



Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia[☆]

Thomas van der Hammen^{a,b,1}, Henry Hooghiemstra^{a,*1}

^aHugo de Vries-Laboratory, Dept. of Palynology and Paleo/Actuo-ecology, University of Amsterdam, Kruislaan 318, 1098 SM Amsterdam, Netherlands

^bTropenbos-Colombia, Apartado Aereo 036062, Bogotá, Colombia

Abstract

The neotropical Amazonian and Andean plant diversity developed mainly during the Tertiary. In Amazonia, Miocene floral diversity seems considerably higher than today. During the Neogene, tropical taxa entered newly created montane area, and montane taxa entered the tropical lowlands. The general decrease of temperature during the upper Neogene and especially during the Quaternary glacial periods may have caused considerable extinctions in the lowlands. Representation of pollen of apparently principally montane taxa (*Podocarpus*, *Hedyosmum*) in Miocene, Pliocene, and Quaternary sediments of Amazonia and surroundings, is still difficult to interpret in terms of temperature decrease at low elevation. Changes in precipitation may have profound impact on the composition of vegetation communities; *Ilex* and Melastomataceae increase significantly in many glacial pollen records. Increase of *Weinmannia* in Amazonian pollen records seems the best indicator of downward migration of montane vegetation belts. A temperature lowering at sea-level of $4.5 \pm 1^\circ\text{C}$ during the Last Glacial Maximum (LGM) seems reasonable; it may have caused a downslope migration of some 700 m of the lower montane vegetation belt; lower montane arboreal species may have been able to grow in higher elevation areas (> 500 m) of Amazonia, increasing background pollen values of montane taxa in the area.

Difference between a cool and wet Middle Pleniglacial (60–28 ka BP), and a cold and dry Upper Pleniglacial (28–14 ka BP; thus including the LGM) is evident in Andean and Amazonian records; statements about environmental conditions of the ice-age Amazon should be specified chronologically. The Middle Pleniglacial is a time of accumulation of fluvial sediments. The Upper Pleniglacial is a time of incision of the rivers in their sediments; sedimentation started again in the Lateglacial (since ca. 13 ka BP) and the Holocene, when lake levels rose again. Based on simplified considerations of precipitation changes and evaporation we estimate that LGM rainfall may have been reduced by values of ca. $45 (\pm 10\%)$; Amazonian and Cordilleran lakes dried up; dry rain forest was locally replaced by savanna, savanna forest, or cerrado-type vegetation; dry rain forest, savanna forest, and pure savanna was locally replaced by extensive semi-desert dune formations (lower Rio Branco area in present-day central Amazonia). The present-day centers of higher rainfall (> 2500 mm) surrounded by areas of lower rainfall, are refuge areas of the very wet rain forest and of the very high plant diversity (300 plant species per 0.1 ha), and they should have been that equally, or more, during the dry climate intervals (plant diversity of drier forests is in the order of 100–150 species per 0.1 ha). Both extinction and speciation in isolation under precipitation and temperature stress may have taken place in these refugia. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

In many fields of research the study of the Quaternary history of northern South America has made much

progress in recent time. To understand the geological, ecological, and palynological history of the Amazon basin, an area which is relatively unknown, knowledge of its Neogene past is necessary. Estimation of the temperature depression during the Last Glacial Maximum (LGM) relies on understanding of the ecological requirements of montane tree taxa, such as *Podocarpus*, *Hedyosmum*, *Ilex*, and *Alnus*. These trees have different histories which are of crucial importance to infer paleoecological conditions during Quaternary episodes. Understanding of the present-day high biodiversity of the neotropical rain forests requires knowledge of its development during the Tertiary. Assessment of paleoecological conditions at various places in the modern Amazonian rain forest area

[☆]This paper is dedicated to dr Alvaro José Negret, director of the Museo Natural of the Universidad de Cauca, Popayan, who passed away in June 1998. We benefited immensely from his impressive knowledge on the natural history of Colombia, his scientific network, and field experience during recent projects

*Corresponding author. Tel.: 0031-20-5257857; fax: 0031-20-5257662.

E-mail address: hooghiemstra@bio.uva.nl (H. Hooghiemstra).

¹Participating in the 'Netherlands Centre for Geo-ecological Research' (ICG), and the 'Institute of Biodiversity and Ecosystem Dynamics' (IBED).

and surrounding drier vegetation types, requires understanding of the geological, geomorphological, and climatological history. The distribution of aridity in the Amazon basin during the Last Glacial is only partly known, which hampers progress to solve the debate about the existence of forest refugia surrounded by savanna-like vegetation, a hypothesis put forward some 30 years ago (Haffer, 1969), and later supported by a.o. Prance (1973), Steyermark (1979), Gentry (1992) and Van der Hammen and Absy (1994). In particular, Colinvaux advocates that there is no convincing evidence for a significantly drier LGM Amazon basin and does not accept the idea that the present area of Amazonian rain forest was significantly reduced during the LGM (Colinvaux, 1979, 1996; see also the references in Hooghiemstra and Van der Hammen, 1998).

The objective of this paper is to show the importance of little known data from the Tertiary, that are important for a correct evaluation of the vegetation history during the Quaternary, to present the paleoenvironmental history of northern South America in general, and of Amazonia especially. It is mentioned here that all radiocarbon dates mentioned in this paper are expressed as ^{14}C yr BP.

2. Development of the neotropical flora and vegetation during the Tertiary

There is a considerable number of publications on Upper Cretaceous and Tertiary geology and palynology of northern South America, a history of some 70 million years (e.g. Van der Hammen, 1954, 1957, 1961a, b, c, 1970; Van der Hammen and Wijmstra, 1964; González, 1967; Van der Hammen et al., 1973; Regali, et al., 1974; Van der Hammen and Cleef, 1983/84; Muller et al., 1987; Hoorn, 1990, 1993a, b, 1994a, b, c, 1996; Hoorn et al., 1995). In the Paleocene several recent plant families and genera are recognized, such as Bombacaceae and *Mauritia*. Since then species (types of pollen) appeared and disappeared throughout time but the general tendency is a continuous increase of diversity and increase of taxa that correspond to recent types. In the Eocene there is a high diversity in the tropical forest, and temperatures and rainfall were higher than at present. It is in the Upper Eocene that we recognize families such as Malpighiaceae, and genera such as *Alchornea* and *Podocarpus*. In the Miocene the generic composition of the flora is already very similar to the present and the diversity is very high: e.g. 280 pollen types in river valley sediments of the Amazonian Caquetá area (Hoorn, 1994a) as compared with 140 types in Holocene river sediments of the same area. The number of species in recent vegetation is approximately 140 per 0.1 ha (Urrego, 1994, 1997).

During the entire Tertiary there were changes in climate, sea-level and tectonic events. These continuously affected the present day Andean area, which belonged at that time mainly to the lowlands, and was in continuous connection with the present day Orinoquia-Azonian. Brackish water entered far into Amazonia, from the Caribbean and Pacific, and possibly also from the Atlantic, during the Middle Miocene, creating large areas with mangrove vegetation (e.g. Hoorn et al., 1995). During the Early and Middle Miocene, rivers in present day western Amazonia ran westward and northward towards the Caribbean, via the Maracaibo area, and possibly towards the Pacific. When the Colombian Eastern Cordillera and the Cordillera de Mérida started their first important uplift, some 12 million years ago, the river system changed completely and the present-day Orinoco and Amazon river systems were formed. Temperature changes took place during the entire Neogene, cooler phases interrupting a climate that was mostly warmer than today. During the Pliocene the climate seems to have been generally cooler than during the Miocene, and during the final part, approximately between 3 and 2.5 million years ago (= Ma BP), a strong cooling produced the first glacial period and the start of the Quaternary, as documented in pollen record Funza-2 (e.g. Hooghiemstra and Cleef, 1995).

Thus, during the entire Tertiary, and especially since the beginning of the Miocene, there were frequent environmental changes that created different types of stress, that may have led to extinctions, but may have been also one of the factors favouring the strong evolution and speciation that has led to the very high biodiversity of the neotropical flora. The upheaval of the Andean mountain chain stimulated the evolution/adaptation of montane taxa, and permitted the entrance of genera from the austral-antarctic, and later from the holarctic floras into the temperate and cold areas of the neotropics, where new neotropical taxa were formed, adapted to the new circumstances.

2.1. Early history of some 'modern' montane trees

Higher representation of pollen of montane trees in Amazonian lowland records of Last Glacial age, such as *Podocarpus*, *Hedyosmum*, *Ilex*, and *Alnus*, is often used as evidence of cooler conditions than at present (see the re-evaluation of available pollen records in this article). Here we discuss the early history of such taxa in order to precise the ecological conditions that may be potentially inferred in Late Quaternary records. The location of all pollen sites mentioned in the text are indicated in Fig. 1.

In the Upper Eocene, pollen grains of *Podocarpus* are found in Brazil and Colombia, together with the tropical pollen flora. In the Early Miocene percentages up to 8% were found in tropical pollen spectra of the Caquetá area

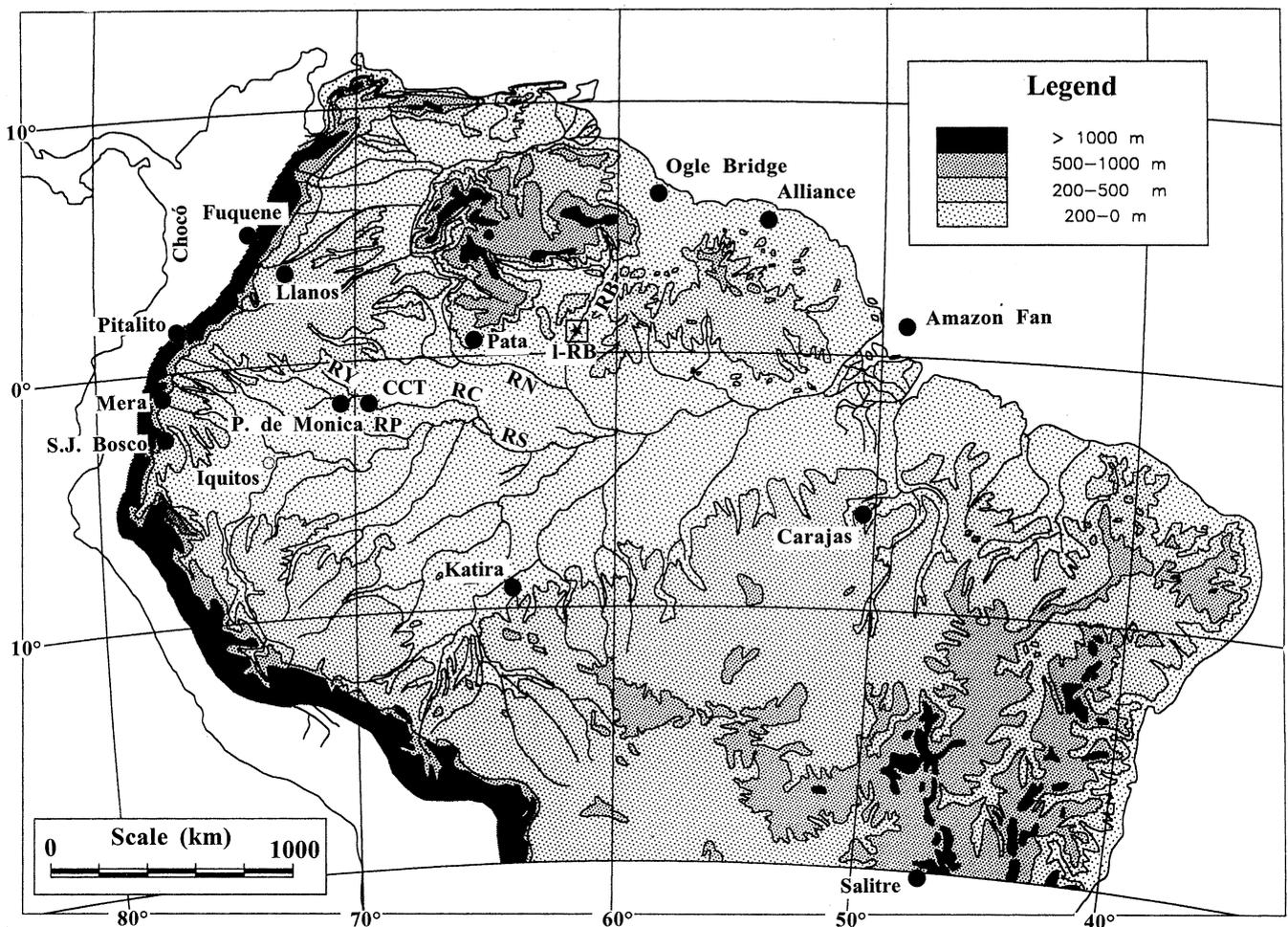


Fig. 1. Altitudinal intervals in the Amazon basin and the location of pollen sites mentioned in the text. 1-RB = lower Rio Branco area; RB = Rio Branco; RN = Rio Negro; RS = Rio Solimos; RC = Rio Caquetá; RY = Rio Yari; RP = Rio Putumayo; CCT = sections Cameleon, Cahuinari and Totumo.

