AMAZON LOWLAND AND GUAYANA HIGHLAND. HISTORICAL AND ECOLOGICAL ASPECTS OF THEIR FLORISTIC DEVELOPMENT [1]

by

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Resumen

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La evolución de la flora de la planicie Amazónica está estrechamente interconectada con la de la meseta de Guayania. Se admite que el levantamiento de la formación arenisca de Roraima, (meseta de Guayania), ocurrió antes de lo supuesto anteriormente habiendo ocurrido recién en el Neogeno y durado posiblemente hasta el Pleistoceno.

Se propone la hipótesis de que la mayor diferenciación de una flora psamófila de llanura, implicando la asociación simbiótica con micorrizas ectótrofas, tuvo lugar en la placa arenisca de la formación Roraima antes de su levantamiento en el Cretácico superior y Neogeno. Con el levantamiento la mayor parte de los elementos de esta flora especializada quedaron en la planicie cálida sobre hábitats de arena blanca periféricos al conjunto de montañas insulares y a la meseta de Roraima. Tales suelos arenosos se derivaron por erosión del macizo de Roraima. En la meseta misma, posiblemente de manera simultánea con el levantamiento, evolucionó una flora predominantemente endémica a partir de migraciones provenientes principalmente de los Andes, así como del escudo central Brasileño. En la flora actual de la planicie amazónica, una gran dicotomía separa la flora ectotrófica psamófila desarrollada sobre arenas blancas, de la flora no ectotrófica desarrollada sobre latosoles.

1. Introduction

Amazonia as a phytogeographical region is understood in the following to comprise the Amazon lowland and the lowland of Guayana. The latter, sometimes considered as representing a separate floristic region, has a flora different from that of Amazonia in the strict sense only on specific level. As delimited to include the Guayana lowland, Amazonia is quite homogeneous and clearly different from the rest of the Neotropical flora through a high degree of generic, let alone specific, endemism.

With the exception of the region of the crystalline shields, Amazonia is generally considered geologically young, and so its flora often is supposed to be. This is apparently in contrast to the Guayana Highland because this represents one of the oldest land regions of South America that has not been inundated since the Middle Cretaceous, i. e. for at least 100 million years (Harrington, 1962). It is a region of table mountains, which in the central part are nearly 3.000 m high, while peripherically dispersed inselberge are raised only to lower altitudes. For this region Mary and Phelps (1955) coined the term "Pantepui", which ecologically more pre-

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[1] Dedicated, with affection and admiration, to Dr. José Cuatrecasas on occasion of his 85 th birthdy.

cisely was defined by **Huber** (1987). It harbours a flora characterized by bizarre life forms and, at least on specific level, by some degree of endemism, and is generally considered as evolutionarily very ancient.

The purpose of the following is to analyse the floristic relationship between the two regions against an ecological and geological background. Previous floristic analyses, which included the area under discussion, were given by **Smith** (1962), **Raven** and **Axelrod** (1974), and specially **Gentry** (1982). The latter author had pointed to two geological events that had great impact upon the development of the neotropical flora: (1) The closing of the Central American landbridge in the Pliocene, which led to a floristic interchange between Central and South America, and (2) the Andean orogenesis, which was followed by adaptive radiations in numerous lineages, leading to the occupation of the newly created habitats. Here I want to focus upon various neglected aspects of the physical setting and genesis of the Guayana Highland and the adjacent lowlands in relation to their floristic history. These aspects include (1) the timing of the uprise of the Roraima sandstone formation: should it be younger than generally accepted, the consequences for our ideas concerning the age of the Guayana flora would be enormous; (2) the scarcity of nutrients, which prevails in the Guayana Highland and in parts of the Amazonian ecosystem as well (**Irion**, 1978); this is a decisive ecological determinant that cannot be neglected when discussing the origins of the Amazon and Guayana flora. Apart from these geological and ecological aspects, I will also deal with the immigration of northern hemisphere taxa that have enriched the neotropical flora to a much larger extent than accepted up to the present.

