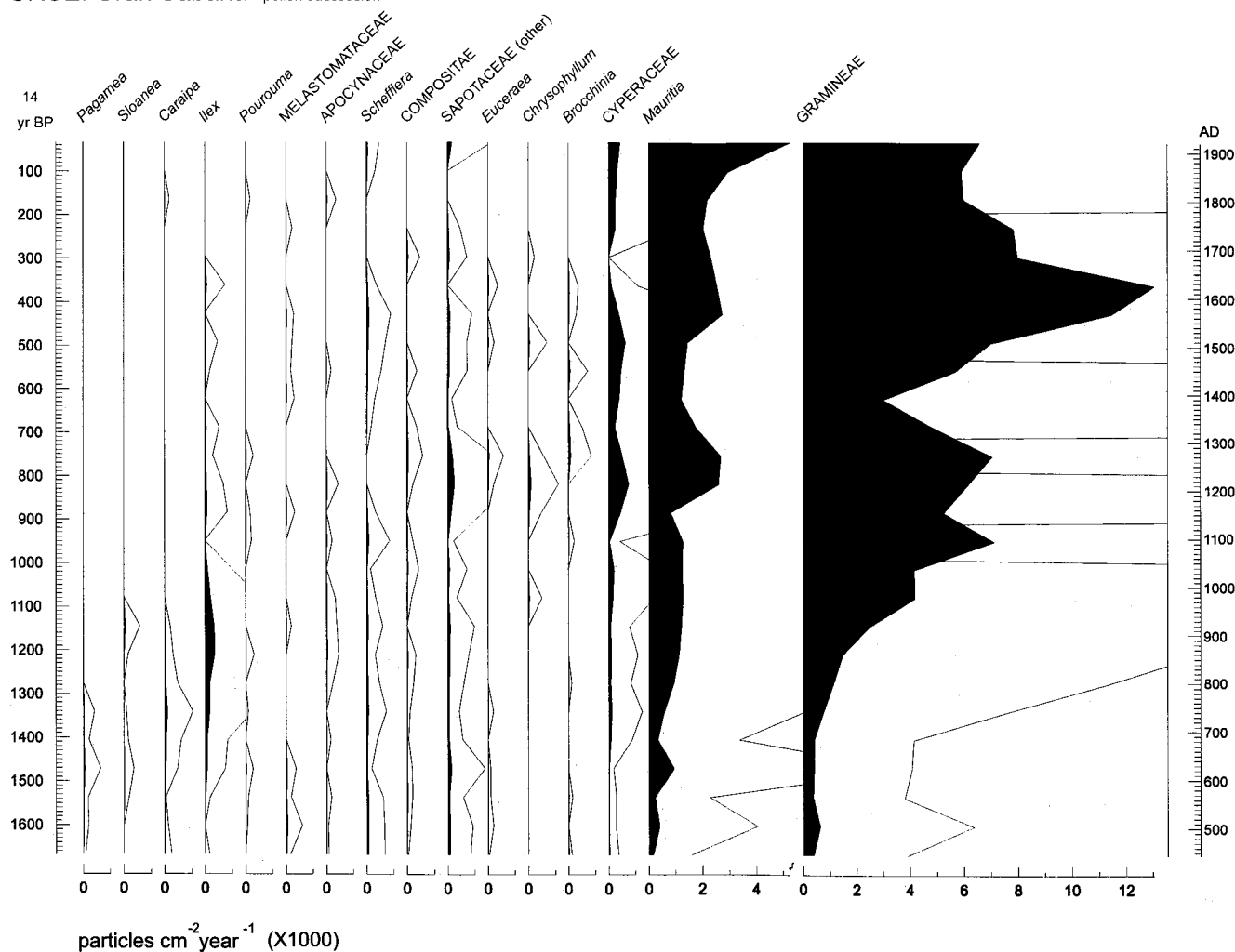


Figure 8 Influx of pollen types found, ordered sequentially. Solid lines are 10× exaggeration.

between them. In order to provide more comparative results, all surface samples taken in the Gran Sabana during the course of previous studies followed the same procedures as above. The stratigraphical sequence studied covers the last 1.6 k ^{14}C yr BP and consists of a 2.6 m core of clay sediments from the bottom of the valley, within the *morichal*. Sampling and palynological methods used to produce the initial slides, as well as radiocarbon dates, are detailed in Rull (1991, 1992). From the same residues stored in silicone oil, new slides were prepared using the same mounting medium, without sealing, in order to preserve the size of pollen grains and spores (Rull and Rinaldi, 1988). The pollen sums range from 373 to 706 pollen and fern spores (average 457); however, counts of important but scarce taxa (especially trees and shrubs) were extended in order to generate representative numbers for statistical analysis (Rull, 1987). Identification were improved using herbarium material (Herbario Nacional de Venezuela, Botanical Institute, Caracas VEN), especially for fern spores, where the colonisers of burnt areas, notably *Pteridium* and *Sticherus*, could be recognised. With reference to charcoal counts and identification, only particles larger than 50 μm were considered, because the lower ones might have been transported by thermal currents, and thus represent not only local but also regional or extraregional fires (MacDonald, 1996). The particles analysed were further subdivided into three size categories, in order to test their behaviour: class I, 50–

100 μm ; class II, 100–250 μm ; class III, more than 250 μm . Concentration values for charcoal particles were estimated by counting introduced exotic pollen of *Kochia scoparia* (Salgado-Labouriau and Rull, 1986). Diagrams were plotted using PSIMPOLL (version 2.25), and statistical analyses were performed with SIMSTAT (version 1.01) and MVSP Plus (version 2.2). Dates were interpolated between 1.18 k ^{14}C yr BP at 180 cm (Rull, 1991) and present-day at the top of the section. Below 180 cm, dates were extrapolated, assuming a constant sedimentation rate. Calibrated AD years were calculated according to Stuiver and Pearson (1993), using the program CALIB (version 3.0.3).