(Hoorn, 1994a), and up to 30% in tropical pollen spectra of Venezuela (Lorente, 1986). In the Middle Miocene tropical pollen flora of Venezuela, up to 30% *Podocarpus* is found, in the Late Miocene up to 22%, and in the Pliocene up to 60% (Lorente, 1986). It is important to state that in the Lower Miocene the first important upheaval of 12 million years ago, had not yet taken place. In the Upper Miocene tropical lowland sediments in the present-day Eastern Cordillera of Colombia values as high as 50% of *Podocarpus* are found, including phases of abundant *Mauritia* (Wijninga, 1996; Wijninga et al., 1999) and some *Weinmannia* pollen.

In a section of Lower Pliocene age of the same area, a spectrum with tropical lowland pollen contains 6% *Podocarpus*, 10% *Hedyosmum*, and 4% *Ilex*. Pollen spectra from a Middle Pliocene peat section, deposited at an elevation of c. 1500 m, contains > 10% *Podocarpus*, > 40% *Weinmannia* and > 15% *Hedyosmum*, together with *Rapanea* (= *Myrsine*), *Ilex*, Apocynaceae, and Bombacaceae (Van der Hammen et al., 1973). Later, at the

same site and stratigraphic level, a peat interval with > 50% *Podocarpus* pollen and *Podocarpus* wood was found (Wijninga, 1996). As to *Hedyosmum*, a few pollen grains are regularly found in Miocene sediments in Amazonia (Hoorn, 1994a) and in equally lower tropical pollen spectra of Miocene age from the present-day Eastern Cordillera. They become more abundant (10%) in Lower Pliocene tropical spectra (with Bombacaceae, *Mauritia*, and *Podocarpus*, see above) and in younger sediments.

From these data we have to conclude that *Podocarpus* entered northern South America in the Late Eocene to Oligocene and species, adapted to the tropical lowland (warmer than today), must have existed since then and throughout the Miocene and Pliocene. The species that are found today in Amazonia and surrounding lowlands should, therefore, most probably be the descendants of these earlier tropical lowland species (see below). *Hedyosmum* should also have developed one or several species adapted to the tropical lowland climate during the

Miocene and the Pliocene, and the present-day lowland species are probably descendents of them.

3. Vegetation zonation pollen deposition

For a correct interpretation of pollen data in ecological and climatic terms, knowledge of the vegetation and its relation to pollen deposition is crucial. Here we discuss the relationship between vegetation zonation and pollen deposition in tropical lowland sites and on the eastern slopes of the Andes, which faces the Amazon basin.

Up to 20% *Hedyosmum* pollen was found in organic sediments of 4700 BP in the Caquetá area (Colombian Amazonia; Urrego, 1997), and up to 60% in Holocene lake sediments of the southern Colombian Llanos (Wijmstra and Van der Hammen, 1966). In a lake of the lower Magdalena Valley, percentages up to 25% were found (Wijmstra, 1967).

Alnus is found today principally from 1700 to 3500 m and is a great pollen producer, whose pollen easily reaches the tropical lowlands, especially by river transport. The genus entered South America one million years ago (Hooghiemstra and Cleef, 1995), and pollen is found since then at all altitudes. Above 2000 m, values may be locally very high, especially produced by alder marsh forest and by alder forest in river valleys. Values in the proper tropical lowlands of Amazonia are seldom more than a few percent, but in river sediments of the lower Magdalena valley 5–15% of *Alnus* pollen is frequently found in Holocene deposits, and up to 18% is found in early Middle Quaternary tropical lowland deposits near Cartagena (Colombian Caribbean area; Sole de Porta, 1960).

From the eastern slopes of the Andes, facing towards Orinoquia–Amazonia, quantitative releves of vegetation and the corresponding pollen deposition from the upper forest line to the tropical lowlands are available (Grabandt, 1980). Similar transects are available from the three northern Andean Cordilleras, from the paramos to the lowlands, including also the western slopes of the Western Cordillera, to the Chocó lowland rain forest (Melief, 1989; Rangel, 1999).

One transect, along the eastern slopes toward the Llanos (3800–600 m) is of special importance (Grabandt, 1980). Between 1200 and 1400 m, on river terraces, there is forest with abundant *Weinmannia* (cf. *W. engleriana* or *W. pinnata*; up to 20% of the trees), *Hedyosmum*, *Brunellia*, *Myrsine* (= *Rapanea*), *Viburnum* and Ericaceae, with abundant palms (*Catoblastus*, cf. *Iriartea*), *Alchornea*, Sapotaceae, Annonaceae, *Erythroxylon*, *Heliocarpus*, *Heliconia*, etc. Pollen rain percentages of *Weinmannia* are some 40% at 1400 m, 50% at 1380 m, 6% at 1300 m, 4% at 1200 m and 3% at 1100 m and there is almost 1% at 900 and 600 m altitude, at the lowermost end of the

transect. *Hedyosmum* is represented in the pollen spectra by values up to 14% (1400 m) and 5% at 1100 m, *Myrsine* by 2% (down to 700 m), Ericaceae by up to more than 10% (down to 700 m). The total inventories of these forests and their pollen deposition spectra show an apparent mixture of high Andean taxa and tropical lowland forest taxa, under conditions of relatively high rainfall (3000–4000 mm) with sandy terrace deposits as a substrate.

An overview of all the data on vegetation and pollen available shows that percentages of pollen of *Hedyosmum* up to 10% may occur in the tropical lowland zone, up to 6% of *Weinmannia* (at ca. 400–500 m altitude), and up to 2% of *Myrsine* and 3% of *Alnus*. In the relevée at ca. 700 m altitude, on the higher Llanos terraces (foothills) at Sacama (Colombia), 10% of the individual trees were found to be *Myrsine* together with 15% *Byrsonima*, 30% *Befaria*, 13% *Clusia*, 12% *Miconia*, and some *Xylopia*, *Guarea*, *Chiococca* and *Phyllanthus*. *Alnus* occurs from 1700 m up to 3000 m, and locally up to 3500 m. Background values of *Alnus* are between 2 and 20% in lake deposits and bogs; higher values are related to the actual presence in the local vegetation (Hooghiemstra, 1984). In the Middle Holocene peat of the Pitalito Basin (1300 m altitude) up to 12% *Alnus* is found, and up to more than 20% in the Early Holocene (Bakker, 1990). *Alnus* may form dense sands along rivers; pollen is then easily transported downstream resulting in relatively high percentages of pollen in the sediments at elevations below their actual presence in the vegetation. *Quercus* has its principal distribution between 1900 and 3500 m altitude, but locally oak forest is present as low as 1000 m (Cleef and Hooghiemstra, 1984). *Cecropia* occurs from the tropical lowland up to 2100–2300 m, and is well represented in the pollen rain; above 2100 m only very low values are found (< 0.5%). *Mauritia* is abundant in marsh areas below 500 m, where very high pollen percentages may be found (both in savanna and rain forest areas), but it is found also on table mountains as high as at least 800 m (e.g. in Carajas).

3.1. Present day 'montane' elements in the neotropical lowland flora

Several montane species are also represented in the tropical lowlands, in rain forest areas, or in savanna or cerrado area. *Podocarpus*, well represented in the montane area, has several species in the lowlands. *P. magnifolius* occurs on humid Andean slopes (Panama, Venezuela, Brazil up to Bolivia), in Putumayo (Colombia), and on low sandstone hills in the west Amazonian Caquetá area (Duivenvoorden and Lips, 1993, 1995; Sánchez-Sáenz, 1997), and in the Darien (Torres-Romero, 1988). *P. sellowii* (Mainieri and Pires, 1973) in eastern Amazonas, and *P. guatemalensis* in the Pacific coastal lowlands (including Gorgona Island, 0–100 m;

Torres-Romero, 1988). *Hedyosmum*, equally abundant in montane areas, has species in the tropical lowlands of Brazil and in the Chocó lowland forest (Gentry, 1986). *Myrsine*, abundant in montane areas, occurs on terraces in the lower tropical area (humid to dry), and it has at least two species in the Cerrado of Brazil.

The very wet Chocó area (Colombian Pacific) provides an interesting example of the relation of very high annual rainfall and montane elements in tropical lowland areas. Gentry (1986, p. 80) makes the following statement, that we quote here literally because of its importance: “Another interesting feature of the Chocó pluvial forest is that plant families that are usually restricted to the Andean uplands occur at or near sea-level. While these taxa rarely achieve the ecological importance they have at higher altitudes, their mere presence at such low altitudes is noteworthy. Examples from 0.1 ha samples include *Hedyosmum*, *Ilex*, *Panopsis*, *Meliosma*, and *Talauma*. Elsewhere in the Chocó region the presence of *Podocarpus* on Gorgona Island and probably elsewhere, and of the only known lowland species of *Brunelliaceae*, *Brunellia gentryi* Cuatr. in Chocó Department, and *Brunellia hygrothermica* Cuatr. in Valle Department, are even more extraordinary. In general, the floristic difference between lowland and montane forests seems much less clearly demarcated on the Pacific than on the Amazonian side of the Andes”. The Chocó biogeographic area receives rainfall from 4000 to 9000 mm, Amazonia from 1500–2000 to 4000–5000 mm, indicating that high pluviality may be the direct or indirect cause of the presence of montane taxa in the tropical lowlands. For reason of these specific conditions, it is unclear to which degree the altitudinal floristic distribution in Chocó can be used by extrapolation to Amazonas. The few palynological studies in Chocó (Behling et al., 1998; Jaramillo and Bayona, 1999) cover only part of the Holocene preventing comparison of the glacial times conditions.

4. Paleoenvironmental interpretations

4.1. Lake levels and climate

Lakes that are independent of river systems may have very low sedimentation rates. In general there is a maximum level, above which the water will leave by overflow or infiltration. Under these circumstances the lake will have a maximum level if annual rainfall in the lake is greater than the annual evaporation. If such a lake in an area with modern annual rainfall of, e.g. 3000 mm and an evaporation of 1700 mm dried up totally, the rainfall must have diminished 1300 mm in the past. These considerations may give an additional approximate indication on the order of climate change. Both Lake Carajas (Absy et al., 1991) and Lake Pata (Colinvaux, 1996) dried

up during the LGM, just like Lake Fuquene (Van Geel and Van der Hammen, 1973) in the northern Andes, and peat bog Lagoa Salitre in Central Brazil (Ledru, 1992, 1993). Sometimes the upper part of the period of ca. 30,000–13,000 BP is missing, and sometimes the lower part or the entire interval. But around 20,000 BP almost all lakes seem to have dried up (Ledru et al., 1998). Evaporation in the Amazonian lowland is between 1000 and 1650 mm (values of < 100–600 mm occur on higher Andean slopes). In the analysis of Amazonian data, there is a certain relationship between rainfall and evaporation: between 3500 and 3000 mm rainfall the evaporation is between 1050 and 1250 (1450) mm. Around 2500 mm rainfall the evaporation is between 1150 and 1350 (1650) mm (Figueroa and Nobre, 1990).

Present-day rainfall in the Carajas area may be estimated as ca. 1800 mm. If evaporation is on the order of 1300 mm, a rainfall decrease of 500 mm, or more, would be required to dry up an isolated lake that does not receive water from surface runoff. As the lake studied receives some surface runoff, the decrease in rainfall might be estimated as > 500 mm. Present-day rainfall in the Lake Pata area should be > 3000 mm. If we use a maximum evaporation of 1500 mm, a decrease in rainfall of at least 1500 mm would be required to dry up the lake which does not seem to receive surface runoff. In both cases, lower temperatures that might cause lower evaporation, and hence would need a greater decrease in rainfall, are not taken into account; inflow of water from surface runoff would equally require a greater decrease of precipitation. A loss of water to the ground water system would have the opposite effect, but this may only be of minor importance for the principal and the central part of the lakes, where fine-grained sediments seal the bottom. These data can only be provisional and approximate, but in combination with those deduced from dune fields and colluviation they may be compared with the data derived from vegetation change.

