The African rain forest during the Last Glacial Maximum, an archipelago of forests in a sea of grass

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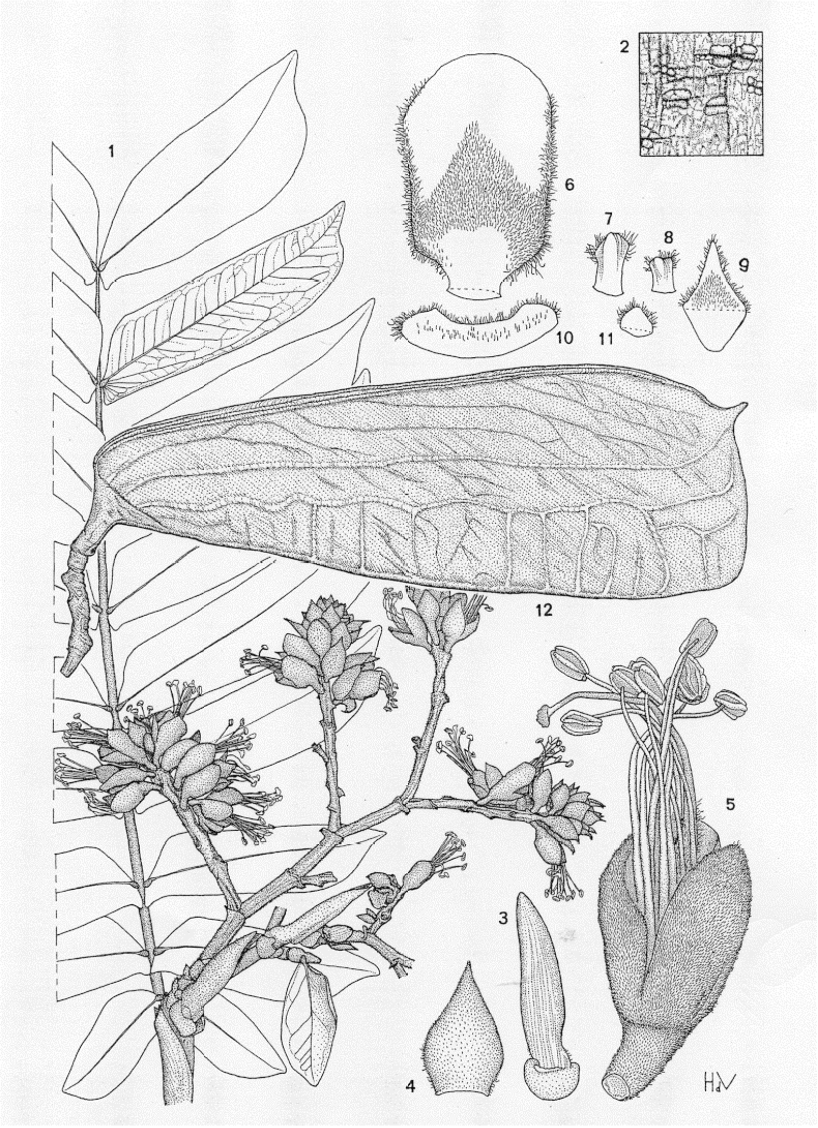
To

X11 and his forest friends



Tetraberlinia moreliana Aubrév. with the typical Caesalpinioid explosively opening pod (drawing by H. de Vries)

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Samenvatting

Het Afrikaanse regenwoud tijdens het Laatste Glaciale Maximum, een archipel van bossen in een zee van gras.

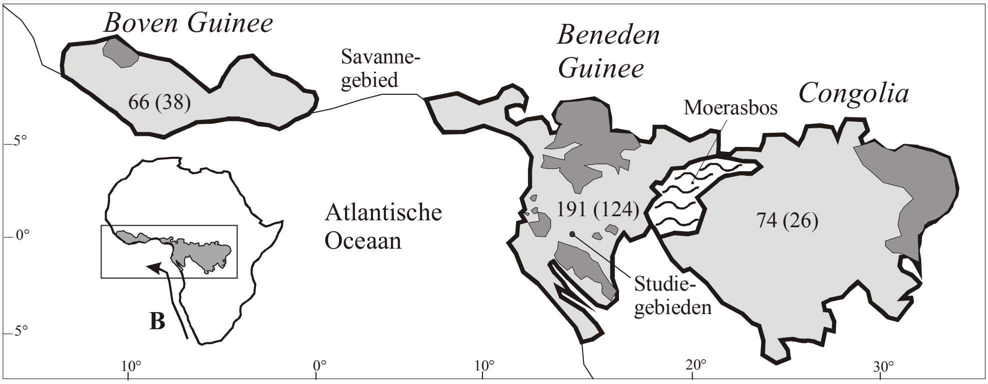
Tijdens het hoogtepunt van de laatste ijstijd (18.000 jaar geleden) was het Afrikaanse regenwoud kleiner in oppervlakte en opgedeeld in kleinere gebieden dan tegenwoordig, omdat het klimaat koeler maar vooral droger was. De geringere neerslag was vooral het gevolg van een koudere Tropische Zuid-Atlantische Oceaan, veroorzaakt doordat de Benguela Golfstroom in die periode verder naar het noorden reikte. Dit versterkte en verlengde het koele droge seizoen. Tijdens een krachtig koel droog seizoen valt er geen regen en is het permanent bewolkt. Men neemt aan dat onder deze drogere omstandigheden het bos zich alleen heeft kunnen handhaven in heuvels, die regelmatig in mist gehuld waren en zo het regentekort compenseerden. Dergelijke gebieden duidt men aan als refugia. Na het einde van de laatste ijstijd breidde het bos zich vanuit de heuvels uit en nam het omliggende grasland weer in.

Boskolonisatie vanuit de refugia is een langzaam proces van pionier- naar climaxvegetatie. Boomsoorten die horen bij de laatste fase van dit proces zullen het dichtst bij de refugia staan. De Caesalpinioideae zijn zulke soorten, want zij verspreiden zich langzaam. Ook wordt aangenomen dat ze droogtegevoelig zijn en daardoor tijdens de ijstijden alleen in de refugia hebben overleefd. Omdat het langzame verspreiders zijn, zullen ze ook nu nog in of dicht bij de refugia staan. Het blijkt echter dat ze voor een groot deel tussen de refugia voorkomen. Dit kan betekenen dat de Caesalpinioideae zich veel sneller hebben verspreid sinds het einde van de ijstijd (zo'n 10.000 jaar geleden) of dat ze droogte toleranter zijn dan gedacht en nooit tussen de refugia zijn uitgestorven.

Om dat te achter halen zijn de Caesalpinioideae in twee bos-grasland mozaïeken in centraal Gabon bestudeerd. Beide studiegebieden liggen tussen de refugia in en de omstandigheden lijken nog het meest op droge omstandigheden van tijdens het hoogtepunt van de laatste ijstijd. In beide gebieden blijken de Caesalpinioideae bijna alleen maar aanwezig langs beken en rivieren. Soorten die elders ook voorkomen vertonen niet zo'n duidelijke voorkeur. Het feit dat zij alleen langs beken voorkomen die niet opdrogen of op plaatsen waar ze voor een belangrijk deel van de dag in de schaduw staan toont, aan dat ze droogte gevoelig zijn.

Beide gebieden hadden ook een duidelijk andere soortensamenstelling die niet kon worden verklaard door verschillen in habitat. Tevens werd vastgesteld dat de Caesalpinioideae noch vanuit het dicht bijzijnde refugium beide gebieden via hun gewone verspreiding hebben kunnen bereiken, noch via onregelmatige verspreiding van hun zaden over grotere afstand langs rivieren en beken. Het enige alternatief was dat zij de laatste ijstijd ter plaatse moeten hebben overleefd.

Het feit dat ze kennelijk nooit uit beide studiegebieden zijn verdwenen is te danken aan een heuvelgebied waaruit beken stroomden die niet opdrogen tijdens het droge koele droge seizoen. Deze heuvelrug is heden ten dage tijdens het koele droge seizoen regelmatig gehuld in laag hangende bewolking. Onder deze mistige omstandigheden kan het bos op de heuvelrug extra vocht onttrekken wat voorkomt dat de beken opdrogen. Dat voorkomt weer dat Caesalpinioideae nu niet uitdrogen tijdens dit droge



Het Afrikaanse laagland regenwoud (lichtgrijs) verdeeld in 3 regio's, Boven Guinee, Beneden Guinee en Congolia met het totaal aantal soorten Caesalpinioideae en tussen haakjes het aantal soorten dat alleen in die regio voorkomt (endemisch). Donkergrijs: heuvelgebieden en plateau's; B: de Benguela Golfstroom.

seizoen, en zo moet het ook zijn gegaan tijdens de laatste ijstijd immers anders waren deze boomsoorten er niet meer.

De aanwezigheid van Caesalpinioideae in het laagland wordt dus voor een belangrijk deel bepaald doordat uit heuvelgebieden beken en rivieren stromen die niet opdrogen tijdens het koele droge seizoen. Dit toont aan hoe belangrijk heuvelgebieden moeten zijn geweest voor het overleven van het regenbos tijdens het hoogtepunt van de laatste ijstijd. Dit komt ook tot uitdrukking in het grootschalige patroon van de Caesalpinioideae binnen het Afrikaanse regenwoud. Het Afrikaanse regenwoud bestaat uit drie gescheiden regio's (zie bovenstaand figuur). Caesalpinioideae kunnen niet tussen de regio's migreren. De verschillen in soortenrijkdom tussen de regio's moeten dus zijn ontstaan doordat in de ene regio meer soorten zijn uitgestorven of in de andere meer zijn ontstaan.

Het feit dat in Beneden Guinee zoveel meer Caesalpinioideae voorkomen wordt toegeschreven aan het feit dat er minder soorten zijn uitgestorven. In Gabon (het zuidelijk deel van Onder Guinee) komen nog de meeste Caesalpinioideae soorten voor. Dit is ook het gebied met de meeste heuvelgebieden die bovendien zijn begroeit met groen blijvend regenwoud. Deze heuvelgebieden voorkomen dat beken en rivieren opdrogen. De aanwezigheid van Caesalpinioideae in het omringende laagland heden ten dage en het feit dat ze zich eigenlijk niet verspreiden toont aan dat beken en rivieren tijdens het hoogtepunt van de laatste ijstijd ook niet opdroogden ondanks het langere hogere seizoen.

Dus, de heuvels beschermden niet alleen het bos in de heuvels, maar zij bepaalden ook mede de hoeveelheid regenbos in het laagland. Tussen de grote heuvel refugia overleefde een lappendeken van kleinere bosrestanten, of te wel een archipel van bos in een zee van grasland.

Résumé

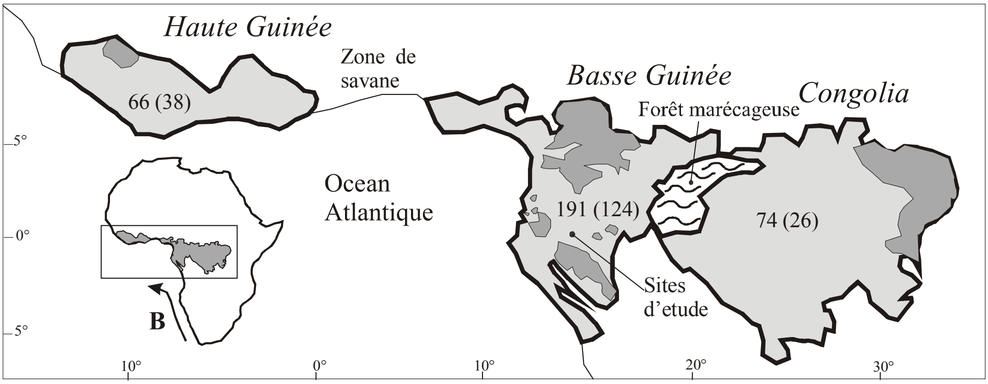
La forêt tropicale sempervirente humide africaine pendant la Dernière Glaciation Maximale: un archipel de forêts dans une mer des herbes.

Pendant la Dernière Glaciation Maximale (18,000 ans BP), les forêts tropicales humides Africaines avaient des aires réduites et reparties en surfaces parce que le climat était plus froid et sec. La réduction des précipitations était principalement due au refroidissement de l’Océan Atlantique Sud Tropical parce que pendant cette période le courant marin de Benguela arrivait plus au nord. Ainsi le prolongement d’une saison sèche froide était favorisé. Pendant une longue saison sèche froide, il n’y a ni soleil, ni pluies. Sous ces conditions de sécheresse accentuée, l’on croit que les forêts n’auraient pu survivre que sur les collines et les régions de hautes altitudes à cause de la présence des nuages et du brouillard due à l’absence de pluie. Ces reliques forestières sont considérées comme des refuges. Après cette période de glaciation, les forêts se sont répandues à partir de ces collines et ont occupé les savanes avoisinantes.

Cette expansion des forêts est un processus lent qui va d’un stade pionnier à une végétation climax et les espèces climax qu’on y trouve sont très proches de celles qu’on rencontre dans les refuges. Les Caesalpinioideae font partir de ces espèces car elles sont très sensibles aux stresses et se dispersent très lentement. C’est ainsi qu’on pense que pendant le dernière glaciation, les Caesalpinioideae n’auraient survécu que dans les refuges forestiers et que de nos jours, on espère encore les trouver très proches de ces refuges parce qu’elles ont un mode de dispersion très lent et sont très sensibles aux conditions de sécheresse prolongée. Contraire à cette hypothèse on les retrouve également très loin de ces refuges ou entre ces refuges. Ceci est peut être du soit au fait que les forêts étaient plus restreintes que l’on ne pense, soit que les Caesalpinioideae on pu se disperser plus rapidement après la période de glaciation (près 10,000 AP) et qu’elles se sont bien adaptées aux conditions climatiques actuelles qui règnent en Afrique Equatoriale.

Si la distribution des Caesalpinioideae s’était complètement réajustée ou adaptée aux conditions environnementales actuelles, sa richesse floristique et la distribution de ses espèces endémiques devraient refléter les différences écologiques qu’on retrouve dans les forêts sempervirentes humides. Ceci peut être testé car les forêts tropicales africaines sont constituées par trois régions différentes et qui diffère par sa surface, son climat et la diversité de ses habitats (qui est surtout déterminée par la topographie). Les Caesalpinioideae se distinguent par une répartition particulière de leurs espèces endémiques (voir figure ci-dessous). Cependant cette répartition ne reflète pas les différences écologiques et abiotiques existantes qu’on rencontre dans ces régions. Seulement les zones d’altitudes et la région de Basse Guinée sont caractérisées par une grande richesse floristique nonobstant le fait les Caesalpiniodeae ne se trouvent pas uniquement sur ces collines. Le taux élevé d’endémisme dans chacune de ces régions peut s’expliquer par une longue période d’isolement. La richesse floristique de la région de Basse Guinée s’explique également par le fait qu’il y a eu moins de disparition des espèces pendant les périodes de glaciation.

Afin d’expliquer pourquoi il y a eu un faible taux de disparition des espèces dans la région de Basse Guinée, nous avons étudié les Caesalpinioideae dans deux mosaïques de forêt-savane dans la région centrale du Gabon. Cette région possède des



La forêt africaine sempervirente de basse altitude (gris), réparties dans 3 régions, Haute Guinée, Basse Guinée et Congolia avec le nombre des espèces d'arbres de Caesalpinioideae et le nombre des espèces endémiques entre parenthèse pour chaque région. Gris foncé: collines et plateaux; B: le courant marin de Benguela.

caractéristiques qui ressemblent à celles qui ont existé pendant le dernières glaciation maximale. Les deux sites étudiés avaient une composition floristique différente, pourtant cette différence n'est pas liée à la diversité des habitats existants. Il a été établi que l'aire de distribution des Caesalpinioideae ne pouvait pas arriver à ces endroits à cause de leur mode de dispersion très lente (la dispersion balistique des graines par l'explosion de la gousse ne permet pas aux Caesalpinioideae de se disperser sur une longue distance). Même par une dispersion occasionnelle sur une longue distance par l'eau à travers les rivières ou les ruisseaux. La seule alternative qui explique la présence des Caesalpinioideae dans ces sites est celle d'une survie de ces espèces dans ces endroits pendant les Dernière Glaciation Maximale.

Le fait que ces espèces aient pu survivre dans ces sites nous ont amener à analyser comment elles ont pu résister aux conditions climatiques défavorables qui ont existé pendant les saisons sèches très froides. Les Caesalpinioideae étaient presque absentes le long des ruisseaux asséchés pendant ces saisons sèches et froides, et se rencontraient beaucoup plus le long des rivières qui étaient bien drainées. La présence de l'eau était déterminée par une série de petites collines qui permettaient de stocker et de préserver l'eau de pluie pendant la saison pluvieuse par infiltration qui était ensuite utilisée pendant la saison sèche. De plus les forêts d'altitudes recueillaient également de l'eau à partir de l'humidité provenant du brouillard et des nuages. Toute cette eau permettait ainsi aux rivières de ne pas s'assécher pendant les saisons sèches très froides, permettant ainsi aux Caesalpinioideae de survivre pendant le Dernière Glaciations Maximale.

La présence des Caesalpinioideae dans les forêts de basses altitudes est étroitement liée à celle de l'eau provenant des collines pendant les saisons sèches très froides. Ceci démontre l'importance de ces collines et des zones d'altitudes pour la survie des forêts sempervirentes humides au cours des Dernière Glaciation Maximale. Il ressort de cette analyse que le faible taux de disparition des espèces dans la région de Basse Guinée peut s'expliquer par la présence de plusieurs rivières et collines dans cette région. En d'autres termes la présence des collines et des zones d'altitudes ont joué un rôle primordial dans la distribution actuelle des forêts de basses altitudes. De plus, des reliques forestières ont survécu entre les différents refuges formant ainsi des îlots de forêts dans une mer herbeuse.

Summary

The African rain forest during the Last Glacial Maximum, an archipelago of forests in a sea of grass

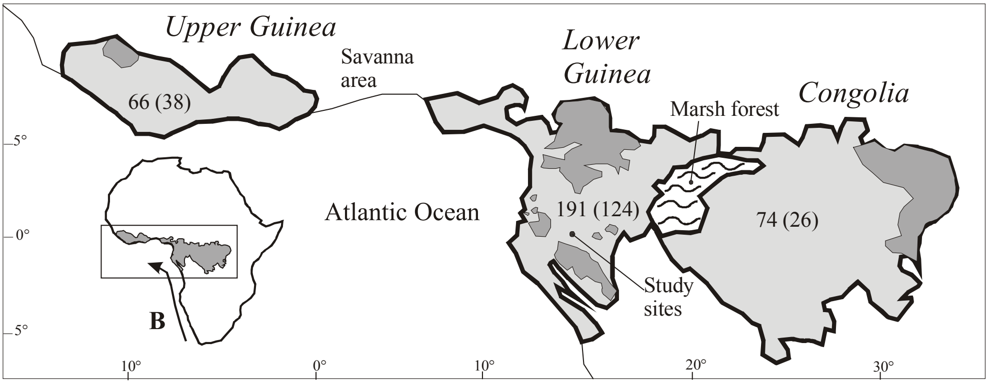
During the Last Glacial Maximum (18,000 yrs ago) the African rain forest was smaller in surface area than today and fragmented, because the climate was cooler, but, more importantly, also drier. The lower rainfall was mainly due to a colder Tropical South Atlantic Ocean, as the Benguela Current reached further north and strengthened and lengthened the cool dry season. During a strong cool dry season, rainfall ceases completely and the sky is permanently overcast. Under these dry conditions the forest was believed only to have survived on hills, where mist frequently occurred compensating for the absence of rainfall. Such areas are indicated as refuge areas. After the end of the last ice age the forest expanded from the hills and colonized the surrounding grassland again.

Forest colonisation is a slow process from pioneer- to climax vegetation. Tree species typical for the last phase in this process will occur closest to the refugia. The Caesalpinioideae are such species, since they disperse slowly. It is assumed that they are drought sensitive and therefore only survived in refuge areas. Because they are slow dispersers, they are expected to occur close to the former refugia. However, in contrast to this assumption, they are found mainly in between refuge areas. This means either that the Caesalpinioideae have dispersed much faster since the end of the last ice age (some 10,000 yrs ago) or that they are drought tolerant and never became extinct in between refuge areas.

To determine which of the two options is most plausible the Caesalpinioideae were studied in central Gabon between forest refugia. The two study sites most closely resemble the dry conditions during the Last Glacial Maximum. In the two study sites the Caesalpinioideae were almost exclusively present along streams and rivers. The same species elsewhere do not show such a preference. The fact that they only occur along permanent streams and in shady places for a larger part of the day shows that they are drought sensitive.

The two studies sites show a clear difference in species composition, which cannot be related to differences in habitat. Moreover, neither their presence in the two study sites can be explained by range expansion by their normal from the closest refugium nor by occasional long distance dispersal events along streams and rivers. The only alternative is that they survived the Last Glacial Maximum in situ and never became locally extinct.

The fact that they apparently never disappeared from the two sites is facilitated by a range of hills from which streams part that do not dry up during the cool dry season. These hills are often shrouded in mist during the cool dry season and extra moisture is drawn from the mist by the forest which prevents that the streams dry up. This in turn protects the Caesalpinioideae against desiccation during the present-day cool dry season and by the presence of the Caesalpinioideae in these two study sites. This must have been so during the Last Glacial Maximum, despite the longer cool dry season.



The African lowland rain forest (light grey), divided in 3 regions, Upper Guinea, Lower Guinea and Congolia with the number of Caesalpinioideae tree species and between brackets the number of species only found in that region (endemic). Dark grey: hills and plateaus; B: Benguela current.

The presence of Caesalpinioideae in the lowland is determined by the water coming from the hills during the cool dry season. This shows how important hilly areas must have been for the survival of the rain forest during the Last Glacial Maximum. This is also evident from the large scale pattern of the distribution of the Caesalpinioideae within the African rain forest. The rain forest consists of three regions (see figure above). Caesalpinioideae are unable to migrate between them and hence differences in species richness can only be explained by differences in extinction and speciation between them.

The fact that Lower Guinea is so much more species rich in Caesalpinioideae is attributed to the fact that less species became extinct. Gabon (southern Lower Guinea) is richest in Caesalpinioideae and it is also the hilliest region covered with evergreen lowland rain forest. These hills prevent the streams and rivers in the lowland to run dry and the presence in between the forest refugia in combination that the virtually do not disperse shows that these same streams and rivers also did not dry up under the drier conditions during the Last Glacial Maximum.

In other words, hills did not only preserve the forest on them but also arround them in the lowland and in between the forest refugia an array of small forest fragments presisted, i.e. a reticulate forest in a matrix of grass.

Chapter 1 Caesalpinioideae, forest refugia and upwelling

1.1 Introduction

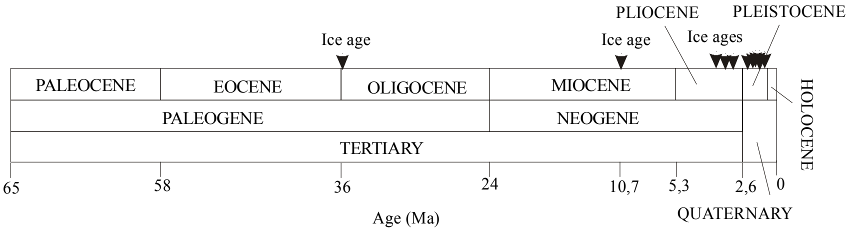
The Caesalpinioideae are the basal subfamily of the Leguminosae and they form one of the largest and oldest groups of tropical tree species among the Angiosperms (Herendeen et al., 1992; The Angiosperm Phylogeny Group, 2003). There are some 152 genera and over 1900 species world wide (Cowan et al., 1981). The earliest fossil representatives date back to the late Cretaceous (70-65 Ma BP; Muller, 1981) and their former distribution once extended to the temperate zones (Herendeen, 1992; Herendeen & Crane, 1992). Presently, the Caesalpinioideae show their highest taxonomic diversity in tropical Africa south of the Sahara (Raven & Polhill, 1981).

Below the Sahara the highest diversity of genera and species is found in the African lowland rain forest where members of the Caesalpinioideae are among the most common tree species encountered (e.g. White, 1983). In some parts of the rain forest they dominate as large stands of a single or few species (e.g. Germain, 1957; Newbery et al., 2004). At the wet end of the rainfall gradient they dominate the forest by species diversity (Aubréville, 1968; Letouzey, 1968). Only in the drier periphery of the rain forest are they less abundant or absent (Evrard, 1968; Letouzey, 1968; Swaine, 1996).

The extent of the African lowland rain forest has not always been the same. There were periods during the Pleistocene when climatic conditions were drier than today. Subsequently, the extent of lowland rain forest was also smaller (e.g. Maley, 1991; Morley, 2000). In roughly the past 3 million years the African rain forest contracted and expanded regularly due to fluctuating humidity and aridity related to orbital forcing (most notable to precession maxima; Tiedemann et al., 1994). These climatic changes caused some parts of the rain forest to become replaced by drier vegetation formations, e.g. grassland. Other parts remained forested to shape the so-called forest refugia. The locality of these forest refugia remains hidden within the present-day lowland rain forest, because the forest is now larger than during the maximum of the last ice age, i.e. the Last Glacial Maximum (LGM).

Locating forest refugia in Africa has been pursued among others by mapping the distribution of slowly dispersing plant species (Sosef, 1994). The idea is that after the end of the last ice age, i.e. during the Holocene, such plant species dispersed not at all or only a short distance away from the forest refuge areas. Therefore, they are considered forest refuge indicator species. The Caesalpinioideae with ballistic seed dispersal are also slowly dispersing tree species. Their seeds are dispersed by explosive opening of their woody pods and only travel tens of meters (Hart, 1995; Newbery et al., 2004; van der Burgt, 1997). The Caesalpinioideae can therefore be considered refuge indicator species and their present patterns of distribution may reveal where the rain forest persisted during the Last Glacial Maximum.