Results and interpretation

Surface samples

The arrangement of Gran Sabana samples in the space of the first two axes of a detrended correspondence analysis (DCA) clearly reflects vegetation patterns in a horizontal gradient along axis 1 (Fig. 2). Samples taken in the *morichales*, around rivers or lakes, are at the left-hand side of the plot, whereas those from gallery forests are placed at the right-hand side. Savanna and mixed forest samples remain

in the middle, but the savanna 'region' is very close to the *morichal* one, indicating their palynological similarity. This agrees with the assertion of Huber (1994b) about the botanical similarity between these two living communities. Axis 2 contributes only to the separation within the gallery forest 'area', probably reflecting composition differences between large gallery forests near major rivers (KUK-0) and smaller ones along little streams.

Aquatic plant representatives (*Sagittaria* and *Myriophyllum*) and taxa typical of flooded areas (*Xyris*, Eriocaulaceae and *Mauritia*) are shown on the left-hand side of the diagram, hence, the horizontal gradient of axis 1 also represents a flooding trend. Indeed, all the samples from *morichales* and savannas were taken from inundated soils, whereas those from forests come from very humid but water-unsaturated substrates, and the intermediate ones (UR-M and AF-0) may vary seasonally. Gramineae is placed almost exactly between the savanna and the *morichal* 'areas', which indicates the importance of this family in both areas. The mixed forest 'region' is surrounded by pollen of Cyperaceae, trees (*Mahurea* and Moraceae) and ferns (*Polypodium*, *Monoletes* and *Triletes*), which suggests some heterogeneity in their composition, due to disturbance.

The gallery forest 'region' is close to trees (*Schefflera*, *Chaetocarpus*, Apocynaceae, Myrtaceae) on the upper side, and trees (*Euceraea*, Sapotaceae), epiphytes (Bromeliaceae), shrubs (*Ilex*) and ferns (*Ptedidium*) on the lower side. The

coincidence and proximity of the latter two genera—which are secondary colonisers of burnt areas (see above)—might indicate some forest-disturbance component for axis 2.

Three of these surface samples were taken at Urué, representing the gallery forest (UR-B), the transition between it and the *morichal* (UR-M) and the *morichal* properly (UR-0). The sample from the gallery forest is dominated by pollen from trees (*Schefflera*, Sapotaceae and Moraceae), whereas herbs (Gramineae, Cyperaceae) are scarce (Fig. 3). In the transition, the trees show a notable decrease and Gramineae and Cyperaceae dominate, whereas in the *morichal* all the elements except *Mauritia* and Gramineae are scarce. The main tree representatives showed an exponential decline from the gallery forest to the *morichal*, whereas Gramineae and *Mauritia* show an inverse trend, suggesting low dispersion capacity, and local dominance of the most important pollen types. The more characteristic palynological elements of the forest–*morichal* transition are the Cyperaceae. Among the spores, the almost linear decrease of *Alsophila* from the gallery forest to the *morichal*, and the scarce occurrence of *Sticherus* in the three samples, are noteworthy. In summary, the pollen from surface sample sediments in Urué represents primarily the local vegetation and therefore comparable assemblages in the stratigraphical record will reflect the succession of local vegetation.