4.2. Glacial temperatures in the Andes and Amazonian lowlands

The interpretation of temperature change on the basis of pollen spectra may be based on direct comparison with present-day pollen rain in relation to temperature or, after translation of pollen spectra to present day vegetation, to temperature. However, genera of plants may have a wide altitudinal range of distribution, pollen is transported by wind and water outside the area where it was produced, and genera with species with limited altitudinal range in the mountains may have species adapted to very dry or very wet conditions in the tropical lowlands. Moreover, genera or species may have different altitudinal distribution in dry and in wet climatic conditions (e.g. montane taxa in very wet tropical lowland as was mentioned before). We need to be careful with

reconstruction of past temperatures. Reconstruction of temperature in the Andes between 4000 and 1500 m altitude has been relatively certain, because of the considerable number of sites (LAPD, 1996), the relatively clear zonation of vegetation and species, and the relatively abundant data of the present-day relation of altitude, vegetation and pollen rain with temperature and rainfall. So we have relatively reliable reconstructions for the variation of temperature at ca. 2500 m in the northern Andes for the last 3 Ma (Hooghiemstra, 1984; Hooghiemstra and Ran, 1994; Hooghiemstra et al., 1993) with an amplitude on the order of 8°C. For the Last Glacial and Lateglacial there are relatively abundant data from above 1500 m, and relatively few below. Bakker (1990) plotted the present day and the Last Glacial to Lateglacial temperatures of 12 sites from Colombia, Ecuador and Panama, against altitude (data from between 650 and 3500 m) and reconstructed lapse rates (Fig. 2). The present-day lapse rate was found (as known) to be 0.6°C/100 m, and the glacial one 0.7°C/100 m. Thus, glacial lapse rates were steeper than modern, as already supposed (e.g. Van der Hammen, 1989), and in agreement with the fact that the lapse rate is higher in dry compared to wet air. Glacial temperatures in the tropical lowlands might have been 4°C lower than today, if we extrapolate these data to sea-level. The values calculated on the basis of the analysis of the Huascarán ice cap in Peru at 6050 m altitude (Thompson et al., 1995) agree well with these lapse rates.

Original data on LGM sea-surface temperatures of CLIMAP (1976) indicated that tropical sea-surface temperatures (SST) were only 2°C lower than today. However, the first computer reconstruction of land

surface temperatures based on the CLIMAP data (Gates, 1976), showed land surface temperatures between 2 and 8°C lower than today (average ca. 5°C) in Amazonia. Recently, Stute et al. (1995) concluded on the basis of the analysis of noble gases and the age of groundwater that average cooling for the LGM in northeastern Brazil at 400 m altitude was on the order of $5.4 \pm 0.6^\circ\text{C}$, and the LGM SST in the area were calculated to have been 5°C lower than today. All these data together suggest a maximum temperature lowering for the tropical lowland of northern South America on the order of 4–5°C (Farrera et al., 1999; Bush et al., 2000).

4.3. History of river sedimentation and dune fields

Data from the Amazonian Middle Caquetá River valley in Colombia indicate wide spread deposition of terrace gravels, sands, silts and clay during the wet (and relatively cold) Middle Pleniglacial (ca. 26,000–> 55,000 BP; Van der Hammen et al., 1992a; see also Ledru et al., 1996). These gravels form today the lower terrace of the river. Incision took place during the Upper Pleniglacial, between ca. 26,000 and 13,000 BP, and (finer-grain) sediment accumulation in the present day flood plains started some 13,000 years ago and has continued to the present-day (Van der Hammen et al., 1992b). Similar wide spread lower terrace deposits were dated as Middle Pleniglacial age in Peru (36,500 BP; Räsänen et al., 1987; Rasanen et al., 1990; Campbell and Romero, 1989), and peat in fluvial terrace material on the lower Andean slopes toward Amazonia in Ecuador was dated 33,520 and 26,530 BP (Liu and Colinvaux, 1985; Colinvaux and Liu, 1987). In the Upper Rio Negro basin

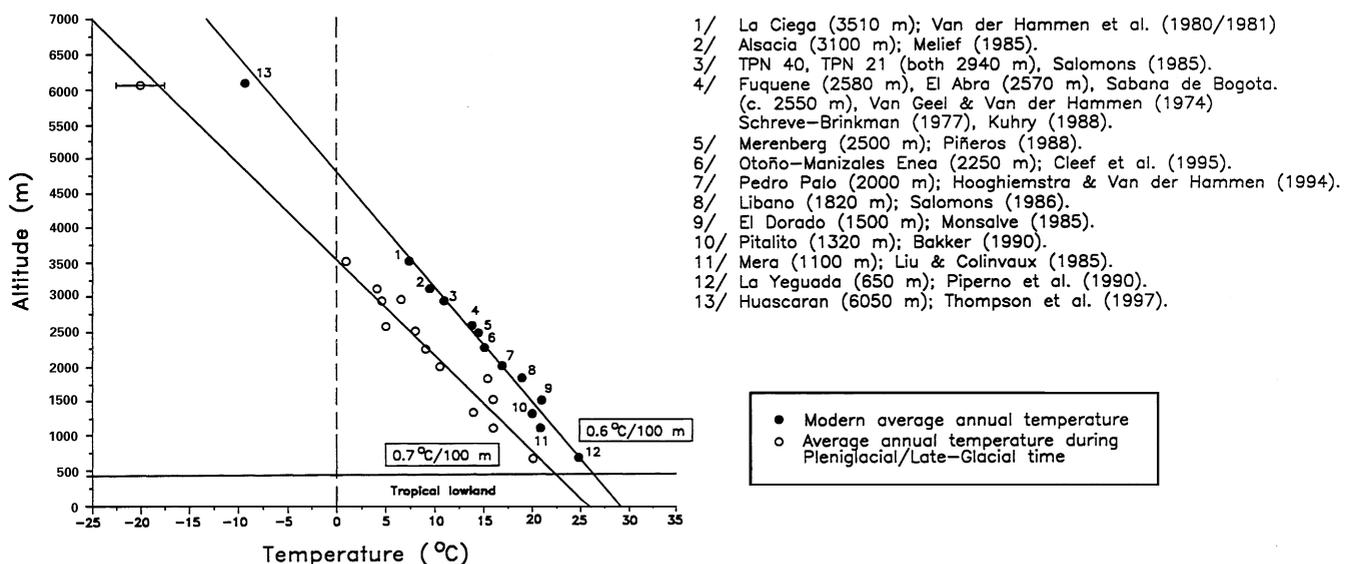


Fig. 2. The relation of altitude and average annual temperature for sites in Ecuador, Colombia and Panama from where paleo-data are available, for the present and for the upper part of the Last Glacial. Lapse rate is ca. 0.7°C/100 m for the Last Glacial (based on the data compiled by Bakker (1990) and the high altitude temperature reconstructed by Thompson et al. (1995).

of Brazilian Amazonia, the Tiquié Formation river deposits with pebbles and organic material, were dated between 27,000 BP and infinite age (corresponding in age to the lower terrace of the Caquetá), and younger terrace deposits have an age range between 13,500 and 4000 BP (Latrubesse and Franzinelli, unpublished manuscript). This being a river originating in Amazonas, shows that the increased rainfall established for the Middle Pleniglacial Andes, should also have effected the lowlands. There are extensive alluvial fans built by the rivers from the Andes when they reach the lower slopes toward Orinoquia and Amazonia, and the latest extensive fans seem to be of Middle Pleniglacial age, and of the same age as the lower terrace of the Amazonian rivers.

From the palynological and Quaternary geological studies in the northern Andes, we know that the Middle Pleniglacial is, in general, a very wet and relatively cold period, with some changes toward somewhat warmer and colder intervals, while the Upper Pleniglacial (including the LGM) is very cold and very dry (Ledru et al., 1996). During the Middle Pleniglacial, glaciers of the Andes reached their maximum extension and huge masses of sand and gravel of glaciofluvial origin were deposited on the high plains. During the Upper Pleniglacial glaciers retreated (related to the very dry climate), lakes on the high plains dried up and glaciofluvial sedimentation diminished and was restricted to the higher area of the Andes. Therefore, there seems to be a close relationship between the climate and sedimentation sequence in the Andes, and the sedimentation and erosion sequence in Amazonia (and Orinoquia).

In the Colombian and Venezuelan Orinoquia (present day areas of savanna and dry forest) there was extensive development of dune fields during the Late Quaternary, today stabilized and covered with vegetation, and there is a cover of loessic material on the higher Llanos. There are only two dates from the base of some dunes in Venezuela (Roa Morales, 1979), indicating a Lateglacial age. The formation of dunes requires the availability of sands and the lack of, or very sparse vegetation, and in such areas there may be repeated reactivation of dunes during dry climate intervals (very locally, where man has destroyed the vegetation, there may be anthropogenic reactivation). Maps of these very extensive dune fields show the complete Late Quaternary change of the savanna and dry forest vegetation into a type of sand desert (Roa Morales, 1979). In the Bolivian Amazonia, sand dunes are reported that have been dated as a dry Holocene interval and a strong regression of the forest (e.g. Servant et al., 1993). It eventually might be a reactivation of older aeolian deposits, but there are no data to confirm that supposition.

An important area of Late Quaternary dune fields is located in a central area of Amazonia: on both sides of the lower Branco River, extending from the Ananaú

River west to the Aracá River and north shore of the Rio Negro (1°30'N to 1°S, and 60°30'W to 64°W). These dunes show several phases of (former) reactivation. Today, the dune fields are traversed by modern drainage, and the water table is high enough to create marshy areas (Nelson, 1994; Carneiro Filho and Zinck, 1994). The area is partly covered by dense woody campina vegetation, partly by Amazonian forest. In the Colombian and Venezuelan Llanos (Orinoquia), the area with former dunes has annual rainfall values between 2000 and 1500 mm, and in the central part 1000 mm. To create the semi-desert conditions needed for the extensive formation of dunes, 500 mm or less rainfall is probably required. This would imply a minimum decrease of rainfall of 1000–1500 mm, some 50–60%. In the lower Rio Branco-Rio Negro dune area, the present day rainfall should be somewhat below 2000 mm. Here again a decrease of some 1000–1500 mm, as compared to the present (50–60%), would be required. In Rondonia (Katira section; Van der Hammen and Absy, 1994), with present day rainfall between 2000 and 2500 mm, the rain forest was replaced by a pure grass-savanna, and strong colluviation prevailed (incomplete vegetation cover). To create those conditions, a rainfall below 1000–500 mm would be required, that is a decrease of 1000–1500 mm as compared to the present (50–60% reduction). All these data point to a considerable reduction of rainfall in Amazonia on the order of 1000–1500 mm, corresponding to some 50–60%. For Lake Fuquene, at 2580 m in the Eastern Cordillera of Colombia (annual rainfall ca. 1000 mm), a reduction to 100–400 mm was estimated, a reduction of > 600 mm, i.e. 60% at least; Van Geel & Van der Hammen, 1973).

In summary, considering the possibility of some error, we may conclude that a general reduction of rainfall in northern South America during the LGM may have been in the order of at least 40–50%.

5. Vegetation, biodiversity, and climate

When rainfall is above 2000 mm, closed rain forest is the natural vegetation. Between 2000 and 1500 mm the number of deciduous species increases, and below 1500 mm there is dry forest or cerrado and savannas. Although a dry type of forest is, in principle, possible between 1000 and 1500 mm rainfall, the conditions for forest growth are relatively marginal, and edaphic and atmospheric factors (fire) may determine if the local vegetation cover is dry forest (often deciduous), low bush, or open grasslands. Below 750–500 mm, conditions become those of half-desert and the probability of sand desert conditions may increase when the soil is sandy.