Table 1.1. Geological time table showing the ice age periods. Ice age: accumulation of ice at the poles.



1.2 The history of the African rain forest

Tropical rain forests were once considered to represent the most stable ecosystems on earth, unaffected since time memorial. However, fossil pollen records showed that the rain forest communities have been shaped and moulded during the last 36 Ma. Below, the history of the African rain forest is set within the concepts and processes of global cooling. For a more detailed review see Maley (1996) and Morley (2000).

Periods of global cooling and Ice ages

In the tropics solar radiation absorbed during the day exceeds the (infrared) radiation lost during the night in all seasons. At the poles the opposite occurs. The reason why the tropics do not become increasingly hotter and the poles increasingly colder is because the atmosphere and ocean currents transfer the surplus of heat from the tropics to the poles. This continuous movement of air masses and ocean currents is referred to as the general circulation, and it has always existed as a response to the imbalance in heat distribution.

Only in the last 36 Ma years (Table 1.1) has this imbalance led to the formation of a polar ice sheet at the South Pole (marking the end of the Eocene) and later also at the North Pole (late Pliocene). The establishment of ice on the poles indicates that during the last 36 Ma global climate changed from warm and humid (the “greenhouse world”) to colder and drier (the “ice house world”). Part of the answer as to why this happened, lies in plate tectonics, mountain formation, opening and closing of oceanic gateways and changes in concentrations of green house gases.

However, these settings have remained fairly similar during the last 2 Ma, the most intensive period of global cooling, and therefore the occurrence of ice ages has been attributed to orbital forcing only, i.e. changes in the sun-earth geometry (Fig. 1.1). These changes include the distance between the earth and the sun, i.e. the *eccentricity*, the shift in the seasons, i.e. the *precession* of equinoxes, and the tilt of the earth, i.e. the *obliquity*. The three variables are superimposed and have different cycles, 100 kyrs, 13-29 kyrs (depending on the tilt) and 41 kyrs, respectively. Eccentricity (i.e. the glacial-interglacial cycle) in turn depends of the position of the other planets in our solar system (Chambers et al., 1996).

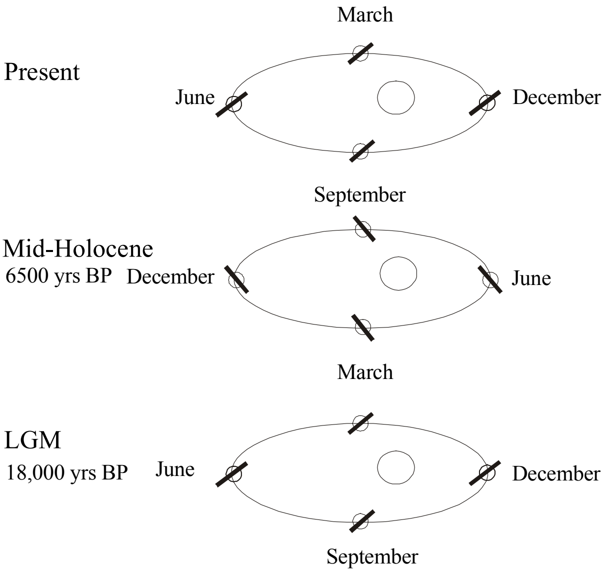


Fig. 1.1. The earth-sun geometry for the LGM, mid-Holocene and at present. For further explanation see text.

Eccentricity determines the total amount of energy received at the low latitudes, whereas precession and tilt of the earth determine the pole-equator thermal gradient. A decrease in total amount of solar energy may lead to the growth of the polar ice sheets, but a steeper pole-equator thermal gradient may as well. Being superimposed the effects either reinforce or weaken one another in cooling the poles. Periods of reinforcement cause glacial periods which alternate with interglacial periods when the cooling is weakened. The effect of their alternation on the vegetation has been mainly traced by interpreting the stratification of fossil pollen records and other metabolic proxies, which give an indication of the dominant vegetation in the region during the period of deposition.

Presently, the dominance of a vegetation formation (e.g. forest or tundra) at a certain latitude is determined by the global distribution of temperature and moisture, which divide climate into latitudinal zones (zonal climate). In the past, the zonation of climate shifted due to orbital forcing and consequently the associated vegetation also shifted or changed. Cooling of the poles caused a shift southward of the vegetation formations of the northern hemisphere (e.g. Elenga et al. 2000) and the disintegration of certain vegetation formations into formations unparalleled with forms extant today (Sharon, 1998).

However, certain changes in vegetation observed in fossil pollen records do not coincide with changes in the volume of polar ice within the 100 kyrs cycle of eccentricity. This makes it difficult to classify these periods as either glacial or interglacial ones (the periods are referred to as stadials and interstadials) and the shorter periodicity suggests that these changes are related to the cycles of precession and obliquity. Although these cycles may not always have led to the accumulation of ice on the poles, reconstruction of the change in vegetation formation does, nonetheless, indicate a change in global climate.

Climate and vegetation simulation

Presently, the earth is in a phase of global warming due to orbital forcing accelerated by human activity. In response to the threat of global warming and the need to separate warming due to human activity from orbital forcing much effort has been put to increase our understanding of the general circulation, i.e. the ocean-atmosphere interface. Part of this is achieved by simulating global climate and by testing the validity of the (programme) output with rainfall records. General circulation models incorporate several orbital configurations and different levels of CO_2 as input. The approach is mainly component based and resolution of the output is improving.

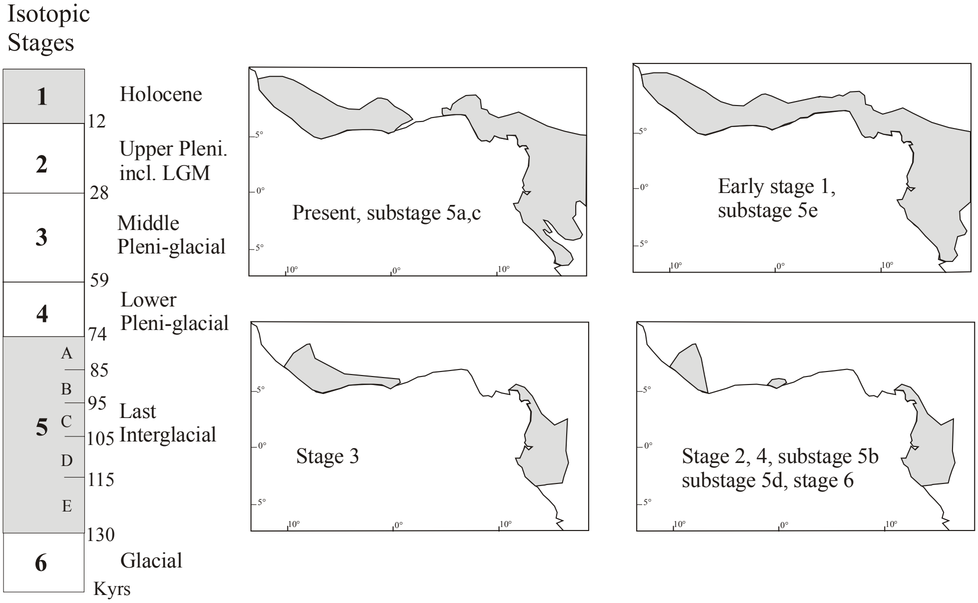
Since the amount of solar radiation and seasonality is also determined by orbital forcing, similar general circulation models are used to quantify global warming due to the natural process. Simulations of paleo-climate therefore focus on configurations which represent opposing extremes in the earth-sun geometry, such as the LGM (18,000 yrs BP), and the mid Holocene (6,000 yrs BP, fig. 1.1). The outputs of these simulations are related to proxies or substitutes in the record deposited in those periods, like marine, alluvial, and palynological records. Linked with paleo-vegetation simulation models vegetation dynamics are inferred from palynological records and species present in the records are classified into functional species groups (Jolly et al., 1998; Marchant et al., 2002). The strength and accuracy of these models largely depend on the number of records.

The latest simulated reconstruction of biomes (vegetation formations) for central Amazonia during the LGM was based on the Leaf Area Index (LAI). This is a measure for the amount of leaf-layers within a vegetation, which allows distinguishing between grassland, evergreen and deciduous rain forest (Cowling et al., 2001). The simulation-output did not show the fragmentation of Amazonia, but neither did it reconstruct the present-day situation according to the remote sensing vegetation classifications (Eva et al., 2002). Nonetheless, the simulation showed that the central part of Amazonia is most sensitive to changes in climate related to orbital forcing and reduced CO_2 levels. Similar LAI-based simulations are not yet available for equatorial Africa.

The latest forest dynamics in Africa

The last 150.000 years represent a full glacial and interglacial cycle (Table 1.2). Changes in global climate during this period are recognised by changes in oxygen isotopic in marine and ice cores. Marine oxygen isotopic stages (OIS) correspond with changes in the dominance between forest and grassland as represented by pollen percentages in fossil pollen records in tropical Africa (Dupont et al. 2000). The changes between forest and grassland do not fully correspond with the glacial-interglacial cycle. The forest tends to be smaller during glacial periods (OIS 2-4 and OIS 6) than during the last interglacial period (OIS 5), but there were periods (5b, 5d) during the last interglacial (OIS 5) when the forest was as small as during the LGM in terms of pollen percentages. These vegetation changes within a glacial or interglacial period are referred to as stadials and interstadials and the shorter periodicity suggests that these changes are related to the cycles of precession and obliquity.

Table 1.2. Sequence of the Isotopic stages during the last 150 kyrs and the reconstruction of the forest cover (grey) for each stage in West and Central Africa (after Dupont et al. 2000).



Palynological records identified four periods within the Upper Pleniglacial (OIS 2) and Holocene (OIS 1) during which either forest or grassland dominated: 1) 28,000-20,000 yrs BP, 2) 20,000-10,000 yrs BP, 3) 10,000-2,500 yrs BP, 4) 2,500 yrs BP-present. These observations are based on fossil pollen records from Lake Bosumtwi in Ghana ((Maley & Livingstone, 1983), Lake Barombi Mbo in Cameroon (Maley & Brenac, 1987), marine pollen records from off the Ghana shore (Lezine & Vergnaud-Grazzinni, 1993) and off the Niger River delta (Dupont & Weinelt, 1996). The more recent Holocene changes in vegetation are supported by pollen records from lakes in Cameroon and Congo (Elenga et al., 1991; Reynaud & Maley, 1994; Schwartz et al., 1990; Vincens et al., 1999).

The period from 20,000-10,000 yrs BP, is traditionally referred to as the terminal phase of the last ice age with its culmination around 18,000 yrs BP (LGM). During this period the rain forest was at its smallest and intermixed with species from montane genera such as *Podocarpus*. The end of this period (10,000 yrs BP) is considered the end of the last ice age and the onset of the Holocene. In the period before the terminal phase of the last ice age (28,000-20,000 yrs BP), the rain forest was equally dominant (in pollen percentages) as today with the only difference that *Podocarpus* was present whereas now it is virtually absent.

After the end of the last ice age (10,000 yrs BP) the African rain forest expanded and in the early Holocene it even bridged the Dahomey Gap (Dupont & Weinelt 1996), which presently separates the west-African from the central-African rain forest. Later in the Holocene, around 2,500 yrs BP, the forest in Atlantic central Africa became reduced and pollen percentage returned to values as before the LGM (Elenga et al., 1991; Reynaud & Maley, 1994; Schwartz et al., 1990; Vincens et al., 1999).

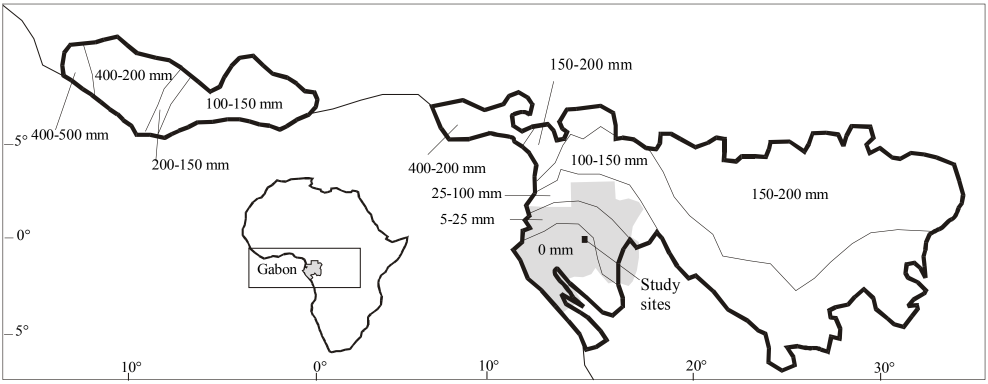


Fig. 1.2. The cool dry season: mean monthly rainfall in July (1920-1980) within the African rain forest. Bold line outline: lowland rain forest, grey area: Gabon.

Simulations of the vegetation dynamics for the LGM (18,000 yrs BP) showed that rain forest was smaller than today and that the forest was intermixed with montane species (Elenga et al., 2000). Simulations for the mid-Holocene (6000 yrs BP) showed that the Sahara received more rainfall than today and that it was covered by vegetation. The mid-Holocene and Last Glacial Maximum time-intervals were chosen because they represent configurations in the earth-sun geometry (orbital forcing) which are either similar to today, i.e. LGM, or opposite, i.e. mid-Holocene (Fig 1.1). In the present earth-sun configuration, as well as during the LGM, the summer in the Northern Hemisphere (boreal summer) occurs at the longest distance from the sun (cooler summers), whereas in the mid-Holocene it is closest to the sun (warmer summers).

During the mid-Holocene the Inter Tropical Convection Zone (ITCZ) or monsoon rains had shifted further north over the Sahara which allowed permanent vegetation to develop (Prentice et al., 2000). Although climate conditions in the Sahara became wetter, fossil pollen records showed that the rain forest in equatorial Africa was smaller than today (Prentice et al., 2000). The northward shift of the monsoon rains in Africa during mid-Holocene cannot be explained by warmer boreal summers alone, it also requires changes in the sea surface temperature in places of upwelling (Texier et al., 2000). The northward shift of the ITCZ or monsoon rains is the combination of warmer boreal summers and, colder austral winters (Southern Hemisphere), i.e. more increased upwelling of cold deep sea water in the Gulf of Guinea.

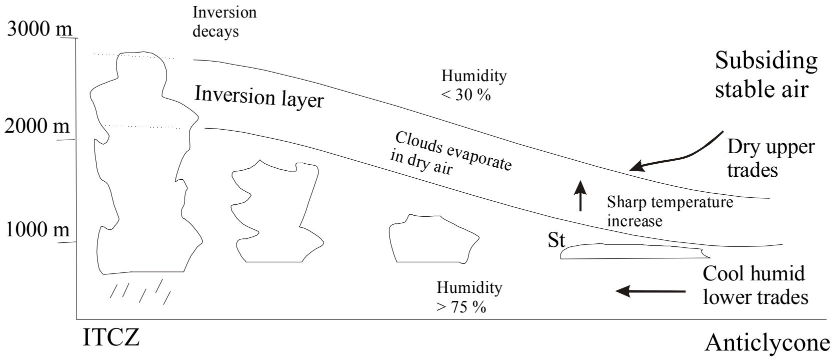


Fig.1.3. Cross-section of the atmosphere, showing the trade wind inversion over the southern tropical Atlantic Ocean. St: stratiform cloud cover (after Buckle 1996).

Upwelling

Increased upwelling of cold deep sea water in the Gulf of Guinea has affected the African rain forest since the establishment of the Benguela current in the late Miocene (Maley, 1996; Morley, 2000). Oceanographic studies on the Benguela current showed that the current was stronger during glacial periods in the Plio-Pleistocene causing more upwelling of cold deep sea water in the Gulf of Guinea (Berger & Wefer, 2002; Dieter-Haass et al., 2002; Giraudeau et al., 2002). Recently, a direct relationship was shown between increased upwelling, i.e. colder sea surface temperatures and an increase of grassland at the expense of lowland forest in equatorial Africa during the mid-Pleistocene period (1.2 Ma-450 kyrs; Schefuss et al., 2003).

Upwelling of cold deep-sea water still influences climate today. Anomalies and variations in rainfall, lengthening and shifts in seasonality monitored since the middle of the last century could be related to variations of upwelling and associated sea surface temperatures (Camberlin et al., 2001; Janicot & Fontaine, 1997; Moron et al., 1995). Even el Niño/la Niña events of the Southern Oscillation in the Pacific Ocean only had a weak impact on the climate in equatorial Africa compared to SE Asia (Moron et al., 1995). This shows how strong the upwelling system of the Benguela current determines climate over equatorial Africa and it strengthens the concept that variations in upwelling intensity and associated SST are the mechanism which forced vegetation dynamics in the past.

Upwelling in the south-eastern Atlantic Ocean is not fundamentally different from upwelling in the south-eastern Pacific Ocean (the Southern Oscillation). In the south Pacific Ocean, a high-pressure system induces a branching-off of cold seawater from the Antarctic circumpolar current. The strength of this current varies, and El Niño and La Niña events are a departure of the normal or dominant state of upwelling. The seesaw of increased and decreased upwelling in the South Atlantic Ocean can also be described in terms of a “La Niña” or an “El Niño event”, which are extremes within the oscillation of the system and a temporary departure of the “normal” or dominant state of upwelling.

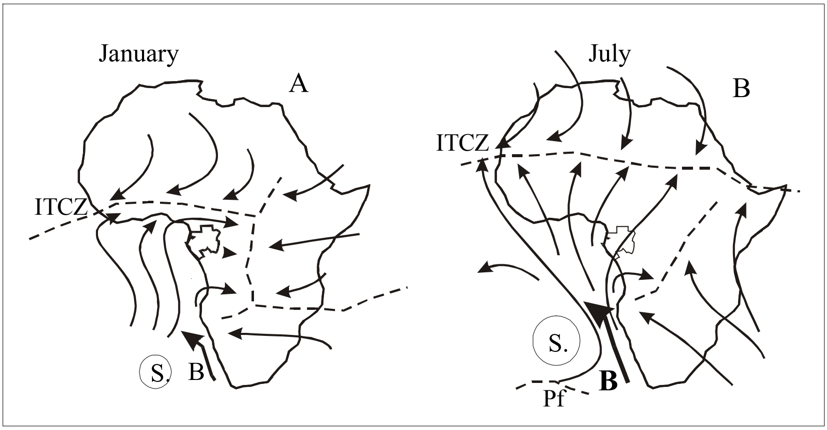


Fig. 1.4. Mayor air streams (arrows) and air boundaries (dotted lines) in January and July. ITZC: Inter Tropical Convection Zone, S.: St Helene anticyclone, B: Benguela current (bold arrow), Pf: polar front (after Buckle 1996).

A long-term departure from the present-day dominant state of the system is put forward to explain the millennial-scale changes in the dominance between grassland and lowland rain forest as mentioned above (Maley, 2001). During the LGM cold SST were dominant (a la Niña state) whereas directly after the LGM, in the early and middle Holocene (9,000-4,000 yrs BP), they were warmer (an el Niño state). From the mid-Holocene onward SST became progressively colder (6,500-2,800 yrs BP) until 2,500 yrs BP when warm SST and associated climate caused the Atlantic part of the rain forest to be replaced by grassland or to be subjected to a temporary invasion by secondary species.

Upwelling of cold deep-sea water still takes place along the coast of West Africa (Ivory Coast), and along the coast of south and central Africa (with the exception of Cameroon). The upwelling of cold deep-sea water in the equatorial region varies over the year and is strongest in July and August. During this period the high-pressure system (St. Helene) reaches its most northerly position dominating the weather over the African rain forest on the neighbouring landmass (Fig. 1.3 and 1.4). The African rain forest flanking the Atlantic Ocean becomes overcast by stratiform cloud cover. During this period rainfall and daily maximum air temperatures drop (Flohn, 1982; 1987; Maley, 1987; 1989). Therefore, this dry season is hereafter referred to as the “cool dry season” to distinguish it from the normal cloudless or “hot dry season”.

The impact of this cool dry season is not the same everywhere (Fig. 1.2). In Ivory Coast, Ghana, southern Cameroon and Equatorial Guinea drizzly rains and misty conditions occur. Therefore, the drop in rainfall is not as stressful for the forest when compared to the hot dry season which occurs around January when there is direct solar radiation (Veenendaal et al., 1996). The impact of the cool dry season is much stronger in Gabon where all rainfall ceases completely. Only in the more elevated areas misty conditions prevail, which are known to alleviate the absence of rain fall (Bruijnzeel & Proctor, 1995; Troll, 1956). A longer and drier cool dry season over a larger part of the rain forest than is presently the case is the main cause of the deforestation of equatorial Africa.

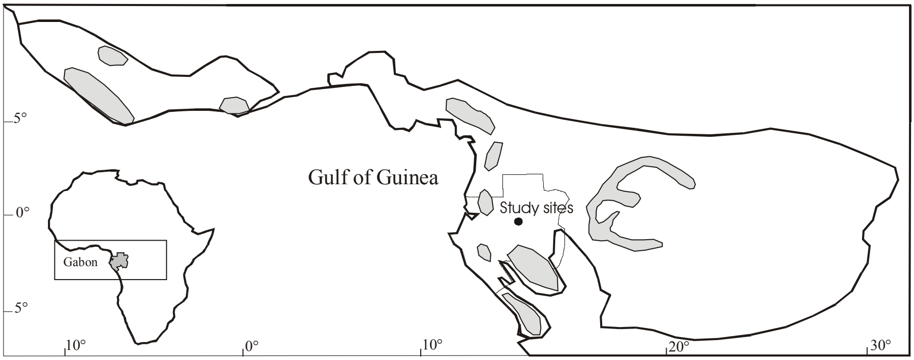


Fig. 1.5. Reconstruction of the African rain forest during the last glacial maximum (18,000 yrs BP) based on paleoclimate and refuge indicator species (only the lowland rain forest refuge areas are shown, simplified after Maley, 1996). Grey areas: the lowland refugia, bold line: limit of closed-canopy lowland rain forest.

Reconstruction

Knowing the weather conditions during the cool dry season, it was assumed that during the LGM the African rain forest would have had the best change of survival in elevated areas where drought stress would have been lowest due to the prevailing cloud forest conditions (Maley, 1987). Therefore, the first reconstruction of the rain forest extension during the LGM showed postulated refuge areas in the elevated areas of West Africa, Atlantic Central Africa (Gabon/Cameroon) and in the foothills of the Ruwenzori Mountains in eastern Central Africa (Maley, 1987).

In later reconstructions several lowland refuge areas were added based on patterns of plant species richness and endemism; i.e. two refuge areas along the coast in West Africa (Cape Three Points and Cape Palmas; Sosef, 1994; Van Rompaey, 1993), supported by fossil pollen records (Lezine & Vergnaud-Grazzinni, 1993) and one in the interior of central Africa based on a centre of endemic animals (Colyn et al., 1991). The latest reconstruction based only on fossil records does not show a fragmented forest in Atlantic equatorial Africa (table 1.2 OIS 2) (Dupont et al. 2000).

Another source of information has come from *Begonia* species of the sections *Scutobegonia* and *Loasibegonia*, a group of rain forest herbs which deposit their seeds right at their base. Because of their inefficient seed dispersal, these forest herbs were thought not to have been able to disperse far out of the forest refuge areas in which they survived the LGM (de Wilde, 1988; Sosef, 1994). Mapping the distribution of these slowly dispersing forest herbs confirmed the location of the postulated forest refugia and two new smaller refugia were postulated in elevated areas of the Doudou Mountains in Gabon and Mayumba in both Congo's (Sosef, 1994; Sosef, 1996).

However, their restriction to elevated areas or hills may not necessarily be due to historical reasons only. Some of the *Begonia* species inhabit rocky creek beds, a habitat restricted to hilly areas and hence their restriction to hills could alternatively be explained by their ecological preference. Another observation which compromises their validity as forest refuge indicators is that several populations are located outside the postulated refuge areas, which cannot be readily explained by a range expansion during the Holocene.

The Caesalpinioideae, like the begonias mentioned above, are slowly dispersing plant species. Their distribution within the African lowland rain forest is also not exclusively restricted to the postulated refuge areas (Rietkerk et al., 1996). The observation that slow dispersing plant species are present outside the postulated refuge areas suggests that either less forest disappeared during the LGM (i.e. the reconstructed refugia are wrong) or that occasional long-distance dispersal events occurred over the Holocene. This thesis tries to gain insight in how slow dispersing plant species were affected by forest reductions related to increased upwelling.

1.3 The ecological-historical opposition

By studying the present-day distribution ecology of the Caesalpinioideae and making historical inferences about the forest during the Last Glacial Maximum this thesis verges on what is referred to as the ecology-history opposition (Crisci, 2001). Both ecology and historical biogeography study species distributions. Ecologists try to explain species distributions in terms of contemporary processes and principles (e.g. climate, habitat, competition) whereas historical biogeographers do so in terms of evolutionary processes and principles (e.g. dispersal, extinction and speciation).

The *ecological* aim of this thesis is to establish how contemporary processes and environmental conditions in two lowland rain forest-savanna mosaics (Lopé and Mitendi) in central Gabon determine the distribution of Caesalpinioideae tree species with explosively opening pods (Fig. 2.1). Studying their distribution ecology is complicated because they show a low-abundance within the study sites and also form near monodominant stands or groves. This asks for a different approach as the standard procedures based on at random sampling and performing multivariate analyses are not efficient or effective. This will be addressed in the next chapter.

The *historical* aim is to assess the impact of increased upwelling during the LGM on the African rain forest and to improve the reconstruction of the forest cover during the LGM. The historical aim is possible because Caesalpinioideae are slow dispersers (forest refuge indicators) and because they were studied in areas which most closely resemble the environmental conditions during the LGM, i.e. where the impact of the cool dry season is strongest with a low mean annual rainfall.