URUÉ. Gran Sabana spores succession

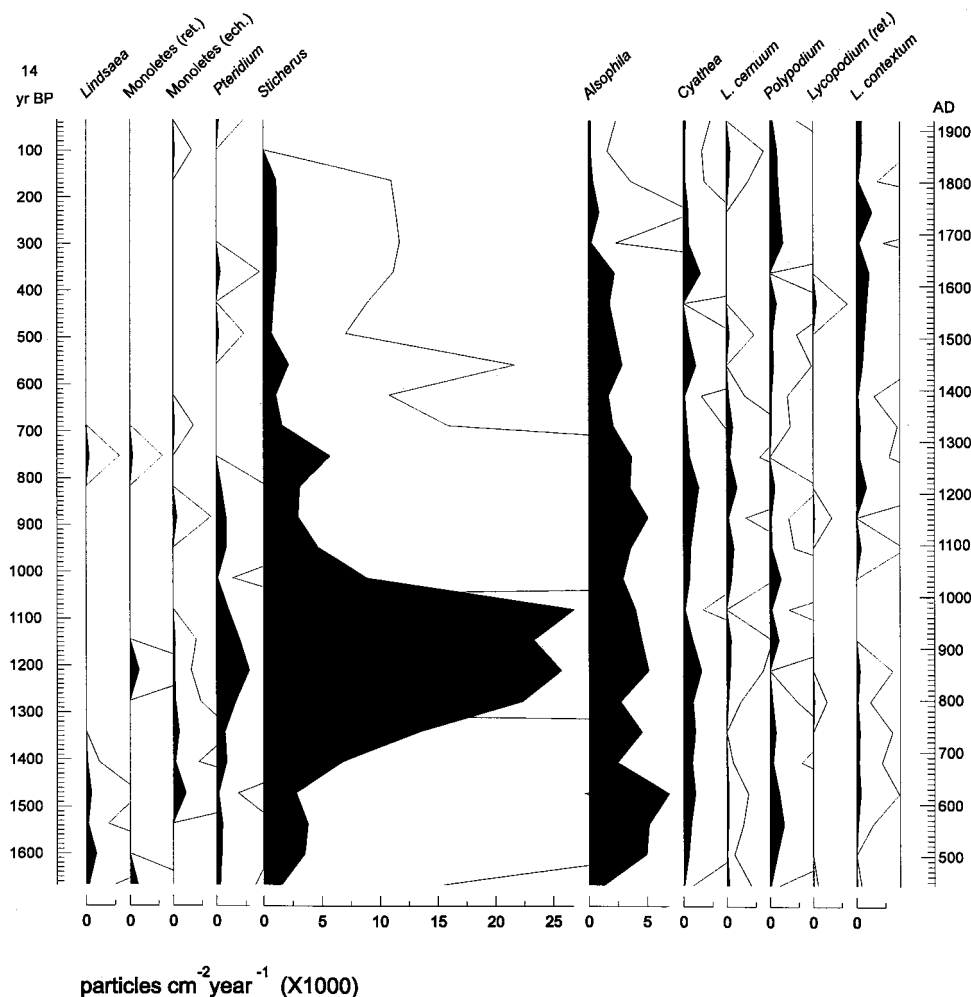


Figure 9 Influx of fern and allied spores found, ordered sequentially. Solid lines are 10× exaggeration.

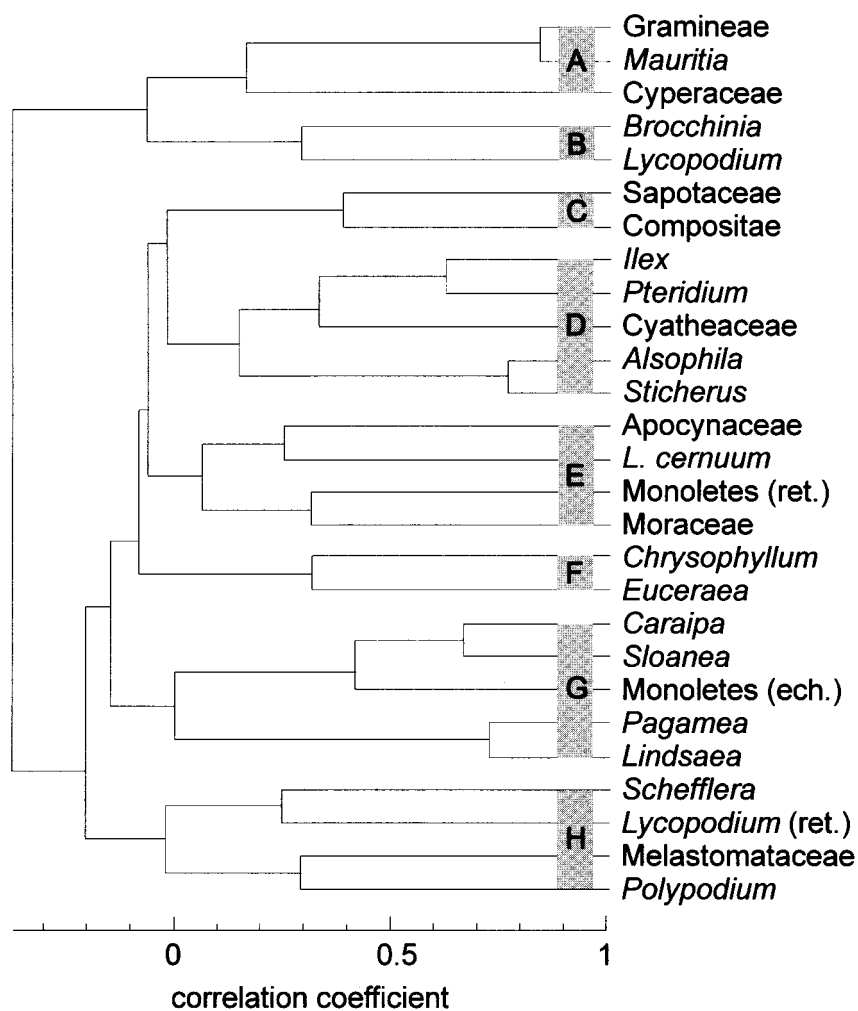


Figure 10 Cluster analysis and the resulting palynomorph assemblages (see text for details).

Charcoal

Two main phases can be recognised in the charcoal diagram (Fig. 4); the first characterised by three peaks of class II and III particles, and the second of low particle deposition. This suggests three main events of higher fire intensity in Urué around 1.47, 1.15 and 0.95 k ^{14}C yr BP respectively. The highest fire intensity seems to have been reached at about 0.95 k ^{14}C yr BP. After this, a phase of low fire incidence is assumed, extending up to about 0.15 k ^{14}C yr BP, when a final charcoal increase coincides with a dry climatic phase (Rull, 1991) that could have favoured the occurrence of fires. Although the same three peaks of the first phase can be seen in the class I particles, they are not easily distinguishable from others by themselves. It is probable that a significant number of the particles between 50 and 100 μm originated elsewhere (regional fires) and have been transported and mixed with the local ones from Urué. On the other hand, although class III particles show the same trend as Class II ones, they are too scarce to be considered significant for statistical purposes. Therefore, only those particles between 100 and 250 μm will be used as indicators of local fires, as well as in quantitative analyses.

