

CHAPTER 7

PALAEOCLIMATES AND THEIR CONSEQUENCES ON FOREST COMPOSITION

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1. Introduction

The analysis of most plant populations in natural forests clearly retraces the mechanisms of sylvigenesis, based on the occurrence of small-scale incidents - in particular treefall gaps - more or less regularly distributed in time and space (van der Meer *et al.* chapter 24). However, a number of 'anomalies' detected in the population structure or in the distribution of some species cannot be adequately explained by the internal dynamic processes which occur on the century time scale. Plants react at different speeds to perturbations, and major events, even very ancient ones such as the perturbations recorded in the sediments, have probably also left a durable mark in the present organisation of the vegetation. We can therefore hypothesise that relatively ancient events, which would have occurred on a much larger scale than treefall gaps, would have caused large modifications of the forest ecosystems and left long-lasting tell-tale signs.

This article constitutes a brief synthesis of a multidisciplinary approach of the forest ecosystem viewed on a several thousand years scale.

2. The past recorded in the sediments

2.1 PALAEOFIRES

The charcoal layers found in the soil are the most obvious indicators of palaeofires (Soubies 1980, Saldarriaga 1994, Tardy 1998). In the hyperhumid forest zone of French Guiana (Boyé *et al.* 1979, Puig *et al.* 1981), annual rainfall exceeds 3000 mm distributed over 280 days. In the less humid areas of Amazonia, extensive forest fires can develop during exceptionally severe dry seasons - like the fires of the Roraima in 1998, or those of 1988, when 80,000 km² were destroyed (J. Ronchail personal communication) - but in French Guiana no-one has such an incident in memory. The traditional agriculture, like elsewhere in tropical forests, is based on slash-and-burn techniques which proceed by the felling of trees on a plot and by the on-the-spot burning of the woody debris at the end of the following dry season. Tardy (1998) shows that charcoal layers are generally independent of the levels of human occupation. The presence of Man in America is attested since 30,000

BP at least, and agriculture since 6,000 BP (Grand Atlas de l'Archéologie 1990, Lorenzo 1994, Vilhena Vialou *et al.* 1994, Behling 1996, Roosevelt *et al.* 1996), but evidence for tropical rain forest agriculture is only found since 2,500 BP in Meso-America (Linares 1984). Saldiarraga (1994), based on indirect proofs, estimates the agriculture in Colombia (areas of Amazon and Rio Negro) to 4,000 BP. However, in French Guiana, intensive archaeological searches undertaken in the Petit Saut area over 275 archaeological sites (Puaux 1993, Tardy 1998) have not yielded any remains anterior to 2,000 BP, while palaeofires appeared a long time before this, during the periods 10,000-8,000 BP, 6,000-4,000 BP and 2,000 BP to present time.

The fact that these fires, whether they are of natural or human origins, have been able to develop in hyperhumid forests, suggests that the dry seasons and the resulting water losses had then been extremely severe.

2.2 EROSION UNDER FOREST COVER

Today, the physical erosion of the forest floor is minimal under primary forest cover. The thick vegetation considerably reduces the impact of heavy rains. Moreover, the forest floor is entirely colonised by a dense mat of surface roots which 'filter' particles. During heavy rains, the flow of small streams and rivulets rises sharply but very small amounts of solid matter are actually torn from the forest floor, and the water flow merely reorganises ancient sediments. Large-size elements are never driven from the forest floor into the stream beds. However, recent investigations (Charles-Dominique *et al.* 1998, Charles-Dominique & Servant 2000) along the course of the Nouragues River have uncovered remains of alluvial terraces that are quite unlikely under the present-time vegetation cover and which could only have arisen during periods of intensive erosion (Fig. 1). The lower terrace (1 m