The impact of the cool dry season on the African rain forest is strongest in Gabon. Furthermore, in central Gabon mean annual rainfall is also relatively low (1500 mm per year). Also the topography of the study areas allowed to asses how the impact of the cool dry season is on elevated areas and lowland, because the study sites comprise both hills and lowland. Finally, the two study sites are situated between two postulated forest refugia, which allows us to test the range expansion of the Caesalpinioideae over the Holocene.

While studying the distribution ecology within the study areas and the biogeographical pattern of the Caesalpinioideae tree species within the African rain forest present-day ecological and climatological processes and principles were applied as much as possible in order to explain processes that took place in the distant past. Consequently, shifts in upwelling of cold deep-sea water during the LGM and the Holocene are regarded as phases of rain forest habitat destruction (increased upwelling) and rain forest habitat formation (decreased upwelling). Similarly, expansion of the rain forest over the Holocene is considered a process comparable to primary succession, i.e. the colonisation of grassland by forest.

The vegetation dynamics as observed from fossil pollen records reflect the adaptations of plant species to changing environmental conditions, i.e. to obtain a new equilibrium with “contemporary” conditions. Fast dispersing species reach equilibrium more quickly than slow dispersing ones (Haydon et al., 1993; Ricklefs & Schluter, 1993). The Caesalpinioideae, as slow dispersing species, need more time than most other tree species to fully expand their range, i.e. before they reach equilibrium with present-day factors. The question underlying the ecology-history opposition is whether there is any historical signal left in the present-day distributions of the Caesalpinioideae. This is addressed in the next chapter together with the complicating difficulties studying the Caesalpinioideae as low-abundance tree species with a clumped distribution.

Chapter 2

Ecological data, clumped distributions and historical signal

2.1 Introduction

The present-day distribution and ecology of the Caesalpinioideae was studied in two low rainfall areas, Lopé and Mitendi (Fig. 2.1). The traditional approach would be to collect plot-data at random within these sites. However, the fact that Caesalpinioideae occur in a very low abundance poses a problem. Along three 5 km-transects of a general forest survey in Lopé they occurred only in a very small portion of the transect-segments (1.2 %- 4.3 % - 9.1 %; White, 1992).

Therefore, obtaining robust data set from the forest by random sampling would be a very time and effort consuming. Deliberate sampling, on the other hand, has the repercussion that statistical tools to analyze the data become restricted as most of them assume a random sampling from a population. This dilemma does not only apply to the Caesalpinioideae studied here, but to biodiversity studies in general, as the majority of the plant species in the tropical lowland rain forest occur in a low abundance (Hubbell, 2001). Not studying their distribution ecology because of statistical repercussions seriously hampers to gain insight into the ecology of rain forests in general.

An additional complicating difficulty studying the distribution ecology of the Caesalpinioideae with ballistic seed dispersal is their clumped (gregarious) distribution. At a regional scale they are common (100 x 100 km; Fig. 5.3), at a meso-scale they show a low abundance (10 x 10 km; Fig. 2.1), and on a local scale (100 x 100 m) they show monodominance. Recording their distribution in vegetation plots (20 x 20 m to 50 x 50 m) would only produce complete or near monodominance of one or two species and analyzing such a data set at a meso-scale with ordination or classification programs will not result in a sensible output. Therefore, a different approach is needed to study species with clumped distributions in relation to abiotic processes.

Studying the Caesalpinioideae for historical inferences related to the LGM is precarious. In previous research, regional patterns of species richness and endemism were presented as proof for the existence of Pleistocene forest refugia in Africa (Hamilton, 1976; Livingstone, 1982) and South America (Haffer, 1969; Prance, 1973). Later it appeared that these patterns were also explained by present-day rainfall and other climate-related variables (Bongers et al., 1999; Gentry, 1988; Givnish, 1999; Hall & Swaine, 1981), biased collection densities (Nelson et al., 1990), restricted habitat (ecological endemism; Tuomisto et al., 2003), or mid-domain effect (ter Steege & Zagt, 2002). Since the historical signal in these patterns was not evident, caution should be taken on how present-day distribution patterns may provide information about the distribution of the rain forest during the Last Glacial Maximum.

In this chapter the ecological data obtained by non-random sampling and the problems dealing with clumped distributions are discussed. To obtain a historical signal from ecological data, a catchment-scale based landscape-approach is discussed and a scenario of climate aridification at a catchment-scale is developed and applied to infer forest and species dynamics at local-, meso- and regional spatial-scale from present-day to an evolutionary time-scale.

2.2 Traditional approach

Multivariate analyses and random sampling

The usual approach studying spatial patterns in plant species distributions is by randomly sampling a vegetation, recording their abundance in plots and analyzing the plot data set by running multivariate analyses, i.e. a direct, indirect gradient or canonical correspondence analysis, e.g. Principle Component Analysis (PCA), Dedrended Component Analysis (DCA), or Canonical Correspondence Analysis (CCA) or a classification analysis such as Two-Way INdicator SPecies ANalysis (TWINSPAN).

The objective of these programs is to obtain clusters of plots (or species) which show a higher similarity in species composition (or co-occurrence) than other clusters within the same analysis. The clusters may form a gradient (ordination) or disjunction (classification) in a multi-dimensional space. This differentiation is searched for because the repeated co-occurrence of species at a spatial scale is an indication for underlying abiotic processes. The inference is that in a patch with a certain environment only equally competitive species co-occur.

The preference of a species for a certain habitat or environment (represented by the cluster of plots) is quantified by its abundance. Abundance can be measured at plot level (local-scale), i.e. the average relative number of individuals of a certain species per plot (mean relative abundance), and above plot level (meso-scale) as the relative number of plots in which a certain species occurred (species relative frequency).

To prove that the plot data has a non-random signal a (Monte Carlo) permutation analysis is performed. This analysis is needed, because in certain areas species composition in terms of relative abundance varies without any obvious change in environment. This phenomenon is also known as “a random walk in ecological space” or ecological drift, and these changes are considered to be neutral demographic fluctuations between equally competitive species (Hubbell, 1997; Hubbell, 2001).

Caesalpinioideae in Lopé

White (1992) carried out a general forest survey in Lopé following the standard approach where three 5-km transects were placed in two different geological formations. These two formations are very distinct: one formation comprises a range of hills with an altitude between 400 and 700 m with deep valleys (referred to hereafter as upland), the other consists of an undulating lowland with an altitude between 100 and 300 m (referred to hereafter as lowland; Martin et al., 1981). Their regolith (weathering profile) and associated soil-type is also different. The upland has a clayey regolith and the lowland a sandy regolith (Prain et al., 1990).

Two 5 km-transects were situated in lowland and the other one in the upland. The three 5 km-transects were 5 m wide and the total number of individuals enumerated with a DBH >10 cm were 760, 974 and 1026, respectively. Along the two lowland transects only 3 Caesalpinioideae species were encountered, represented by 9 (1.2 %) and 33 individuals (4.3%), respectively. Along the upland-transect 12 species were encountered represented by 94 individuals (9.1 %). Almost half of the individuals of the latter transect belonged to a single species, *Augouardia letestui* Pellegrin.

White (1992) analyzed the three 5 km-transects for classification (TWINSPAN) and ordination (CANOCO). The transects were divided in 100 m segments (0.05 ha). Only the species recorded in at least three segments were used in the analyses, to reduce the stochastic occurrence of species on the transects. None of the Caesalpinioideae were included in the analyses, not even the most abundant species *Augouardia letestui*. The multivariate analyses showed that the upland-transect had a different species composition than the two lowland-transects. Conclusion was that the forest on the two geological formations had a different species composition.

From this general forest survey some statements for the Caesalpinioideae with a ballistic seed dispersal may be inferred as to their distribution over the two geological formations. The Caesalpinioideae showed a low-abundance in both lowland and upland, because no species was recorded in more than three segments. In the upland 12 species (94 individuals) were found and in the lowland 3 (42 individuals). So, it seems that the Caesalpinioideae with a ballistic seed dispersal are more species-rich and abundant in the upland than in the lowland. A preliminary assumption based on this data would be that the upland has more appropriate habitat fitting the requirements of these Caesalpinioideae, either by surface area of habitat diversity.

Clumped distributions

It is of course debatable how reliable these inferred statements are, since they are based on only 136 individuals. Additional data (by deliberate sampling) was collected by completing 71 plots (20 x 20m). In these plots all individuals with a “diameter at breast height” (dbh) of more than 5 cm were recorded, from which “mean relative abundance” or “species relative frequency” can be calculated.

In the plots usually one Caesalpinioideae tree species was the single dominant species. Species did not co-occur often, not even the three most common species in Lopé: *Cryptosepalum staudtii* Harms, *Julbernardia brieyi* (De Wild.) Troupin and *Guibourtia demeusii* (Harms) J.Léonard. The near monodominance of species in plots poses a problem analyzing the data set with multivariate programs. As mentioned above in order to obtain clusters of plots or species in a multi-dimensional space species have to co-occur. In this case running a multivariate analysis would result in at least three clusters where in each cluster the species composition of the plots would be dominated by one of these three most common species. The conclusion from such an analysis would be that there are three (sub)forest types in Lopé where environment is notably different.

This could be a fair conclusion, but knowing how multivariate programs work it is clear that clumped distributions flaw the output. Hence, no realistic classification or ordination is obtained when studying the distributions of the Caesalpinioideae the traditional way. Another way by which the faulty output is revealed is by mapping these three forest types. The subsequent map would show a close intermixture of three very distinct forest types at a meso-scale. The sharp boundaries between the forest types would suggest a sharp change in environment, which does not exist in the field.

A similar situation exists in western Cameroon (Korup National Park) where the Caesalpinioideae species *Microberlinia bisculata* A.Chev. formed very distinct single dominant stands. The sharp boundary of these stands did not represent any abrupt change in environment or changes in phosphorus concentrations as was previously thought (Newbery et al., 1988). Their existence was more plausibly explained by the combination of their specific ecology as “non-tolerant shade bearers”, their short distance seed dispersal and forest disturbances in the 19th century (Newbery et al., 2004).

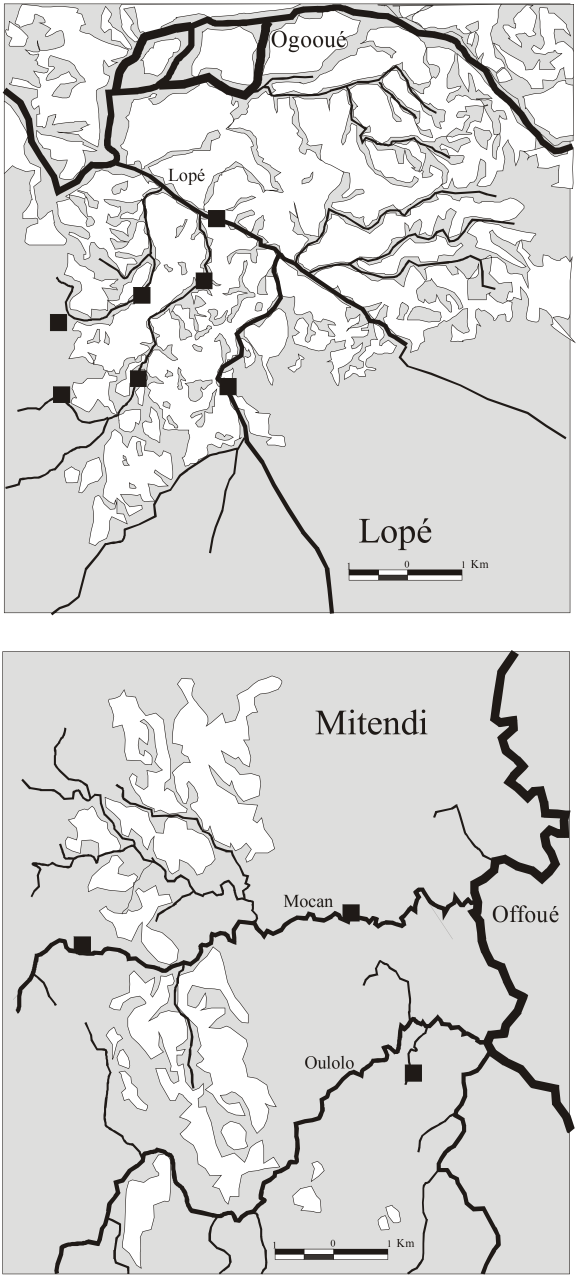


Fig. 2.1. The study sites Lopé and Mitendi showing the distribution of one of the more common species *Neochevalierodendron stephanii* (A. Chev.) J.Léonard (black squares); (grey: forest; white: grassland).

2.3 The alternative approach

Deliberate sampling

The question to be answered is whether the Caesalpinioideae indeed show a preference for the upland in terms of species number and abundance. It is clear from the above that the traditional approach does not work in the case of the Caesalpinioideae. Collecting the additional data by at random sampling is very time and effort consuming, because of their low abundance. Therefore, the data was collected by deliberate sampling, which is allowed when certain preconditions are met.

Deliberate sampling meant that the Caesalpinioideae were searched for in the forest and recorded where they were encountered. Obtaining data in this way runs the risk of becoming biased. Therefore, as a precondition it has to be certified that in this case the two geological formations are thoroughly prospected and that “all” species present are found. In other words, the absence of a species in one of the formations has to be a true absence and not a sampling error. To meet this precondition the Lopé and Mitendi study areas (both ca. 10 x 10 km) was intensively prospected for almost a year.

Normally, a higher abundance or change in abundance is tested with statistical tools based on at random sampling. Since the data of the Caesalpinioideae was not collected at random, their preference for either the lowland or upland has to be tested differently. The only robust test available in this case is the homogeneity-test or chi-square test. Hence, the hypothesis to be tested is: are the Caesalpinioideae species equally abundant in the upland as in the lowland. Because of their clumped distribution a complicating difficulty with the Caesalpinioideae is how to measure their abundance from which their preferences for either the upland or lowland may be derived.

Mean relative abundance is not very sensible, because of the monodominant of species in the majority of the plots they occurred. Species relative frequency can also not be used because the homogeneity-test (chi-square test) does not work with proportions. Therefore, an alternative abundance was used based on the characteristic distribution of the Caesalpinioideae. Their distribution consisted of a complex of subpopulations, i.e. a metapopulation. In each subpopulation at least two plots were completed placed in such a way that all the species were recorded to maximize efficiency. The abundance of a species was measured as the number of times that it occurred in a metapopulation, i.e. species absolute frequency.

By deliberate sampling 27 Caesalpinioideae species with a ballistic seed dispersal were encountered; 17 species in the lowland (310 individuals), and 16 species in the upland (215 individuals). So, in contrast to the data obtained by random sampling, the lowland and upland are equally rich in Caesalpinioideae species. This discards the preliminary assumption that there is more appropriate habitat in the upland fitting the requirements of the Caesalpinioideae.

The 27 Caesalpinioideae species were not homogeneously distributed over the upland and lowland (see Chapter 3 for methods and results). The lowland and upland have a different species composition in terms of the Caesalpinioideae with a ballistic seed dispersal. This shows that the Caesalpinioideae as a low-abundance species group show the same differentiation in distribution between the upland and lowland as the common tree species from the general forest survey.

Landscape approach

The traditional approach does not elucidate why the Caesalpinioideae tree species differentiated in their distribution response between the two geological formations. So, in order to answer this question an alternative approach was developed, one based on landscape ecology, geobotany, biogeography and chorology (Farina, 1998). In these disciplines the spatial unit is central, e.g. region, area or catchment. At a particular spatial scale the atmosphere (climate) and the lithosphere (topography and geology) create abiotic circumstances in a spatial unit. Within this spatial unit these factors create an environment suitable for only a selected group of equally competitive species which in turn determines the physiognomy (appearance) of the vegetation formation.

The Lopé and Mitendi study sites both consist of two geological formations which differ in altitude, geology (associated regolith or weathering profile) and topography (geomorphology) (Martin et al., 1981; Prain et al., 1990). Each formation has its own typical characteristics, which can be described and measured in terms used in geology, geomorphology and meteorology. These three factors determine microclimate and hydrology, which in turn create a certain environment which by competition results in different vegetation formation composed of a certain combination of plant species from a regional species pool.

A principle factor determining the distribution of plant species are the hydrological processes in the regolith, i.e. the upper part of the lithosphere (Huggett, 1995; Ripl, 1995). The subsurface water flows determine the abiotic and biotic soil related processes and concentrations of soil nutrients such as phosphorus (P), nitrogen (N) and organic matter (C), oxygen and pH (Moore et al., 1993; Schimel et al., 1985). The regolith in combination with topography determines the direction of the soil water flows (e.g. percolation and through flow) and the availability of water (i.e. soil matrix potentials), and where water shortages will occur and how severe plant water stress will be (Walsh, 1996).

The approach developed here was to describe the two geological formations in terms used in geology, geomorphology and soil hydrology to characterize the abiotic situation. In geological terms the Lopé and Mitendi sites were classified in two spatial units, i.e. the upland and lowland. The transition between the two is very abrupt. Each spatial land-unit has a different altitude, regolith (and associated soils) and geomorphology. The topography of the two land-units was described in terms of slope-units as used in geomorphology to make a representative slope profile (Dalrymple et al., 1968). Such a description would also allow to makes inferences on soil hydrology along the slopes and within catchments. These descriptions at local (slope-unit), meso- (slope-profile) and macro- scale (land-unit) were nested in a hierarchical classification following Canters et al. (1991).

The classification of the Lopé study site in abiotic terms served to test whether the differences (or similarities) in distribution ecology of the Caesalpinioideae reflected differences (or similarities) in the abiotic situation. For instance, the three most common Caesalpinioideae tree species in Lopé, *Cryptosepalum staudtii*, *Julbernardia brieyi* and *Guibourtia demeusii* rarely co-occurred. If the distribution of each species would reflect a difference in “enviroment” or “habitat” then each species would have a different position within the classification. Visa versa, if these three species have a similar position within the classification it is a strong indication that species have similar requirements. The fact that they rarely co-occur is due to other reasons than environment alone. This will be elaborated upon in the next chapter.

2.4 Present-day distribution patterns and historical signal

Drought stress in the past

Ecological data on the distribution of the Caesalpinioideae with ballistic seed dispersal was collected for historical inference, because fossil pollen records and other alternative proxies dating back to the Last Glacial Maximum (18,000 yrs BP) in or close to the study area are absent. In past research, using ecological data for historical inference has led to misconceptions about Pleistocene refugia (Hamilton, 1976; Livingstone, 1982). To avoid such misinterpretations any ecology-related variation within present-day distribution patterns must be removed to obtain a valid historical signal.

Equally important is how information from present-day distribution patterns is extrapolated to make inferences about the rain forest during the LGM. To make such inferences a model is required which links ecology with paleo-ecology. Paleorecords showed that climate in equatorial Africa was drier during the Last Glacial Maximum (Chapter 1). To arrive at a reconstruction of the forest refugia a model is needed which describes how a regional drop in rainfall affects the distribution of evergreen trees at a smaller spatial scale. Such a model can be developed by applying the principle of uniformitarianism.

The principle of uniformitarianism does not mean that the present and the past are identical, but that the present provides an image to understand the past. In other words, for the rain forest to become contracted during the LGM, drought stress must have increased and this is only possible by the same mechanisms as observed today. The lower levels of CO_2 during the LGM reinforced the drought stress caused by the decrease in rainfall (Cowling et al., 2001). The present-day transition from forest to savanna is determined by a change in (zonal) climate, i.e. where rainfall is low and strongly seasonal (e.g. Gentry, 1988; Givnish, 1999). A decrease in annual rainfall is possible by a reduction of rainfall during the rainy season(s) and/or a prolongation or deterioration of the dry season(s). A prolongation of the dry season is more likely to cause a spatial contraction in forest cover, because it prolongs the period of soil water shortage as a result of strong evapotranspiration.

Evapotranspiration is strongest during the dry season when long spells of solar radiation are uninterrupted and heat up the plant-soil complex, lowering the moisture content of the complex. Soil water shortages (expressed in negative soil matrix potentials) are lower and reach permanent wilting point more frequently (i.e. leaves loosing their turgor) in the drier exterior of the rain forest than in the wetter parts of the rain forest (Veenendaal et al., 1996). Similarly, soil matrix potentials close to the surface reach low values more quickly and more frequently than at larger depths (Veenendaal et al., 1996).

The occurrence of soil water shortages is not only determined by evapotranspiration. Also important are the local conditions of the regolith and/or topography which are able to compensate for or deteriorate the regional climatic situation (Daws et al., 2002; Van Rompaey, 1993). Studies on soil (slope) hydrology showed that soil water shortages along a slope are more likely to occur at the summit than along the stream bank, because water will accumulate at the lowest point (Atkinson, 1978; Bras, 1990; Fig. 3.5).

Model and scenario

Plant species will primarily respond to changes in soil water shortages and not directly to changes in rainfall. Therefore, the regional drop in rainfall has to be translated in a change in soil water flows and quantities. For this translation between rainfall and soil moisture flows the catchment-scale (within 10 x10 km) was chosen. The catchment approach allows using and applying the knowledge and principles of drainage basin hydrology. This makes it possible to indicate where in the catchment a drop in precipitation is most likely to cause water shortages.

An additional advantage of the catchment approach as a model is that it facilitates reconstructing the situation for the LGM and creating a model. The main difference between the LGM and the present-day situation is the amount of rainfall intercepted in the catchments. The topography and regolith within a catchment will have changed less, because the erosion of catchments in general is a slow process, or changes rapidly only occasionally. When considering that a prolongation of the dry season is most likely to have caused a spatial contraction in forest cover, the input of rainfall is even less important. Since there is little or no rainfall during the dry season, soil moisture flows in the catchments are mainly determined by the regolith and topography of the catchment.

With the catchment as the basal unit or system a change from wet to drier climatic conditions and the response of drought sensitive species can be worked out. The starting point of this scenario is a catchment in a wet part of the rain forest where the dry season does not cause soil water shortages (negative soil matrix potentials), not even in the highest parts of the catchment, i.e. on summits or ridges. In this catchment evergreen forest is the dominant vegetation and drought-tolerant tree species have a low abundance or are absent.

When over time rainfall during the dry season becomes increasingly less, evapotranspiration becomes increasingly stronger. The stronger evapotranspiration will first create lower soil matrix potentials at the higher parts of the catchment, i.e. on the summits and upper half of the slopes (backslope; Daws et al., 2002). Simultaneously, the upper part of the regolith is more often and more quickly depleted from its moisture than deeper regions (Veenendaal et al., 1996). Under these conditions drought-sensitive plants on the summit and backslope experience drought stress, in particular shallow-rooting plants, e.g. herbs, understory shrubs, seedlings and saplings. Their mortality rate will increase during the dry season and so will that of old trees (Condit et al., 1995).

Increased gap-formation due to the fallen old trees opens up the canopy contributing to a further depletion of moisture in the plant-soil complex (Kapos et al., 1997; Lovejoy et al., 1986). Under these conditions seedlings and saplings of drought-tolerant tree species are competitively stronger and they will have increased opportunities to reach the canopy. In time, the low-abundant drought-tolerant tree species will take over the dominant position in the canopy from the drought-sensitive tree species. As drought stress increases the same process will continue further down the slope lower into the catchment, limiting the drought-sensitive tree species to the stream banks where soil matrix potentials remain positive. When ultimately the stream in the catchment dries up during the dry season, the drought-sensitive species will become locally extinct.

Historical inferences

The scenario above describes how a regional drop in rainfall and increase of the length of the dry season creates water shortages within the catchments in that region. The scenario can also describe the reverse process, i.e. when the dry season weakens. As drought-sensitive species are competitively stronger under wetter conditions with an increasing absence of water shortages they become the dominant forest trees in the catchment. The relative abundance of drought-sensitive and drought-tolerant tree species within catchments will oscillate in response to aridification and humidification of climate, which in equatorial Africa is the response to the oscillation of upwelling of cold deep sea water in the Gulf of Guinea (Chapter 1).

In this model also elements of historical biogeography, like extinction, dispersal and speciation events can be incorporated. The extinction of a species starts first with extinctions at catchment-scale. When this happens in all the catchments in the region where the species occurs, this is a permanent extinction event. After a species has become locally extinct in one catchment it can only be re-colonized from another catchment by dispersal, i.e. a dispersal event. When these colonizing individuals come from a catchment far away it is referred to as an occasional long-distance dispersal event. The speciation of a species is more complicated, as a new species can occur by both limited extinction between catchments and by dispersal events. The first depends on the formation of a non-equilibrium metapopulation and the latter is the result of founder-effects related with dispersal events.

A metapopulation is created when a previously continuous distribution of a drought-sensitive tree species becomes fragmented. This will happen when after a permanent regional drop in rainfall drought-sensitive species become restricted to the lower parts of the catchments. The spatial isolation of a species in subpopulations is not enough to cause a (allopatric) speciation event, because when species have seeds or pollen which disperse well, the exchange of genetic material between subpopulations will still occur. For speciation to happen also sexual isolation between subpopulations is needed in combination with population reductions (Comes & Kadereit, 1998; Hamrick, 1994; Sork et al., 1999; Young et al., 1996).

Speciation can only occur when subpopulations continue to decrease, thereby forcing genetic differentiation (Hamrick, 1994; Sork et al., 1999) and only when the genetic variation continues to differentiate by genetic drift (Barret & Kohn, 1991; Ellstrand & Elam, 1993). This kind of speciation is non-adaptive and only means that the former most frequent alleles, c.q. the associated characteristics of the species are no longer dominant and rarer alleles are allowed to manifest. These new species may merge later during a phase of climate humidification and form species complexes (Hewitt, 1999).