Gentry (e.g. 1986) showed that there is a close relationship between biodiversity (number of species per area) and rainfall. He found that this number rises from

50 species (diameter > 10 cm) at 1000 mm rainfall, to 250 species per 0.1 ha at 4000 mm and more of rainfall. This is an important relationship, which produces considerable differences of biodiversity even within the area of the Amazonian forest, and that the actual centers of high rainfall (> 3000 mm) in Amazonia may be considered as a type of 'modern refugia of very wet forest' for many species that are not found in the areas of lower rainfall. The number of species per 0.1 ha in tierra firme forest in the area with rainfall > 3000 mm (Duivenvorden and Lips, 1993, 1995) is on the order of 300 (in the fluvial valleys on the order of 150), and in the area of drier tierra firme rain forest with rainfall between 1500 and 2000 mm (in the Carajas area) on the order of 120 species (Ferreira Da Silva and Cleef, 1991).

Along the slopes of the Andes, from snowline to tropical lowland, there is an upper zone of open paramo vegetation (above ca. 3500 m), a zone of Andean forest (ca. 3500 to ca. 2300–2100 m), a zone of subandean forest (ca. 2300–2100 to ca. 1200–1000 m), and a zone of tropical lowland forest (ca. 1000–0 m). The transition Andean-subandean forest is floristically relatively important, as it is the upper limit of a large number of tropical families and genera. Going upward from the lowlands to the high Andes, there is a gradual decrease of the number of species per minimum area, or per community, from 300–200 (or less, some 50 in dry areas) to 50–20 in the paramos. So biodiversity (species density) is positively correlated with both rainfall and temperature (Van der Hammen, in press b).

6. The Last Glacial climatic sequence

When considering climatic change during the Last Glacial it is important to take into consideration the considerable differences within this period. The sequence is defined by global climatic change (recognizable by vegetation change, isotopic changes in marine and ice cores, lake level changes etc.; e.g. Peterson et al., 1979; Livingstone and Van der Hammen, 1978; Van der Hammen, 1974, 1995). Marine oxygen isotopic stage 5 (OIS 5) represents the Last Interglacial and Early Glacial interstadials. OIS 4 corresponds to the Lower Pleniglacial cold phase of terrestrial stratigraphy with an age of approximately 70,000–60,000 BP. OIS 3 corresponds to the Middle Pleniglacial, a period that lasts from approximately 60,000–28,000 BP. It is a long period with a generally cold (but not so cold as stages 4 and 2) and wet climate; lake levels are high in many places, there is also extensive river sedimentation in many regions. Around 40,000 BP there is a very cold interval. OIS 2 (ca. 28,000–13,000 BP) includes the LGM when climatic conditions are very cold and very dry. Many lakes have very low levels or dry out, global conditions are cold and dry. During the transition of stages 2–1, the Lateglacial (ca.

13,000–10,000 BP) there is a sudden increase in temperature and rainfall, and most lake levels rise around 12,500 BP, especially in the tropics (Martin et al., (1997) showed a valuable concept on astronomical forcing of South American rainfall). There is a short, cold interval between 11,000 and 10,000 BP (Younger Dryas stadial), locally also somewhat drier, and 10,000 BP is the beginning of the Holocene. Hence, the Last Glacial shows periods with a very different climate. The difference between a wet and relatively cold Middle Pleniglacial and a very cold and partly very dry Upper Pleniglacial both in the Andes and in Amazonia is of importance. For the northern Andes, the very cold ($7 \pm 2^\circ\text{C}$ lower than today) and dry climates may have lasted only some 20,000 years (30% of the time of the Last Glacial), the moderately cold ($5 \pm 2^\circ\text{C}$) and wet climates some 50,000 year (70% of the time of the Last Glacial).

6.1. Re-evaluation of available pollen records

We will now re-evaluate the most significant pollen diagrams from Amazonia and surrounding tropical lowland that include at least part of the Last Glacial.

6.1.1. *Katira (Rodonia, Brasil, ca. 9°S, 63°W; Van der Hammen, 1972; Absy and Van der Hammen, 1976; Van der Hammen and Absy, 1994)*

The sequence analyzed consists of 13 m of a valley infill in an area covered with rain forest and annual rainfall between 2000 and 2500 mm. The lowermost humic layer dominated by *Mauritia* and other trees (*Didymopanax*, *Hedyosmum*, *Weinmannia-type*, *Curatella*, *Ouratea*, *Podocarpus*, and *Ilex*) has ages of 41,000 and 49,000 BP and delta ^{13}C values of -29% , and represents (rain) forest with *Mauritia*. The sediments above this layer are dominated by grass and herb pollen (Compositae, *Cuphea*, *Labiatae*); the age of the largest fraction of C (alkali soluble) is $18,500 \pm 150$ BP with a delta ^{13}C value of -16% , confirming the dominance of tropical grasses (a small quantity of organic residue, that should be re-deposition of older material (44,000 + 2000 – 3000 BP) has similar values of ^{13}C). The sediments of the upper part of the section are colluvial, indicating an incomplete vegetation cover. Pollen analytical, ^{13}C , and sedimentological-geomorphological data assure a reliable interpretation: (1) a Middle Pleniglacial age *Mauritia* swamp, tropical wet to dry forest elements (including some elements normally common in savanna and savanna forest, like *Didymopanax* type, *Ouratea*, and *Curatella*), and a group consisting of *Ilex*, and very low values of *Podocarpus* and '*Weinmannia type*', followed by (2) an Upper Pleniglacial age grass-savanna with herbs (*Cuphea*, Compositae, *Labiatae*, Cyperaceae), practically devoid of trees and with an incomplete vegetation cover permitting colluviation. The climate should have been of rather extreme dryness (rainfall most probably below

1000–500 mm). This means a reduction of rainfall of 50–60% as compared to the present.

6.1.2. *Guyana and Surinam (Van der Hammen, 1961c, 1963; Wijmstra, 1969, 1971)*

Pollen diagrams of several borehole sections from the coastal plain of the Guyana basin show repeated Quaternary low sea-level stands alternating with high sea-level sands. The high stands are represented by the extension of marsh forest and mangrove forests, the low stands by the extension of grass-savannas with herbs (*Compositae*, *Cuphea*) and savanna shrubs and forest with abundant *Byrsonima*, *Curatella*, and *Didymopanax* type. *Alnus* pollen grains are sometimes present, both during high and low sea-level stands (up to 5% in the Holocene). The Last Glacial low sea-level (dated between > 45,000 BP and some time before ca. 8400 BP) is well represented both in Guyana and Surinam. The Ogle Bridge section (Georgetown; 6°50'N, 58°10'W) shows a well developed mottled soil at approximately 23 m depth and almost 100% grass pollen. Borehole Alliance (Surinam; ca. 55°30'W, 5°50'N) shows the low sea-level interval at the same depth, grass pollen percentages between 40 and 70%, and *Byrsonima* pollen percentages between 10 and 45%.

The data show that during the Last Glacial, extensive grass-savannas and savanna bush and low forest (of *Byrsonima*, *Curatella*, and some others) extended in what at the present day is the coastal plain of Guyana and Surinam, at that time far above sea level and deeply eroded by the rivers. It should be emphasized that these were dry savannas high above sea level, not comparable to the local edaphically determined 'wet savannas' of the present coastal plain. Present-day rainfall on the Guyana site is 2500 mm and on the Surinam site 2000 mm. A decrease of more than 1000 mm is required in the west and > 500 mm in the east, to explain the glacial time vegetation.

6.1.3. *Carajas (Brazil, 6°20'S, 50°25'W; Absy et al., 1991; Sifeddine et al., 1994).*

This is a lake section from a narrow plateau (mesa) at 700–800 m altitude in eastern Amazonia, with annual precipitation between 1500 and 2000 mm. In the rain forest surrounding the hill, relative seasonal dryness is evidenced by patches of deciduous trees. Patches of open or dense treelet-scrub savannas cover the plateau surface. The sediment sequence of ca. 6 m shows three sedimentary cycles, each of them starting with a sandy layer rich in siderite, changing upward to an organic-rich silt. The sandy layers have pollen assemblages of dominantly savanna elements, the organic-rich ones dominantly forest elements. The periods with savanna are dated between 23,000 and 13,000 BP, 40,000 BP, and around 65,000 BP. Like several other lakes from that period (Salitre, Patas, Fuquene) the lake must have dried up. This is an

important fact as it shows that evaporation exceeded precipitation. Under the present dry conditions with rainfall between 1500 and 2000 mm (ca. 1800 mm), evaporation at 700–800 m altitude might be estimated 1300 mm. To dry up the lake, a rainfall decrease of > 500 mm would be necessary (> 30%). Lower temperatures would have decreased evaporation, requiring a larger decrease in rainfall, although this might have been compensated by some increase of evaporation because of the drier air; if surface runoff entered the lake, a higher minimum decrease would be required.

The interpretation of the pollen diagram was based on a study of the recent vegetation and of pollen rain in relation to vegetation (Ferreira Da Silva and Cleef, 1989; Cleef and Ferreira Da Silva, 1994; Sifeddine et al., 1994). It could be concluded that more than 60% of the recent and Late Holocene pollen rain on the plateau and the lake was not from the plateau itself but from the forest vegetation around and below the plateau (*Aparisthmmum*, *Celtis*, *Trema*, *Cecropia*, *Piper*). *Borreria* is abundant in both dry and temporarily flooded savannas. The savanna and low lake level intervals mentioned, alternate with forest and high lake level intervals. In the Middle Pleniglacial, these forests are composed of *Ilex* and Melastomataceae (the remarks in Collinvaux et al., 1996; Colinvaux, 1997) that grasses and herb components are high throughout, and that the arboreal elements are associated with the open vegetation of the site, are incorrect as is evident from the above mentioned studies). The more than 60% of arboreal pollen from the surrounding lower area are very much reduced (almost none) during the dry savanna intervals, even so the driest parts of these intervals are not represented. There is a Holocene interval of extension of grasses and (almost) disappearance of the outer forest elements around 6000 BP associated with the abundant presence of charcoal particles in the sediment. This interval seems to correspond also to a drier interval, but with the strong influence of fire, possibly caused by the presence of man (at least since 8000 BP).

The results show without any reasonable doubt that during the known glacial temperature minima (ca. 20,000, 40,000, and 65,000 BP) the climate in the area was much drier, resulting in the drying up of the lake and the extension of savanna-type vegetation, and the disappearance or reduction of bush vegetation on the plateau and of the forest in the lowlands around the plateau. During the driest intervals that caused the disappearance of the lakes, the reduction of rainfall may be estimated as > 500 mm (> 30%), while the change of forest to savanna, and savanna forest or cerrado-type vegetation in the area would require equally a decrease of at least 500 mm. The composition of the local Middle Pleniglacial forest and *Ilex* (and Melastomataceae), not represented in the present local vegetation recalls the typical high presence of *Ilex* in glacial time Amazonian sediments of the other sites (as compared to the Holocene).

6.1.4. *Pantano de Monica (Lower Caquetá area, east of Araracuara, Colombia; 0°42'S, 72°04'W; Van der Hammen, in press a)*

This is a pollen diagram from almost 4 m of sediments, from a marsh forest on a low area on the lower terrace of the Caquetá River at ca. 150 m alt., in an area with ca. 3060 mm of rainfall and average annual temperature of 25°C. The area is within extensive Amazonian rain forest. Time control is as follows: 6120 ± 80 BP at 200 cm, 11,230 ± 100 BP at 281 cm, and 36,000 ± 1900/-1500 BP at 381 cm. The 36,000 BP date is from the top of sandy terrace elements; the rest of the sediment is clay with small wood remains. Extrapolation of the two younger dates downward suggests an age between ca. 13,000 and 17,000 BP for the basal part of the clayey sediments (and a hiatus at the limit of sand and clay). The pollen spectra of this Upper Pleniglacial interval are very different from the Lateglacial and Holocene ones. It starts with very high percentages of Myrtaceae, upward gradually replaced by Melastomataceae and then by *Ilex*, which reaches 15%. *Mauritia* pollen is present in the entire interval, but is lacking in the lowermost sample, and *Symphonia* and *Clusia* (elements of the modern marsh forest) start in the uppermost part of the interval discussed here. There is some *Podocarpus* pollen (1.5%), some Gramineae pollen (2.5%), *Borreria* (1%), and Compositae (Tubuliflorae; 1.5%). This composition recalls that of the Carajas area and that of other Amazonian sites mentioned here, in Last Glacial time. As to the probable hiatus during the lower part of the Upper Pleniglacial, this coincides with other sites like Carajas and Lake Pata, and could well be related with the driest climatic interval, around 20,000 BP, when there was incision of the rivers in their lower terrace sediments and the site of our section seems to have been dry, or under erosion. There is no reasonable doubt that during the Upper Pleniglacial rain forest continued to be present in this area, although there was a marked change in composition, and the presence of a number of elements seems to indicate that there may have been some more dry and open vegetation locally in the area (possibly on well drained sandy soils).