2. Landscape history fo Amazonia and Guayana

The Amazon river follows an ancient depression that existed since the Mesozoic and the continuation of which can be traced in Africa (**Grabert**, 1983). As long as Africa was connected with South America and the Atlantic Ocean did not yet exist, the drainage from the Amazon region was directed into the Pacific (**Katzer**, 1903). Following the opening of the Atlantic Ocean in the Jurassic, a watershed between the Atlantic and Pacific Ocean originated, the remnants of which habe been demonstrated by **Grabert** (1967). This watershed obviously extended along ancient mountain chains and can partially be identified from the Roraima mountains via the Serra do Divisor to the Serra dos Parecis. It ceased to function when with the lifting of the Andes the drainage into the Pacific was blocked up. Through the uplift of the Andes bays were cut off from the Pacific and became transformed into freshwater; several elements of the original marine fauna, such as dolphins (**Grabert**, 1984) and some kinds of fish (**Lüling**, 1969), became adapted to freshwater conditions and at present form part of the limnic fauna of the Amazon region. However, it is not only these marine and later freshwater molasse-lakes of the Subandean region that document the lacustrine-fluviatil history of Amazonia. During major parts of the Tertiary and the Pleistocene in the Amazon lowland freshwater lakes of vast extension must have existed, which left mighty deposits of clay, sand and gravel. These deposits are up to 300 m high and are known as Solimoes clays and Barreiras clays, of which the former may have originated in the Miocene, while the for the latter different age estimates ranging from the Upper Cretaceous to the Pliocene have been suggested.

Clearly the lacustrine-fluviatil history of Amazonia is documented by sediments only as far as the waters involved were carrying rich suspended material. Since the sediment load of contemporaneous so-called "black"- and "clear-water" rivers of Amazonia is extremely low, it is suggestive to conclude that during several limnic periods of the landscape development of Amazonia no sedimentation at all has taken place. The clastic sediments that had been deposited in the Amazon Basin previous to the upheaval of the Andes or before the breakdown of the ancient watershed between the Pacific and Atlantic, can only have originated from the erosion of the crystallinous rocks or of sandstones of Cretaceous or older age. Thus one can conclude that all rivers of Amazonia previous to the uplift of the Andes and later those that did not rise in the Andes were poor in nutrients. Consequently the richness in nutrients of Amazonia, caused by white water rivers and specially by the Amazon river itself, is geologically a recent phenomenon. It is quite possible that after anthropogenic deforestation of the foot hills of the Andes in early historic time, i. e. before the arrival of the Europeans, the sediment load of the Amazon has increased (**I. Walker**, person. comm. 1988). This is suggested by the experience that on the Tertiary land surface of Central Amazonia deforestation in urbanized regions produces a surface run-off rich in sediment load, while forest creeks rising in the same region carry clear water (**Walker**, 1987).

The table mountains of Guayana are built up by sandstones of the Roraima formation which discordantly overly the Precambrian crystalline of the Guayana Shield and are up to 3.000 m high. Besides cross-bedded sandstones, probably of fluviatil origin, quartzites an schists take part in the Roraima sequence. The whole sequence originated during the Precambrian; Gansser's (1974) idea of an Mesozoic age of the upper portion has since been discarded (**Gosh**, 1985).

When considering the age of the uplift of the sandstone plateau, attention has to be paid to the presently topmost layer, the "Mataui", sandstone, which is transformed into an extremely hard crust by the dissolution, migration and liberation of silicate (Grabert, 1976a). This hardened layer together with the existence of three systems of nearly vertical fractures (Briceño & Schubert, 1985) must have been instrumental in shaping the characteristic landscape morphology with its deeply incised valleys and escarpments. However, as Grabert has pointed out, the process of silification required a tropical lowland climate with changing humidity: Silicic acid can only be dissolved under high temperature, and only under a low velocity of flow of phreatic water silica remains in form of a gel, and only under temporary desiccation silical gel can dehydrate and crystallize. Since in the present highland position silification of the sandstone cover seems unlikely, Graber (1976a, b) has hypothesized that this process may have taken place in the tropical lowland. Following tectonic events in the genesis of the Caribbean Andes he assumed an upheaval of the Roraima block to have taken place in the Neogene and older Pleistocene. However, previously to the silification of the Mataui layer, a considerable amount of material of the Roraima series may have been removed by erosion of overlying strata; Urbani (1977) gave an estimate of several of thousands meters of sediments. Thus possibly upheaval and erosion of the Roraima formation have taken place in various cycles that may date back into the Mesozoic or earlier (Schubert and Briceño, 1987).