Speciation by founder effect plays a role in dispersal events, e.g. when catchments are re-colonized after species with similar requirements became locally extinct due to arid conditions. The group of individuals that reached the vacant catchment only represents a part of the population (or genepool) and by genetic drift they may become different from the mother population (Mayr, 1982). Later, when more individuals arrive, differences will be homogenized (Gaggiotti et al., 2003), but in case the founder group was the result of an occasional long-distance seed dispersal event this may take more time or never occur.

Lopé during the LGM

The model and scenario described above can be used to evaluate how much historical signal there is in the ecological data collected on the Caesalpinioideae with a ballistic seed dispersal in Lopé. The Lopé study site consists of several smaller catchments which straddle the two geological formations (Fig 3.4). The upper segment of the catchment is located in the upland and the lower segment in the lowland. As we saw earlier the Caesalpinioideae species are not homogeneously distributed between the upland and lowland segment. In each segment they were distributed along the lowest part of the catchments forming a metapopulation, i.e. isolated subpopulations (Fig. 2.1). In each subpopulation the presence of a species was recorded in plots.

A historical signal dating back to the LGM can only be present in this plot-data when the Caesalpinioideae persisted in Lopé during the Last Glacial Maximum. According to the Pleistocene forest refugia hypothesis drought stress was so severe that all evergreen tree species including the Caesalpinioideae had become locally extinct outside the refuge areas. Subsequently, all the species now present in the catchments of Lopé arrived by dispersal from the nearest refuge area, the Chaillu Massif. However, arrival in Lopé by their normal dispersal is not a realistic scenario (Leal, 2001). The arrival in Lopé by occasional long-distance seed dispersal events will be tested in Chapter 4. But for now assuming that the Caesalpinioideae persisted in Lopé, the plot data set can serve as a hypothetical test case.

During the LGM climate was drier and the dry season longer which will have reduced the abundance of Caesalpinioideae in the Lopé catchments more than today. Presently, the Caesalpinioideae already form a metapopulation and if they did not become extinct they will have formed a metapopulation during the Last Glacial Maximum as well. Applying the aridification scenario described above to the Lopé catchments, the total number of subpopulations will have been lower and the size of the persisting subpopulations will have been smaller.

Some of the present subpopulations may be the result of recent colonization by water (personal observations). A distinction between old and new subpopulations is not clear and may only be distinquishable by a phylogeographic study (Gaggiotti et al., 2003; Wakeley, 2004). Hence, the present total number of subpopulations in Lopé is the sum of the old subpopulations and new colonizations. Therefore, the total number of subpopulations in which a certain species occurs (i.e. species absolute or relative frequency) does not contain a historical signal.

How many subpopulations there were during the Last Glacial Maximum is unknown. But if the Caesalpinioideae with ballistic seed dispersal did not arrive in Lopé by occasional long-distance seed dispersal events, every species present in Lopé successfully survived the Last Glacial Maximum. Most of the species are only present in either the lowland or the upland. These species can only have survived the Last Glacial Maximum when at least one subpopulation of the species persisted in the land-unit (lowland or upland) to which it is presently restricted. So, the only historical signal in the ecological data on the Caesalpinioideae is their absence or presence in the upland or lowland.

2.5 Conclusions

In this chapter the difficulty of studying the distribution ecology of the Caesalpinioideae with present-day processes and principles was addressed. Their occurrence in near monodominant stands in a low abundance makes the standard approach based on at random sampling and multivariate analyses inappropriate. An alternative approach was developed based on deliberate sampling, a landscape classification and metapopulation abundance. In the next chapter the distribution ecology of the Caesalpinioideae will be analyzed in more detail in terms of present-day processes and principles.

Also the ecology-history opposition was addressed, i.e. the question whether there is any historical signal in the present-day distribution of the Caesalpinioideae? By applying the principle of uniformitarianism a model and scenario at catchment-scale was developed to infer a historical signal from present-day ecological data. The answer in the particular case of Lopé is that the historical signal in the present-day distribution data collected for the Caesalpinioideae can only be inferred from their absence or presence in the two geological formations.

Chapter 3 Regional drought stress and local compensation

3.1 Introduction

Climate is one of the principle factors determining species richness and species distributions within tropical lowland rain forests (Aplet et al., 1998; Clinebell et al., 1995; Gentry, 1982; Gentry, 1988; Givnish, 1999; Linder, 2001; Specht & Specht, 1993; ter Steege et al., 2002; Wright, 1992). The decrease of species richness towards the periphery is due to increasing drought stress, i.e. negative soil matrix potentials (Becker et al., 1988; Veenendaal et al., 1996; Wright, 1992). At the periphery of the West African rain forest (Fig. 3.1) soils (regolith) become regularly depleted of moisture during the dry season (December/January), whereas along the coast at the wet end of the rainfall gradient this happens only occasionally (Veenendaal et al., 1996).

Regional species composition of the West African rain forest (Upper Guinea) changes along this rainfall gradient (Hall & Swaine, 1981; Van Rompaey, 1993). Bongers et al. (1999) studied twelve tree species from the regional species sample of (Van Rompaey, 1993) in relation to drought stress related variables, e.g. mean annual rainfall, length of dry season, soil water deficits, etc. Species which did not correlate with any of the climatic variables were located in the middle of the regional species synoptic table of (Van Rompaey, 1993), whereas species which did correlate were located either at the top or bottom of the synoptic table. So, the response curves of these twelve species calibrate the change of regional species composition and confirm that drought stress is the principle force arranging species along the rainfall gradient.

Within the regional change in species composition along the rainfall gradient, also a local change in species composition was observed along slopes. This local change in species composition was also thought to reflect a differentiation in water availability (Van Rompaey, 1993). However, soil matrix potentials were not measured. This idea, however, is supported by hill slope hydrology (Atkinson, 1978; Bras, 1990), and by measurements from a low rainfall area in Panama (Daws et al., 2002). In Panama, soil matrix potentials during the dry season on the dissected plateau corresponded with the regional low, but at the valley bottoms they were comparable with those of high rainfall areas (Daws et al., 2002).

In equatorial Africa also a second and different dry season occurs around July and August (Fig. 1.2 and 3.2) when the meteorological equator (ITCZ) reaches its most northern position (Leroux, 1983). This drop in rainfall does not create drought stress at the periphery of the West African rain forest (Veenendaal et al., 1996), because drizzly rains conserve soil moisture. Also the desiccating effect of direct solar radiation is absent, because of the persistent cloud cover caused by the inland flowing maritime air masses (Leroux, 1983; Maley & Elenga, 1993). But, in Gabon this dry season is more severe as rainfall ceases completely (Saint-Vil, 1977). This is the so-called “cool” dry season (Chapter 1), because daily maximum air temperatures remain relatively low due to the persistent (stratiform) cloud cover which blocks direct solar radiation for more than a month and without which the earth’s surface is not heated up.

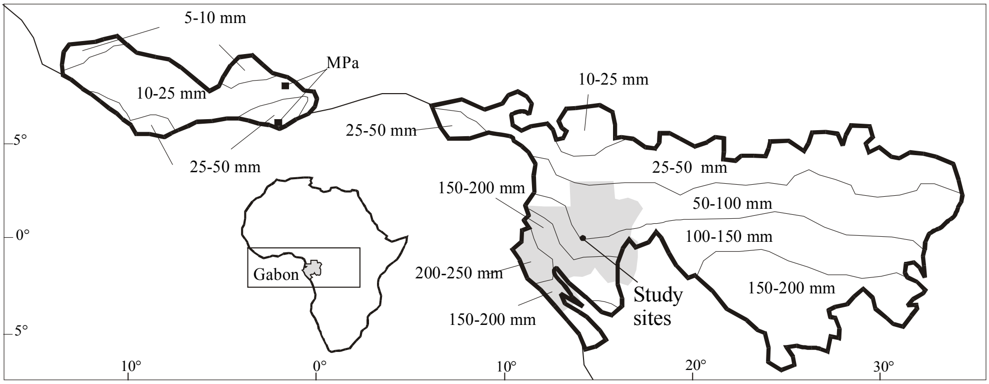


Fig. 3.1. The hot dry season: mean monthly rainfall in December (1920-1980) within the African rain forest showing the study sites and the areas where soil matrix potentials were measured in Ghana (MPa). Bold line: outline lowland rain forest, shaded area: Gabon.

The main difference between the "hot" dry season in December/January and the cool dry season in July/August is the exposure to direct solar radiation, c.q. evapotranspiration. Evapotranspiration depletes the plant-soil system from its moisture during the hot dry season. During the cool dry season the rate is low because there is no direct solar radiation. Furthermore, elevated areas experience less drought stress, because of the low cloud cover, which creates misty, cloud forest-like conditions. These misty circumstances provide an extra input of moisture into the plant-soil complex (Bruijnzeel & Proctor, 1995; Troll, 1956). In other words, drought stress during the cool dry season is different from drought stress during the hot dry season, and during the cool dry season elevated areas experience less drought stress than the lowland.

The impact of the hot and cool dry season on the rain forest community and on evergreen drought sensitive tree species in particular is unknown or has not been analysed separately (Bongers et al., 1999; Hall & Swaine, 1976; Linder, 2001; Swaine, 1996; Veenendaal et al., 1996). Understanding how the rain forest community is affected by the hot dry season will gain insight into how the rain forest became disturbed during the Late Holocene (Chapter 1) or how it will be affected by global warming. Studying the impact of the cool dry season will improve our understanding of how the forest responded during periods of increased upwelling of cold deep seawater, like during the LGM. To assess the impact of the two dry seasons, the distribution of Caesalpinioideae tree species was studied in Lopé and Mitendi, two sites in a larger forest-savanna mosaic within the Gabonese rain forest.

In Lopé the Caesalpinioideae grow almost exclusively along streams (White & Abernethy, 1997). This is an indication that they are affected by drought stress, because elsewhere the same Caesalpinioideae species are not restricted to rivers and streams under wet climatic conditions (Aubréville, 1968; Evrard, 1968; Letouzey, 1968; Newbery et al., 1988; Newbery & Gartland, 1996; Wieringa, 1999). However, the Caesalpinioideae are low-abundance species and a thorough prospection is needed to confirm this observation. Furthermore, it has to be verified that habitat is not the principle force arranging species distributions within the low rainfall areas. The need for such a procedure is clear when reviewing the general forest survey completed in Lopé.

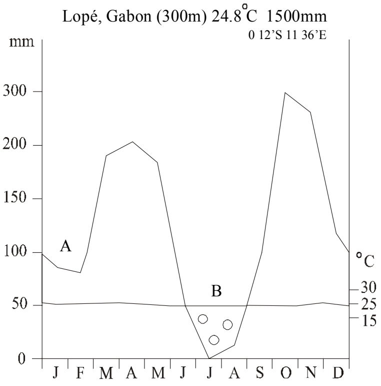


Fig. 3.2. Climate diagram of Lopé showing the mean monthly temperature and mean monthly rainfall; A) hot dry season, B) cool dry season. The section with circles is considered as an arid period according to the conventions of Walter and Lieth (1960-1967).

Drought stress or habitat

In Lopé, a general forest survey showed that the upland and lowland had a different species composition (White 1992). The upland was characteristically inhabited by members of the Olacaceae and the lowland by *Aucoumea klaineana* Harms (White, 1992). *Aucoumea klaineana* is dominant in the lowland because of forest history. This species is a savanna colonizer and apparently in the past there was more grassland in the lowland than in the upland. This may be due to the sandy regolith present in the lowland. Its low retention capacity enhances the occurrence of drought stress (i.e. negetative soil matrix potentials) and the occurrence of extreme drought stress with forest destruction (an arid event), like El Niño-years in SE Asia.

Similarly, the presence of the Olacaceae in the upland may be related to the clayey regolith and subsequent lower chance of drought stress to occur. But it may also be their mineral requirements to root in a clayey regolith. Equally possible is that they may be restricted to the upland because of the (minor) difference in altitude or a specific habitat created by the relief of the upland. It is not possible to tell which of the three, altitude, relief or regolith, is most important, because the Olacaceae were not studied in contrasting conditions/environments. The only conclusion to be drawn from the data collected by White (1992) is that they are restricted to the upland because of the environment as created by altitude, relief and regolith.

The study of White (1992) did not have sufficient data on the Caesalpinioideae to verify whether they were also differently distributed over the upland and lowland (Chapter 2). This study provides a thorough prospection to study them in more detail and under different hydrological regimes. The two study sites were classified at landscape level into smaller spatial-units. This made it possible to retrace a difference between the two geological formations to a difference in "habitat" as determined by altitude, relief or regolith. Also by studying them in areas with a similar "habitat", but a different hydrological regime, the influence of drought stress could be assessed.

3.2 Study sites and methods

Study sites

Lopé (0°12'S, 11°36'E) and Mitendi (0°35'S, 11°41'E), situated in central Gabon, are forest-savanna mosaics (*c.* 10x10 km) enclosed by lowland rain forest *c.* 50 km apart (Fig. 4.1). Regional mean annual rainfall is relatively low, between 1500 mm and 1700 mm (Saint-Vil, 1977). In Lopé the mean annual rainfall is 1500 mm (1984-2001). A more precise figure is not available for Mitendi, but as it is situated further south along the rainfall gradient it is expected to have a slightly higher mean annual rainfall (Saint-Vil, 1977). Rainfall is interrupted by two dry seasons; the cool dry season in July and August when all rainfall ceases and the hot dry season in December and January. The latter is not always evident as rainfall never ceases completely (Fig. 3.2).

The two forest-savanna mosaics straddle north-south orientated geological formations (Martin et al., 1981; Prain et al., 1990). The most prominent feature in the landscape is a low altitude folding zone (400-700 m) or upland, which has deep valleys and a clayey regolith. The upland is flanked to the east by lowland (100-400 m) with gently rolling hills. The transition between upland and lowland is abrupt like an escarpment. In Mitendi the most eastern part is a dissected plateau with deep valleys like the upland. The Mitendi lowland has a clayey regolith like its flanking upland, whereas in Lopé the lowland has a sandy regolith.

The open landscape of the two study sites is most eminent in the lowland of Lopé, where grassland dominates more than in Mitendi (Fig. 2.1). The forest is present along streams as gallery forest, which varies in length and width. Patches of forest are also present on the ridges of varying size. Most of the streams have their origin in the upland, except for a few streams in the most eastern parts of the study areas (Fig. 3.4). During the hot dry season all streams remain flowing in both study areas, but during the cool dry season streams in the easternmost part of Lopé dry up or become insignificant.

Landscape classification

To come to a more detailed description of the study areas, the landscape was classified from a broad to a small-spatial scale based on a hierarchy of topography, regolith and hydrology following (Canters et al., 1991). At a local-spatial scale, the upland and lowland were described in slope-units, represented in diagrammatic slope-profiles following (Dalrymple et al., 1968). This landscape classification was adopted because of the low abundance of the Caesalpinioideae species and their rare co-occurrence in plots (Chapter 2).

Normally the vegetation is sampled together with a set of potentially explanatory abiotic variables. Running a multivariate analysis, e.g. Canonical Corresponds Analysis (CCA) calculates how well the distribution of species and plots correspond with the recorded abiotic variables. Here, the abiotic variables are defined as habitat in the landscape classification, i.e. land-unit (macro-habitat), slope-profile (meso-habitat) and slope-unit (micro-habitat). This classification will serve to characterise the preference of a species for a "habitat".

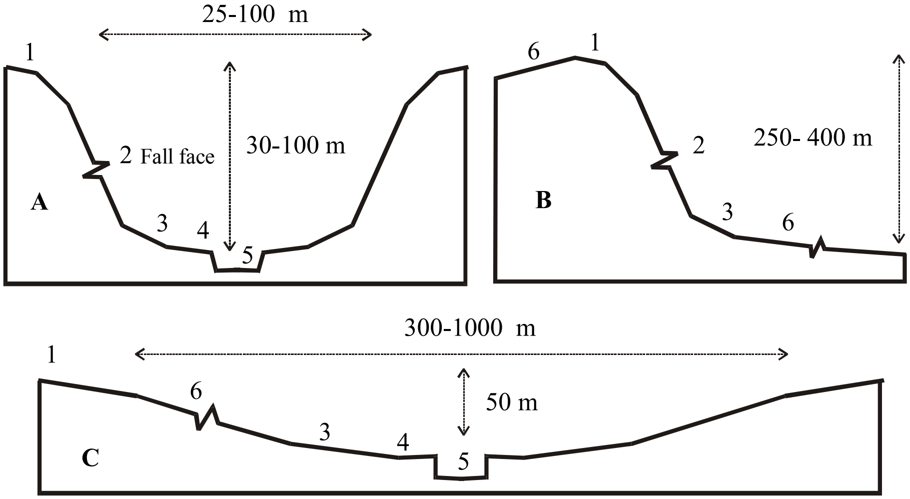


Fig. 3.3. Slope-profiles with estimated depths and widths: **A**: narrow valley, **B**: escarpment, **C**: wide valley. Slope-units: 1: summit, 2: fall face, 3: colluvial, 4: alluvial, 5: channel bed, 6: transportation mid slope.

Sampling and analysis

The low abundance of the Caesalpinioideae forced a non-random sampling procedure. The only statistical test available in this case is the homogeneity-test (chi-square test). It tests whether the Caesalpinioideae species are homogeneously distributed over the i.e. land-units (macro-habitat), slope-profiles (meso-habitat) and slope-units (micro-habitat). The absence or presence of a species in a habitat was determined by thoroughly prospecting the two study areas (by deliberate sampling) for a period of nine months. Each land-unit was sampled until no more new species were found, i.e. when the “species-area” curve reached an asymptote.

The “species-area” curve (Fig. 3.6) was constructed by hand, because Monte-Carlo simulations are not applicable to non-random data sets. The unit of “area” in the curve was represented by subpopulations. In each subpopulation two plots (20 x 20 m) were completed to register all the species. In each plot all individuals above 5 cm dbh were measured, from which “mean relative abundance” and “species relative frequency” can be calculated. However, these measures of abundance are unsuitable in this approach to test the preference of a Caesalpinioideae species for a certain habitat, instead the metapopulation-abundance was used, i.e. the number of subpopulations a certain species occurred in (see also Chapter 2).

Voucher specimens of all species encountered are kept in the herbaria of Libreville, Lopé and Wageningen (LBV, SEGC, WAG; Appendix 1).

Drought stress and soil hydrology

The Lopé and Mitendi study sites consisted of several smaller catchments (schematically represented in fig. 3.4). The catchment-scale approach makes it possible to indicate where within the catchment water shortages are most likely to occur during the dry season (Chapter 2). During the hot dry season drought stress is mainly driven by a stronger evapotranspiration-rate, whereas during the cool dry season mainly by soil hydrology.

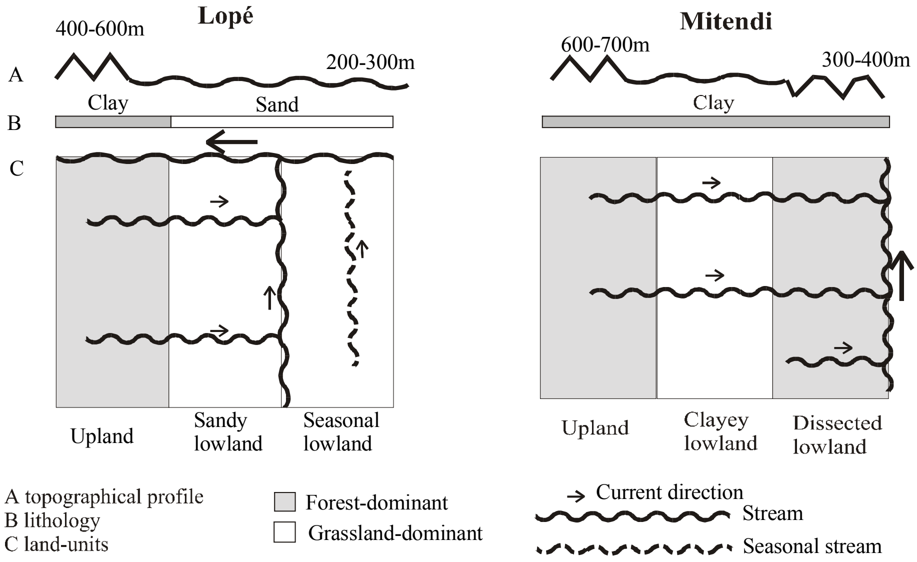


Fig. 3.4. A schematic representation of the study sites divided into land-units.

In the hot dry season the stronger evapotranspiration will first create lower soil matrix potentials at the higher parts of the catchment and later also at the lower parts (Daws et al., 2002). Since rainfall does not cease completely during the hot dry season, the higher parts of the catchments are regularly re-wetted and small currents of through-flow will continue to flow down stream. The situation in the upland and lowland will not be very different, although the higher altitude of the upland may reduce the force of evapotranspiration as daily maximum temperatures in elevated areas are slightly lower (Thibault et al., 2004).

During the cool dry season all rainfall stops and the presence and amount of water is only determined by runoff, i.e. soil moisture flows. Runoff consists of several flows of which the most important one to plants is through-flow (Bras, 1990; Viessman & Lewis, 1996). In principle, as long as there is drainage water in the streams it implies that there is still soil moisture, although, depending on relief, soil moisture availability may be concentrated in the lower parts of the catchment (Bras, 1990; Viessman & Lewis, 1996).

During the cool dry season, contrary to the hot dry season, the level of drought stress between the upland and lowland is different. During the cool dry season the upland of Lopé and Mitendi are frequently shrouded in mist. The misty conditions are an extra input of moisture as water condenses on the leaves of the vegetation and becomes available when it drips on the forest floor (Bruijnzeel & Proctor, 1995; Troll, 1956). Under these cloud forest conditions negative soil matrix potentials cannot develop and hence there is no drought stress in the upland during the cool dry season.

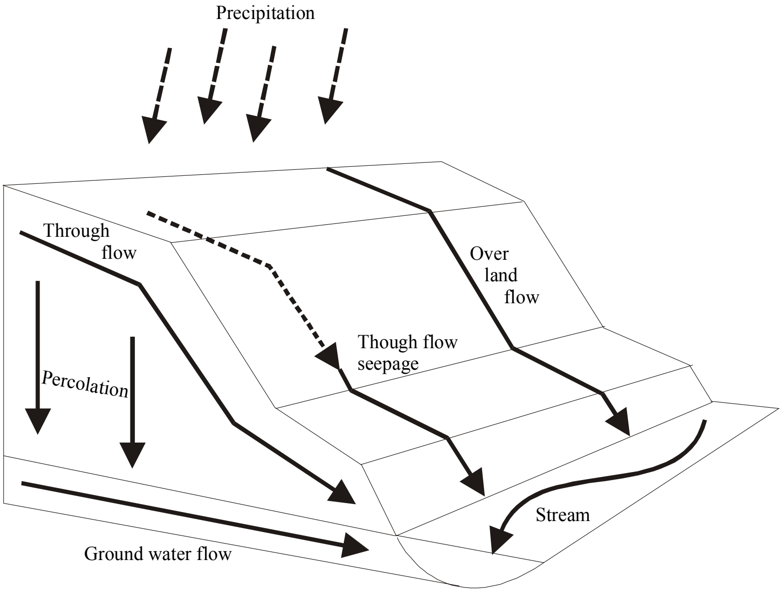


Figure 3.5 Soil moisture flows on hill lopes (from Atkinson 1978).

3.3 Results

Landscape classification

The landscape was classified at a broad spatial scale which resulted in three land-units per site (Fig. 3.4). In Lopé: 1) the Lopé (clayey) Upland, 2) Sandy Lowland, i.e. the lowland with permanent streams, and 3) Seasonal Sandy Lowland, i.e. the lowland with seasonal streams. In Mitendi: 1) the Mitendi (clayey) Upland, 2) Clayey Lowland, i.e. the clayey lowland with a gentle relief, and 3) the Dissected Lowland, i.e. the clayey lowland with deep valleys.

Three distinctive profile types emerged (Fig. 3.3): A) the deep or narrow-valley slope-profile, B) the steep escarpment slope-profile, and C) the gentle wide-valley slope-profile. The “fall face” slope-unit (2) is characteristic for narrow-valley (A) and the escarpment slope-profile (B) and it is absent in the wide valley slope-profile (C). The escarpment slope-profile (B) does not have the alluvial slope-unit (4) and it is also not symmetrical like the narrow and wide valleys. Narrow valleys are characteristic for the Lopé and Mitendi upland-units and the wide valley for the lowland land-units. The Dissected Lowland in Mitendi has both narrow and wide valleys.

Species richness

In 126 plots 42 Caesalpinioideae species were recorded, 27 species in Lopé, and 29 species in Mitendi (see Appendix 1) and all six land-units were sufficiently sampled (Fig. 3.6). Species richness was not equally distributed over all six land-units. Poorest in Caesalpinioideae tree species were the Seasonal Sandy Lowland and the Clayey Lowland with 3 species and no species, respectively. The Lopé Upland and the adjacent Sandy Lowland harboured 17 species each, the Mitendi Upland 18 species and the Dissected Lowland 19 species.

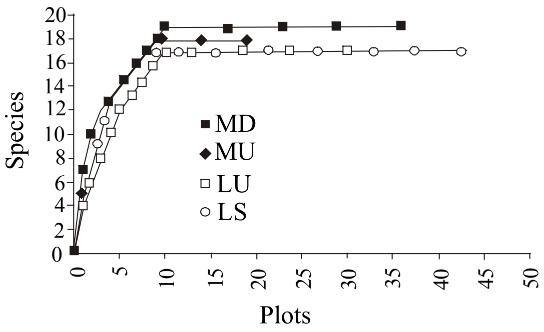


Fig. 3.6. Species-area curves for the species of Caesalpinioideae of the four land-units, MD: Mitendi Dissected Lowland, MU: Mitendi Upland, LU: Lopé Upland, LS: Lopé Sandy Lowland.