6.1.5. *Lake Pata (Brazil, 0°16'N, 66°41'W; Colinvaux et al., 1996; Colinvaux, 1996, 1997)*

A section from a lake at 300 m altitude surrounded by rain forest with a present-day rainfall above 3000 mm. The total section presented is 165 cm long, representing some 43,000 years. According to the radiocarbon data, the average sedimentation rate is on the order of 0.1 mm/yr during the last 6000 years, 0.01 mm/yr between 6000 and 14,000 BP, and 0.04 mm/yr between 14,000 and 18,000 BP. Between 18,000 and 31,000 BP the average sedimentation rate was 0.008 mm/yr and it is evident that there could be considerable hiatus in this interval. This assumption is supported by Ledru et al.

(1998). Between 31,000 and 39,000 BP the sedimentation rate is much higher, 0.4 mm/yr, and between 39,000 and 42,000 BP it is 0.13 mm/yr. The sedimentation rate is, in general, very low and pollen content is relatively high, both facts indicate that very little sediment is transported into the lake by surface runoff. The interval between 14,000 and 31,000 BP is nodular yellowish clay, and we interpret this as evidence that the lake fell dry regularly; there should be a considerable hiatus near the base of the nodular yellowish clay, covering a considerable part of the 18,000–31,000 BP time interval (the lower part of the Upper Pleniglacial). This means that the lake dried up during the lower part of the Upper Pleniglacial, and was intermittently dry during the upper part of the Upper Pleniglacial. This corresponds very well with the interpretation of this period as a very dry one. To dry out, evaporation should have been greater than the rainfall, and if the present day rainfall is taken as 3000 mm and evaporation as 1700 mm, the rainfall should have been at least 1300 mm lower than today. This is, of course, a very rough estimation that only indicates the order of magnitude. But that seems to indicate that the rainfall conditions would correspond to the drier rain forest with some deciduous species, like that of today's lowland Carajas.

The Middle Pleniglacial interval (30,000–42,000 BP) shows the highest sedimentation rate, and continuously high water levels. This indicates a climate with rainfall high enough to maintain the lake at a high water level; the sedimentation rates, even four times higher than in the Holocene, seem to indicate a higher influx of surface runoff from the surroundings with some sediment, and might indicate higher values of rainfall than during the Holocene. *Podocarpus*, *Ilex* and *Weinmannia* type, present with low representation in this record, were also found in low percentages in the Middle Pleniglacial samples of Katira (Rondonia), and *Podocarpus* and *Ilex* in the Upper Pleniglacial of Pantano de Monica (Van der Hammen, 1999a). *Myrsine*, present in Lake Pata record, has several species in the cerrado vegetation, *Humiria* has several species on the low sandstone mesas and in the proper rain forest of Amazonia, and so have *Podocarpus* and *Ilex*, and probably *Hedyosmum*, but *Weinmannia* is so far only known from elevations above about 900 m. In the representation of these taxa there might be a lower temperature signal. We will come back to the significance of the representation of the pollen of these genera in the Amazonian lowland; the increase of Melastomataceae and *Ilex* in glacial time is very interesting and is similar to the forest in Carajas during Middle Pleniglacial time.

6.1.6. *Mera and SanJuanBosco (Ecuador, 1°29'S, 77°06'W and 3°3'S, 78°27'W, respectively; Liu and Colinvaux, 1985; Bush et al., 1990)*

Both sites are on the eastern Andean slopes with rainfall that might be around 4000 mm. The Mera site is at

1100 m altitude and consists of peat and silts as part of a sequence of river sediments. The section represents the time interval from ca. 34,000 to 31,000 BP; hence the upper part of the Middle Pleniglacial, a very wet period in the Andes. In the lower silts there is up to 15% *Alnus* pollen and 15% of grass pollen. The overlying peat shows: *Alnus* between ca. 2 and 6%, a few percent of *Podocarpus* (up to 5%) and *Ilex*, *Hedyosmum* 5–10%. *Weinmannia* up to 25%, indicating local presence in the surrounding forest. We have seen that on the eastern slopes of the Andes, on and around fluvial deposits, *Weinmannia* is well represented down to at least 1200 m. The percentages of *Hedyosmum* correspond to those found at present between 1100 and 1400 m, and the percentages of *Alnus* correspond to values found in the Middle Holocene peat of the Pitalito Basin (1300 m); the higher representation in the silt as in the peat may indicate river water transportation from *Alnus* forest higher up the river. The *Podocarpus* values cannot give an answer about its local presence, nor about a lowering of temperature. We think these data are insufficient to conclude with any certainty about a considerable lowering of temperature; the *Weinmannia* percentage may indicate a lowering of more than 100 m, and if the Pitalito Basin values were maxima for the 1300 m altitude, we might conclude of a possible lowering of 200 m at least. So, from the available pollen data we cannot conclude with certainty on a temperature lowering more than 2°C, although a value of 4°C is not impossible. Values on lowering of temperature from the high plain of Bogotá for the time interval 34,000–31,000 BP area on the order of $3(\pm 1)^\circ\text{C}$.

The San Juan Bosco section is from an altitude of 900 m from a sequence of fluvial sediments (boulders, gravels, sand and clay). The lowermost clastic sediments contain up to 45% *Alnus*, and the uppermost up to 40% *Weinmannia*; Melastomataceae pollen is rather abundant (10–30%) and there is little *Hedyosmum*, *Podocarpus*, *Ilex*, and *Cecropia*. There are two dates of approximately 31,000 and 26,000 BP. The sequence resembles that of the Mera record, the *Alnus* peak is in fluvial sediments and the pollen grains could very easily have been fluvially transported. That seems not to be the case for *Weinmannia*, whose pollen production is much lower. If that is correct, a lowering of at least 300 m may be accepted, a minimum decrease of some 2°C.

Both sedimentary sequences correspond to fluvial sediments and are dominantly silts, sands and boulders. They seem to correspond to the top of the Middle Pleniglacial sequence of fluvial Amazonian and cordilleran deposits (the lower terrace of Amazonia). The situation is very similar to that further north, where forests with abundant *Weinmannia* are found on fluvial sediments at altitudes down to 1200 m. The transect of vegetation and pollen sedimentation along the eastern slopes of the Andes (Grabandt, 1980) was not taken into account by

Bush et al. (1990) with the arguments that there is *Quercus* (oak) in the northern Andes, that is not present in Ecuador. However, *Quercus* does not occur on the eastern slopes of the northern Andes.

The experience is that fluvial sediments both in the Andes and Amazonia frequently contain wood, fluvially transported and deposited in the sediments. They may come from very far, especially on relatively steep slopes and with relatively high energy as in the case of the Middle Pleniglacial high rainfall period. So, the presence of *Podocarpus* wood and even of *Drimys* cannot tell us with any degree of certainty about their presence at the site, especially as pollen values of the first are extremely low and those of the second are absent. All this wood may very easily have come from higher up the slopes.

As to the *Alnus* pollen, the higher values are from the lower silts. They go together with higher values of grass pollen, and the spectra were compared with pollen spectra from alder carr in the ‘Sabana de Bogotá’, calling it ‘alder-meadows’. This, however, is an error, as the small remnants of alder carr on the high plain are surrounded by large extensions of man-made meadows and the higher grass percentages in this case come from outside the carr. The most probable interpretation of the pollen content of the silts is that a good part of it is water-transported from higher elevation. We have to conclude that 7.5°C lowering of temperature suggested by Bush et al. (1990) cannot be accepted on the basis of the available evidence. The suggested mixture of tropical and montane elements is not a special glacial time phenomenon, as is evident from the vegetation and pollen sequences published by Grabandt (1980). It is general characteristic of the transitional zone between the subandean forest (lower montane forest) and the lower tropical belt; in this case the phenomenon is apparently enhanced by pollen and wood most probably fluvially transported.

6.1.7. Cameleon, Cahuinari-II and Totumo sections (Middle Caquetá Valley east of Araracuara, Coloumbia)

Several sections from the lower terrace of the Caquetá River (of Middle Pleniglacial age) were sampled for pollen analysis and radiocarbon dating. The radiocarbon dates and the sections have already been published (Van der Hammen et al., 1992a). Here we mention some of the palynological results of pollen diagrams that are now being prepared for publication (Espejo, unpublished data). Section Cameleon is a ca. 1 m thick peat clay bed; the uppermost part was dated 55,200 + 4000/ – 2700 BP. Rain forest elements dominate; there is an almost continuous curve for *Podocarpus* (up to 5%), a continuous curve for *Ilex* (up to 10%), Melastomataceae (up to 25%). Gramineae and Compositae are represented (up to 5%). *Mauritia* is almost absent. Section Cahuinari-II is a 60 cm thick interval of gray sandy clay with wood and leaf remains.

The top is dated $40,000 \pm 1100$ BP, the middle part $46,400 \pm 1700/-400$ BP, and the base $> 50,000$ BP. The diagram shows the presence of some *Byrsonima*, *Didymopanax* type, and of *Ouratea*. There is a continuous *Mauritia* curve with values between 5 and 25%. Section Totumo is a 1 m thick section, 6 m below the top of the terrace, with a date of $30,640 \pm 240$ BP at the top, and of $49,100 + 3800/-2600$ BP in the lower part. Besides the presence of many tropical rain forest elements there is a succession of Myrtaceae (ca. 20%) followed by Lecythidaceae (up to 35%), and finally a maximum of *Ilex* of 35% (*Ilex* is present in the entire section). The Gramineae and Compositae curves show percentages up to more than 10%. There is some *Podocarpus* only in three samples (ca. 1%), otherwise it is absent. *Mauritia* is absent in the lower and middle part of the section, and only present with 2% in the uppermost part.

These Middle Pleniglacial sections show rather different pictures, but in general considerably higher values of *Ilex* than in Holocene sections of the same area, sometimes higher values of Myrtaceae and/or Melastomataceae, locally higher values of grass pollen and Compositae, sometimes *Podocarpus* up to 5% and sometimes absent, *Mauritia* sometimes present with up to 25%, or almost absent. It has to be stressed that all of these elements are present in the Holocene sections, sometimes reaching higher percentages (Myrtaceae, Melastomataceae, *Mauritia*), sometimes being (almost) absent; *Podocarpus* is now and then found in the Holocene, but mostly below 1%. The presence of *Byrsonima* together with *Didymopanax* type, *Ouratea* and Gramineae suggest that some more open or dry forest vegetation may have been present, maybe on sandy terrace soils.

6.2. Pollen in Amazon delta and other off shore sediments

We have seen that the Amazon River system suffered important changes during the Last Glacial. The river discharge was very high during the Middle Pleniglacial, related to a substantial increase of rainfall in the Andes and Amazonia, the rivers carried much sediment that was deposited in Amazonia as 'lower terrace' sediments. During the Upper Pleniglacial, water carried by the rivers was seriously reduced because of the reduction of rainfall, and the rivers incised in the terrace sediments, some 10 m in the middle course. The incision was much deeper in the lower course of the Amazon River, where it may have been 100 m or more, related to the lower sea-level during glacial time (Irion, 1976). This phase of important erosion is apparently also registered in the sedimentary record of Atlantic deep-sea sediments west and north of South America, in the form of deep-sea arkosic sands, related to the glacial aridity (Damuth and Fairbridge, 1970).

Recently the results of palynological analysis of cores from the submarine delta of the Amazon River were published (Haberle, 1997; Hoorn, 1997). The sediments

contain much reworked pollen from older sediments. The glacial sediments are characterized by higher percentages of organic remains (like woody vessels), corroded pollen and spores, high values of fern spores and fungal spores, and by an increase of *Alnus*, *Hedyosmum*, and *Podocarpus*. Tropical lowland tree pollen is present together with grass pollen and Compositae (these last two slightly higher during the glacial period). This result of thorough mixing of elements of different sources is difficult to interpret. However, it seems clear that there should be a relation between (1) the strong erosion in the river system, when older sediment of the lower terrace and older, were removed and deposited in the submarine delta, and (2) the abundant organic material (peat, tree trunks) present in the lower terrace that may have provided the organic material, and part of the sometimes corroded pollen grains. At present-day the lower parts of river banks inside the rain forest may be slightly eroded by water level fluctuations and water velocity; such places are covered by abundant fern vegetation which may explain high percentages of fern spores during erosional phases.