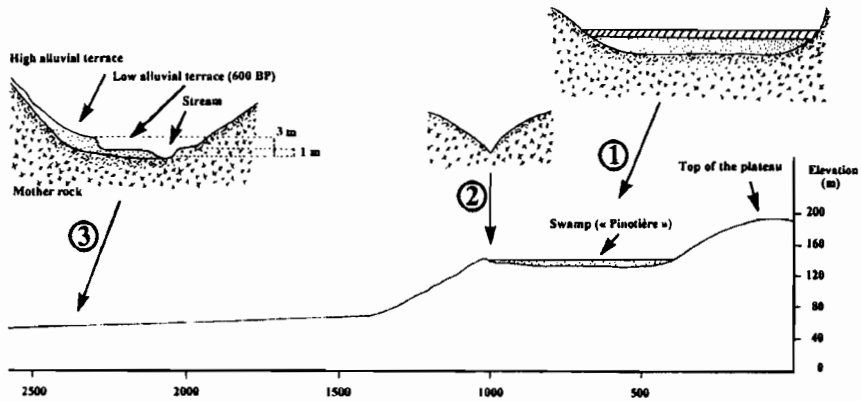


Figure 1. Longitudinal profile of the pina swamp, and transversal profile of the Nouragues stream at the levels 1, 2 and 3.