Species richness was also not equally distributed among the three slope-profiles. Poorest in species was the escarpment slope-profile with 3 species in Lopé and 1 species in Mitendi. Species richness in wide and narrow slope-profiles were not very different with 17 species (Lopé /13 species (Mitendi) versus 18 (Lopé) and 14 species (Mitendi), respectively (Fig. 4.1 B). Species richness was also not equally distributed among the slope-units within each profile (Fig. 4.1 A). The Caesalpinioideae showed a strong preference for the alluvial and colluvial slope-units of valleys (81 % of all 126 plots); in Lopé (χ^2= 76.3, d.f. 26, α = 0.01) and in Mitendi (χ^2=73.5, d.f. 28, α = 0.01).

Species distributions

In the Lopé site 27 species were recorded in 71 plots (Table 3.1). These species were not homogeneously distributed between the Lopé Upland and Sandy Lowland (χ^2= 71.0, d.f. 26, α = 0.01). 4 species were very rare and represented by only one individual. 10 species were restricted to the Sandy Lowland and 10 species to the Lopé Upland. 7 species were recorded in the Sandy Lowland and Lopé Upland. Of these 7 species only *Neochevalierodendron stephanii* and *Scorodophloeus zenkeri* were equally distributed between the two land-units. *Cryptosepalum staudtii* and *Guibourtia demeusii* showed a strong preference for the Sandy Lowland and *Brachystegia mildbraedii* for the Lopé Upland.

At the Mitendi site 29 species were recorded in 55 plots (Table 3.1). Also in Mitendi species were not homogeneously distributed between the Mitendi Upland and Dissected Lowland (χ^2=63.9, d.f. 28, α = 0.01). Eight species were rare and only represented by one individual. 10 species were restricted to the Mitendi Upland and 11 species to the Dissected Lowland. 8 species were recorded in both the Mitendi Upland and the Dissected Lowland. 4 out of these 8 species showed no clear preference for one of the two land-units, for example *Julbernardia pellegriniana* and *Scorodophloeus zenkeri*. Some showed a preference for the Dissected Lowland, such as *Gilbertiodendron ogoouense*, and others for the Mitendi Upland, e.g. *Neochevalierodendron stephanii*, (Table 3.1).

Table 3.1. Species abundance as measured in number of plots per land-unit (as defined under "sampling"). LS: Lopé Sandy, LU: Lopé Upland, MD: Mitendi Dissected, MU: Mitendi Upland.

	LS	**LU**	**MD**	**MU**
Julbernardia brieyi	8			
Aphanocalyx djumaensis	6			
Crudia gabonensis	3			
Cynometra schlechteri	3			
Gilbertiodendron grandistipulatum	3			
Baikiaea robynsii	2			
Tessmannia dewildemania	1			
Berlinia auriculata		1		
Tessmannia anomala		1		
Baikiaea insignis	1	1		
Brachystegia mildbraedii	1	3		
Guibourtia demeusii	7	2		
Cryptosepalum staudtii	10	1		
Berlinia bracteosa	5		6	
Anthonotha macrophylla	4		1	
Hymenostegia klainei	2		6	
Pellegriniodendron diphyllum	3	1	2	
Neochevalierodendron stephanii	4	4	3	9
Scorodophloeus zenkeri	1	1	6	10
Eurypetalum batesii		1	6	3
Sindoropsis letestui		5	5	5
Julbernardia pellegriniana		2	13	11
Augouardia letestui		2	8	
Hymenostegia pellegrinii		4	5	
Julbernardia seretii		2	1	
Oddoniodendron micranthum		3		1
Tetraberlinia bifoliolata		3		1
Librevillea klainei			1	
Anthonotha triplomeris			2	
Gilletiodendron pierreanum			2	
Hymenostegia felicis			2	
Crudia harmsiana			1	2
Aphanocalyx margininervatus			4	3
Gilbertiodendron ogoouense			7	1
Gilbertiodendron brachystegioides				4
Bikinia media				4
Leonardoxa africana				3
Gilbertiodendron dewevrei				2
Gilbertiodendron preusii				2
Aphanocalyx heitzii				1
Aphanocalyx microphyllus				1
Erythrophleum ivorense				1
Total no. of species	17	17	19	18

Within the Dissected Lowland most of the species were also not homogeneously distributed over the narrow (MD-n) and wide valleys (MD-w) (χ^2= 42.9, d.f. 18, α = 0.001). 6 species were restricted to the wide valleys and 4 to the narrow valleys, while 9 species were present in both narrow and wide valleys (Table 3.3).

In other words, the Caesalpinioideae species showed a strong preference for valley bottoms in both Lopé and Mitendi. Species composition of the upland and lowland valleys was different in Lopé as well as in Mitendi. Species composition also differed between the narrow and wide valleys within the Dissected Lowland of Mitendi. The Caesalpinioideae species were virtually absent in the lowland with seasonal streams (Seasonal Sandy Lowland) and completely absent in the Clayey Lowland in Mitendi despite the permanent streams.

3.4 Discussion

Habitat differentiation or drought stress in Lopé

Species composition between the Lopé Upland and Sandy Lowland was different, which is a difference in macro-habitat. This difference between the two land-units cannot be attributed to a differentiation in micro-habitat (slope-units), because they mainly inhabited the alluvial and colluvial slope-units in both land-units. This would only be the case when the species restricted to the Lopé Upland inhabited the "fall-face slope-unit", which is the slope-unit absent in the lowland. Also the species present above the colluvial/alluvial slope-units in the Lopé Upland (*Sindoropsis letestui*, *Neochevalierodenderon stephanii* and *Hymenostegia letestui*) does not explain the difference in species composition, because they were also present at the colluvial and alluvial slope-units. Since micro-habitat does not explain why the upland and lowland are different, it must be related to a difference in meso-habitat (slope-profile), macro-habitat (regolith) or altitude, singly or in combination.

At this point the difference in species composition between the Lopé Upland and Sandy Lowland does not directly infer a difference in drought stress, since the colluvial/alluvial slope-units are kept at field capacity (i.e. no negative soil matrix potentials) by the permanent presence of water in the streams. The influence of drought stress is only apparent when comparing it with the same "habitat", but without the presence of water, i.e. the Seasonal Sandy Lowland and the colluvial slope-units of the Escarpment-profile. In the Seasonal Sandy Lowland there were only 3 species along the dried up streams (compare the Sandy Lowland with 17 species) and no species at the colluvial slope-units of the Escarpment-profile.

The Seasonal Sandy Lowland is only different from the adjacent Sandy Lowland by the absence of water in streambeds during the cool dry season. A dried up streambed means that soil moisture in the catchment is absent or at least low, i.e. negative soil matrix potentials or drought stress. If the streams of the Sandy Lowland were not fed by drainage water from the Lopé Upland they would also dry up and be equally poor in Caesalpinioideae species. The colluvial slope-units of the Escarpment profile are also not fed with water passing (influent seepage). If the only requirement for the establishment of the Caesalpinioideae were the colluvial/alluvial habitat than the Seasonal Sandy Lowland should be as species rich as the Sandy Lowland. Similarly, the colluvial slope-units of Escarpment-profile should be as species rich as those of the Lopé Upland. This is not the case.

Table 3.2. Species abundance as measured in number of plots in the upper and lower half of the valleys in Lopé and Mitendi. Upper half: slope-units 1,2 and 6; Lower half: slope-units: 3 and 4 (see fig. 3.3).

	Lopé		**Mitendi**	
	lower half	upper half	lower half	upper half
Anthonotha macrophylla	4		2	
Anthonotha triplomeris			2	
Aphanocalyx djumaensis	6			
Aphanocalyx heitzii			1	
Aphanocalyx margininerv			4	2
Aphanocalyx microphyllus			1	
Augouardia letestui	2		6	
Baikiaea insignis	2			
Baikiaea robynsii	2			
Berlinia auriculata	1			
Berlinia bracteosa	5		4	
Bikinia media			2	
Brachystegia mildbraedii	4			
Crudia gabonensis	3			
Crudia harmsiana				
Cryptosepalum staudtii	10	1		
Cynometra schlechteri	3			
Erythrophleum ivorense			1	
Eurypetalum batesii		1	6	2
Gilbertiodendron brachystegioides			3	
Gilbertiodendron dewevrei			2	
Gilbertiodendron grandistipulatum	3			
Gilbertiodendron ogoouense			6	
Gilbertiodendron preusii			4	
Gilletiodendron pierreanum			1	1
Guibourtia demeusii	7	2		
Hymenostegia felicis			2	
Hymenostegia klainei	2		4	
Hymenostegia pellegrinii	2	2	4	
Julbernardia brieyi	8			
Julbernardia pellegri	2		10	7
Julbernardia seretii	2		1	
Leonardoxa africana			3	
Librevillea klainei			1	
Neochevalierodendron stephanii	4	4	2	5
Oddoniodendron micranthum	2	1	1	
Pellegriniodendron diphyllum	2	2	2	
Scorodophloeus zenkeri	2		2	11
Sindoropsis letestui	1	4	1	5
Tessmannia anomala	1			
Tessmannia dewildemania	1			
Tetraberlinia bifoliolata	2	1	1	
Total no. of species	26	9	25	7

So, the presence of water in the streams primarily determines the distribution of the Caesalpinioideae in Lopé, i.e. the situation during the cool dry season. But this situation does not explain why the Caesalpinioideae restricted to the Lopé Upland are not present in the Sandy Lowland. It also does not explain why they are restricted to the bottoms of the narrow valleys. During the cool dry season drought stress in the upland is low or absent, because it is frequently shrouded in mist. The mist provides sufficient moisture to continue through-flow seepage at the colluvial slope-units. This shows that through-flow from the summit along the slope is not interrupted during the cool dry season. This observation also excludes the possibility that the streams are fed only with water by deep percolation at ground water level, because through-flow seepage at the colluvial slope-unit is situated above the ground water level (Fig. 3.5).

Mitendi and narrow valleys

In Mitendi, a difference in species composition was also recorded between the Mitendi Upland and the Dissected Lowland (macro-habitat). Like in Lopé, this also cannot be attributed to a difference in micro-habitat, because all species were recorded at the colluvial/alluvial slope-units. The difference in species composition between the two land-units is only partly explained by the exclusive habitat of wide valleys in the Dissected Lowland, i.e. a difference in meso-habitat (slope-profile). 11 species were restricted to the Dissected Lowland of which only 5 were restricted to the wide valleys, the remaining 6 species were present in the narrow valleys within the Dissected Lowland (Table 3.1).

The narrow valleys in the Mitendi Upland have a higher altitude and they are deeper than those of the Dissected Lowland. This difference could explain the difference in species composition. However, this difference is also shared with the Lopé Upland which is most similar in species composition to the Dissected Lowland (Fig. 4.5). If altitude and depth of the valleys determined species distributions, than the narrow valleys of the Mitendi Upland and the Lopé Upland should have been most similar.

The difference in species composition between the narrow valleys of the three land-units does not reflect the differences in habitat. Subsequently, these differences can be considered as three random walks in ecological space. This means that all species in the narrow valleys are equally competitive. Consequently, their presence and abundance in the narrow valleys is determined by random population dynamics like local extinction and dispersal events. However, their restriction to the colluvial/alluvial slope-units is not determined at random, because in all three land-units they are not homogenously distributed among the slope-profile. The same distribution response in all three land-units by equally competitive species suggests that their restriction to the bottom of valleys is caused by the same mechanism.

Drought stress during the hot dry season is considered to be this principle mechanism, because during the dry season in a low rainfall area in Panama soil matrix potentials remained positive at valley bottoms unlike outside the valleys on the plateau (Daws et al., 2002). The Dissected Lowland is also a dissected plateau and closely resembles the situation in Panama. The upper part of the Dissected Lowland is much more exposed to solar radiation during the hot dry season than the narrow valleys. A longer exposure to direct solar radiation increases the loss of moisture from the soil-plant complex by evapotranspiration (i.e. desiccation).

Table 3.3. Species abundances in number of plots (as defined under “sampling”) in narrow and wide valleys in the Mitendi Dissected Lowland. MD-n: Mitendi Dissected narrow valley, MD-w: Mitendi Dissected wide valley. *: not exclusively restricted along streams.

	MD-n	**MD-w**
Hymenostegia pellegrinii	3	
Anthonotha triplomeris	2	
Pellegriniodendron diphyllum	2	
Crudia harmsiana	1	
Hymenostegia klainei	5	1
*Scorodophloeus zenkeri**	4	1
*Julbernardia pellegriniana**	3	9
Augouardia letestui	2	6
*Sindoropsis letestui**	2	3
Eurypetalum batesii	2	2
Aphanocalyx margininervatus	1	3
*Neochevalierodendron stephanii**	1	2
Gilletiodendron pierreanum	1	1
Gilbertiodendron ogoouense		7
Berlinia bracteosa		6
Hymenostegia felicis		2
Julbernardia seretii		1
Librevillea klainei		1
Anthonotha macrophylla		1
Total no. of species	13	15

Similarly, the summits and ridges of the Lopé and Mitendi Upland are also more subjected to desiccation, and hence soil matrix potentials will be lower (negative) than in the narrow valleys during the hot dry season. The greater exposure at the “open” Escarpment slope-profile would also explain the absence of Caesalpinioideae at the colluvial slope-unit of this slope-profile. Furthermore, species restricted to narrow valleys in Lopé and Mitendi and present elsewhere outside Lopé and Mitendi are not restricted to narrow valleys (Aubréville, 1968; Evrard, 1968; Letouzey, 1968; Newbery et al., 1988; Newbery & Gartland, 1996; Wieringa, 1999). Therefore, their restriction to narrow valleys in both low rainfall areas is a strong indication that they are restricted because of drought stress and not because of habitat requirement.

Wide valleys

Species composition between the wide valleys of the Dissected Lowland and Sandy Lowland showed a low similarity (0.29). This difference in species composition is not neutral and explained by the difference in regolith between the two land-units (macro-habitat). The near absence of Caesalpinioideae species in the wide valleys of the Seasonal Sandy Lowland was already explained by the dried-up streams during the cool dry season. But dried-up streams cannot explain the absence of Caesalpinioideae species in the Clayey Lowland. In fact, except for the difference in regolith the Clayey Lowland resembles the Sandy Lowland in relief, altitude and grass as the dominant vegetation (Fig. 3.4). The gallery forest of the Sandy Lowland is inhabited by 17 species of Caesalpinioideae whereas in the Clayey Lowland it virtually consists of the semi-deciduous tree species *Aucoumea klaineana* Harms. This indicates the presence of drought stress along these permanent streams.

Exposure to desiccation in the wide valleys is higher than in the narrow valleys as trees are exposed during the whole day. Evergreen tree species like the Caesalpinioideae can only cope with drought stress (i.e. high evapotranspiration rates) by transpiring more soil moisture, because they cannot shed their leaves like deciduous tree species. Water uptake is obtained by extending their root system (Heilmeier et al., 1997; McIntrye et al., 1995; Pritchard et al., 2000), i.e. by growing rootlets into water-filled macropores (e.g. (Singer & Munns, 1992). The total volume of macropores is higher in sandy soils than in clayey soils. The coarser texture of sandy soils facilitates the infiltration of rain water, but for the same reason it also retains less soil moisture (i.e. a lower retention capacity). However, in this case the banks along all the permanent streams are kept at field capacity (i.e. no negative soil matrix potentials) by influent seepage.

All streams are kept at field capacity, but the total amount of soil moisture available is not the same. This depends on the size of the streams and the regolith the water passes through. Larger streams are able to “irrigate” larger volumes along their streambed by influent seepage, because the water pressure is higher than along smaller streams (e.g. Bras, 1990). Similarly, in sandy soils (regolith) more water from the streams is able to filtrate, because of their open texture compared to clayey soils. In other words, at the colluvial and alluvial slope-units of the Sandy Lowland more soil moisture is available than along the Clayey Lowland or Dissected Lowland. Therefore, the higher number of Caesalpinioideae species in the Sandy Lowland can be explained by a higher availability of soil moisture to compensate for the high transpiration, i.e. the higher total volume of water-filled macropores.

The difference in species richness of Caesalpinioideae between the Clayey Lowland and Dissected Lowland and the presence of a closed-canopy forest in the Dissected Lowland may also be explained by a difference in total volume of macropores. The Dissected Lowland has been more eroded by the same streams than the Clayey Lowland. This difference in erosion shows that the regolith of the Dissected Lowland is less stable that of the Clayey Lowland. Stability is, among other factors, determined by the amount of macropores. This explains why sandy formations are less stable and in this case why the Dissected Lowland is more eroded than the Clayey Lowland. A higher total volume of macropores in the clayey regolith of the Dissected Lowland as compared to the clayey regolith of the Clayey Lowland also predicts a higher water availability.

Hot dry season versus cool dry season

The two dry seasons have a different influence on the distribution of the Caesalpinioideae. The complete absence of rainfall in the cool dry season causes the streams in the Seasonal Sandy Lowland to dry up as a result of which there are very few Caesalpinioideae tree species present in that land-unit. The difference between narrow and wide valleys is mainly determined by drought stress during the hot dry season. During the hot dry season canopy trees in wide valleys are more exposed to direct solar radiation than trees in narrow valleys.

The hot dry season eliminates the possibility that a difference in drought stress during the cool dry season between the upland and the lowland can be seen as an explanation for the differences in Caesalpinioideae richness and composition. If only the cool dry season existed, Caesalpinioideae tree species would probably not be restricted to the narrow valleys in the upland, as the upland is frequently shrouded in mist and no drought stress would exist. But now drought sensitive Caesalpinioideae tree species are restricted to the narrow valleys because of the hot dry season.

But, whatever the impact of the cool and hot dry season on the distribution of the Caesalpinioideae tree species in this part of Gabon, without the upland both the Lopé and Mitendi sites would have been much poorer in Caesalpinioideae tree species. Without the upland streams the lowland would have dried up during the cool dry season, and the situation now limited to the Seasonal Sandy Lowland would apply to the entire area. Similarly, without the upland there would be no narrow valleys where the Caesalpinioideae tree species could find refuge against the desiccating effect of the direct solar radiation during the hot dry season. This shows that hydrology and geomorphology can provide local compensation when regional climate conditions cause drought stress at a regional scale.

Future global warming will lower mean annual rainfall and increase the length of the hot dry season in the tropical latitudes. In such a case the African lowland rain forest will shrink and drought-sensitive species will highly depend on local relief and hydrological features such as narrow valleys. The opposite, global cooling, would also cause the African lowland rain forest to shrink as mean annual rainfall will also become lower and the cool dry season longer. In such a case drought-sensitive species would highly depend on the presence of permanent streams and rivers or on elevated areas where drought stress would be reduced by mist.

3.5 Conclusions

Two low rainfall areas straddle different geological formations with different characteristics in altitude, relief, hydrology and regolith. The vast majority of the Caesalpinioideae species were not homogeneously distributed over these geological formations resulting in differences in species composition and richness. The differences between land-units could be retracted to differences in relief and more particularly to a difference in shape valley. Soil matrix potentials were not measured. Differences in drought stress within and between catchments were deduced by applying drainage basin hydrology. By this catchment-approach it could be established that drought stress is the principle force determining the distribution of the Caesalpinioideae species in these two low rainfall areas.

In Gabon, the hot dry season is not as severe as the cool dry season, according to the conventions of Walter and Lieth (1960). It is shorter and rainfall does not cease completely. Nevertheless, the hot dry season seems to have a stronger influence on the distribution of the Caesalpinioideae, since strong evapotranspiration during this period keeps most of the Caesalpinioideae restricted to the lower parts of the catchments. But the impact of the cool dry season is obscured by the upland. This geological formation acts as a large container of soil moisture irrigating the adjacent lowland. Without this drainage water Caesalpinioideae species richness in Lopé and Mitendi would have been much lower.

Studies on species richness and species distributions dealing with drought stress usually deal with many data points over a regional rainfall gradient, data points with the size of Lopé and Mitendi (Bongers et al., 1999; Gentry, 1988; Linder, 2001; Swaine, 1996; Van Rompaey, 1993). Studying the present two “data points” at a smaller scale revealed that species richness and distributions are determined in a much more complex way, and are not only related to climatic factors, but also to the underlying bedrock and associated soils, relief, and hydrology.

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Chapter 4 The Holocene expansion and microrefugia

4.1 Introduction

During the Last Glacial Maximum (LGM) the Arctic polar ice sheet was larger than today and subsequently cold-sensitive species from north and central Europe migrated south to areas in Spain, Italy, Greece and the Balkan (e.g. Hewitt, 1999). During the Holocene, after the end of the last ice age, these species migrated northwards again, which is referred to as the Holocene Expansion (Clark, 1998). A similar range expansion occurred in equatorial Africa after drought-sensitive forest species had become restricted to forest refuge areas during the LGM as a result of a drier climate (Fig. 1.3; Maley, 1996).

After the end of the last ice age, the forest refuge areas merged and the African lowland rain forest continued to expand. In the early Holocene the forest even bridged the Dahomey Gap (Dupont & Weinelt, 1996; Toussou, 2002). Later, in the mid-Holocene (6000 yrs BP), its distribution became smaller as the meteorological equator was situated further north over the Sahara. This exposed the southern part of the African lowland rain forest to a drier climatic regime (Prentice et al., 2000). In the late Holocene (some 2,500 yrs BP) parts of the Atlantic Central African rain forest became disturbed due to an arid climatic event (Elenga et al., 1991; Reynaud & Maley, 1994; Schwartz et al., 1990; Vincens et al., 1999). This arid climatic event is hereafter referred to as the Late Holocene Perturbation (LHP).

The forest expanded after the disturbances during the LGM and LHP by colonising the surrounding savanna-dominated landscape until forest fragments were united. At present, a large complex of forest-savanna mosaics still exists within the Gabonese rain forest and of which the Lopé and Mitendi study sites are part (Fig. 4.1). The forest around the savanna patches is dominated by the tree species *Aucoumea klaineana* Harms (Burseraceae). This canopy tree species is a savanna coloniser (White et al., 2000). The closed canopy forest which this species presently forms, indicates that in the recent past (one generation ago) the savanna complex was larger than today.

At present, the savanna patches persist because rainfall is low and because colonisation by the surrounding forest is prevented by frequent burning. In and around the savanna patches Caesalpinioideae tree species with a ballistic seed dispersal are present along streams (White, 1992; White & Abernethy, 1997). Caesalpinioideae tree species are considered to be late successional species because they expand their range slowly and because they are drought-sensitive (Chapter 3). As late successional species, they are among the last species to arrive in the forest expansion process, but yet they occur together with an early successional tree species such as *Aucoumea klaineana*.

There are two possibilities which may explain the presence of Caesalpinioideae with a ballistic seed dispersal intermixed with the wind-dispersed *Aucoumea klaineana* savanna-coloniser. The Caesalpinioideae could have arrived in Lopé and Mitendi by dispersal during the Holocene (the expansion scenario), or they were never restricted to the closest refuge area, the Chaillu Massif, and survived the LGM and LHP in situ (the in-situ scenario).

The traditional expansion scenario is that the evergreen rain forest in Gabon became restricted to refuge areas, in this case the Chaillu Massif (Fig. 4.1). This means that evergreen tree species, such as the Caesalpinioideae species became locally extinct in Mitendi and Lopé. In the early Holocene the forest expanded and during this period the Caesalpinioideae with ballistic seed dispersal must have reached Lopé and Mitendi. Later, during the LHP, the forest became disturbed and patches of forest along rivers and streams survived (like in SE Asia after el Niño-years) where Caesalpinioideae persisted. The alternative in-situ scenario is that the Caesalpinioideae persisted in Lopé and Mitendi and never became restricted to the Chaillu Massif.

The expansion scenario assumes that the Caesalpinioideae expanded their range from the Chaillu Massif by their normal ballistic seed dispersal. This appears not very probable. The maximum possible distance a Caesalpinioideae species can have covered since the LGM and during the Holocene is 36 km (18,000 yrs BP; Leal, 2001). The distance by the same calculation from the start of the Holocene to the mid-Holocene, (6,000 yrs BP) would be 12 km. This is not sufficient to arrive in Lopé from the closest refuge area, the Chaillu Massif, some 100 km further south. Secondary dispersal by rodents potentially adds 25 m (Jansen, 2003) to the 60 m dispersal distance per generation (van der Burgt, 1997), but even enlarging the distance to 100 m is not sufficient as then the maximum range expansion distance is only 20 km.

Many of these Caesalpinioideae were observed along streams and rivers (White, 1992; White & Abernethy, 1997) and secondary long-distance dispersal by water has been shown to facilitate fast range expansion (Cain et al., 2000; Campbell et al., 2002; Thébaud & Debussche, 1991). Occasional long-distance dispersal events, however, are difficult to observe (Cain et al., 2000) and their occurrence can only be established indirectly by testing whether species richness and composition are in equilibrium with present-day environment. If the Caesalpinioideae in Lopé and Mitendi reflect an equilibrium situation, then occasional long-distance dispersal must have occurred, when assuming the expansion scenario is correct.

In an equilibrium situation species composition is solely determined by the result of physiological limitations and competitive interactions (Krebs, 1985). Subsequently, similar “habitat” or environment in Lopé and Mitendi should have a “similar” species richness and composition. For instance, the narrow valleys in the upland of Lopé and Mitendi are characterized by the same regolith, altitude, depth of valley and valley shape. Therefore, species composition should show only minor differences. Ecological data in terms of species composition generally tends to vary with distance and within the same environment.

In Panama the change in species composition (species turnover) between adjacent one-hectare plots was only 30 % (Sørensen index value of 0.7). But over longer distances (beta-diversity) species turnover decayed rapidly (Sørensen index value of 0.1-0.15) which was explained by high habitat variation over distance (Condit et al., 2002). Species turnover in the western Amazon was more constant with Sørensen index values between 0.3-0.4 (30%) as habitat showed low variation (Condit et al., 2002).