7. General discussion

The lowland forest and its flora could develop and evolve continuously during the entire Tertiary in a climate generally warmer than today. In the Miocene, biodiversity was very high, and there are indications that it may have been even considerably higher than it is now. The uplift of the Eastern Andes in the Miocene and Pliocene changed fundamentally the drainage patterns and the climate: the present-day Amazons and Orinoco river systems were formed (Hoorn et al., 1995), rainfall must have increased in present day western Amazonia, and on the eastern Andean slopes. The Pacific rain forest was separated from the Amazon forest, resulting in a stronger endemism. The creation of the Andes opened the way to the development of its flora and vegetation zones, by evolution/speciation upward from the tropical lowland flora, and by evolution/speciation of taxa immigrated from the south (austral-antarctic region), and from the north (holartic region). Later, neotropical Andean elements could enter the tropical lowland and create new lowland species; global cooling since the Miocene may have been an important factor. *Podocarpus* seems to have formed species adapted to the tropical warm climate since the Oligocene and Miocene, and the present-day Amazonian species might be their descendants. In the Upper Miocene there is locally even very abundant *Podocarpus* together with *Mauritia*, and other tropical taxa, like Bombacaceae, and also 'Andean' taxa like *Weinmannia* and *Ilex*. The general lowering of temperature during the Neogene, and the increase of rainfall related to the upheaval of the Andes both may

have stimulated the entrance of montane taxa into the tropical lowland flora. It seems that the drier climatic zones, actually present north and south of Amazonia, with a.o. savanna, savanna forest, deciduous forest, cerrado, established gradually in their present day position in the course of the Miocene and Pliocene, when pollen data include the extension of grasses, Compositae and other herbs, eventually together with *Byrsonima* and *Curatella*.

When discussing glacial vegetation and precipitation in Amazonas it is necessary to treat separately the dry Upper Pleniglacial and the wet Middle Pleniglacial. As to the Upper Pleniglacial dry period, there is convincing evidence of a dry grass savanna with incomplete vegetation cover leading to colluviation in Katira (Rondonia), and to savanna vegetation (and a strong decrease of rainfall) in Carajas. There is savanna vegetation during low sea-level sand in Guyana and in Surinam, and there were extensive Late Quaternary dune fields in the lower Rio Branco to Rio Negro region and extensive Late Quaternary dune fields in the Colombian and Venezuelan Llanos (Orinoquia). Savannas and associated dry forests and cerrado vegetation are found in areas with rainfall below 1500 mm. The formation of large dune fields require the presence of sand and rain fall at least below 1000 or 500 mm. Comparison with the present day rainfall in these areas, a decrease of > 500 mm and of more than 1000–1500 mm should be required as minimum (a reduction of 50–60%) for this change.

The impact of dryness and temperature lowering on the vegetation and flora, repeated every glacial interval of the Quaternary, may have led to considerable extinctions instead of to extensive speciation. The fact that biodiversity of the Miocene seems to have been greater than the Holocene supports this view. Plotting Gentry's species density values in relation to rainfall on the precipitation map of Amazonia, we see that the present-day high rainfall centers should have a high number of species per 0.1 ha and the lower rainfall area less (with values from some 300 to 100). Thus decrease in rainfall may result in a loss of species, especially if migration is difficult or impossible. The specific composition of these relatively wet and dry forests is moreover partly different. Another conclusion is that the present-day centers of high rainfall are relatively isolated by the areas of lower rainfall and might be considered a type of present-day 'refugia' for a number of wet forest species. These areas may have become still more isolated during the dry glacial intervals and may have had a still more pronounced function as 'refugia' (areas where wet forest species could survive the generally adverse conditions). If under these conditions of relative isolation and adverse conditions without escape, speciation occurred, is difficult to answer but it seems probable that extinction dominated (see also Bush, 1994). However, these areas of higher rainfall may

have been somehow existent during the entire Quaternary (Hooghiemstra, 1997) and at least the Upper Pliocene, and as such, they may have been centers of speciation.

When we plot principle sites with paleodata on a rainfall map of Amazonia and surroundings and accept that no fundamental changes in this pattern occurred besides a general reduction of rainfall (see discussion in Hooghiemstra, 1995, 1997), we can compare the reconstructed vegetation and the reduction of rainfall with the present one. We may extrapolate the data on the basis of the general reduction of rainfall, and so reconstruct an approximate tentative vegetation/rainfall pattern that may serve as a first, partly hypothetical, image of the LGM in Amazonia (Fig. 3). This image depends on the accuracy of the rainfall map and might change somewhat when more detailed data become available. Data from Lake Pata (Colinvaux et al., 1996) and the presence of dune fields in the Lower Rio Branco-Rio Negro area are in accordance with this picture. Gallery forest and varzea vegetation must have existed along the rivers, but in view of the strong incision of the rivers in their Middle Pleniglacial sediments, their extension during maximum dryness and lower sea-level may have been limited.

8. Conclusions

(1) The neotropical flora developed principally during the Tertiary. Tectonic movements, sea-level changes causing marine transgressions and regressions, and changes of river systems were important sources of environmental dynamics. There was a positive balance between evolution and extinction, reaching extraordinarily high biodiversity in the Miocene. Uplift of the Andes in the course of the Tertiary increased biodiversity by evolution, migration, and adaptation of the montane floras.

(2) The effect of Late Neogene temperature decrease, and especially of the Quaternary glacial cycles on the tropical lowland flora was apparently negative for biodiversity (negative evolution-extinction balance), as there is no escape in the tropical lowlands for temperature decrease and only partly for a considerable decrease of rainfall. The increase in rainfall due to the uplift of the Andes may have had locally a positive effect on biodiversity.

(3) The entrance of originally montane taxa into the tropical lowland flora may have been stimulated by the Neogene climatic cooling. The adaptative evolution of principally tropical taxa to the montane areas (Andes, Tepuis) might have taken place during much of the Tertiary, especially during the Neogene. Very high rainfall, like today in the Chocó, is also related to the presence of montane taxa in the tropical lowland flora.

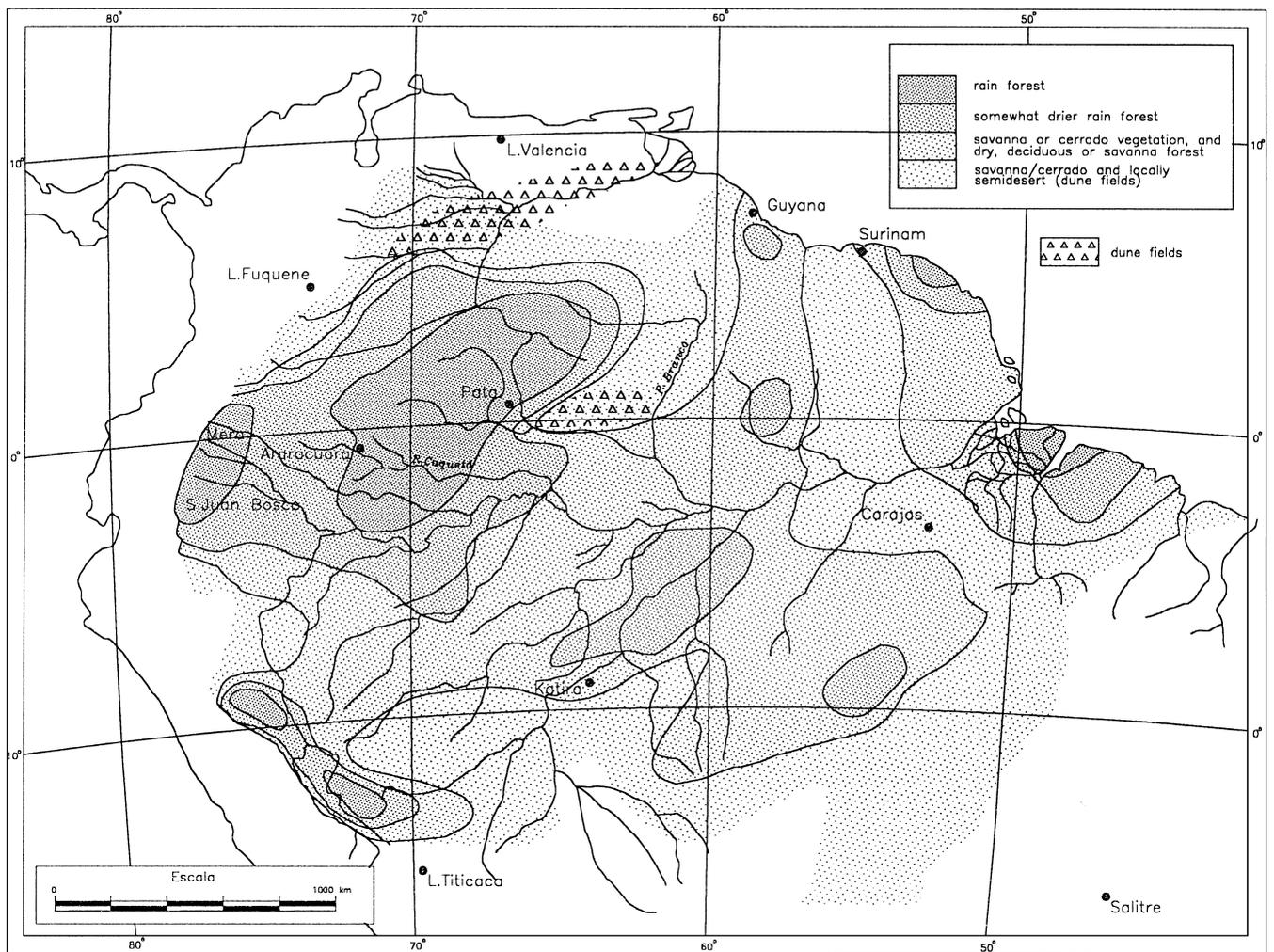


Fig. 3. Reconstruction of the possible vegetation pattern in the Amazon basin and surroundings during the Last Glacial Maximum, some 20,000 BP, based on the present day rainfall map of Figueroa and Nobre (1990) and a general reduction of c. 40% rainfall as suggested by the interpretation of the paleo-data presented. All the data from sites from where paleo-data are available are in agreement with this reconstruction. (This is a further elaboration of earlier maps presented by Van der Hammen and Absy, 1994).

(4) Compared to modern values, temperature lowering during the LGM in the high Andes was ca. 8°C, in the tropical lowlands possibly 4–5°C.

(5) The difference between a wet and cool Middle Pleniglacial (60,000–28,000 BP), and a dry and cold Upper Pleniglacial (28,000–13,000 BP) including the LGM, is evident both in the Andes and Amazonia. Lapse rates were approximately 0.7°C/100 m during the dry Upper Pleniglacial and may possibly have been 0.6°C/100 m during the wet Middle Pleniglacial (equal to modern value).

(6) During the Middle Pleniglacial (ca. 60,000–28,000 BP) wet climate in both the Andes and Amazonia caused extensive fluvial sedimentation in both areas. Glaciers in the Andes reached their maximum extension. The climate was fluctuating, temperatures were somewhat higher than during the Upper Pleni-

glacial, but there was one very cold and dry interval around 40,000 BP. Lowland temperatures may have been equal to or higher than those during the Upper Pleniglacial.

(7) During the Upper Pleniglacial (28,000–13,000 BP) the climate was relatively dry and cold. Glaciers in the Andes were less extensive. Rivers in Amazonia incised in the Middle Pleniglacial sediments. Savannas and drier types of forests extended and replaced locally rain forest. Dune areas developed in several present-day savanna and forest areas. Rainfall may have been reduced some 30–50% in most of northern South America. Around 20,000 BP there should have been a 'dryness crisis' during which isolated Amazonian lakes dried totally, like some of the larger Andean lakes.

(8) At the beginning of the Lateglacial (13,000–10,000 BP) rainfall increased again, lake-levels rose (both

in the Andes and Amazonas), and sedimentation started again in the river valleys and continued in the Holocene.

(9) Pollen of principally montane taxa (*Podocarpus*, *Hedyosmum*) is present in the Miocene, Pliocene, and Quaternary sediments of Amazonia and surroundings, sometimes abundantly. These genera have modern species in the tropical lowlands. *Weinmannia* occurs as low as 900 m in the mountains, and is found in the Upper Miocene sediments together with abundant *Podocarpus* and *Mauritia*. Low values of *Weinmannia* are found in Pleniglacial sediments of Amazonas. *Podocarpus* pollen is more frequent in Last Glacial sediments than in the Holocene: apparently the background values increased because of a more frequent presence in the area. Increased background values of *Weinmannia* may point to downslope migration into the area between 400 and 1000 m, increasing background values in the area.