Palynological succession

Overall, pollen shows an increasing trend in concentration, with minor variations (Fig. 5). Its higher values are not

attained until about 0.9 kyr BP, coinciding with a marked decrease in charcoal content. This suggests that fires inhibited plant growth until this time, and the present vegetation could not be fully established until their intensity and/or frequency diminished. Despite this controlling character of fire on vegetation, the relationship between pollen and charcoal values shows a non-significant correlation ($r = 0.235$, $p = 0.247$), which indicates that once established, plant communities were affected by other forcing mechanisms. Fern and allied spores show a similar trend to that of charcoal, being more abundant in the lower half of the diagram, and almost disappearing when charcoal content diminished. The correlation between them is significant, indicating a more intense control of fern abundance by fires, but other factors may also be involved, because the dispersion of the residuals in a linear regression model (which showed the best fit) is relatively high (Fig. 6). Algal remains, although scarce, show a similar trend to pollen ($r = 0.568$, $p = 0.002$), suggesting similar controlling mechanisms. As algae respond directly to the climatic water balance that determines the existence or not of water bodies in which they grow, it is possible that minor variations in both pollen and algae reflect changes in climatic humidity. Local hydrological changes, however, could not be discounted on the evidence available. Fungal spores are present in similar abundances throughout the entire diagram, but with important oscillations. Their abundance in the zone of highest charcoal values suggest that fires did not inhibit fungal growth. Furthermore, a low but significant correlation exists between them and the pollen ($r = 0.429$, $p = 0.029$), suggest-

URUÉ. Gran Sabana associations

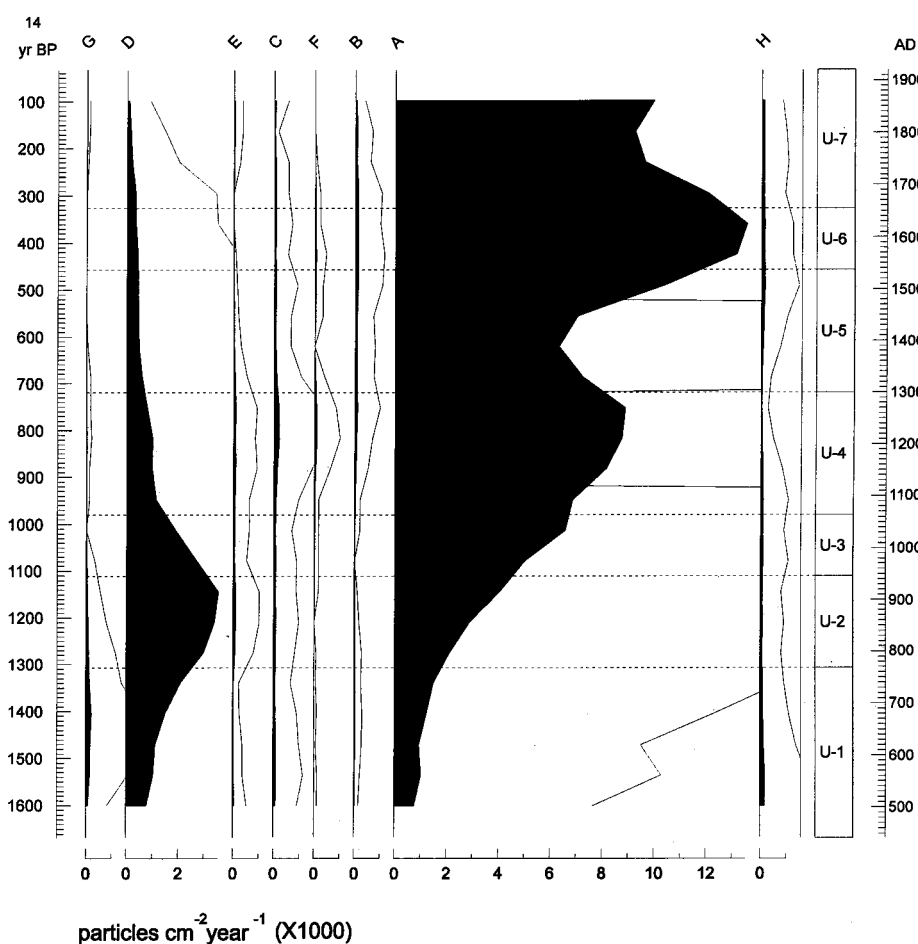


Figure 11 Smoothed diagram of the palynomorph influx assemblages, ordered sequentially (see text for details). Solid lines are 10× exaggeration.

ing that similar factors (probably climate) also affected fungal populations to some extent. Fungal spores were treated as a whole, however, and taxonomic differentiation between them is necessary in order to obtain a clearer picture.

The percentage pollen diagram is shown in Fig. 7, and the sequence of colonisation can be seen in Figs 8 and 9. The first elements were trees and shrubs. Herbs (Gramineae) had started to increase at about 1.2 kyr BP, just after the second charcoal peak, but they did not become important until about 0.95 kyr BP, coinciding with the charcoal decrease. The increase of *Mauritia*, *Brocchinia* and Cyperaceae occurred later (ca. 0.8 kyr BP), close to the increase of algae (Fig. 5), indicating flooded environments. The most striking feature of the pollen record is the sudden and marked increase in *Sticherus* after the first charcoal peak, and its spectacular decline after the second one. *Pteridium* shows the same behaviour, but in lower numbers, and *Alsophila* also shows a decreasing trend.

In order to reconstruct the plant succession, a more detailed analysis was carried out. Pollen and spores were grouped into assemblages through cluster analysis, using the Pearson's product-moment correlation coefficient and the unweighted centroid agglomerative method on log(e)-transformed influx values. The eight assemblages found (Fig. 10) were plotted in a sequential way (Fig. 11). The diagram was divided into seven zones through the method of optimal

splitting by information content. Each pollen assemblage is considered to represent a plant association, and each pollen zone a seral stage, which can be interpreted using both the known autoecology of the taxa involved and the present sedimentation patterns of their pollen. The whole sequence is thus a 'palynoseré' and represents the ecological succession of the local vegetation.