The isolated inselberge, which extend to the Tafelberg in Surinam in the East and to the Sierra Macarena at the foothills of the Andes in the West, indicate an earlier vast extension of the Roraima formation that may have covered an estimated area of 1 million km^2 (Gansser, 1974). Up to the present three quarters of this surface have been eroded or are weathered. Thereby immense masses of sand must have been liberated, which were deposited mainly at the northern and southern fringe of the Guayana highland. Thus the northern savannas of Fench Guayana, Surinam and Guyana, the Rupununi savannas of Guiana and the vast white sand area between Rivers Orinoco and Negro and in the basin of the Rio Negro preferentially owe their existence to this process. Also the high proportion of sand contained in sediments deposited during the Miocene and Pliocene in greater distance such as in eastern Venezuela and Trinidad may be due to the weathering of Roraima sandstone (Gansser, 1974).

It would be wrong, however, to regard all white sand deposits around the Guayana highland an in the Amazon basin as products of the decay of sandstones. It could be shown that quartz sands of the Upper Rio Negro region according to their contents of heavy metals have originated from selective lixiviation of soils that in turn had originated from the weathering of crystallinous rocks (Schnütgen and Bremer, 1985). Equally, Klinge (1965) and Chauvel et al. (1987) have described the spatial relationship between latosols and podzols formed on the Barreiras layers of Central Amazonia, which points to an origin of white sands through selective loss of clay minerals. This may indeed be the most frequent mechanism of the origin of white sands in Amazonia, although other mechanisms certainly exist as well (see Ab' Saber, 1982).

While the nutrient poverty of latosols is well known, this is even more accentuated on bleached sands (see the analytical data of Anderson, 1981; and Bremer and Schnütgen, 1987). Therefore it is understandable that the latter soils carry only low woodland and scrub communities with reduced biomasses.

3. Floristic history

Against this ecological and geological background the floristic history of Amazonia appears in new light. It is obvious that many species and genera and even taxa of higher rank are restricted to, or occur predominantly, on nutrient-poor white sands in the Guyana highland, its slopes, or on low-lying savannas ("Amazonas savannas", Hubert, 1982) in and bordering Guayana. The close affinity between the flora or the savannas adjacent to the northern border of the highland and those in the middle and upper elevations of the highland itself has been recognized by Fanshawe (1952) and van Donselaar (1968). Fanshawe argued that in the past the sandstone plate of the Roraima formation had a greater extension than in the present. Through erosion some part of the crystalline basement was exposed, and later during a period of flooding white sands were deposited. Thus he concluded that the flora of the Pakaraima highland on Roraima sandstone is the oldest flora, which had given rise to the flora of the crystalline shield, from which in turn the savanna flora originated. In contrast to this schematic concept I prefer the idea the differentiation of a psammophilous flora began in the Upper Cretaceous or in the Palaeogene under tropical lowland conditions upon a substrate derived from Roraima sandstone. Here the typical taxa must have differentiated and diversified, which until the present are linked to nutrient-poor lowland habitats, both inundatable and non-inundatable. The uplift of the sandstone massif up to altitudes of nearly 3.000 m led to a dramatic change of environmental conditions. The dissection and marginal erosion of the sandstone massif created new habitats in the warm-tropical lowland, in which the original Guayana sandstone flora could persist. Some of its representatives may have adapted to meso and microthermic conditions which exist above 1.200 m, possibly concomitantly with the uplift or subsequently to it. On the whole the flora of the upper stories of the table mountain region appears as a geologically younger flora, in which only a limited number of elements has persisted since the Cretaceous or Palaeogenic lowland phase. The rich representation of Andean elements in the flora of the Guayana highland shows that it is not predominantly a preserved ancient flora. On the contrary, relatively late, i. e.

in the Neogene, an influx of taxa from surrounding areas is supposed to have taken place. Their subsequent radiation was determined by the very special environmental conditions of these tropical mountains, such as their climate, nutrient stress and isolation.