(10) *Alnus* pollen is easily transported by water and may reach even the tropical lowlands in considerable quantities. Hence, great care should be taken when temperature lowering is inferred from pollen associations in sediments from river valleys and brooks. *Alnus* entered South America ca. 1 Ma BP. *Quercus* entered ca. 340,000 yr BP and is locally found as low as 1000 m in the interior of the northern Andes, but *Quercus* is not present on the eastern flank of the Eastern Cordillera facing Orinoquia and Amazonia.

(11) The species composition of the tropical lowland wet forest during the Last Glacial was probably not fundamentally different from the present one, but relative proportions were different. Besides a slight increase of background pollen values of some elements, like *Podocarpus* and *Hedyosmum*, and some specific montane elements like *Weinmannia*, there is a relative important increase of values of *Ilex* and Melastomataceae. But it is not yet clear what this means in climatic or adaptive terms (a response to drier or cooler climatic conditions might be one possibility).

(12) During the Quaternary the repeated lower temperatures and especially the lower rainfall had a strong impact on the distribution of vegetation and flora. There is a positive relation between temperature and biodiversity (number of species per area) and between rainfall and biodiversity. So biodiversity must have been seriously affected by glacial climate. This seems to be confirmed by the fact that Miocene Amazonian river valley sediments contain twice as many pollen taxa as the Holocene sediments. The Neogene lowering of temperature, and especially the long sequence of Quaternary ice ages, seem to have caused major extinction, in a situation of no escape of warmer and wetter areas.

(13) The present-day Amazonian centers of higher rainfall are refuge areas for wet forest species. These centers became more pronounced during glacial climates. It is possible that in these areas there was, and is, speciation in relative isolation.

(14) Using the map of present-day rainfall and the principal paleoecological data, accepting that the reduction of rainfall on the order of ca. 30–50% was generally true throughout the area, a probable LGM scenario for the distribution of rainfall and vegetation can be made. This reconstruction corresponds to the known data on vegetation change and dune fields, but may be adapted to future new data on modern rainfall patterns and new paleo-data.

Acknowledgements

Cooperation with Colombian institutes and universities during the past 40 years made the elaboration of these data possible. We thank the Netherlands Organization for Scientific Research (NWO) for their decision to focus in the '1997 Huygens Lecture' on Amazonas. We thank Paul Colinvaux for his generous contribution to this lecture, which gave the stimulus to prepare this paper. We thank M.P. Ledru and G. Seltzer for critical and stimulating comment on an earlier draft of the manuscript, which improved it substantially.

References

- Absy, M.L., Van der Hammen, T., 1976. Some palaeoecological data from Rondonia, southern part of the Amazon basin. *Acta Amazonica* 6, 293–299.
- Absy, M.L., Cleef, A.M., Fornier, M., Servant, M., Siffedine, A., Da Silva, M.F., Soubies, F., Suguio, K., Turcq, B., Van der Hammen, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60,000 dernières années. Première comparaison avec d'autres régions tropicales. *Comptes Rendus Academie Scientifique Paris* 313, 673–678.
- Bakker, J., 1990. Tectonic and climatic controls on Late Quaternary sedimentary processes in a neotectonic intramontane basin (The Pitalito Basin, south Colombia). Ph.D. Thesis, Wageningen Agricultural University, 160 pp. (Also in: 'The Quaternary of Colombia', 16).
- Behling, H., Hooghiemstra, H., Negret, A.J., 1998. Holocene history of the Chocó rain forest from Laguna Piusbi, southern Pacific lowlands of Colombia. *Quaternary Research* 50, 300–308.
- Bush, M., 1994. Amazonian speciation: A necessarily complex model. *Journal of Biogeography* 21, 5–17.
- Bush, M.B., Colinvaux, P.A., Wiemann, M.C., Piperno, D.R., Liu, K.B., 1990. Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Research* 34, 330–345.
- Bush, M.B., Stute, M., Ledru, M.-P., Behling, H., Colinvaux, P.A., De Oliveira, P.E., Grimm, E.C., Hooghiemstra, H., Haberle, S., Leyden, B.W., Salgado-Labouriau, M.-L., Webb, R., 2000. Paleotemperature estimates for the lowland Americas between 30°S and 30°N at the last glacial maximum, in press.
- Campbell, K.E., Romero, L., 1989. The Quaternary geology of Departamento de Madre de Dios, Peru. In: Congreso Peruana de Geología, Lima. Proceedings Lima Soc. Geol. del Peru, p. 6.
- Carneiro Filho, A.C., Zinck, J.A., 1994. Mapping paleo-aolian sand cover formations in the northern Amazon basin from TM images. *ITC Journal* 3, 270–282.

- Cleef, A.M., Hooghiemstra, H., 1984. Present vegetation of the area of the high plain of Bogotá. In: Hooghiemstra, H. (Ed.), *Vegetational and Climatic History of the High Plain of Bogotá, Colombia: A Continuous Record of the Last 3.5 million Years*. *Dissertationes Botanicae*, Vol. 79. J. Cramer, Vaduz, pp. 42–66. (Also in: 'The Quaternary of Colombia', 10).
- Cleef, A.M., Ferreira Da Silva, M., 1994. Plant communities of the Serra dos Carajas (Pará) Brazil. *Boletim do Museu Paraense Emílio Goeldi Nova Série Botanica* 10 (2), 269–281.
- CLIMAP Project Members, 1976. The surface of the ice age earth, *Science* 191, 1131–1137.
- Colinvaux, P.A., 1979. The ice-age Amazon. *Nature* 278, 399–400.
- Colinvaux, P.A., 1996. Quaternary environmental history and forest diversity in the neotropics. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. The University of Chicago Press, Chicago, pp. 359–405.
- Colinvaux, P.A., 1997. The ice-age Amazon and the problem of diversity. NWO Huygens Lecture 1997, The Hague, The Netherlands Organization for Scientific Research (NWO), pp. 7–30.
- Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* 274, 85–88.
- Colinvaux, P.A., Liu, K.-B., 1987. The Late-Quaternary climate of the western Amazon basin. In: Berger, W.H., Labeyrie, L.D. (Eds.), *Abrupt Climatic Change*. Reidel, Dordrecht, pp. 113–122.
- Damuth, J.E., Fairbridge, R.W., 1970. Equatorial Atlantic deep-sea arkosic sands and ice-age aridity in tropical South America. *Bulletin Geological Society of America* 81, 189–206.
- Duivenvoorden, J.F., Lips, J.M. 1993. *Ecología del paisaje del Medio Caquetá*. (Landscape ecology of the Middle Caquetá basin). *Tropenbos Colombia*, Vol. IIIA (Explanatory notes to the maps/Memoria explicativa de los mapas) & IIIB (10 Maps/10 Mapas), 301 pp.
- Duivenvoorden, J.F., Lips, J.M., 1995. *A Land-Ecological Study of Soils, Vegetation, and Plant Diversity in Colombian Amazonia*. *Tropenbos Series*, Vol. 12. The Tropenbos Foundation, Wageningen, The Netherlands, 438 pp. (Also in: 'The Quaternary of Colombia', 20)
- Farrera, I., Harrison, S.P., Prentice, I.C., Ramstein, G., Guiot, J., Bartlein, P.J., Bonnefille, R., Bush, M., Cramer, W., von Grafenstein, U., Holmgren, K., Hooghiemstra, H., Hope, G., Jolly, D., Lauritzen, S.-E., Ono, Y., Pinot, S., Stute, M., Yu, G., 1999. Tropical climates at the last glacial maximum: a new synthesis of terrestrial palaeoclimate data I. Vegetation, lake-levels and geochemistry. *Climate Dynamics*, in press.
- Ferreira Da Silva, M., Cleef, A.M., 1991. Plant communities of the Serra da Carajas (Para, Brasil). *INQUA Symposium Sao Paulo*, pp. 269–274.
- Figuerola, N., Nobre, C.A., 1990. Precipitation distribution over central western tropical South America. *Climanalise* 5 (6), 36–42.
- Gates, W.L., 1976. Modeling the ice-age climate. *Science* 191, 113–1144.
- Gentry, A.H., 1986. Species richness and floristic composition of Chocó region plant communities. *Caldasia* 15, 71–91.
- Gentry, A.H., 1992. Tropical forest biodiversity: distribution patterns and their conservational significance. *Oikos* 63, 19–28.
- González, A.E., 1967. A palynological study of the Upper Los Cuercos and Mirador formations (Lower and Middle Eocene; Tibú area, Colombia). Ph.D. Thesis, University of Amsterdam, E.J. Brill, Leiden, 68 pp 30 plates.
- Grabandt, R.A.J., 1980. Pollen rain in relation to arboreal vegetation in the Colombian Cordillera Oriental. *Review of Palaeobotany and Palynology* 29, 65–147.
- Haberle, S., 1997. Upper Quaternary vegetation and climate history of the Amazon basin: correlating marine and terrestrial pollen records. *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 155, pp. 381–396.
- Haffer, J., 1969. Speciation in Amazonian forest birds. *Science* 165, 131–137.
- Hooghiemstra, H. (1984). *Vegetational and climatic history of the high plain of Bogotá, Colombia: a continuous record of the last 3.5 million years*. *Dissertationes Botanicae*, Vol. 79. J. Cramer, Vaduz, 368 pp. (Also in: 'The Quaternary of Colombia', 10).
- Hooghiemstra, H., 1995. Environmental and paleoclimatic evolution in Late Pliocene-Quaternary Colombia. In: Vrba, E.S., Denton, G., Burckle, L.H., Partridge, T.C. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, USA, pp. 249–261.
- Hooghiemstra, H., 1997. Tropical rain forest versus savanna: two sides of a precious medal? A comment. NWO Huygens Lecture 1997. The Netherlands Organization for Scientific Research (NWO), The Hague, pp. 31–43.
- Hooghiemstra, H., Cleef, A.M., 1995. Pleistocene climatic change and environmental and generic dynamics in the north Andean montane forest and paramo. In: Churchill, S.P., Balslev, H., Forero, E., Luyeyn, J.L. (Eds.), *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, pp. 35–49.
- Hooghiemstra, H., Melice, J.L., Berger, A., Shackleton, N.J., 1993. Frequency spectra and paleoclimatic variability of high-resolution 30-1450 ka Funza I pollen record (Eastern Cordillera, Colombia). *Quaternary Science Reviews* 12, 141–156.
- Hooghiemstra, H., Ran, E.T.H., 1994. Late Pliocene-Pleistocene high resolution pollen sequence of Colombia: an overview of climatic change. *Quaternary International* 21, 63–80.
- Hooghiemstra, H., Van der Hammen, T., 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth-Science Reviews* 44, 147–183.
- Hoorn, C., 1990. Evolución de los ambientes sedimentarios durante el Terciario y el Cuaternario en la Amazonica Colombiana. *Colombia Amazonica* 4 (2), 97–126.
- Hoorn, C., 1993a. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. *Palaeogeography Palaeoclimatology Palaeoecology* 105, 267–309.
- Hoorn, C., 1993b. Geología del nororiente de la Amazonia Peruana: la formación Pebas. In: Kalliola, R., Puhakka, M., Danjoy, W. (Eds.), *Amazonia Peruana. Vegetación Húmeda Tropical en el llano Subandino*. Proyecto Amazonia, Universidad de Turku (PAUT) and Oficina Nacional de Evaluación de Recursos Naturales (ONERN), Jyväskylä, pp. 69–85.
- Hoorn, C., 1994a. Fluvial palaeoenvironments in the intratropical Amazonas Basin (Early Miocene-early Middle Miocene Colombia). *Palaeogeography Palaeoclimatology Palaeoecology* 109, 1–54.
- Hoorn, C., 1994b. An environmental reconstruction of the paleo-Amazon river system (Middle-Late Miocene NW Amazonia). *Palaeogeography Palaeoclimatology Palaeoecology* 112, 187–238.
- Hoorn, C., 1994c. Miocene palynostratigraphy and palaeoenvironments of northwestern Amazonia. Evidence for marine incursions and the influence of Andean tectonics. Ph.D. Thesis, University of Amsterdam, 156 pp.
- Hoorn, C., 1996. Miocene deposits in the Amazonian foreland basin. *Science* 273, 122–123.
- Hoorn, C., 1997. Palynology of the Pleistocene glacial/interglacial cycles of the Amazon Fan (Holes 940A, 944A, and 946A). *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 155, pp. 397–409.
- Hoorn, C., Guerrero, J., Sarmiento, G.A., Lorente, M.A., 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* 23, 237–240.
- Irion, G., 1976. Quaternary sediments of the upper Amazon lowlands of Brazil. *Biogeographica* 7, 163–167.
- Jaramillo, C., Bayona, G., 1999. Mangrove distribution during the Holocene in Tribugá Gulf, Colombia. *Biotropica*, in press.