Figure 11 shows a replacement of assemblage D by assemblage A as the dominant plant association. Assemblage D characterises seral stage U-2 and is composed of *Ilex*, *Pteridium*, *Sticherus*, *Cyathea* and *Alsophila*, *Sticherus* being dominant. These fern genera are typical of the *helechaes* that colonise burnt areas, whereas *Ilex* is a shrub also common in the secondary vegetation after fire (see above). Therefore, assemblage D probably represents a *helechal* intermingled with patches of *Ilex* shrubs (*matorrales*?). On the other hand, assemblage A (Gramineae, Cyperaceae and *Mauritia*) is representative of savannas and *morichales*, and dominates from seral stage U-4 onwards. The dominance of *helechaes* coincides almost exactly with the second fire event, whereas its replacement by the savanna and *morichales* took place just after it. Associations representing other vegetation types are obscured by the comparatively higher abundances of grass pollen and fern spores, but they also show sequential trends (Fig. 12), revealing their importance in the reconstruction of the ecological succession. Assemblage G is almost

URU . Gran Sabana minor associations

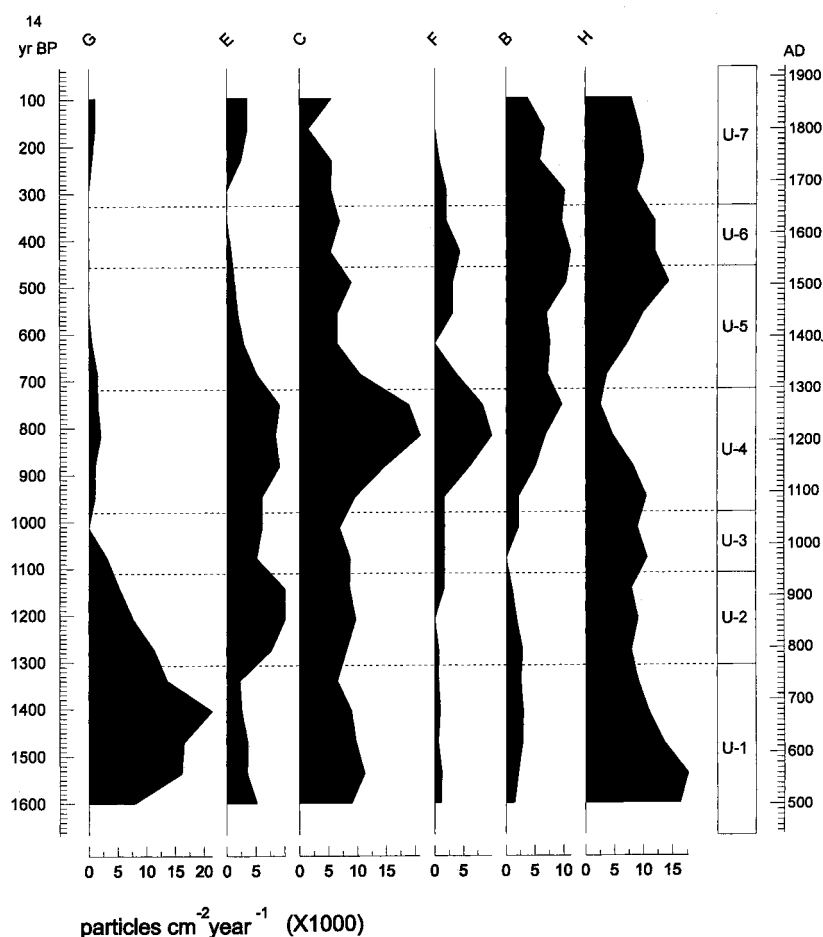


Figure 12 Smoothed diagram of minor palynomorph influx assemblages, ordered sequentially.

restricted to stage U-1, and disappears later. It is composed of pollen of trees from montane and gallery forests (*Caraipa*, *Sloanea*, *Pagamea*) and some ferns (*Lindsaea* and echinate *Monoletes*). Their abundance, however, is not enough to represent *in situ* gallery or mixed forest, as compared with those of surface spectra (Rull, 1991). There is no modern analogue for seral stage U-1, but its composition and low pollen and spore numbers suggest a combination of grasses, ferns and trees scattered or in patches, most probably an open forest, which has been cleared previously by the action of fire. It is important to note that the first fire event occurred at about the middle of this stage, and assemblage G initiated a definitive decreasing trend, which suggests the complete burning of the secondary open forest. Assemblage H remained, although it also shows periods of slight decrease. This too is composed of trees (*Schefflera*) and ferns (*Lycopodium*, *Polypodium*). The pollen of *Schefflera* is important in the present-day gallery forest of Urué (Fig. 3), and therefore assemblage H might reflect a similar community in the vicinity at that time. As some *Schefflera* species, however, are frequently colonisers (Hernández, 1994b), these also could be secondary forests. Stage U-2 corresponds to a *helechal* as stated before, and stage U-3 represents its transition to savanna. In it, minor associations are scarce or decreasing, except for H again. As in U-1, however, no modern analogues are available, so far. These first three stages and the base of U-4 represent the more

frequently burnt vegetation, which is characterised by the trend: open secondary forest → *helechal/matorral* → transitional savanna.