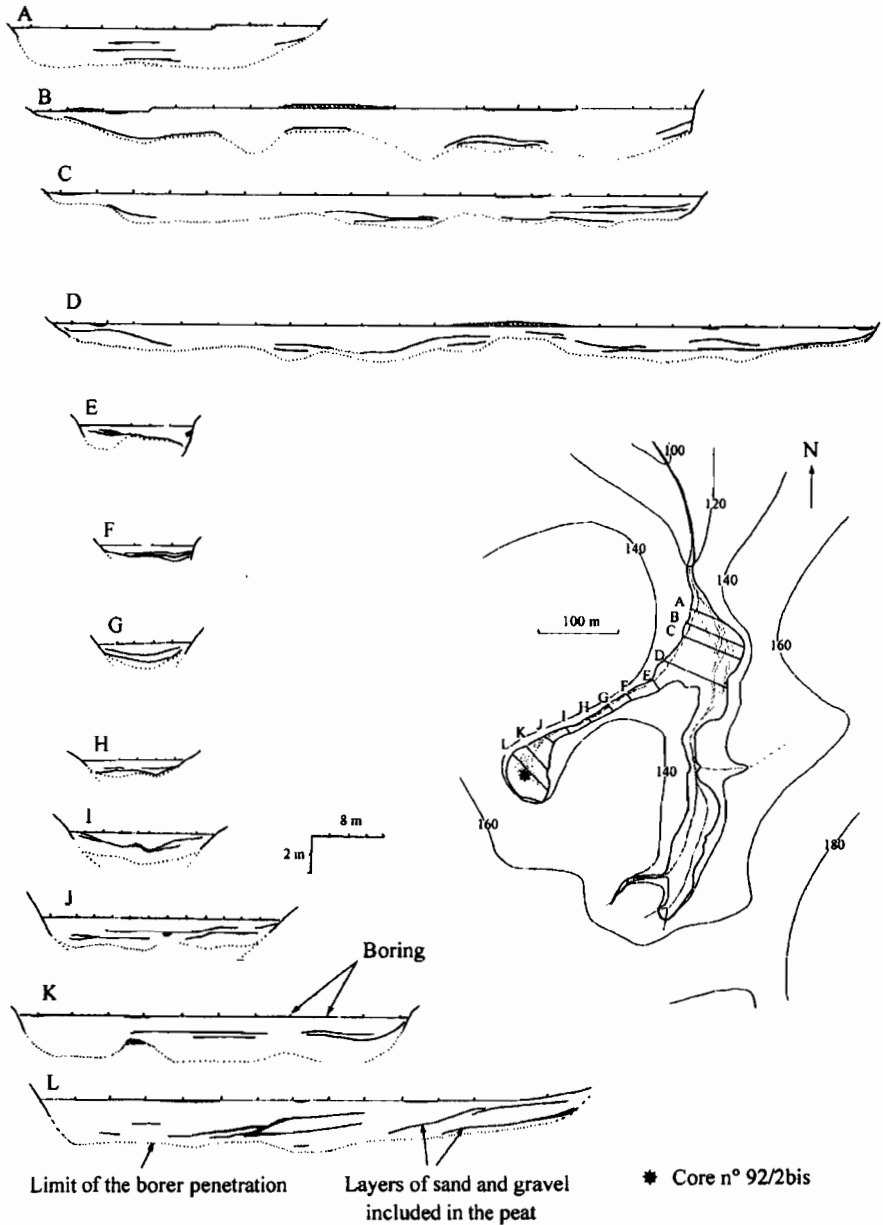


Figure 2: Transversal profiles of the pina swamp (cf. level I of Fig. 1) showing the layers of sand and gravels included in the peat.

high) sits on a bed of clay and sand containing charcoal fragments, seeds and dead leaves. The examination of the seeds reveals a great abundance of pioneer species: *Henriettea spp*, *Miconia spp*, Melastomatacea, *Cecropia obtusa*, *C. sciadophylla*, Cecropiaceae, *Goupia glabra*, Celastraceae, etc. These taxa are characteristic of important disturbances of the forest cover at the time.

Ancient tree stumps still rooted in place were discovered on the border of and under this terrace, during the excavation of the river banks on 80cm width. The carbon datings of these woody remains are difficult to interpret: 810 ± 60 years BP, 1250 ± 50 years BP, 1390 ± 40 years BP, 2380 ± 50 years BP and 4310 ± 50 years BP. Successive events may have preserved these stumps from decomposition by successively embedding them in silt and uncovering them several times. The latest sedimentation event would correspond to the formation of the lower terrace and would be contemporary with the dead leaves deposit, dated 530 ± 70 years BP, which is undoubtedly too fragile to have undergone several reorganisations. A higher (3 m) and older terrace has also been discovered but has not been dated so far.

Geomorphological and sedimentological studies recently undertaken on the lower terrace completed these data and made it possible to identify several major trends of the morphogenetic evolution of the Nouragues stream catchment area throughout the Holocene. The ^{14}C datings of several charcoal debris and organic matter found in the deposits will soon yield a precise chronology of these events. Recurring acute erosion phases were reconstructed, materialised on one hand by an increased input of detritic matter in the valleys (coarse and sandy alluvia) and, on the other hand, by a severe destabilisation of the slopes (mass landslides and colluvial deposits). Such morphogenetic events seem clearly correlated with disturbances of the forest ecosystem. The episode of superficial scouring for which evidence can be found on the right bank of the Nouragues stream necessarily implies a significant degradation of the vegetation cover (palaeofire?) at the time. The event began around 530 ± 70 years BP (^{14}C dating undertaken on the above-cited lower terrace of the Nouragues stream). In two of the Nouragues tributaries, the Cascade and Kwak streams, the presence of sandy hydromorphic clays and organic clays interbedded in the alluvial sands attest a radically different orientation of the morphogenesis. It signals one to several episodes of low sedimentary activity linked with the development of poorly drained habitats: wandering meanders depositing their load of suspended matter in floodplains probably covered by dense hygromorphic vegetation. No such processes can be found at work today in either catchment area: on the contrary, evidence supports that a decisive reversal of the dynamic trend has taken place since, reactivating the alluvial water channels. On the other hand, these once-ruling processes share some characteristics with the mechanisms governing sedimentation in present-time pina palms alluvial basins (Rosique *et al.* 2000).