The widespread occurrence of ectotrophic mycorrhiza is a peculiarity of the flora on nutrient-poor bleached sands. At some time it was assumed that this type of mycorrhiza is restricted to temperate regions and mountain forests of the tropics and subtropics (Singer and Morello, 1960). Now it has become apparent that it is frequent in the woodland and scrub vegetation on white sands *(campina, campinarana, igapó* and *bana* vegetation) of Amazonia and certainly beyond this region Singer and Araujo, 1979, 1986). The fungi of the ectomycorrhiza, probably through competion, prevent the growth of litter decomposing basidiomycetes, so that in vegetation rich in ectotrophic mycorrhiza much raw humus accumulates. This is in contrast to forests on latosols, in which litter is readily decomposed. It seems that the possession of ectomycorrhiza is an important adaptation of plant life to extremely nutrient-poor habitats. However, low rates in the decomposition of litter may also be due to the existence of secondary plant products, as has been shown by Lisbôa (1977).

Consequently there is a large number of taxa —mostly at the rank o genus— that are specialized with all species for such habitats. In the Guayana highland and its surroundings the most impressive examples are the families Rapateaceae and Humiriaceae. Maguire (1958) wrote that hardly another family is more characteristic for the Guayana region than Rapateaceae. They comprise herbs that grow in humid forests, in humid or inundatable savannas and in similar habitats. Their centre of distribution is the Guayana highland and its periphery, to which some 60 of the more than 80 known species are restricted. Equally the Humiriaceae, a family of 8 genera and more than 50 species of trees and shrubs, have their centre of distribution in the same region, where their primary differentiation is supposed to have taken place (Cuatrecasas, 1960). Most of these species are bound to bleached sands, although some occur on latosols. The small family Thurniaceae, comprising only three herbaceous species, is restricted to the Guayana highland and its surroundings, and the Ochnaceae/Luxemburgieae equally there have their centre. Other characteristic taxa were listed by Maguire (1970) and Gentry (1982).

If one considers the present distribution and habitat preferences, a phytogeographical element can be envisaged that has differentiated and diversified in the tropical lowland on substrates derived from the Roraima formation and from there has radiated into surrounding lowland regions, while only rarely adaptation for meso and microthermic conditions of the mountain climate has occurred. The following taxa could be mentioned as examples:

Aldina
Dicymbe
Macrolobium
Eperua
Humiriaceae
Terminalia sect. *Pachyphyllum*
Raveniopsis and *Ravenia* the genera of the Ochnaceae/Luxemburgieae
Moronobea and *Lorostemon*
many genera of the Rubiaceae, such as *Henriquezia, Retiniphyllum, Pagamea, Gleasonia, Duroia* a.m.o.
Micrandra
Senefelderopsis
Rhodognaphalopsis (= *Pochota*, p. p.)
Sipanea
genera of the Sapotaceae such as *Glycoxylon* and *Neoxythece*
Rapateaceae
Thurniaceae,
etc.

Early representatives of these lineages must have reached the Guayana region at primordial stage of the floristic development of South America and must have become adapted for the nutrient-poor conditions. However, the effects of "peinomorphosis", i. e. the consequences of nitrogen and phosphorus stress, are not so strongly marked as in the flora of Australia (see van Steenis, 1979) possibly because during the development of the Guayana region there were no arid phases. Generally, these lineages must have been unable to adapt for meso and microthermic conditions.

On the other hand there are phytogeographic elements that occur predominantly in the highland and were considered as specially ancient; Steyermark (1986) has listed and discussed them. Striking examples are provided by the endemic representatives of the Compositae/Mutisieae, the endemic genera of the Bromeliaceae, the genera of the Bonnetiaceae, that have hardly entered the lowland, and the Ericaceae, that equally are nearly absent from there. However, in contrast to earlier ideas (see Maguire, 1970), these lineages do not seem to be particularly ancient taxa, which were present in the highland since the Cretaceous. It rather seems to me that after the uplift to the Andes they have dispersed from there to the Guayana highland, where they have radiated without penetracting into the warm lowland; the Brazilian Shield may have contributed as well. Thus the strong floristic affinities between the Andes and the Guayana highland, emphasized by Steyermark (1979, 1986), can be explained. As in other tropical mountains, the mountain climate has triggered the evolution of the life form of unbranched or poorly branched giant rosette plants *("caulirosulae"* of Cuatrecasas, 1979), that typically appear in the Mutisieae, Bonnetiaceae, Ochnaceae and other families. Apart from this growth form the coriaceous leaves with their white, gray or ferrugineous indumentum convey a strange impression to this element.