Savannas are fully established in U-4, coinciding with the beginning of the phase of lower charcoal values. The charcoal peak at the base of this stage probably indicates the burning of the transitional vegetation. *Helechales* and open forests strongly decrease, and two new associations appear and become important: B and F. The first one is composed of plants that occur nowadays in peat bogs, and are floristically intermediate between the savannas of the Gran Sabana and the so-called tepuian *herbazales*. Therefore, one of these bogs might have been present at Urué during U-4. On the other hand, both components of association F (*Chrysophyllum*, *Euceraea*) are derived from trees of gallery forests, which indicates an expansion of these communities. Also worth noting are the peaks in associations E and, especially, C, both containing elements such as Sapotaceae, Moraceae and Apocynaceae, which are common in the surface samples of gallery forests (Fig. 2). Influx values however, are below those recovered in modern samples (Rull, 1991), suggesting that these forests did not grow in the bottom of Urué valley. Instead, it was occupied by a *morichal*, since the values of *Mauritia* (Fig. 7) are similar to those found in present *morichal* communities. All these features of U-4 coincide with the occurrence of a humid phase (Rull, 1991), thus indicating that both the decrease in

fire incidence and climate contributed to produce these vegetational changes. In U-5, after a small charcoal peak, all the associations except H experienced a decrease connected to a dry period. The values of *Mauritia* are lower than those corresponding to a *morichal*, hence, the local vegetation was most probably a treeless savanna of lower density than in U-4. The assemblage zone U-6 is similar to U-4, except for associations C, E and F, indicating a drastic reduction in the gallery forests, which did not return to their values of U-4. Finally, another reduction in all the assemblages (F disappeared) coincides with a return of dry climate in U-7. In the upper half, however, an exponential increase of *Mauritia* culminates at the top of the diagram, indicating that a significant expansion of local *morichales* occurred recently. This is synchronous with a slight increase in charcoal influx, suggesting some probable connection. In summary, during the phase of low fire incidence, the succession was controlled mainly by climate, which resulted in an alternation of savannas and *morichales*, as well as the progressive reduction of gallery forests. A summary of the vegetational trends is shown in Fig. 13.

Important changes in diversity that accompanied the successional process are reflected in the continuous impoverishment of communities due to the constant loss of taxa. A stronger decreasing trend can be seen during the phase of higher fire incidence, until the end of stage U-3 (Fig. 14). From here, a small local increase is observed, coinciding with the humidity maximum; however, another decreasing trend began in the middle of U-4, although at a lower rate. There is a significant change in the rate of diversity shift, which means that the impoverishment process slowed down (although it continued) after the third charcoal peak. Indeed, four taxa (mainly trees) disappeared from U-1 to U-3 and only one in U-4–U-5. The impoverishment process, however, began again after the first drought event, which resulted in the disappearance of 10 more taxa in about 300 yr. This indicates that climate has continued to be an important

controlling factor in the degradation of the vegetation in Urué.

Discussion: comparison with present-day studies

Studies of present-day ecosystems suggest that, in the Gran Sabana, burning of 'primary' forests seems to be followed by natural degradation of the secondary vegetation to savanna, even in areas where there is no evidence of additional external disturbances (Fölster and Dezzeo, 1994). The succession reconstructed in the present work agrees with this suggestion but, in this case, it starts with secondary communities; therefore, the burning of the assumed 'primary' forests of Urué that occurred before 1.6 k ^{14}C yr BP (probably close to 1.8 k ^{14}C yr BP) has not been recorded. The first stages in the sequence are interpreted as open secondary forests with ferns and grasses, and probably *matorrales*, derived from clearing of the forest by fire. The next is the burning of the open forests, and the establishment of a *helechal*. This represents an important difference between an undisturbed secondary successional process, characterised by the succession of several ligneous secondary communities (Fölster and Dezzeo, 1994), and others in which secondary vegetation is being burnt again. Furthermore, it supports the idea that the existence of a phase of *helechales* is dependent on repeated burning (Hernández and Fölster, 1994), and this is reinforced by the significant correlation between charcoal and fern spores, as well as by the almost exact correspondence of their curves during stage U-2 (see Figs 5 and 8). Todd (in Hernández and Fölster, 1994) related the occurrence of a *helechal* to early successional stages, when the humus in the soil is still abundant, whereas the

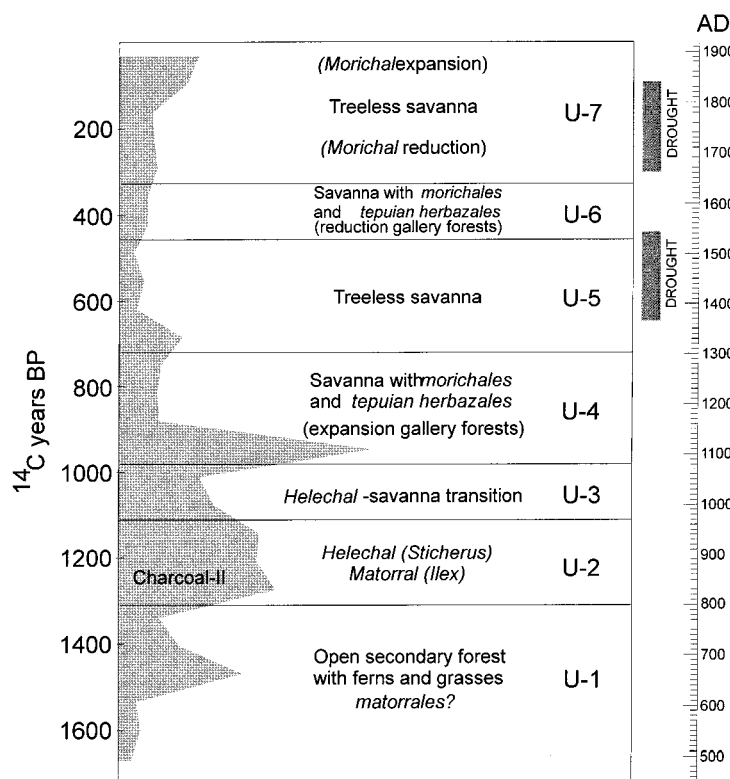


Figure 13 Summary of the interpreted vegetation stages and succession for Urué. The grey area is the class II charcoal influx.