The study of a pina palm swamp, a little further upstream and lodged in a plateau depression, also displays traces of several periods of intensive erosion (Fig. 2). In this case, layers of sand and gravels a few centimetres thick have been found included within clayey-organic sediments or peat. The reconstitution of the soil profiles reveals up to three such layers one above the other, with a slight slope towards the centre of the swamp, suggesting transport of material by runoff. One of these layers, with its upper limit at -85 cm, has been dated just under 1,570 BP. Another, located between -131 and -140 cm (Ledru *et al.* 1997), would be about 3,000 years old. In order to explain such alluvial deposits, knowing that the

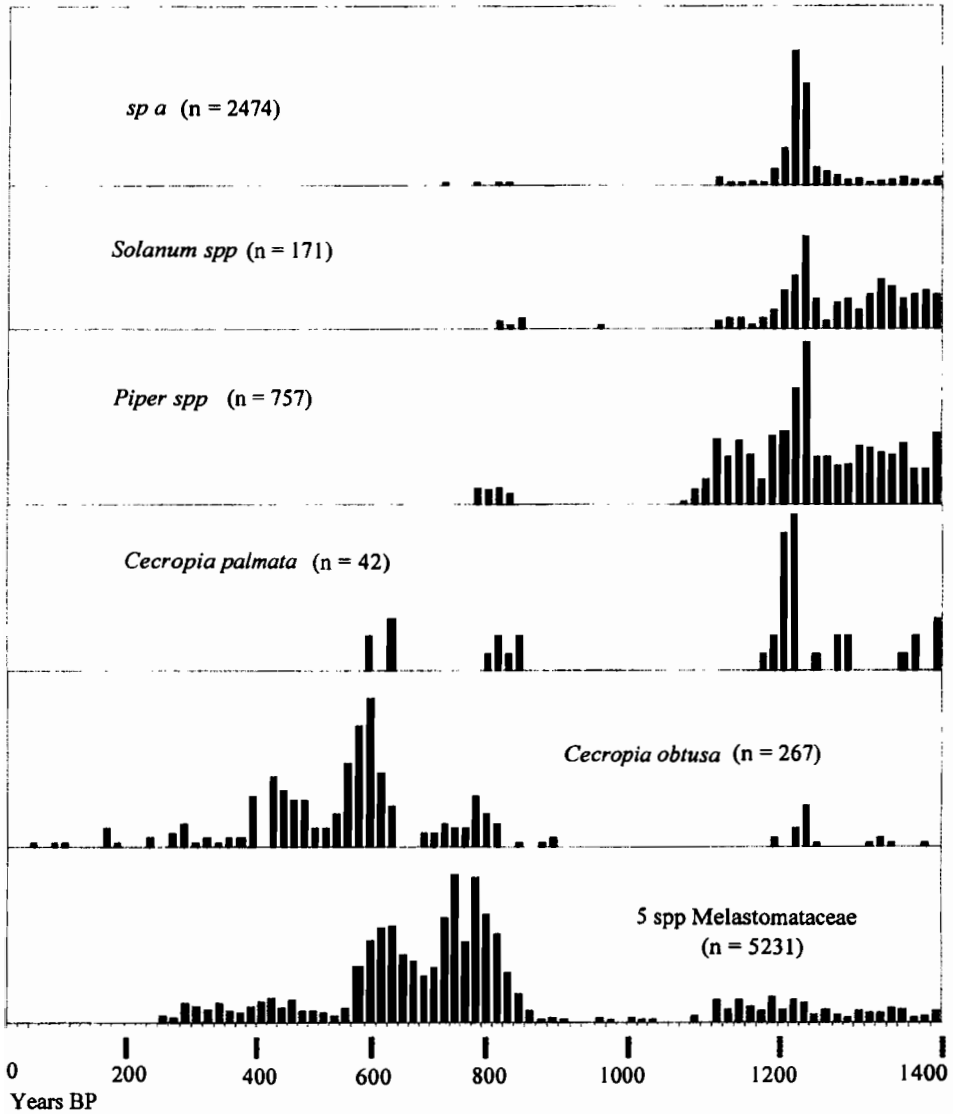


Figure 3a. Seed analysis of the peatbog core (in number of seeds).