If the Caesalpinioideae are not in equilibrium with present-day factors then it is possible that they are still expanding their range. Therefore, the two areas were aligned along the postulated line of the forest expansion during the Holocene from the Chaillu Massif northward to Mitendi and Lopé. To assess whether the Caesalpinioideae with ballistic seed dispersal reflect environmental conditions (an equilibrium situation), historical contingency or succession (a non-equilibrium situation), the species richness and composition between Lopé and Mitendi were compared.

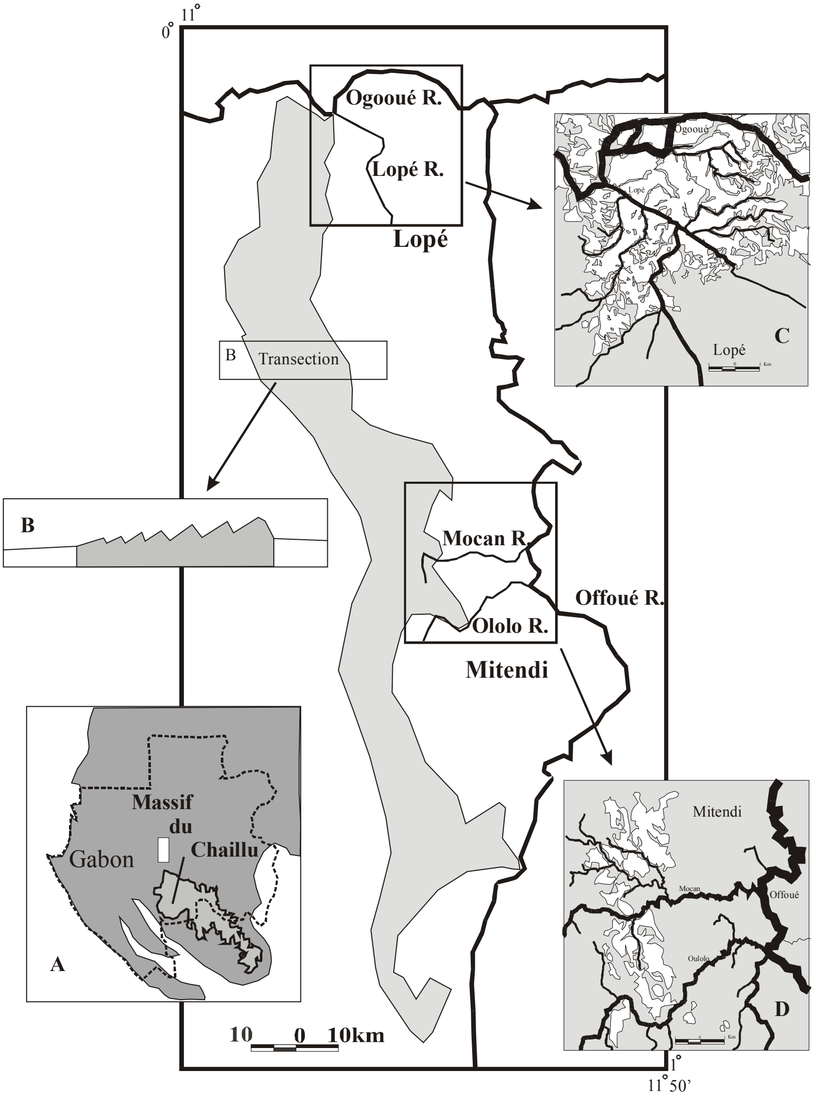


Fig. 4.1. Location of the two study sites, Lopé (C) and Mitendi (D) in Gabon (A). The connection with the closest refuge area by the major streams and rivers and the low altitudinal folding zone (400 -700 m; shaded) are indicated. A cross-section of the shaded area shows the ruggedness of the folding zone flanked on both sides by a gentler geomorphology (B). A schematic view of the study sites is given in Fig. 3.4. Within each site the plots form a polygon with a maximum distance of 10 km between most distance plots.

4.2 Study sites and methods

Study sites and Caesalpinioideae

The study sites are briefly described and placed in a context of the Holocene expansion. The two study sites, Lopé (0°12'S, 11°36'E) and Mitendi (0°35'S, 11°41'E), are part of a larger forest-savanna complex in central Gabon. In the previous chapter Lopé and Mitendi were classified at landscape level into six land-units (Chapter 3). In this chapter the land-units where the Caesalpinioideae were absent or almost absent were excluded, i.e. the Sandy Seasonal Lowland and the Clayey Lowland. The four remaining land-units the Lopé Upland, Sandy Lowland, Mitendi Lowland and Dissected Lowland served to test whether their species richness and composition reflected equilibrium with "habitat".

Habitat in the land-units was classified into slope-profile (meso-habitat) and slope-units (micro-habitat; see Chapter 3). All the Caesalpinioideae in the four land-units were recorded at the colluvial and alluvial slope-units of permanent streams. Differences in species composition between land-units were explained in more detail as differences between narrow and wide valleys (Chapter 3). The differences between narrow and wide valleys were related to differences in exposure to direct solar radiation during the hot dry season. In this case emphasis is on the "habitat" or environment they represent and how their characteristics determine the distribution of the Caesalpinioideae tree species.

Equilibrium vs. non-equilibrium

The two most similar land-units in terms of abiotic characteristics are the Lopé and Mitendi Upland. They have the same clayey regolith, altitude and geomorphology (Prain et al., 1990). The largest difference is between the Sandy Lowland, and the other three land-units, because of its sandy regolith and gentle relief. The Dissected Lowland is mixture of the two study sites on a smaller scale, with both wide and narrow valleys. The species richness and composition were determined for the two types of valleys and compared with the narrow and wide valleys of the other land-units.

Sørensen similarity indices were calculated to establish which habitat-units were most similar. The indices were not tested with permutation simulations to verify whether they represented a genuine signal, because it was already shown that the Caesalpinioideae were not homogenously distributed over the land-units and wide/ narrow valleys (Chapter 3). Within a study site (short distance) Sørensen similarity index values between similar habitat-units above 0.7 (70%) were considered as neutral variation (random walks in ecological space), and between study sites (long distance) a value above 0.3 was considered as neutral according to the findings of Condit et al. (2002) in South America.

A non-equilibrium situation may indicate that the Caesalpinioideae tree species are still expanding their range. Therefore, also riverine range expansion was tested. For the Caesalpinioideae tree species to have arrived from the Chaillu Massif in Mitendi and Lopé they must have come down stream along the Offoué and partly along the Ogooué. From there on they colonised the smaller streams upstream into Mitendi and Lopé (Table 4.3D). As a consequence, species composition in Lopé would be a subset of the species present in Mitendi and similarly species along smaller streams a subset of species present along the Offoué and Ogooué.

Table 4.1. Number of species and plots per slope-unit (A), number of species per type of slope-profile (B).

A

slope-unit	species	plots
1: summit	2	10 (7.9%)
2: fall face	0	0
6: transp.	4	14 (11.1%)
3: colluvial	42	43 (43.1%)
4: alluvial	41	59 (46.8%)
5: channel	0	0

B

	Lopé	Mitendi	
Escarpment	3	1	
Wide valley	17 (LS)	11 (MD-w)	
Narrow valley	17 (LU)	18 (MU)	14 (MD-n)

4.3 Results

Species richness

In total 42 Caesalpinioideae tree species were recorded in 126 plots, 27 species in Lopé, and 29 species in Mitendi (Appendix 1). All four land-units were almost equally species-rich: 17 species in the Lopé Upland, 17 species in the adjacent Sandy Lowland, 18 species in the Mitendi Upland, and 19 species in the Dissected Lowland (Table 4.1B). All four land-units were sufficiently sampled (Fig. 3.6).

The three slope-profiles differed in species richness (Table 4.1 B), as well as the slope-units within each profile (Table 4.1 A). The Caesalpinioideae showed a strong preference for the lower slope-units: 81 % of all 126 plots were situated at a colluvial and alluvial slope-unit. The remaining 24 plots (19 %) were located at or near the summit of the upland. The escarpment slope-profile was very species poor in contrast with the narrow and wide valleys (Table 4.1 B).

Land-units

Species composition varied remarkably between the Mitendi and Lopé site and between the four land-units. 13 of the 27 species (48%) in Lopé were restricted to or "endemic" for Lopé and in Mitendi 14 of the 29 species (48%). Only two species were present in all four land-units (Table 4.2). The Sørensen similarity index values (Fig. 4.2 and Table 4.2) were lower between the Lopé Upland and Mitendi Upland (0.34), than between the Lopé Upland and the Dissected Lowland in Mitendi (0.50). Values between lowland and upland within a site were almost equal (0.41 and 0.43 in Lopé and Mitendi, respectively) and similarly, within upland and lowland between Mitendi and Lopé (0.34 and 0.33, respectively). The lowest value was between the Mitendi Upland and the Sandy Lowland (0.11).

Narrow versus wide valleys

The Mitendi Dissected Lowland (MD) was analysed separately having both narrow (MD-n) and wide valleys (MD-w; Fig. 4.2 B and Table 4.2). Species richness in the narrow and wide valleys was almost similar, 14 and 11 species, respectively, but species composition was considerably different (Sørensen similarity index 0.43). The narrow valleys (MD-n) of the Dissected Lowland showed a higher similarity with the narrow valleys of the Lopé Upland (0.60) than with the close by narrow valleys of the Mitendi Upland (0.44). Wide valleys (MD-w) differed considerable in species composition with the wide valleys of the Sandy Lowland (0.29).

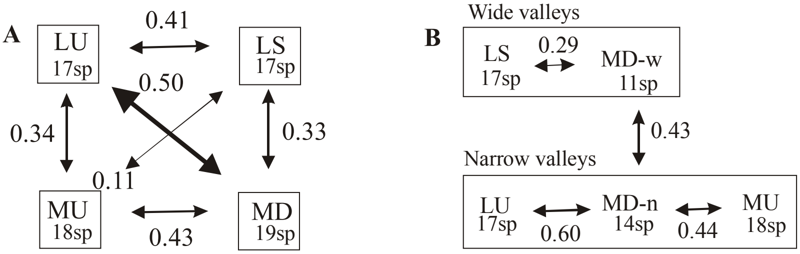


Fig. 4.2. Sørensen similarity values between the four land-units (A), and between narrow and wide valleys (B). LU: Lopé Upland, LS: Lopé Sandy lowland, MU: Mitendi Upland, MD: Mitendi Dissected lowland, MD-w: MD wide valleys, MD-n: MD narrow valleys. Sørensen index is $S_{12}/[0.5(S_1+S_2)]$ where S_{12} is the number of shared species between two sites (e.g. LU and LS) and S_1 is the total number of species in site 1 (LU) and similarly S_2 (LS).

Riverine range expansion

The plots were aligned along the postulated range expansion routes given in Table 4.3D. It shows that species composition of the narrow valleys in the Dissected Lowland and Mitendi Upland are not a subset of the species occurring downstream along the Ololo, Mocan or Offoué River. Species such as *Aphanocalyx margininervatus*, *Eurypetalum batesii* or *Julbernardia pellegriniana*, which are present in narrow as well as in wide valleys, may have obtained their current distribution by expanding their range upstream. But there are other species, e.g. *Anthonotha triplomeris*, *Pellegriniodendron diphyllum* or *Oddoniodendron micranthum*, which are exclusively present in narrow valleys.

A similar observation is made when going from the Offoué River in Mitendi to Lopé. Species composition along the Ogooué River is completely different from the species composition along the Offoué River (Table 4.3C). Also species composition in the narrow valleys of Lopé Upland is not a subset of the intermediate streams in the Sandy Lowland, Ogooué or Offoué River (Table 4.3C).

The only species in Lopé which may have expanded their range from the Ogooué River upstream into the Sandy Lowland are *Guibourtia demeusii* and *Aphanocalyx djumaensis*. They are both present along the Ogooué and Lopé River, but there are other species such as *Berlinia bracteosa* or *Tessmannia dewildemania*, which are only present along the Lopé River, and other species such as *Oddoniodendron micranthum* or *Tertraberlinia bifoliolata*, which are only present in the Lopé Upland.

Occasional long-distance seed dispersal events other than by water were not considered very probable, because there were no Caesalpinioideae tree species with a ballistic seed dispersal present in the inter-fluvial forest patches. The distance between these forest patches and the riverine forest with Caesalpinioideae was sometimes not more than one hundred metres. This is in contrast to wind or animal-dispersed Caesalpinioideae tree species such as *Hylodendron gabunense* Taub., *Distemonanthus benthamianus* Baill. or *Detarium macrocarpum* Harms which were present in both riverine forest and inter-fluvial forest patches.

Table 4.2. Differences in species composition between the four land-units, and species composition of the narrow and wide valleys. LU: Lopé Upland, LS: Lopé Sandy lowland, MU: Mitendi Upland, MD: Mitendi Dissected lowland, MD-w: MD wide valleys, MD-n: MD narrow valleys. For explanation of the species abbreviations see Appendix 1. Framed species are “endemic” for a land-unit or slope-profile.

	LS	**LU**	**MD**	**MU**
Neo ste	1	1	1	1
Sco zen	1	1	1	1
Pel dip	1	1	1	
Jul pel		1	1	1
Eur bat		1	1	1
Sin let		1	1	1
Bai ins	1	1		
Bra mil	1	1		
Cry sta	1	1		
Gui dem	1	1		
Ant mac	1		1	
Ber bra	1		1	
Hym kla	1		1	
Jul ser		1	1	
Aug let		1	1	
Hym pel		1	1	
Odd mic		1		1
Tet bif		1		1
Aph mar			1	1
Cru har			1	1
Gil ogo			1	1
Aph dju	1			
Bai rob	1			
Cru gab	1			
Cyn sch	1			
Gil gra	1			
Jul bri	1			
Tes dew	1			
Tes ano		1		
Ber aur		1		
Ant tri			1	
Gil pie			1	
Hym fel			1	
Lib kla			1	
Aph hei				1
Aph mic				1
Bik med				1
Ery ivo				1
Gil bra				1
Gil dew				1
Gil pre				1
Leo afr				1

	LS	**MD-w**	**LU**	**MD-n**	**MU**
Eur bat		1	1	1	1
Jul pel		1	1	1	1
Aug let		1	1	1	
Ant mac	1	1			
Ber bra	1	1			
Hym kla	1	1		1	
Bai ins	1		1		
Bra mil	1		1		
Cry sta	1		1		
Gui dem	1		1		
Pel dip	1		1	1	
Neo ste	1		1	1	1
Sco zen	1		1	1	1
Sin let			1	1	1
Aph mar		1		1	1
Gil ogo		1			1
Gil pie		1		1	
Hym pel			1	1	
Jul ser			1	1	
Odd mic			1		1
Tet bif			1		1
Cru har				1	1
Aph dju	1				
Bai rob	1				
Cru gab	1				
Cyn sch	1				
Gil gra	1				
Jul bri	1				
Tes dew	1				
Hym fel		1			
Lib kla		1			
Tes ano			1		
Ber aur			1		
Ant tri				1	
Aph hei					1
Aph mic					1
Bik med					1
Ery ivo					1
Gil bra					1
Gil dew					1
Gil pre					1
Leo afr					1

4.4 Discussion

Species composition

Species composition of the four land-units (MU, MD, LU, LS) differed considerably (Fig. 4.2 A, Table 4.2). Shared species varied from 11% (0.11) between the Mitendi Upland and Sandy Lowland to 50% (0.50) between the Lopé Upland and Dissected Lowland. With Sørensen index values well below the 0.7 (70%) differences in species composition between the land-units should be well explained by habitat variation as was the case in Panama (Condit et al., 2002).

The dissimilarity in species composition between the Lopé Upland and Sandy Lowland (0.41) can be attributed to differences in regolith, valley shape and altitude. Similarly, in Mitendi differences in altitude, regolith and the presence of wide valleys could explain the difference in species composition between the Dissected Lowland and Mitendi Upland (0.43). When comparing only the narrow valleys of the Dissected Lowland with those of the Mitendi Upland the Sørensen index value slightly increases from 0.43 to 0.44.

The Lopé Upland and Mitendi Upland share only 34 % of their species. This species turnover with distance (beta-diversity) within the same geological formation is comparable with values observed in the Amazon (Condit et al., 2002). In the Amazon this value remained fairly constant with distance, which might be expected in a lowland rain forest with little habitat variation. The same may also be valid within the upland as a geological formation where characteristics like regolith, altitude and relief changes little. However, the Lopé Upland shares 60% of its species with the narrow valleys of the Dissected Lowland. The only habitat they share is the shape of the narrow valleys (meso-habitat).

Non-equilibrium

The Mitendi Upland, Lopé Upland and Dissected Lowland only share the habitat of narrow valleys. If the presence of this habitat would explain the higher similarity in species composition between the Dissected Lowland and Lopé Upland, than it remains unexplained why there is a larger difference with the more close by narrow valleys of the Mitendi Upland. It was already suggested that differences in species composition between these narrow valleys were neutral and did not reflect any differences in environment, so-called random walks in ecological space (Chapter 3).

When considerable differences in species composition like in this case do not reflect differences in habitat or environment they are considered to represent a non-equilibrium. The question is how this non-equilibrium could have developed. Condit and colleagues (2002) suggested that the species turnover they observed was influenced by dispersal limitation and speciation. This is also supported by the theory of island biogeography and simulations (MacArthur & Wilson, 1967; Ricklefs & Schluter, 1993). An equilibrium in species diversity between islands can only exist when species are able to disperse between them.

The Caesalpinioideae with a ballistic seed dispersal have a very limited seed dispersal (van der Burgt, 1997) and the narrow valleys in the land-units can be considered as islands. When seed dispersal between the narrow valleys of the three land-units is rare, than differences in species composition can be explained by speciation, extinction events or occasional long-distance seed dispersal events. Local speciation is not very likely since all species also are present outside Lopé and Mitendi.

Table 4.3. Species composition of postulated migration routes (A, B, and C) along the streams in Mitendi and Lopé. Arrows indicate migration directions. Off.: Offoué River, Og.: Ogooué River, Lopé: Lope River, Olo.: End of Ololo River, Mid.: intermediate Ololo River, Nar.: narrow valleys. Moc.: Mocan River. Mid.: intermediate streams, MU1: Mitendi Upland valley mouth, MU 2: idem, middle of valley, MU3: idem, end of the valley. Framed species are “endemic” to a section of a river or stream.

A

	Off.	**Olo.**	**Mid.**	**Nar.**
Hym kla	1			
Hym fel	1			
Lib kla	1			
Aph mar	1			1
Gil pie	1			1
Gil ogo	1	1		
Eur bat	1	1	1	1
Jul pel	1	1	1	1
Ber bra		1		
Hym pel			1	1
Jul ser			1	
Sco zen			1	1
Sin let			1	1
Cru har				1
Ant tri				1
Pel dip				1

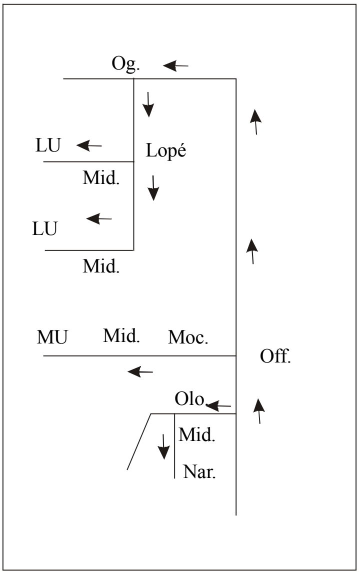
B

	Off.	**Moc.**	**Mid.**	**MU 1**	**MU 2**	**MU 3**
Hym kla	1					
Hym fel	1					
Lib kla	1					
Aph mar	1				1	
Gil pie	1				1	
Eur bat	1				1	
Jul pel	1	1	1	1	1	1
Gil ogo	1	1		1		
Ant mac		1				
Ber bra		1				
Aug let		1	1			
Neo ste			1	1	1	
Sin let			1		1	1
Sco zen				1	1	1
Gil bra				1		1
Gil pre				1		
Ery ivo				1		
Bik med					1	1
Gil bra					1	
Leo afr					1	
Cru har					1	
Gil dew					1	
Tet bif						1
Aph heit						1
Odd mic						1

C

	Off.	**Og.**	**Lopé**	**Mid.**	**LU**
Aph mar	1				
Hym fel	1				
Lib kla	1				
Gil pie	1				
Gil ogo	1				
Eur bat	1				
Jul pel	1				
Hym kla	1			1	
Aph dju		1	1		
Cyn sch		1			
Bai rob		1			
Gui dem		1		1	1
Cry sta			1	1	1
Neo ste			1	1	1
Pel dip			1	1	1
Sco zen			1		1
Cru gab			1	1	
Jul bri			1	1	
Tes dew			1		
Ber bra				1	
Ant mac				1	
Bra mil				1	1
Tet bif					1
Odd mic					1
Sin let					1
Jul pel					1
Ber aur					1
Hym pel					1
Tes ano					1
Aug let					1
Jul ser					1

D



Range expansion

Occasional long-distance seed dispersal events are rare and it is possible that not enough time has passed for an equilibrium situation to have settled. Present-day differences may reflect an intermediate situation. Species may still be developing towards an equilibrium situation, i.e. expanding their range. This expansion scenario implies that species richness is highest along the Offoué and Ogooué from where species richness gradually decreases upstream into the narrow valleys of the Dissected Lowland and Mitendi and Lopé Upland.

But species composition along the Ogooué River is not a subset of the species composition along the Offoué. Similarly, species composition in the Lopé Upland is not a subset of the species composition in the Sandy Lowland. In other words, the shift and differences in species composition along the streams and in the different land-units does not support the scenario that the Caesalpinioideae tree species arrived from the Chaillu Massif via rivers and streams and are still expanding their range (Table 4.2 and 4.3). Hence, local extinction events are the most plausible explanation of the observed distribution patterns.

Local extinctions

The most likely periods for local extinctions to have occured are the Late Holocene Perturbation and the Last Glacial Maximum. However, the Lopé forest-savanna mosaic dates from the start of the Holocene (Peyrot et al., 2003). This means that the Lopé forest-savanna mosaic already existed before and during the early Holocene. According to the expansion scenario species now present in the upland arrived along the streams through the lowland (Sandy Lowland). Presently, these upland species are absent in the lowland, because the "habitat" is not suitable in terms of regolith, altitude or relief. However, if the lowland is not suitable at present, it was also unsuitable during the early Holocene. This means that range expansion during the first half of the Holocene is not very probable.

4.5 Conclusions

In Lopé and Mitendi Caesalpinioideae with a ballistic seed dispersal were observed intermixed with wind-dispersed savanna colonisers such as *Aucoumea klaineana*. Two scenarios were hypothesized. The expansion scenario meant that the Caesalpinioideae were restricted to the closest forest refuge area during the LGM and expanded their range during the first half of the Holocene. Expansion by their normal and secondary rodent dispersal was already dismissed.

Occasional long-distance seed dispersal events by water in the first half of the Holocene could have created an equilibrium situation in Lopé and Mitendi. But this hypothetical equilibrium situation no longer exists, because the large present-day differences in species composition between the narrow valleys are neutral. A still ongoing range expansion of the Caesalpinioideae along streams is also not substantiated.

The only differences in species composition which can be explained by differences in habitat (environment) are within site differences, i.e. between the Lopé Upland and Sandy Lowland and between the wide valleys of the Dissected Lowland with the narrow valleys in the same land-unit and the Mitendi Upland. Differences in species composition between narrow valleys are not explained by species turn over with distance (beta-diversity) or environment and show the influence of historical contingencies.

These differences are explained by assuming they are the result of extinction events related with forest disturbances in the past, because for the Caesalpinioideae dispersal between land-units is non-existent. These extinction events could have happened during the relatively recent LHP. Hence, but it is much more plausible that the Caesalpinioideae never left Lopé and Mitendi during the LGM. Consequently, the in-situ scenario is more probable than the expansion scenario. This means that the present situation in Lopé and Mitendi has remained relatively unchanged since the LGM.

Survival of the Caesalpinioideae and other slow dispersing species like the refuge begonias (Sosef, 1996) outside the larger refuge area in so-called microrefugia was already suggested (Leal, 2001). However, survival in situ outside the refuge areas should not be considered common place. The fact that Caesalpinioideae species are present in these two low rainfall areas is only possible because the upland provides local compensation for the regional drought stress (Chapter 3). Without the permanent streams coming from the upland species diversity would probably have been far less. This shows that the upland, as a minor low-altitude elevated area, not only protects the forest on it but also the area around it. This may be true for elevated areas in general.

Going back to chapter 2, there was the issue whether there was a historical signal within present-day distributions patterns. The historical signal for the Caesalpinioideae consists of their absence/presence in land-units, but only when occasional long-distance seed dispersal events can be excluded. Since the Caesalpinioideae survived the LGM in situ, and long-distance dispersal events play a minor role, the presence of historical signal in their present-day distribution pattern is now confirmed. Static species like the Caesalpinioideae will have more historical signal in their present-day distributions than dynamic species.

In studies in tropical forest dealing with species turnover with distance (beta-diversity) and species similarities, variance (16-59%) within the ecological data is not explained by distance or environment (Duivenvoorde et al., 2002). This could imply that influence of historical contingencies on present-day species distribution patterns is much more important than is presently believed.

Chapter 5 Ice ages, regional species richness and endemism

5.1 Introduction

Plant species are not equally distributed within rain forests, but so-called centres of biodiversity and endemism are recognised. These centres are areas where species and endemics (species with a restricted range) are concentrated. In the African rain forest four such centres are recognised: Upper Guinea, Lower Guinea, Congolia and Kivu (Linder, 2001; White, 1979). These centres are not equally rich in species and endemics. What causes these differences is a matter of discussion between ecologists and historical biogeographers. Ecologists try to explain these patterns with present-day factors and principles like mean annual rainfall, surface area, and habitat diversity, whereas historical biogeographers focus on evolutionary processes and principles like extinction, vicariance or dispersal.