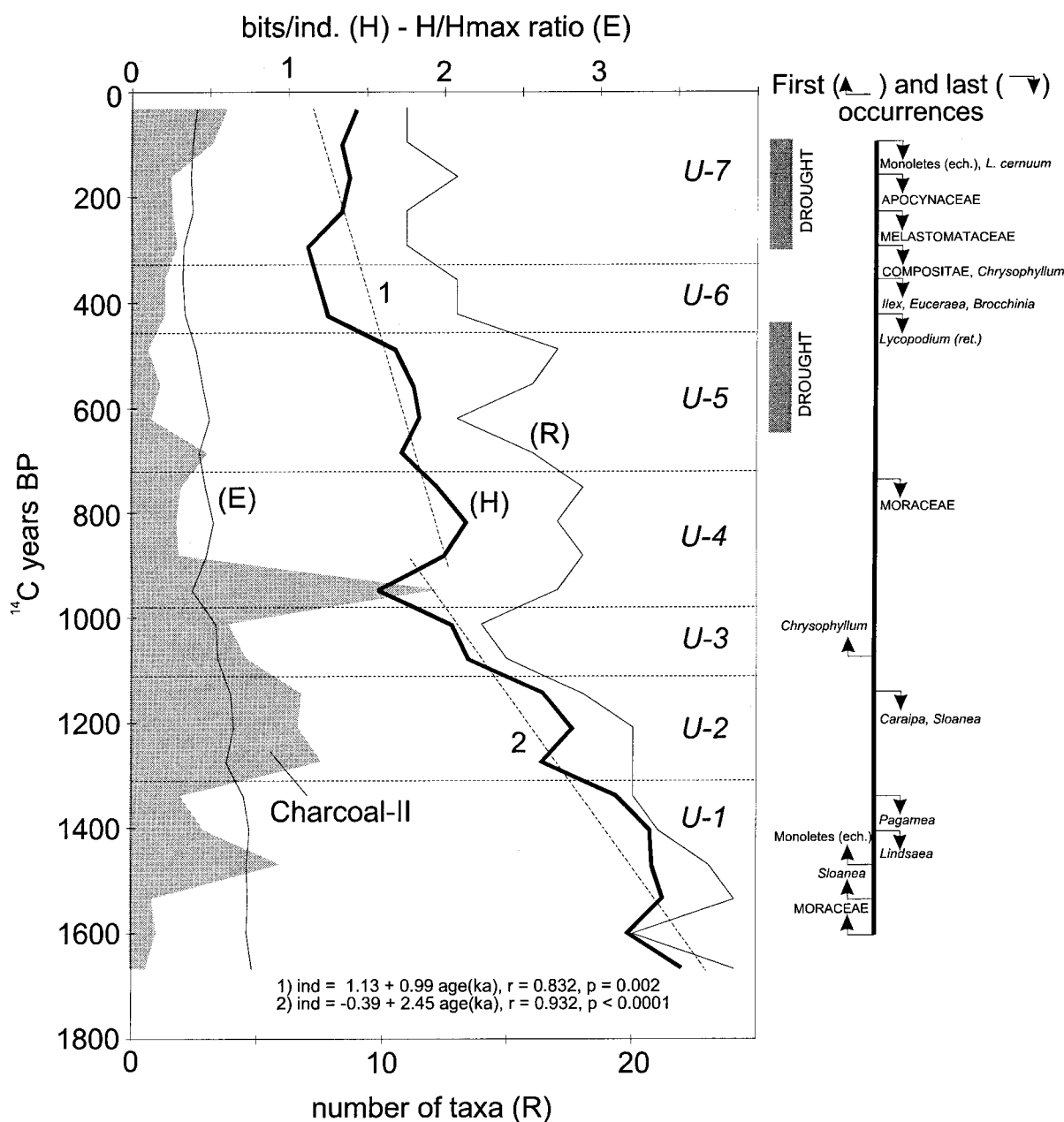


Figure 14 Diversity changes in the palynological assemblages during the succession, and first and last appearances of taxa. R = taxa richness, H = diversity index of Shannon–Weaver (Pielou, 1975), E = equitability.

savanna established later, after the subsequent depletion of soil in organic matter. This is consistent with the palynological reconstruction of Urué, because the *helechal* decreases between stages U-2 and U-3, where no evidence of external forcing factors (e.g. fire, climate) is recorded. The time-stability of these fern communities is also noteworthy (Fölster and Dezzio, 1994). In Urué, they persisted for about 200 yr, which indicates a large amount of humus in the soil, probably as a result of the extensive burning. Although the transition to savanna occurred in stage U-3, the process of degradation continued, but was now controlled by climate instead of fire. Present-day studies suggest that the resulting savannas could be further degraded, due mainly to nutrient losses and mechanical erosion of soils (Fölster, 1986). In Urué, this process has not been observed, because the savanna changed to a *morichal*. It could be argued, however, that this is an unusual situation, because the borehole site is in the bottom of the valley and accumulation of water and nutrients, rather than erosion, is the dominant control

(the vegetation of the adjacent slopes is indeed poor and sparse). Nevertheless, the evidence shows that taxonomic impoverishment and, therefore, degradation, has continued after the fire event (Fig. 14).

It is also interesting to analyse the increase of *Mauritia*. Pollen of *Mauritia* is of local origin, and is restricted mostly to soils where this palm is growing. Therefore, the presence of this pollen in sediments indicates the local occurrence of *morichales* or communities with *Mauritia*. In addition, both the absolute and the relative amounts of *Mauritia* pollen in sediments vary according to the abundance of the parent species in the community (Muller, 1959; Rull, 1991). For this reason, its pollen signal is a reliable indicator of its population dynamics. In Urué, the influx of *Mauritia* pollen to the sediments increased markedly just after the last important charcoal peak. Furthermore, it has been reduced after each fire and also during each drought event (Fig. 15), but its recovery has been almost immediate, and the resulting general trend is of a discontinuous, but overall increase.