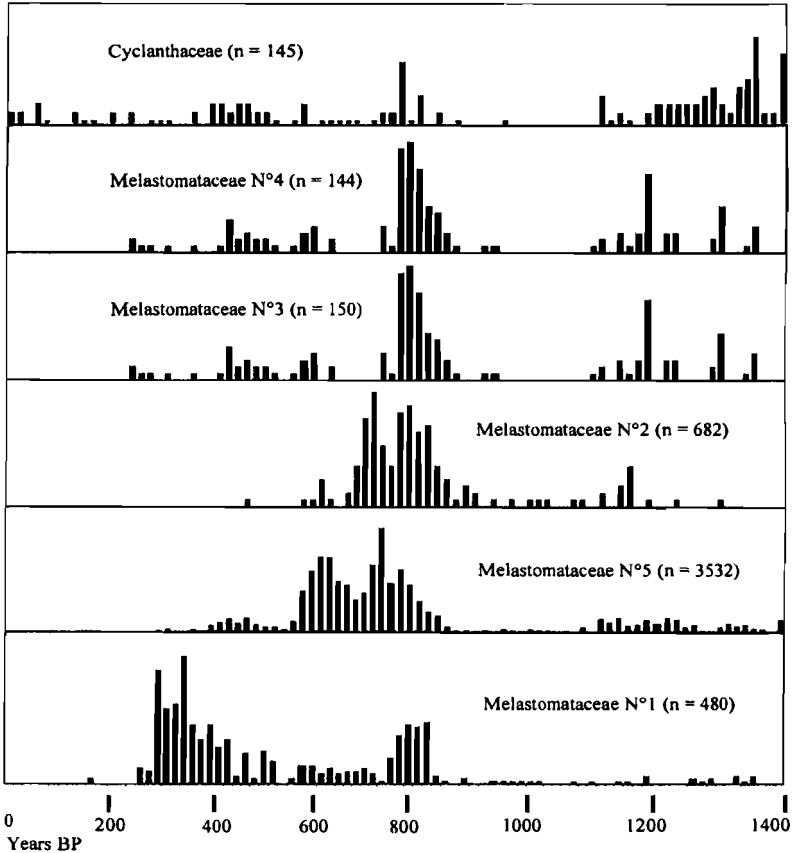


Figure 3b. Seed analysis of the peatbog core (in number of seeds).

swamp does not receive at present any coarse particles during heavy rains, one must consider massive destructions of the forest cover which would have induced intensive soil erosion over large areas. The same goes for the alluvions accumulated further down along the stream bed. Such erosion/alluvion cannot be explained outside large-scale deforestations, such as palaeofires may have generated.

2.3 THE PAST VEGETATION

Past vegetation was studied by analysing the pollen (Ledru *et al.* 1997) and seeds (Charles-Dominique & Servant 2000) contained in core samples collected from a pina swamp. The peatbog cores go back 3,000 years BP for pollen and 1,400 years BP for seeds (Fig. 3). Overall, between 3,000 and 2,000 BP, the forest appears to have been more humid than today, with a higher taxonomic diversity (Ledru *et al.* 1997). Between 1,800 and 1,200 BP, the analyses suggest a marked drying-up and the opening of large areas favourable to

pioneer species, in particular *Cecropia*, *Solanum*, and *Piper*, this phase peaking around 1,600-1,300 BP. Between 1,200 and 900 BP, the forest appears similar to what it is now, but between 900 and 600 BP new disturbances are indicated by the development of pioneer plant assemblages (in particular the family Melastomataceae). These subsided from 600 to 300 BP, and today's pollen and seed assemblages appeared around 300 BP (Fig 3a,b).

The appearance of pioneer species during several consecutive centuries suggest that brief disturbances must have occurred every 10-30 years during each of these periods. Indeed, the observation of forest recovery in a 'modern' gap shows that the short-lived pioneer tree species are progressively replaced within a few decades by mature forest species. Only repeated incidents can therefore explain the maintenance of a widespread secondary vegetation for several centuries.