The first centres of biodiversity and endemism attributed to historical events related to Pleistocene ice ages were observed in the Amazon (Haffer, 1969; Prance, 1973), because palynological records from the Late Pleistocene showed a change from closed-canopy lowland rain forest to open forest savanna mosaics during the last ice age (van der Hammen, 1974). This suggested that the lowland rain forest had been fragmented. Not knowing where the forest fragments persisted, the overlap of species ranges were thought to show a faded trace of their location.

The idea was that in these forest fragments new species evolved (neo-endemics) and extant species survived (paleo-endemics). These species remained restricted in distribution when the forest expanded during the Holocene. In the Amazon this scenario became disputed by ecologists who showed that patterns of species richness were among others related to rainfall or other environmental factors (Gentry, 1982), and that patterns of endemism were partly caused by a bias in collection densities (Nelson et al., 1990) or related to local environmental conditions (Salo et al., 1986).

It is presently not possible to determine whether the African centres of biodiversity and endemism are mainly ecologically or historically determined, because the species samples used are a mixture of species with different biological traits (Linder, 2001; White, 1979). Differences in species richness and endemism between the three centres (Upper Guinea, Lower Guinea and Congolia) observed by White (1979) might be explained equally plausible by present-day environmental differences (mean annual rainfall, seasonality, habitat diversity, area size etc.), as by differences in evolutionary histories (more or less extinction or speciation).

To overcome this problem and to be able to discriminate better between present-day and historical factors samples should not consist of species with mixed dispersal capacity or ecology. For example, comparing the distribution patterns in the Aegean archipelago between butterflies and snails, it appeared that butterflies as dynamic species reflected present-day ecological conditions, whereas snails as static species showed a more relictual pattern (Dennis et al., 2000; Wetler-Schultes & Williams, 1999). This difference between dynamic and static species was also shown in island biogeography simulations (Haydon et al., 1993). So, the distribution patterns of static species are more likely to still show the remnant influence of historical events than those of dynamic species.

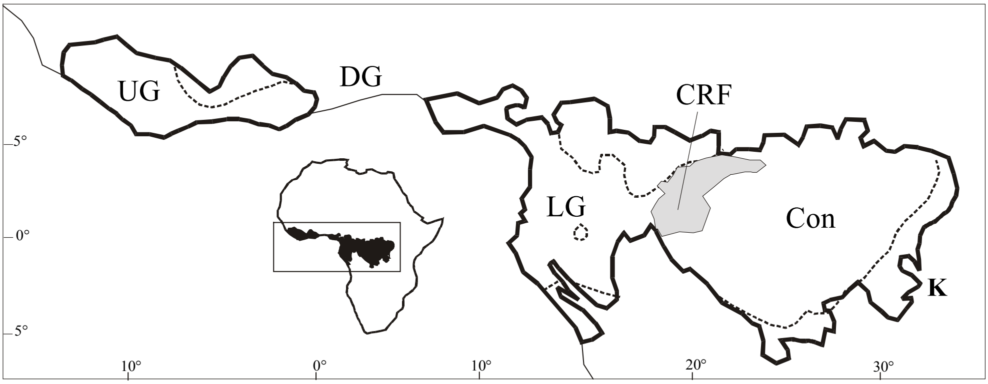


Fig. 5.1. The three lowland rain forest centres of species richness and endemism, Upper Guinea (UG), Lower Guinea (LG) and Congolia (Con) with in between the dispersal barriers, the Dahomey Gap (DG) and the Congo River Floodplain (CRF). Kivu (K) is located outside the lowland rain forest. Bold line: the outline of lowland rain forest (Mayaux et al., 2003). Dashed line: the 1600 mm per year rainfall line/isohyet.

Historical events which affected the distributions of rain forest species are the Last Glacial Maximum (LGM) and the Late Holocene Perturbation (LHP, see paragraph 4.1). During these periods the African lowland rain forest became disturbed due to a drier climate (Chapter 1). The species most likely to be affected by these forest disturbances are evergreen lowland rain forest species. With the increased drought stress they are more likely to become locally extinct than species of the deciduous lowland rain forest. Furthermore, evergreen lowland rain forest species with a limited seed dispersal capacity are also less likely to quickly expand their range during the forest expansion after large scale forest disturbances.

Most of the Caesalpinioideae are evergreen lowland rain forest tree species. The vast majority of these tree species have a ballistic seed dispersal mechanism and they are a closely related evolutionary taxonomic unit. The process of dispersal proved to have a very limited influence on their range expansion over the Holocene (Chapter 4) whereas their drought sensitivity (Chapter 3) makes them susceptible to local extinction during the LGM and LHP. These characteristics allow us to evaluate whether the biogeography of the Caesalpinioideae tree species in terms of species richness and endemism is determined mainly by history or by ecology.

5.2 Methods

The centres

Within the limits of the African rain forest four centres of species richness and endemism were recognised (Linder, 2001; White, 1979), i.e. Upper Guinea (UG), Lower Guinea (LG), Congolia (Con) and Kivu. The latter centre is only recognised by Linder (2001) and Congolia only by White (1979). The Kivu centre coincides with a mountain chain east of the lowland rain forest with an altitude above 1000 m covered with montane forest (Mayaux et al., 2003). This vegetation is characterised by Afro-montane species (Linder, 2001) and because there were only two common Caesalpinioideae tree species this centre was not included in the analysis.

The pattern of species richness and endemism found by White (1979) based on 277 species (comprising herbs, shrubs and trees of various plant families) showed that Lower Guinea was most species rich with 210 species and richest in endemics (71 species); Upper Guinea was less species rich than Congolia with 110 and 146 species, respectively, but almost equally rich in endemics, 33 and 34 species (Table 5.1A). Linder's (2001) results show more or less the same pattern as White's, but comparison is difficult since Linder used a different procedure.

Linder divided sub-Saharan Africa in one-degree grid cells, plotted species distributions over it and counted the number of species per grid cell. Similarity in neighbouring cells was calculated; cells with a high one-degree grid cell endemism were grouped, and defined as "narrow" centres of endemism. White (1979) used overlapping species distributions with similar characteristics. Although the two procedures are different, Upper and Lower Guinea were both recognised as regions with a high endemism and Lower Guinea as a region with a high species richness.

Delimitation

In both cases the centres were geographically not clearly delimited within the African rain forest. Present-day remote sensing techniques and images allow a much better classification of the African rain forest (Mayaux et al., 2003) and subsequently allow an evaluation and a more detailed delimitation of the centres recognised by White (1979) and Linder (2001). To arrive at a better delimitation of the three centres the land-cover map of Africa for the year 2000 derived from SPOT VEGETATION data (Mayaux et al., 2003) was used.

Lower Guinea is defined as the area classified on the map as "closed evergreen lowland forest", and "degraded evergreen lowland forest" covering Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo-Brazzaville and the Mayumba area in RD-Congo (-Kinshasa). Congolia is defined as the "closed evergreen lowland forest", and "degraded evergreen lowland forest" covering RD Congo (-Kinshasa) and excluding the Mayumba area at the Atlantic Coast. At present, Upper Guinea has little primary forest left and it is defined as the area labelled "forest/savanna mosaic", covering Sierra Leone, Liberia, Ivory Coast and Ghana. To consider here only the areas labelled as "closed evergreen lowland forest" and "degraded evergreen lowland forest", as was done for Lower Guinea and Congolia, would only give the present-day protected areas and not the former natural distribution of the lowland rain forest.

On this map the three centres are clearly recognisable because they are separated by zones with atypical (azonal) vegetation formations, i.e the Congo River Floodplain (between LG and Con) and the Dahomey Gap (between UG and LG). The Congo River Floodplain is defined as the area classified as "swamp forest" on the border between Congo-Brazzaville and RD Congo (-Kinshasa). The Dahomey Gap is defined as the area classified as "deciduous woodland", covering parts of Ghana and most of Togo and Benin.

The African centres are dealt with as separate geographical regions (Fig. 5.1) because the centres are separated by wide dispersal barriers, i.e. the Dahomey Gap (DG) and the Congo River Floodplain (CRF). The Dahomey Gap and the Congo River Floodplain are areas in between the centres which represent a zone of at least one hundred kilometres with unfavourable habitat for Caesalpinioideae tree species. In the DG between UG and LG mean annual rainfall is too low to support tropical lowland rain forest. In the CRF in between LG and Con, the permanently inundated state is also unfavourable for Caesalpinioideae (Wieringa, 1999). Therefore, both zones are considered a dispersal barrier for the Caesalpinioideae in general.

Dispersal
The Caesalpinioideae with ballistic seed dispersal have a very low dispersal capacity. Their normal ballistic dispersal does not exceed more than 60 m per generation (van der Burgt, 1997). Evidence for occasional long-distance seed dispersal events was also not found when testing range expansion of the Caesalpinioideae from the Chaillu Massif to Mitendi and Lopé (*c.* 100 km), between Mitendi and Lopé (*c.* 50 km) and within Mitendi between the upland and lowland (*c.* 4 km; Chapter 3). Subsequently, the Dahomey Gap and the Congo River Floodplain, which are more than 100 km wide, are effective barriers which geographically isolate the Caesalpinioideae in each centre, including the few species with a non-ballistic dispersal.

History
As dispersal between centres is assumed to be non-existent, differences in endemics and species richness must have been caused by speciation (i.e. vicariance) and extinction events. Vicariance implies that the formation of the Dahomey Gap and Congo River Floodplain led to the development of a new species at least on one side of the dispersal barrier. Extinction implies that when species became extinct in a centre it remained extinct, because recolonisation from an adjacent centre was not possible. Which of two historical processes, extinction or speciation, has been more important is difficult to assess. Methods to prove former extinctions are very limited. But local speciation is less problematic to detect as it results in specific patterns of taxonomic diversity. This will be investigated by comparing the number of species per genus for each centre.

Ecology
The ecological explanation for higher species richness in one of the centres is habitat diversity and the amount of evergreen rain forest. The factor of habitat diversity was quantified by establishing the surface of elevated area (600-800 m *sensu* (Grubb & Whitmore, 1966) present within each centre. Elevated areas have a higher habitat differentiation than lowland areas because in a hilly landscape there are valleys, ridges, slopes with a different aspect (i.e. orientation towards the north), etc. creating many small-scale gradients and a patchy environment.

The amount of elevated area within each centre was determined by making an altitude map of Africa from elevation data (GEODESK, Wageningen University and Research Centre) using GIS software (Arc View 2.3) and superimposing the outline of the centres as defined above (Fig. 5.2). Similarly, the amount of evergreen rain forest in each centre was determined by superimposing rainfall patterns (GEODESK, Wageningen University and Research Centre). To distinguish (semi-) deciduous forest from evergreen rain forest a mean annual rainfall of 1600 mm was used as cut off-level, similar to the work of Hall and Swain (1981) in Ghana.

Sampling
The present-day abundance of species within or between centres was not considered important within this context. Caesalpinioideae characteristically form a metapopulation, i.e. a complex of subpopulations. Within their present-day distribution pattern older subpopulations dating back to the LGM cannot be readily distinguished from more recent ones established during the Holocene (Chapter 2). Therefore, the only reliable biogeographical signal within their present-day distributions is their absence or presence in a centre.

Table 5.1. Species richness and endemism in the three centres. UG: Upper Guinea, LG: Lower Guinea, Con: Congolia. A: data taken from White (1997) based on 277 plant species, B: This study based on 256 species of Caesalpinioideae. C: Species richness in N Lower Guinea (Cameroon) and in S Lower Guinea (Gabon).

A

White 1979	**UG**	**LG**	**Con**	**Tot**
widespread species	50 (45.5%)	50 (23.8%)	50 (34.2%)	50 (18.1%)
endemic species	33 (30.0%)	71 (33.8%)	34 (23.3%)	138 (49.8%)
UG+LG species	27 (24.5%)	27 (12.9%)	-	27 (9.7%)
LG+Con species	-	62 (29.5%)	62 (42.5%)	62 (22.4%)
UG+Con species	-	-	-	-
total species	110	210	146	277

B

this study	**UG**	**LG**	**Con**	**Tot**
widespread species	9 (13.6%)	9 (4.7%)	9 (12.2%)	9 (3.5%)
endemic species	36 (54.6%)	124 (64.9%)	26 (35.1%)	186 (72.9%)
UG+LG species	19 (28.8%)	19 (9.9%)	-	19 (7.4%)
LG+Con species	-	39 (20.4%)	39 (52.7%)	39 (15.2%)
UG+Con species	1 (1.5%)	-	1 (1.4%)	1 (0.4%)
total species	66	191	74	256

C

Northern LG	125 species
Southern LG	157 species

Considering only the presence or absence of species in a centre also has another advantage. The presence or absence of species in a centre is also partly determined by differences in collection intensities between the three centres. All three centres have not been equally intensely sampled and a bias will be present in this data set. But by only focusing on the absence or presence of species in a centre this bias is as limited as possible, because even a species which has only been collected once or twice will be present in this data set.

The presence or absence of rain forest Caesalpinioideae tree species in each centre as delimited above was determined by critically compiling data from herbarium material, monographs, revisions, floras, checklists, and guides. Species restricted to one centre were classified as endemic. Through this procedure the total number of Caesalpinioideae tree species and the number of endemic species was obtained for each centre. For a more detailed analysis of Lower Guinea this centre was subdivided in a northern half comprising Nigeria and Cameroon and a southern half comprising Gabon, Equatorial Guinea, Congo-Brazzaville and Mayumbe.

5.3 Results

Species richness and endemism

In total 256 rain forest Caesalpinioideae tree species were recorded in the African rain forest (Appendix 2). Almost three quarters (72.9 %) of the species were restricted to one centre (Table 5.1). Upper and Lower Guinea shared 19 species, Lower Guinea and Congolia 39 species, and Upper Guinea and Congolia 1 species. Lower Guinea is the centre with by far the highest species richness (191 species) and highest level of endemism (64.9%: 124 species). Congolia and Upper Guinea are not notably different in richness, but in Upper Guinea the number of endemic species was higher (54.6%: 36 species) than in Congolia (35.1%: 26 species).

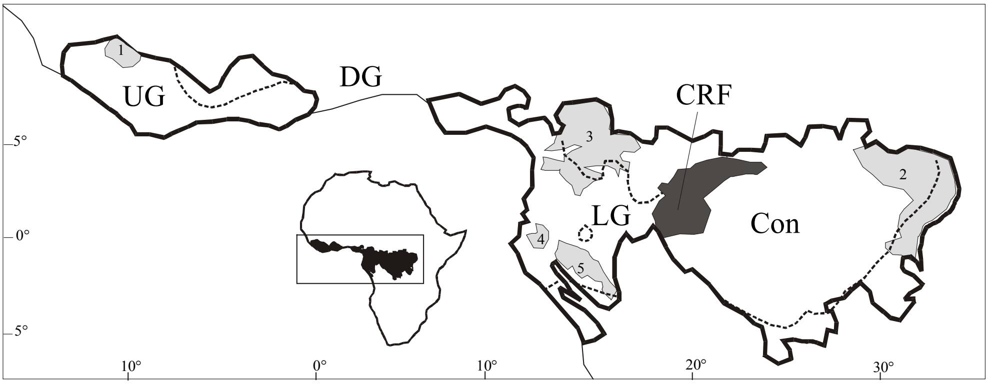


Fig. 5.2. The elevated areas (600-800 m) within the African lowland rain forest (grey areas). 1: Southern flanks of the Guinean Highlands, 2: Ituri Plateau, 3: Cameroonian Plateau, 4: Crystal Mountains, 5: Chaillu Massif. Dashed line: 1600 mm of rainfall per year (abbreviations see fig. 5.1)

The pattern of species richness and endemism of the Caesalpinioideae confirmed the patterns found by Linder and White. But, the differences between the centres were more pronounced (Table 5.1). In White's (1979) sample the percentage of species restricted to one centre was almost 50%, whereas for the Caesalpinioideae this was almost 75%. There is also a large difference in the number of species present in all three centres. In White's sample 50 species (18.1%) were recorded in all three centres, whereas for the Caesalpinioideae only 9 species (3.5%) were common. Also an important difference between White's sample and that of the Caesalpinioideae is the percentage of endemics in Lower Guinea. A quarter (25.6%) of the total species sample of White were endemic, whereas for the Caesalpinioideae this was almost half (48.4%) of all species.

Elevated areas

Habitat diversity in each centre was accounted for by mapping the amount of elevated area (Fig. 5.2). In Upper Guinea the elevated area comprises the southern flanks of the Guinean Highlands (Mt Nimba 1750m), in Lower Guinea the Cameroonian plateau, the Crystal Mountains and the Chaillu Massif, and in Congolia the Ituri Plateau. Most of these elevated areas are covered with semi-deciduous forest, except Mt Nimba, the Crystal Mountains and Chaillu Massif (Fig. 5.2). But none of the elevated areas is densely populated by Caesalpinioideae tree species (White, 1983).

The area with the highest species richness in Caesalpinioideae in Upper Guinea is the coastal area of Liberia and not Mt Nimba (Voorhoeve, 1979). Similarly, in northern Lower Guinea species richness is highest in the coastal region of Cameroon and not on the Cameroonian Plateau (Letouzey, 1968). Also, in Congolia species richness is not highest on the Ituri Plateau, but in the middle of the centre (Lebrun & Gilbert, 1954). Only in Gabon Caesalpinioideae tree species are also present in the Crystal Mountains and the Chaillu Massif. But none of the species is restricted to these elevated areas and the same species are generally more abundant in the adjacent lowland (Aubréville, 1968; Caballé, 1978; Rietkerk et al., 1996; van Valkenburg et al., 1998; Wieringa, 1999).

Table 5.2. Number of Caesalpinioideae species per genus for the three centres. **UG**= Upper Guinea, **LG**= Lower Guinea, and **C**= Congolia.

	UG	**LG**	**C**
Gilbertiodendron	7	18	2
Anthonotha	6	15	7
Hymenostegia	3	13	
Cynometra	4	10	7
Dialium	4	10	9
Aphanocalyx	2	9	6
Tessmannia	1	9	5
Bikinia		9	1
Berlinia	4	8	2
Brachystegia	1	6	1
Didelotia	3	6	1
Prioria		6	1
Daniellia	2	5	2
Tetraberlinia	1	5	1
Guibourtia	4	5	
Plagiosiphon	1	5	
Afzelia	3	4	2
Cryptosepalum	2	4	2
Julbernardia		4	1
Crudia	3	3	3
Gilletiodendron	2	3	
Loesenera	1	3	
Erypetalum		3	
Copaifera	1	2	1
Erythrophleum	2	2	1
Talboltiella	1	2	
Baikiaea		2	2
Leonardoxa		2	2
Microberlinia		2	
Oddoniodendron		2	
Cassia	1	1	1
Pellegriniodendron	1	1	1
Stachyothyrsus	1	1	1
Bussea	1	1	
Detarium	1	1	
Distemonanthus	1	1	
Stemonocoleus	1	1	
Bauhinia		1	1
Lebruniodendron		1	1
Pachyelasma		1	1
Scorodophloeus		1	1
Augouardia		1	
Caesalpinia		1	
Hylodendron		1	
Librevillea		1	
Neochevalierodendron		1	
Sindora		1	
Sindoropsis		1	
Zenkerella		1	
Paramacrolobium	1		1
Polystemonanthus	1		
Michelsonia			1
Pseudomacrolobium			1

Species diversity

In total there are 53 genera. 18 genera (34%) are very species rich in Lower Guinea compared to Upper Guinea or Congolia (Table 5.2). For example, the genus *Anthonotha* is represented by 15 species in Lower Guinea, whereas in Upper Guinea by 6 species and in Congolia by 7 species. Similarly, the genus *Gilbertiodendron*, 18 species in Lower Guinea, 7 species in Upper Guinea and 2 in Congolia. Other genera such as *Brachystegia* are less species rich in Lower Guinea with 6 species, but still better represented than in the other two centres with only one species. Similarly, *Tetraberlinia* with 5 species in Lower Guinea but one species in Upper Guinea and another species in Congolia.

5.4 Discussion

Species richness and endemism of the African lowland Caesalpinioideae tree species was roughly three times higher in Lower Guinea than in Upper Guinea and Congolia. White (1979) and Linder (2001) already showed that Lower Guinea had the highest number of species and endemics. Lower Guinea is also the centre which is least well sampled of the three centres (Breteler, 1992; Breteler, 1996). Therefore, the observed high species richness in Lower Guinea cannot be attributed to a bias in collection densities, as was partly the case in South America (Nelson et al., 1990).

The much lower species richness in the Upper Guinea and Congolia is not explained by less or no evergreen lowland rain forest within its boundaries (Fig. 5.2). It could be that in Lower Guinea there is more habitat fitting the requirements of the Caesalpinioideae in terms of diversity or surface area compared to the other two centres. But equally probable the higher species richness in Lower Guinea may be explained by either less extinction or more speciation compared to the other two centres.

Elevated areas

In all three centres there are elevated areas, but the Caesalpinioideae tree species mainly inhabit the lowland around the elevated areas. Therefore, the high number of Caesalpinioideae tree species in Lower Guinea cannot directly be attributed to more elevated area. However, there is an indirect relationship between the elevated areas and the number of Caesalpinioideae species. In Gabon (S Lower Guinea) the two largest elevated areas are covered with evergreen rain forest (Caballé, 1978) and Gabon is also the region with the highest number of Caesalpinioideae tree species. This suggests that the elevated areas are favourable for the presence of Caesalpinioideae tree species in the surrounding lowland rain forest.

Centre of origin

The higher species richness in Lower Guinea may also be explained when regarding Lower Guinea as the centre of origin or the ancestral area of the Caesalpinioideae. According to this concept individuals dispersed from the centre of origin into Upper Guinea and Congolia, where they became isolated and gradually changed into new species. This means that individuals dispersed across the Dahomey Gap and the Congo River Floodplain, which was considered very unlikely. However, these dispersal barriers were not always as wide as they are today.

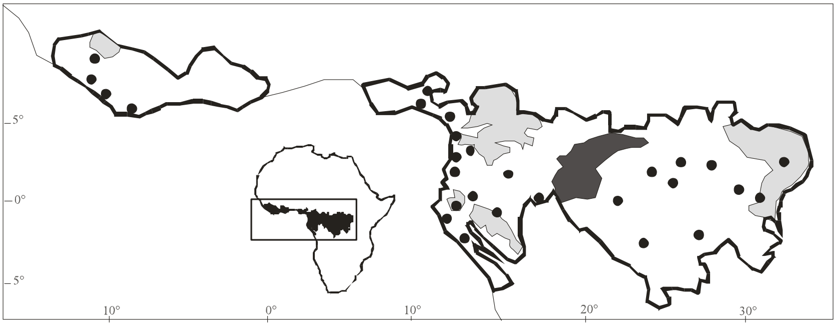


Fig. 5.3. Distribution of *Aphanocalyx microphyllus* (Harms) Wieringa. Grey: elevated areas. (simplified after Wieringa 1999).

During the early Holocene and other periods during the Pleistoceen (Table 1.2) the Dahomey Gap was temporary closed and this may have provided an opportunity for rain forest Caesalpinioideae to migrate between Upper and Lower Guinea and vice versa. However, palynological records from the early Holocene show that the forest that bridged the Dahomey Gap was dominated by deciduous trees such as species of *Celtis* and Sterculiaceae (Toussou, 2002). The Congo River Floodplain will have been smaller during the LGM, but at the same time it will have been flanked by open forest-savanna mosaic like in the Dahomey Gap (Maley, 1996). These are equally unfavourable conditions for the Caesalpinioideae (Wieringa, 1999), especially when there is no local compensation provided by an elevated area (Chapter 3).

This dispersal problem can be circumvented by going back in time to the Neogene when these dispersal barriers did not yet exist, because the African rain forest was situated further north and stretched from coast to coast (Coetzee, 1993; Maley, 1996; Morley, 2000). In this pan-African rain forest species were free to disperse. However, if dispersal was not limited then, why would only a few and not all species disperse out of the central section of the forest (proto-Lower Guinea)? Hence, going back in time does not solve the issue of dispersal; it only increases uncertainties around it. A more plausible scenario is proposed here, which incorporates the present-day dispersal barriers as vicariance-inducing elements in combination with the more recent Pleistocene forest reductions.

Vicariance events

The Dahomey Gap and the Congo River Floodplain dispersal barriers are features of the present-day African rain forest, but their formation dates back either to the Late Miocene or the Middle Pliocene. During the Late Miocene the African continental plate drifted northward (e.g. Dewey et al. 1989; Pfifner 1992), as a result of which the rain forest moved to its present position (Axelrod & Raven 1978). The movement of the forest to the south may also be related to the enlargement of the Sahara over the Pliocene. In either case the formation of the Dahomey Gap and the Congo River floodplain predates the Pleistocene, i.e. the period of intense glaciations.

The formation of the Dahomey Gap and the Congo River Floodplain may have stimulated vicariance events, because it subdivided common ancestral species into either two or three sister populations. As a result of the geographical isolation geneflow between sister-populations became interrupted. This initial geographical isolation may or may not have led to speciation. Speciation becomes more likely when one or both populations pass through a population bottleneck (Hamrick, 1994; Sork et al., 1999). As a population decreases, a part of the genetic variation within the population also disappears, and especially in small populations genetic drift will increase the chances of speciation (Young et al., 1996).

The most likely period that the Caesalpinioideae species populations passed through a population bottleneck is during the unfavourable climatic conditions of the Pleistocene glacial periods and/or those that occurred during periods of increased upwelling of cold deep sea water. Hence, endemic species could accumulate during such a period in each centre. This scenario to explain endemism by vicariance and Pleistocene forest disturbances is still tentative and needs to be supported by phylogenetic biogeographical studies. However, it is far more plausible than the centre of origin scenario.