In this context the Ericaceae are most remarkable: While they are highly diversified in the highland, they are nearly absent from the Amazon lowland, from where I only know *Agarista duckei* and *Gaylussacia amazonica*. Even if the dependence of this family on its peculiar endomycorrhiza may have some significance, it is attractive to speculate that is has been prevented from entering the megathermic zone for climatic reasons.

The ecological differences between bleached sands and latosols are also evident by the contrast between ectotrophic and anectotrophic forests. Consequently the floras typical of these soil types are strictly separated. Frequently entire genera of woody plants occur exclusively or predominantly on one of the two substrates. Others, such as *Hevea*, comprise species adapted either to latosols or bleached sands. In general the elements typical of latosols have wider ranges of distribution in Amazonia; some, such as *Guazuma ulmifolia*, are distributed in the Neotropics beyond Amazonia or, such as *Spondias lutea*, beyond the neotropical realm. It is unknown why in the Neotropics so many elements are restricted to the Amazon lowland (including the Guayana lowland).

Thus the flora of Amazonia exhibits a dichotomy that has largely been overlooked. In contrast to the opinion of Ducke and Black (1953) the borderline between "terra firme" and inundatable land is not the most important ecological limit. The fundamental borderline is rather that edaphically conditioned one, which is reflected by the distribution of the ectotrophic and anectotrophic forest vegetation. The evolution of the ectotrophic white sand flor may have taken place preferably at the southern margin of the Guayana Highland, where white sand habitats of vast extension were available. Exactly this region was suggested by Cuatrecasas (1960) for the early differentiation of the Humiriaceae. The evolution of the flora bound to latosols could have occurred predominantly at the southern margin of Amazonia, where still at present the most fertile soils occur.

Thus the floristic history of the Amazon lowland is illuminated by the floristic and landscape history of the Guayana highland. Trophic conditions are crucial for an understanding of the differentiation of the flora. This is in consonance with my previous analysis (Kubitzki, 1988), in which I pointed to the close floristic relationship between the forests on "terra firme" and the floodplain vegetation of white water rivers ("várzea") on the one hand and between the oligotrophic woodlands and savannas on bleached sands and the vegetation of sand strands of clear and black water rivers on the other.

This sketchy picture of the genesis of the floras of Amazonia and Guayana would be incomplete without mentioning those elements that entered South America after closing of the Central American land bridge in the Pliocene. Raven and Axelrod (1974) have presented an analysis of these elements, which has been completed by Gentry (1982); his conclusion is that the neotropical flora has been enriched only insignificantly by immigration from the North. However, such a conclusion is not tenable any longer. Rohwer (1986) has shown that the very large lauraceous genera *Ocotea* and *Nectandra* (and probably all other neotropical members of the Lauraceae as well) have entered Sotuh America from the North, probably after the closing of the Central American land bridge. This is proven by the distribution of directed floral characters, according to which the more primitive traits occur in Central America and in the Andes, while in the Amazon lowland, in the Guayana highland and South East Brazil nearly exclusively derived characters abound. Since all members of the Lauraceae seem to be ornithochorous, there exists a mechanism for their rapid dispersal. Certainly the about 1.200 species of neotropical Lauraceae have not entered South America as such but have differentiated there, occupying mainly the lower storey of the forest, but entering into other habitats including those on white sand as well. The recent speciation of this group is evident from the frequent occurrence of series of parapatric sister species, which, as it were, are the in situ result of speciation based on geographical differentiation, which seems to be the common situation in the neotropical rain forest (Kubitzki, 1985). I suspect that in the future still other strongly diversified neotropical plant groups will be recognized as recent immigrants from the North.

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