No traces of herbs such as Poaceae and Cyperaceae have been found in the pollen profile to suggest the occurrence of open vegetation types such as woodland-savannas (Ledru *et al.* 1997). Moreover, histological analyses of charcoal remains (Tardy 1998) have always yielded some forest species ever since 13,000 BP. However, tree species diversity is much lower during the two more ancient periods (8,000-7,000 BP and 6,000-4,000 BP) - its specific composition recalling a semi deciduous forest - than from 3,000 BP onwards (Tardy 1998).

3. Traces of the past in present-day ecosystems

3.1 THE VEGETATION TYPES INCLUDED IN THE MAIN FOREST BLOCK

The open vegetation found on rocky outcrops - locally called 'rock-savannas' - and the low forests which surround it only occur on limited surface areas included within the main forest block (c.a. the primary forest extending from the coast to the inland). Most of these patches are found around inselbergs, in the south of French Guiana, between 100 and 300 km from the coast. Two other vegetation types, the liana forests and the bamboo thickets - or 'cambrouzes' - constitute other types of inclusions, the origins and dynamics of which are difficult to explain in the context of present-time sylvigenetic mechanisms. Although an ancient anthropic origin has been proposed in the case of the cambrouzes (Gasc & Sastre 1978), our present state of knowledge on their dynamics is still insufficient. Information can mainly be gathered from the savannas and low forests which have been intensively studied at Nouragues (Larpin Chapter 5, Sarthou Chapter 6).

Overall, in the course of the present relatively humid period, the forest is slowly expanding and gaining over the rock-savannas on its borders. The recovery of the forest is nonetheless extremely slow and even subject to reversals on steep slopes where water runoff is very important.

It is difficult to estimate the age of these open vegetation types, but they are probably very old (as they harbour distinctive plant species) and have undoubtedly suffered variations in surface area over time. Glacial episodes must have determined their maximum extension by inducing severe erosion of the forest soils on much larger areas than today. After the post-glacial forest recovery, more recent phases of erosion probably coincided with dry periods and forest fires, and must have periodically given a new development to these savannas, which would otherwise have disappeared altogether since the end of the latest glacial episode, absorbed by the surrounding forest.

The low forests - sometimes termed 'transition forests' - constitute an original vegetation type generally found on the periphery of rock-savannas. They occupy soils with drier edaphic conditions than in the surrounding high forest (Larpin 1993). The study of their dynamics has highlighted the importance of bird dispersal of seeds in the present colonisation phase of the rock-savannas by this vegetation (Larpin 1993, Théry & Larpin 1993). This present tendency is punctually counterbalanced by perturbations occurring on the ecotone, which are more favourable to the development of the rock-savanna vegetation. Similarly, the surrounding high forest tends to slowly gain over the low forest on its outskirts. Low forests display an original floristic composition: almost 200 plant species are specific to this vegetation type at Nouragues. This clearly indicates that they constitute a distinctive ecosystem as opposed to a 'transition' gradient. These types of forest, well adapted to a number of water constraints, may have known a greater extent in the past and their present distribution would thus correspond to relict patches, like the savannas included within the border zones of the great forest blocks.