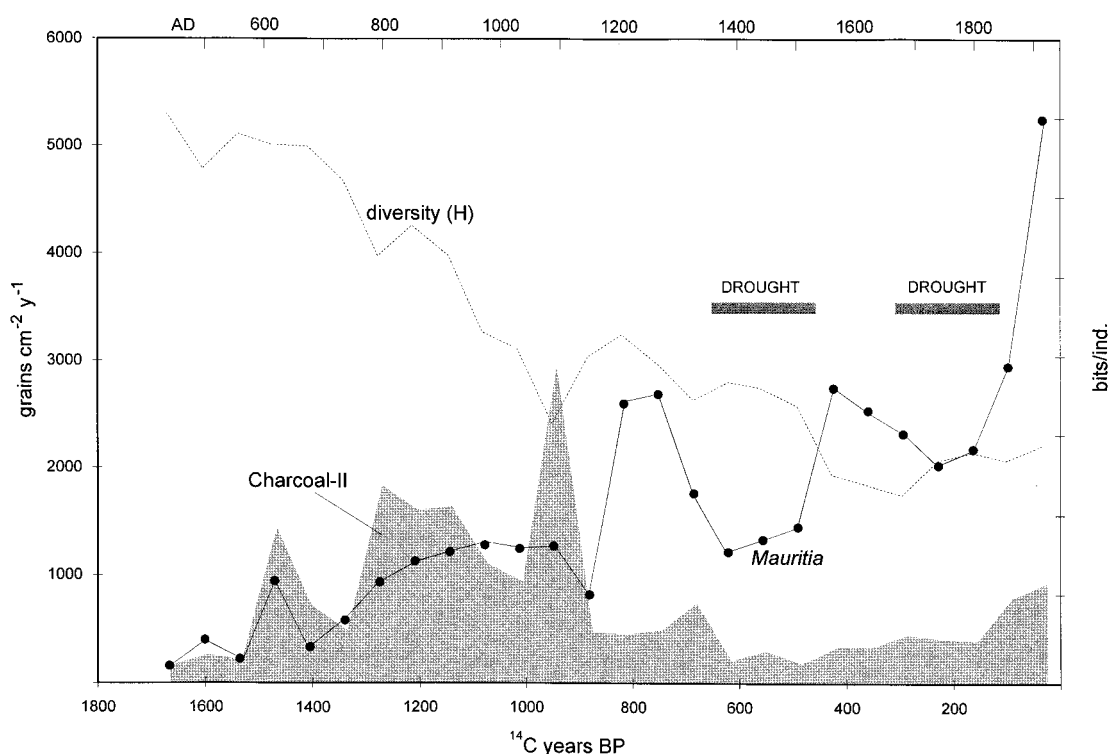


Figure 15 Changes in the influx of *Mauritia* compared with plant diversity and charcoal influx.

This tendency is the inverse of that of practically all the other taxa and is, therefore, connected to the impoverishment process. A significant negative correlation ($r = -0.742$, $p < 0.0001$) exists between *Mauritia* and total diversity (Fig. 15). This palm, therefore, seems to have been opportunistic, and able to colonise rapidly new habitats created by fire and climatic shifts. Based on studies of living *morichales*, González (1987) considers *Mauritia* as a pioneer that colonises the treeless savanna, developing a *morichal*, and finally a swampy forest. The establishment of this assumed final community has not yet been recorded palynologically, but the colonising ability of *Mauritia* is strongly supported in the present work.

Conclusions and final comments

Palynological analysis allowed reconstruction of a secondary succession triggered by fire, from 1.6 k ^{14}C yr BP until the present. The cause of fire (i.e. anthropogenic or not) cannot be deduced from the evidence available. Charcoal counts indicated the occurrence of three main phases of increased fire influence around 1.47, 1.15 and 0.95 kyr BP, followed by an interval of reduced fire intensity, characterised by climatic (humidity) oscillations. During the first phase, three seral stages could be recognised, in a trend from open secondary forests cleared by fire (stage U-1) to a transitional savanna with ferns (U-3). An intermediate stage (U-2) characterised by a *helechal* of *Sticherus* remained near the site for about 200 yr without apparent change. This record supports the results of present-day studies, showing the progressive degradation of the secondary vegetation to savanna over a time-scale of about 600 yr. It also supports the hypothesis that repeated burning after the main fire event is necessary for the establishment of *helechales* (otherwise, the succession proceeds through several woody communities), and that the

transition from them to savannas is a natural process, connected to the decreasing humus content of soils.

The second phase began with the burning of the transitional vegetation and the establishment of wet savannas with peat bogs and *morichales*, linked to a humidity increase (U-4). The following stages are an alternation between treeless savannas (U-5 and U-7) and savannas with *morichales* (U-6), following humidity oscillations controlled by climate. No degradation of savannas resulting from leaching and erosion was observed, probably due to the topographical position of the borehole site, although continuous taxonomic impoverishment due to climatic droughts is apparent. The steady increase of *Mauritia*—and therefore of the *morichales*—in spite of fires and droughts, supports the view that this palm is a coloniser, which reacts rapidly to disturbance by progressively occupying new habitats created by them.

A limitation of this study has been the lack of modern analogues for secondary vegetation types, as the surface samples available from the Gran Sabana region are from undisturbed communities. Owing to the incidence of fire in the region, a survey of modern pollen deposition in burnt areas would be very useful. This requires a close co-operation of palaeoecologists with vegetation ecologists. It is also desirable to carry out more of these palaeoecological studies in other disturbed sites with different vegetation patterns, in order to learn more about the degradation of the vegetation in the Gran Sabana. The results of the present work are very encouraging because of the close correspondence with the data from modern studies.

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