- LAPD, 1996. The Latin American pollen database site inventory. Paleoclimatology Publication Series Report No. 4. World Data Center, Boulder, 58 pp.
- Latrubesse, E.M., Franzinelli, E. (unpublished manuscript). Late Quaternary alluvial sedimentation in the upper Rio Negro basin, Amazonia, Paleoclimatic implications, Brazil.
- Ledru, M.-P., 1992. Modifications de la végétation du Brésil Central entre la dernière époque glaciaire et l'interglaciaire actuel. *Comptes Rendus des Académies des Sciences Paris, Serie II* 314, 117–123.
- Ledru, M.-P., 1993. Late Quaternary environmental and climatic changes in central Brazil. *Quaternary Research* 39, 90–98.
- Ledru, M.-P., Bertaux, J., Sifeddine, A., Suguio, K., 1998. Absence of last glacial maximum records in lowland tropical forests. *Quaternary Research* 49, 233–237.
- Ledru, M.-P., Soares Braga, P.I., Soubies, F., Fournier, M., Martin, L., Suguio, K., Trucq, B., 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. *Palaeogeography Palaeoclimatology Palaeoecology* 123, 239–257.
- Liu, K.-B., Colinvaux, P.A., 1985. Forest changes in the Amazon basin during the last glacial maximum. *Nature* 318, 556–557.
- Livingstone, D.A., Van der Hammen, T., 1978. Palaeogeography and palaeoclimatology. In *Tropical forest ecosystems, a state-of-knowledge report prepared by UNESCO/UNEP/FAO*. Unesco, Paris, pp. 61–90.
- Lorente, M.A., 1986. Palynology and palynofacies of the Upper Tertiary in Venezuela. Ph.D. Thesis, University of Amsterdam, *Dissertationes Botanicae*, Vol. 99. J. Cramer/Borntraeger, Berlin, pp. 1–222.
- Mainieri, C., Pires, J.M., 1973. O genero *Podocarpus* no Brasil. *Silvi Sao Paulo* 8, 1–24.
- Martin, L., Bertaux, J., Correge, T., Ledru, M.-P., Mourguiart, P., Sifeddine, A., Soubies, F., Wirmann, D., Suguio, K., Turcq, 1997. Astronomical forcing a contrasting rainfall changes in tropical South America between 12,400 and 8800 cal yr BP. *Quaternary Research* 47, 117–122.
- Melief, A.B.M., 1989. Relation of pollen rain and vegetation in the Parake Los Nevados transect. In: Van der Hammen, T., Diaz-Piedrahita, S., Alvarez, V.Z. (Eds.), *La Cordillera Central Colombiana, transecto Parque Los Nevados (segunda parte)*. Studies on Tropical Andean Ecosystems, Vol. 3. J. Cramer, Berlin, pp. 517–536.
- Muller, J., de Di Giacomo, E., Van Erve, A.W., 1987. A palynological zonation for the Cretaceous, Tertiary, and Quaternary of northern South America. *AASP Contribution Series* 19, 7–76.
- Nelson, B.W., 1994. Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews* 10, 105–125.
- Peterson, G.M., Webb III, T., Kutzbach, J.E., Van der Hammen, T., Wijnstra, T.A., Street, F.A., 1979. The continental record of environmental conditions at 18,000 yr BP: an initial evaluation. *Quaternary Research* 12, 47–82.
- Prance, G.H., 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazonian basin, based on evidence from distribution patterns in Caryocaraceae, *Chryso balanaceae*, *Dichapetalaceae* and *Lecythidaceae*. *Acta Amazonica* 3, 5–28.
- Rangel, O., 1999. Relacion de lluvia de polen reciente y vegetacion en el transecto Tatama (Cordillera Occidental). In: Van der Hammen et al. (Eds.), *Studies on Tropical Andean Ecosystems*, Vol. 5, in preparation.
- Räsänen, M.E., Salo, J.S., Junger, H., Pittmann, L.R., 1990. Evolution of the western Amazon lowland relief: impact of Andean foreland dynamics. *Terra Nova* 2, 320–332.
- Räsänen, M.E., Salo, J.S., Kalliola, R.J., 1987. Fluvial perturbation in the western Amazon basin: regulation by long-term sub-Andean tectonics. *Science* 238, 1398–1401.
- Regali, M.S., Uesegi, N., Santos, A., 1974. Palinologia dos sedimentos meso-cenozoicos do Brasil. *Boletim técnico da Petrobras* 17 (3), 177–191 and 17 (4), 263–301.
- Roa Morales, P., 1979. Estudio de los médanos de los Llanos Centrales de Venezuela: evidencias de un clima desértico. *Acta Biologica Venezolana* 10, 19–49.
- Sánchez-Sáenz, M., 1997. Catálogo preliminar comentado de la flora del Medio Caquetá. Commented catalogue on the Middle Caquetá flora. *Estudios en la Amazonia colombiana/Studies on the Colombian Amazonian*, Vol. 12. Tropenbos-Colombia, Bogotá, 557 pp.
- Servant, M., Maley, J., Turcq, B., Absy, M.L., Brenac, P., Fournier, M., Ledru, M.P., 1993. Tropical forest changes during the Late Quaternary in African and South American lowlands. *Global and Planetary Change* 7, 25–40.
- Sifeddine, A., Bertrand, P., Fournier, M., Martin, L., Servant, M., Soubies, F., Suguio, K., Turcq, B., 1994. La sédimentation organique lacustre en milieu tropical humide (Carajás, Amazonie orientale, Brésil): relation avec les changements climatiques au cours des 60,000 dernières années. *Bulletin Société Géologie France* 165, 613–621.
- Sole de Porta, N., 1960. Observaciones palinológicas sobre el Plioceno de Cartagena (Colombia). *Boletín de Geología (Bucaramanga)* 4, 45–50.
- Steyermark, J.A., 1979. Plant refuge and dispersal centers in Venezuela: their relict and endemic elements. In: Larsen, K., Holm-Nielsen, L.B. (Eds.), *Tropical Botany*. Academic Press, New York, pp. 185–221.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of tropical Brazil (5°C) during the Last Glacial Maximum. *Science* 269, 379–383.
- Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.N., Henderson, K.A., Cole-Dai, J., Bolzan, J.F., Liu, K.-b., 1995. Late Glacial stage and Holocene tropical ice core records from Huarascán, Peru. *Science* 269, 46–50.
- Torres-Romero, J.H., 1988. Flora de Colombia, 5. Podocarpaceae. Instituto de ciencias Naturales, Universidad Nacional de Colombia, 73 pp.
- Urrego, L.E., 1994. Los bosques inundables del medio Caquetá (Amazonia Colombiana). Caracterización y sucesión, Ph.D. Thesis, University of Amsterdam, 235 pp.
- Urrego, L.E., 1997. Los bosques inundables del medio Caquetá: Caracterización y sucesión. *Estudios en la Amazonia colombiana/Studies on the Colombian Amazonia*, Vol. 14. Tropenbos-Colombia, Bogotá, pp. 1–335 + 2 appendices.
- Van der Hammen, T., 1954. El desarrollo de la flora colombiana en los periodos geológicos I: Maestrichtiano hasta Terciario más inferior. *Boletín Geológico* 2 (1), 49–106.
- Van der Hammen, T., 1957. Climatic periodicity and evolution of South American Maestrichtian and Tertiary floras. *Boletín Geológico* 5 (2), 49–91.
- Van der Hammen, T., 1961a. Upper Cretaceous and Tertiary climatic periodicities and their causes. *Annals of the New York Academy of Science* 95, 440–448.
- Van der Hammen, T., 1961b. Late Cretaceous and Tertiary stratigraphy and tectogenesis of the Colombian Andes. *Geologie en Mijnbouw* 40, 181–188.
- Van der Hammen, T., 1961c. First results of pollen analysis in British Guiana. *Proceedings Fifth International Guiana Geological Conference*, Georgetown, 1959. Publication georgetown Geological Survey Department, pp. 229–231.
- Van der Hammen, T., 1963. A palynological study on the Quaternary of British Guiana. *Leidse Geologische Mededelingen* 29, 125–180.
- Van der Hammen, T., 1970. Ensayo de un esquema en tiempo y espacio de la vegetación y el medio ambiente en el noroeste de Sudamerica. *Revista Academia Colombiana de Ciencias Exactas. Físicas y Naturales* 13 (52), 473–479.

- Van der Hammen, T., 1972. Changes in vegetation and climate in the Amazon Basin and surrounding areas during the Pleistocene. *Geologie en Mijnbouw* 51, 641–643.
- Van der Hammen, T., 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* 1, 3–26.
- Van der Hammen, T., 1989. History of montane forest of the northern Andes. *Plant Systematics and Evolution* 162, 109–114.
- Van der Hammen, T., 1995. Plioceno y Cuaternario del altiplano de Bogotá y alrededores. *Análisis Geográficos*, Vol. 24. Instituto Geográfico 'Augustin Codazzi', Bogotá, pp. 1–142.
- Van der Hammen, T., 1999a. Paleocology of Amazonia. *Boletín Museo Paraense Emilio Gaeldi*, in press.
- Van der Hammen, T., Absy, M.L., 1994. Amazonia during the last glacial. *Palaeogeography Palaeoclimatology Palaeoecology* 109, 247–261.
- Van der Hammen, T., Cleef, A.M., 1983/84. Datos para la historia de la flora andina. *Revista Chilena de Historia Natural* 56, 97–107.
- Van der Hammen, T., Duivenvoorden, J.F., Lips, J.M., Urrego, L.E., Espejo, N., 1992a. Late Quaternary of the middle Caquetá River area (Colombian Amazonia). *Journal of Quaternary Science* 7, 45–55.
- Van der Hammen, T., Urrego, L.E., Espejo, N., Duivenvoorden, J.F., Lips, J.M., 1992b. Lateglacial and Holocene sedimentation and fluctuations of river water level in the Caquetá area (Colombian Amazonia). *Journal of Quaternary Science* 7, 57–67.
- Van der Hammen, T., Werner, J.H., Van Dommelen, H., 1973. Palynological record of the upheaval of the northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. *Review of Palaeobotany and Palynology* 16, 1–122 (Also in 'The Quaternary of Colombia', 2).
- Van der Hammen, T., Wijmstra, T.A., 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. *Leidse Geologische Mededelingen* 30, 183–241.
- Van Geel, B., Van der Hammen, T., 1973. Upper Quaternary vegetational and climatic sequence of the Fuquene area (Eastern Cordillera Colombia). *Palaeogeography Palaeoclimatology Palaeoecology* 14, 9–92.
- Wijmstra, T.A., 1967. A pollen diagram from the Upper Holocene of the Lower Magdalena Valley. *Leidse Geologische Mededelingen* 39, 261–267.
- Wijmstra, T.A., 1969. Palynology of the Alliance well. *Geologie en Mijnbouw* 48, 125–133.
- Wijmstra, T.A., 1971. The palynology of the Guiana coastal basin. Ph.D. Thesis, University of Amsterdam, 62 pp.
- Wijmstra, T.A., Van der Hammen, T., 1966. Palynological data on the history of tropical savannas in northern South America. *Leidse Geologische Mededelingen* 38, 71–90.
- Wijninga, V.M., 1996. Paleobotany and palynology of Neogene sediments from the high plain of Bogotá (Colombia). Evolution of the Andean flora from the paleoecological perspective. Ph.D. Thesis, University of Amsterdam, 370 pp. (Also in: 'The Quaternary of Colombia', 21).
- Wijninga, V.M., Hooghiemstra, H., Van der Hammen, T., 1999. Neogene evolution of the northern Andean flora based on the Colombian paleobotanical record. *Journal of Biogeography*, in review.