3.2 ZOOCHORY, AUTOCHORY AND PLANT DISTRIBUTION

Many plant species in French Guiana disperse their seeds by zoochory, i.e. by means of fruit-eating animals which carry their seeds over a certain distance. The present floristic composition suggests frequent small-scale forest perturbations, as most plant species are capable of quickly recolonising lost ground. A small number of slow-spreading trees exist nonetheless which are not dispersed by animals (autochorous species). Individuals of these species are frequently patchily distributed, a pattern which again cannot be explained solely by today's mechanisms of regeneration. A favoured hypothesis is that these tree species have been eliminated from large areas during the latest palaeofires and that they are now in the process of recolonising from 'microrefuge' patches which these ancient fires have not reached (Riéra & Joly 1996). Tree mapping at Nouragues (85 ha so far) has outlined possible small-scale refuge patches around swamps and springs. More detailed studies on *Eperua falcata* (Caesalpinaceae) show that the older individuals are situated in the centre of the patches, while the younger are distributed mainly on the periphery, as if the population was currently recolonising the plateau from the swampy lowlands (Riéra & Joly 1996). Although the species is not found on the plateau presently, charcoal remains identified to species level prove that it grew there some time ago (Tardy 1998).

4. Discussion

The study of the distribution of species in tropical forest ecosystems has so far approached the problem using two different scales of time and space.

On the local short-term scale, the mechanisms of the sylvigenetic cycle and in particular the key role of treefall gaps have been used to explain the structure and dynamics of the forest mosaic. The mechanisms examined here occur on a scale inferior to the kilometre and on a time scale of 1 to 10^2 years (Oldeman 1974, 1978, Whitmore 1978, Riéra 1995, Riéra *et al.* 1990, Pélissier & Riéra 1993).

On the continental and regional long-term scale, the Holocene refuge theory provides the theoretical framework for the interpretation of global species distributions. Here, the scales used range from 10^4 to 10^8 km² in space, and from 10^4 to 10^6 years in time (de Granville 1992, Haffer 1969, Prance 1973, 1982, Van der Hammen 1974, Vanzolini 1973).

These two axes of investigation can only bring satisfying answers at their own respective scale, and remain unable to explain abnormal population and community organisations (referring to the general distribution pattern). Our approach focuses on an intermediate scale and uses both functional arguments and local evidence for past events.

Exceptional events occurring at several centuries intervals should be taken into account as well as all the common constraints organisms have to face. Their exceptional occurrence explains that they have frequently been ignored in functional ecology models, which are often based on climatic parameter averages. Connell (1978) did consider however that perturbations occurring at a moderate rate could be favourable to the maintenance of a high species diversity. Sporadic catastrophes could give a new impulse to the dynamics of forest ecosystems, maintaining biotopes and species which would otherwise tend to disappear.

The forest fires which have left these numerous tell-tale signs seem to have been the only type of catastrophic event to have affected French Guiana. The crystalline Precambrian shield of the Guianas does not exhibit volcanic nor seismic activity and the region is located close to the equator, between 2° and 6° N, and thereby away from the cyclone routes (Grand Atlas de l'Archéologie 1990). In tropical hyperhumid forests, fires can only develop beyond a certain water stress threshold and have probably been triggered by climatic fluctuations which intensified the effects of the dry season, in particular its duration.

Comparisons made between Amazonia and Western Equatorial Africa underline a fundamental difference between these two regions: in Amazonia, the dry season is cloudless and imposes important water stresses on the vegetation (Guehl 1984), while in Africa (in particular Southern Cameroon, Gabon and Congo), the 'dry' season is overcast and misty, although rainless, and plants are less exposed to water stress (Maley 1996, Schwartz *et al.* 1986). This difference is thought to be caused by the surface temperature of the ocean, in particular the upwelling of cold polar water in the Gulf of Guinea. This important contrast between the two regions could explain the presence of abundant charcoal fragments in Amazonian and Guianan soils, whereas remains of forest fires are rare in West Africa and are generally associated with human settlements (Schwartz 1993).

The tropical rain forests of Amazonia and the Guianas thus appear to be relatively exposed to fire because the intensification of the dry season increases the water deficit. Beyond a certain threshold, any increase in the severity of the dry season could lead to forest fires. Today, this type of catastrophe is prevented by the high air humidity and the short duration of the dry season, but it must be considered in the current context of global warming and increasing human pressure.

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A hummingbird is visiting a passion flower in the forest understorey. *Photo Frans Bongers.*



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