Extinction

Endemism can also be explained by extinction alone in response to the Pleistocene forest disturbances, but it would require a completely different initial setting of the Caesalpinioideae within the African rain forest. It implies that the majority of the Caesalpinioideae tree species have a pre-Pleistocene origin and very few species evolved during the Pleistocene. In such a case a species can only become endemic when it was absent elsewhere beforehand or when it became extinct in the other two centres. For instance, a species endemic for Upper Guinea is endemic, because it became extinct in Lower Guinea and Congolia.

This implies that in the initial situation most of the 256 species were present in each centre. Such an initial situation could be proved if fossil pollen from the Neogene would have been identifiable at species or genus level, which is not possible for the Caesalpinioideae (Salaard-Chebaldaeff, 1990). This initial situation would also imply very high extinction rates, because to arrive at 72 species in Congolia almost 72 % of the 256 species must have become extinct and in Upper Guinea 74 % of all species. These are mass extinctions with a disputable initial situation. The extinction of Caesalpinioideae species is not excluded here, but it is not very likely that it explains the high level of endemism in each of the three centres. Speciation within a centre as a result of rain forest fragmentation in response to orbital forcing may not be ruled out.

Speciation

More than a third of the genera show a very high species richness in Lower Guinea (Table 5.2). No genus shows such a proliferation in Upper Guinea or Congolia. This exceptional pattern suggests that additional speciation within Lower Guinea during the Pleistocene has played an important role in increasing its species richness. It is not suggested here that speciation took place during the LGM, but over the entire Pleistocene, a period of some 2 million years.

Increased upwelling during this period has been identified as the main mechanism by which the forest became fragmented (Chapter 1). Therefore, the macro and micro refugia will have had a similar location during each period of increased upwelling. For refuge begonias there are indications that new species evolved over the Pleistocene (Plana et al., 2004).

Species populations restricted to macro and micro-refugia, especially species with a low dispersal capacity will have been isolated. They may have evolved by a discontinuity of geneflow and population reductions into new species (Chapter 2). So, besides the evolution of endemic species by vicariance there are also strong indications that new species evolved by speciation within a centre as a result of forest fragmentation as proposed by Haffer (1969) and Prance (1973).

5.5 Conclusions

The Caesalpinioideae rain forest tree species showed a very pronounced pattern of species richness and endemism. In Lower Guinea there were roughly three times as many species and endemics than in the other two centres. This difference in species richness and endemism is the result of different extinction and speciation rates between the centres. These differences have most likely been able to accumulate, because the Caesalpinioideae tree species are unable to disperse between centres. Hence, the present-day biogeography of the Caesalpinioideae contains a strong historical signal which is in line with our increasing insight about static species.

The high level of endemism in each centre is mainly attributed to vicariance events related to the formation of the Dahomey Gap and the Congo River Floodplain in combination with the Pleistocene rain forest disturbances. During these disturbances most genera became depleted by the extinction of species and only a few genera (mainly in Lower Guinea) were able to radiate under those conditions.

In all three centres highest Caesalpinioideae species densities are mainly found in the lowland surrounding the elevated areas. Therefore, the high number of species in Lower Guinea cannot be explained by more habitats better fitting the requirements of the Caesalpinioideae tree species, but there was an indirect relationship between elevated areas and the number of species in the adjacent lowland. Particularly in Gabon species richness is high and also in Gabon the elevated areas are covered by evergreen lowland rain forest.

This observation and the knowledge that in Mitendi and Lopé the upland protected the presence of Caesalpinioideae in the adjacent lowland will be used in the next chapter to reconstruct the African rain forest during the LGM.

Chapter 6 **Reconstructing forest refugia**

6.1 Introduction

One of the aims of this thesis is to improve the current reconstruction of the African rain forest during the Last Glacial Maximum or any period of strong upwelling of cold deep seawater. The reconstruction based on increased upwelling, resulting in a prolonged cool dry season, was already discussed (Chapter 1) and situates forest refugia in elevated areas (referred to hereafter by me as the African approach; Maley 1989). The other reconstruction is based on calculating reduced mean annual rainfall as was practised in South America and it situates forest refugia in high rainfall areas (referred to hereafter by me as the South American approach; van der Hammen & Absy, 1994; adapted by Adams & Faure, 1997). A third reconstruction is only based on fossil pollen records (Dupont et al., 2002) and not on reconstructing paleoclimate like the former two approaches.

The latter reconstruction gives a relative measure of the extention of the forest in different parts of tropical Africa based on the relative amount of forest fossil pollen in the records. Records collected off shore and on land in western Africa (Upper Guinea) contained less forest pollen than those of Atlantic equatorial Africa (Lower Guinea). Therefore, a fragmented forest is reconstructed in Upper Guinea and a continuous rain forest in Lower Guinea (Table 1.2, stage 2). The disadvantage of this method is that it heavily relies on terrestrial sites to reconstruct the forest-savanna border. Only three pollen records located at the periphery of the forest were available. Another record not used in this reconstruction is situated in the centre of Lower Guinea (Lopé) and strongly indicates that savanna persisted during the LGM (Peyrot et al., 2003). Hence, according to this method the forest-savanna border in Lower Guinea during the LGM has to be redrawn.

The two approaches based on reconstructing paleoclimate have the advantage they elucidate the mechanism behind the change in forest cover. The South American approach meant calculating how much the mean annual rainfall had to drop to cause a change from closed-canopy rain forest to open forest-savanna mosaic (Adams & Faure, 1997). Rainfall reductions causing such changes postulated for the Amazon and Africa varied between 20% and 45 % (van der Hammen & Absy, 1994; Bush, 1994; Hooghiemstra & van der Hammen, 1998; Thomas, 2000). These reductions were superimposed on the present-day rainfall patterns, and areas where mean annual rainfall is presently highest were considered to represent former forest refugia. According to this method only a relatively small part of the present-day African lowland rain forest area survived the LGM (Fig. 6.1).

The African approach is based on the fact that during the LGM more cool deep-sea water surfaced (upwelling) in the Golf of Guinea, which prolonged the cool dry season (Chapter 1). Under these climatic conditions the forest would have had the highest change of survival in elevated areas where drought stress would have been less due to the cloud forest conditions (Fig. 3.1; Maley, 1987; Maley, 1996; Maley, 2001a). Therefore, elevated areas within the present-day rain forest were postulated as refuge areas.

6.2 Climatic change and seasonality

The two approaches to reconstruct lowland rain forest during the LGM also represents a difference in the perception of climate and climatic change. The South American approach is based upon the assumption that the *pattern* of *mean annual rainfall* is stable and that only the amount of rainfall varies in response to climate change (van der Hammen & Absy, 1994). This assumption is supported by the observation that in the northern hemisphere high rainfall areas remained their present-day position during the LGM (Davis, 1989). The African approach, on the other hand, assumes that the *pattern* of *rainfall during the dry seasons* is stable and that the amount of rainfall varies with seasonality. In other words, areas where drought stress is lowest during the dry seasons are more stable than areas where rainfall is highest during the rainy seasons.

The reconstructions based on the South American (reduced mean annual rainfall) and African approach (a prolonged cool dry season) mainly differ in the presence of forest refugia in Gabon. In the reconstruction based on the African approach, forest refugia are postulated in Gabon, whereas in the reconstruction based on the South American approach they are postulated outside Gabon (compare Figs 1.5 and 6.1). In the traditional expansion scenario this means that the Caesalpinioideae tree species now present in Gabon either arrived from Cameroon and the Congo River Floodplain (the South American approach) or from the elevated areas within Gabon, i.e. the Chaillu Massif and the Crystal Mountains (the African reconstruction, fig. 1.5). But the expansion scenario proved not to be very realistic for the slow dispersing evergreen Caesalpinioideae trees species present in Lopé and Mitendi and for the Caesalpinioideae in general (Chapter 4; Leal, 2001).

Instead, the Caesalpinioideae tree species most likely survived the drier climate during LGM in situ (Chapter 4). This was only possible if there was local compensation for the regional drought stress like the permanent streams in Lopé and Mitendi (Chapter 4). The continuity of the streams during the cool dry season in the study areas was safeguarded by the upland (400-700 m), i.e. a minor elevated area (Chapter 3, 4). Without this elevated area the Caesalpinioideae tree species in Lopé and Mitendi would certainly have become extinct long ago. The hydrological relationship between the upland and the adjacent lowland shows how elevated areas in general prevent streams to run dry in the surrounding lowland during the cool dry season and during the LGM.

The observation that the upland prevented the local extinction of the Caesalpinioideae in Lopé and Mitendi during the cool dry season may also explain why Gabon is so much richer in Caesalpinioideae species than any other section of the African rain forest (Chapter 5). The higher species richness of Caesalpinioideae in Lower Guinea and Gabon in particular was explained by less extinction during periods of increased upwelling during the Pleistocene (Chapter 5). Knowing that elevated areas determine the existence and number of microrefugia in the surrounding lowland explains the higher species richness in Gabon and in Lower Guinea in general. Whether elevated areas remained forested remains unsolved. However, additional support for the stronger seasonality of climate is presented (African approach) rendering a general reduction in mean annual rainfall (South American approach) far less likely.

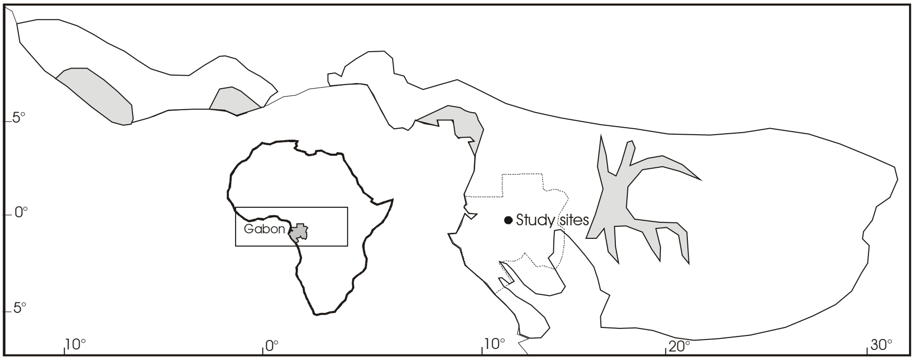


Fig. 6.1. Reconstruction of the African rain forest during the LGM (simplified after Adams & Faure, 1997) based upon superimposing a general rainfall reduction model on the present-day rainfall pattern (the South American approach). The forest refuge area in central equatorial Africa is the Congo River Floodplain, i.e. an azonal refugium.

6.3 Models and the alluvial record

Simulations of the general circulation model, the Community Climate Model (CCM), indirectly also support the African approach, i.e. a greater seasonality. For tropical Africa the CCM-output calculated only a minor reduction in mean annual rainfall (0-200 mm per year) during the LGM (Jolly et al., 1998). Such a minor reduction in mean annual rainfall can not explain the reduction of forest cover as evident from palynological records (Chapter 1).

General circulation models are not focussed on reconstructing seasonality, but the CCM-output for tropical Africa, nevertheless, showed a drop in sea surface temperature in January, i.e. during the hot dry season, and a larger drop in July, i.e. during the cool dry season (Jolly et al., 1998). This suggests that the hot dry season weakened while the cool dry season strengthened. Hence, because the CCM-output showed that mean annual rainfall did not change much, only an increase in seasonality may explain a major change in forest cover.

An extended cool dry season is also supported by a reinterpretation of the alluvial record. The alluvial record provides additional information about climate during the LGM. As fossil pollen records from the LGM are scarce, attempts have been made to reconstruct climate from the alluvial record spanning the LGM. The alluvial record showed a minimum in stream and river sedimentation during the LGM, indicating a general decline in runoff (Thomas, 2000). It was suggested that mean annual rainfall during this period had decreased, but the change in sedimentation can also be explained by a stronger cool dry season dominating the climate.

Presently, some 40% of the mean annual rainfall in the tropics has an intensity greater than 25 mm per hour whereas in temperate regions this is only 5% (Buckle, 1996). During these intensive rain showers rainfall does not have the time to infiltrate the soil and partly continues as infiltration-excess overland-flow creating a peak in discharge of drainage water in streams (Atkinson, 1978; Bras, 1990). Only these intensive rain showers create an overland water flow with sufficient energy and momentum to transport soil particles.

These intensive rain showers can only develop under deep cloud formation (vertical growth), which is particularly likely to occur in unstable moist maritime air (Buckle, 1996). Moist unstable air masses are created over sea when evaporation is high. During the LGM, however, the tropical South Atlantic Ocean was colder due to increased upwelling (Chapter 1) and so moist unstable maritime air masses creating intensive rain storms are not likely to have been a dominant feature of the climate during that period.

Presently, air masses coming from the Atlantic Ocean during the cool dry season are dry and stable and the mainland receives a low intensity of rainfall or none at all (Chapter 1). A longer cool dry season and cooler Sea Surface Temperatures (SST) during the LGM means that all year round the maritime air masses were less humid and more stable. Hence, heavy rain showers were less frequent than today. With less intensive rainfall, there was less infiltration-excess overland water flow and hence less erosion and sedimentation which is in accordance with the alluvial record for tropical Africa (Thomas, 2000).

A new reconstruction

There are strong indications from different scientific fields for a more seasonal climate in equatorial Africa during the LGM than today and especially a stronger cool dry season. A stronger seasonality is also more probable to cause a change in forest cover and a shift in the forest-savanna boundary (Chapter 3). This means that the rainfall pattern during the cool dry season is the principal arranging force determining where forest persisted. The cool dry season can only have been stronger during the LGM where it presently is already evident, like in Gabon, Ghana, Ivory Coast, Equatorial Guinea and Southern Cameroon (Fig. 1.2).

In Liberia, Sierra Leone, northern Cameroon and Congo-Kinshasa the hot dry season is presently stronger than the cool dry season (Fig. 1.2). The hot dry season will have been weaker than today, but in areas where the cool dry season has little impact it will still have had a strong influence, like in Liberia and northern Congo-Kinshasa. Therefore, to obtain a fair reconstruction of the forest during the LGM rainfall patterns during the cool dry season and the hot should be combined and superimposed.

Rainfall during the cool dry season is already nearly or completely absent so no extra reduction has to be calculated. But rainfall during the hot dry season should be reduced by the percentage or amount calculated by simulations and South American approach. In this way in areas receiving less than 1600 mm mean annual rainfall evergreen lowland rain forest would turn into deciduous forest. In areas where the cool dry season dominates elevated areas would remain forested. Elevated areas in the northern part of the African rain forest would have become less forested, especially, the Ituri Plateau and Cameroonian Plateau which are now covered by semi-deciduous forest. In the regions with a dominant cool dry season gallery forest will have persisted in the lowland along permanent streams and rivers coming from elevated areas (Fig. 6.4).

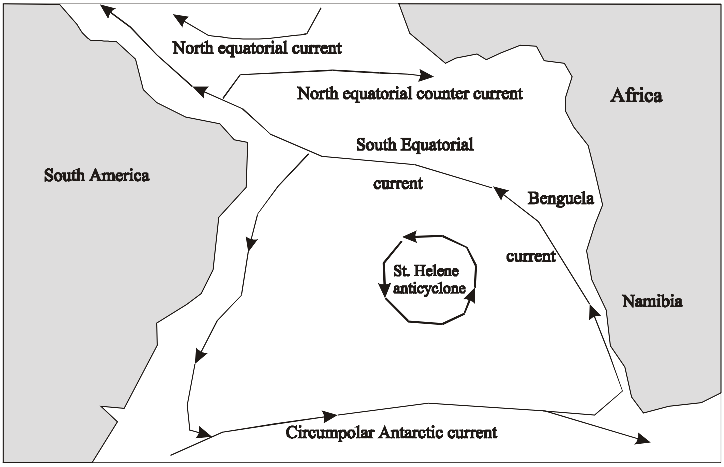


Fig. 6.2. The present-day schematic representation of the sea currents and the St. Helena high pressure system in the Southern Atlantic Ocean (after Berger & Wefer, 2002). The St. Helena anticyclone shifts further north during the boreal summer.

6.5 Trans-Atlantic connections

The presence of Caesalpinioideae in Gabon and in particular their presence in between refuge areas is most plausibly explained by the African approach. The African approach entails that areas where drought stress during dry seasons is lowest are also the areas where the rain forest had the highest change of survival during the LGM. Since the reconstruction by the African approach proves to be the most plausible, the same approach may also give a better reconstruction for South America. Especially, since rain forests on both continents are connected by the same ocean currents.

In South America fossil pollen records during the LGM show a similar situation as in Africa, where closed canopy lowland rain forest turned into (partly) open forest-savanna mosaic (Hooghiemstra & van der Hammen, 1998). But the records are scarce and located at the periphery of the forest. Therefore, there is no consensus whether the climate became drier causing the Amazon rain forest to become fragmented (Bush, 1994; Haffer, 1969; Haffer & Prance, 2001) or whether it only became cooler with a minor contraction at the periphery (Colinvaux et al., 2001). The African situation shows that both possibilities do not necessarily have to exclude each other, but that they can occur simultaneously.

In Africa, climate became cooler and drier due to increased upwelling and lower sea surface temperatures (Chapter 1). The same equatorial current connects both continents across the tropical Atlantic Ocean and a similar phenomenon may have existed in South America during the LGM. Colder coastal waters along South America during the LGM were calculated (CLIMAP Project Members, 1981; Jolly et al., 1998) and therefore, the mechanism by which climate changed in Africa may also partly apply to South America.

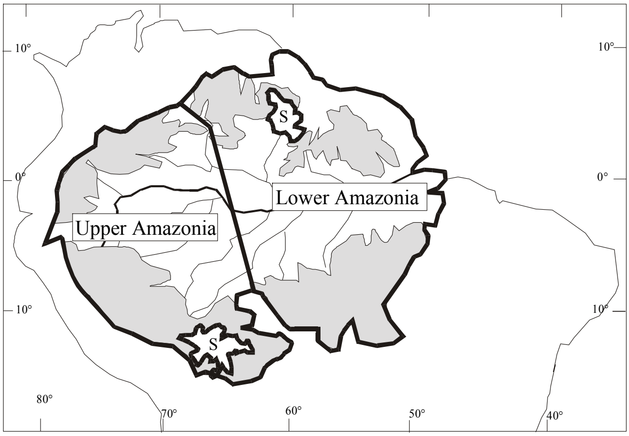


Fig. 6.3 The Amazonian rain forest (bold line), with the main rivers and elevated areas (grey). The division of Upper and Lower Amazonia (after Roucou et al. 2000). S: savanna areas.

The equatorial current connecting the South American east coast and the African west coast is the continuation of the Benguela current (Fig. 6.2). The Benguela current is cold as it branches off from the Circumpolar Antarctic current while driven north-west across the equator it is heated up by direct solar radiation. Subsequently, by the time it reaches the Brazilian coast it is no longer as cold as near Namibia.

A colder South Atlantic Ocean has been identified to cause a reduction in rainfall (anomaly) over NE Brazil and over the Amazon (Moron et al., 1995; Moron et al., 2001; Ronchail et al., 2002; Roucou et al., 2000). Also interannual anomalies in rainfall on both sides of the Atlantic Ocean co-varied with certain configurations of the Atlantic Ocean, i.e. being either colder or warmer than average (Ronchail et al., 2002; Roucou et al., 2000; Ruiz-Barradas et al., 2000). The anomalies in SST affected the eastern part of the Amazon (Lower Amazonia) more than the western part (Moron et al., 1995; Moron et al., 2001; Ronchail et al., 2002; Roucou et al., 2000).

In other words, a colder than average Southern Equatorial current along the African coast will arrive colder than average on the South American coast. A colder tropical Atlantic Ocean due to increased upwelling and associated SST has been identified as having caused the change from closed-canopy rain forest to open forest-savanna mosaic during the LGM (Chapter 1). Present-day minor anomalies in SST cause anomalies in rainfall at both sides of the ocean. Therefore, it is very unlikely that a major change in SST during the LGM only caused a climatic change in Africa and not in South America. Subsequently, the coastal regions of Lower Amazonia must have experienced a cool dry season like in Africa.

Cool dry season

Presently, the stability of maritime air masses reaching South America from the Atlantic Ocean is determined by sea surface temperature of the coastal water (Harzallah & Sadourny, 1995). During the LGM when coastal water had a lower SST air masses would become more stable and release less rainfall. Rainfall may not have ceased completely like presently in Gabon, but nonetheless rainfall would have become reduced. When the Amazon was subjected to a cool dry season it is likely that it responded in a way similar to the rain forest in Africa.

In Africa, elevated areas are fundamental in the survival of the African rain forest, not only by preserving the forest on them, but also by offering favourable conditions for the evergreen species in the surrounding lowland. Therefore, elevated areas within the South American rain forest might well also have been fundamental for rain forest survival, especially in Lower Amazonia which is closest to the influence of the colder sea current. Subsequently, rain forest would have survived on the Guyanan Highlands (macro-refugium) and in the lowland forest limited along streams, rivers and lakes (micro-refugia).

A cool dry season would have affected Upper Amazonia less than Lower Amazonia (Fig. 6.3), because present-day anomalies in SST along the coast of Brazil affect Upper Amazonia less than Lower Amazonia (Moron et al., 1995; Moron et al., 2001; Ronchail et al., 2002; Roucou et al., 2000). Therefore, only the periphery of the Upper Amazonian forest will have experienced drought stress and contracted, whereas the forest in the centre of Upper Amazonia will have mainly experienced cooling causing the descent of montane species.

Climate dominated by a cool dry season due to a colder sea current along the coast of NE South America is a compromise in the debate whether mainly cooling or mainly drying affected the Amazon region during the LGM. It sheds a new light on the possibility of a distinct response within the Amazonian rain forest to the changing climatic circumstances during the Pleistocene Ice ages and the LGM in particular. A cool dry season would cause climate in Lower Amazonia to become predominantly drier and in Upper Amazonia predominantly cooler.

This putative scenario provides an explanation for endemic species observed in the elevated areas at the periphery of the rain forest (Prance, 1973). It suggests that species populations in the elevated areas were temporarily isolated from their sister populations in the central part of Upper Amazonia offering opportunities for genetic differentiation and speciation through vicariance.

Distributions and simulations

A split of the Amazonian forest block in a western and eastern part during the Plio-Pleistocene is also supported by the reconstruction of evolutionary histories of several forest animal groups (da Silva & Oren, 1996; Ron, 2000) and by the disjunct distribution of xeric, drought tolerant plant species (Pennington et al., 2000). The latter study showed that 104 “non-rainforest” species are disjunctly distributed north and south of the Amazon. There are presently no savanna-corridors parallel to the South American coast or Andes, and occasional long distance seed dispersal events are also very unlikely. Therefore, a corridor must have existed during some part of the Pleistocene history to explain these disjunct species.

A split of the Amazonian rain forest during the LGM is not supported by the latest climate-vegetation simulations based on the Leaf Area Index (LAI) (Cowling et al., 2001). Leaf area index was used in order to be able to distinguish between vegetation formations with a different LAI in the simulation, i.e. grassland, deciduous forest and evergreen rain forest. The simulation showed that during the LGM there was no corridor of grassland in between Upper Amazonia and Lower Amazonia but only an incision (Fig. 1 in Cowling et al., 2001).

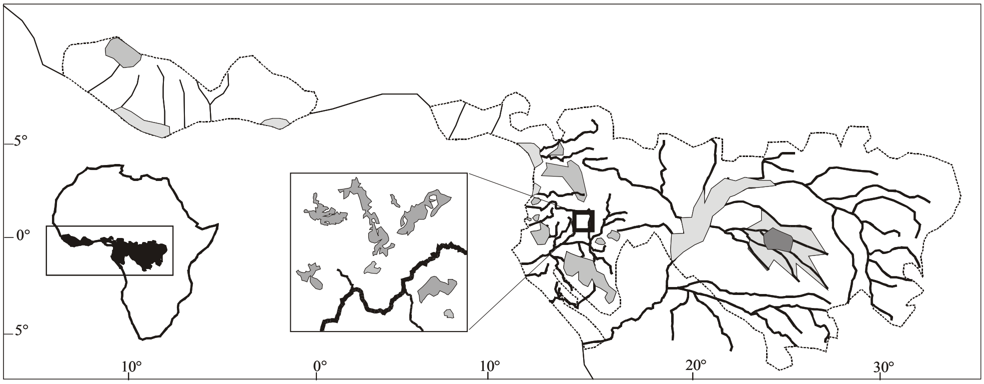


Fig. 6.4. A reconstruction of the African rain forest during the LGM. The amount of refuge areas is underestimated. Dark grey: rainfall refuge , light grey: drier lowland refuge areas and the Congo River Floodplain refuge area, intermediate grey: elevated areas, lines: river refuge areas (i.e. gallery forest). Inset square gives an impression of the situation at a local scale.

Simulations to obtain the modern situation failed as the output did not match with the latest remote sensing vegetation classification map (Eva et al., 2002). This discrepancy may cast doubt on the reconstruction during the LGM, but the simulation does, nonetheless, show that the central section of the Amazonian rain forest is most likely to have been affected by changes in climate related to orbital forcing and reduced atmospheric CO_2 levels.

Presently, that same central section of the Amazon is now the area with the highest diversity of tree species, which is explained as a mid-domain effect since it is not related with rainfall, or seasonality (ter Steege et al., 2003; ter Steege & Zagt, 2002). The mid-domain effect suggests that geographic concentrations of species diversity are due to shared physiographical and physiological boundaries in relation to range-size and unrelated to present-day factors (Colwell & Lees, 2000).

Since this phenomenon is unrelated to present-day factors an alternative historical explanation is allowed and introduced here as the Holocene forest expansion effect. The concentration of tree species in the central section is situated on the border of Upper and Lower Amazonia. During the LGM, the Amazonian forest block was split in an Upper and a Lower part, which subsequently also separated the tree species pool. As Upper and Lower Amazonia merged over the Holocene the two separate species pools converged in this central section. Consequently, what was previously an open forest-savanna mosaic is now the most tree species-rich part of the South American rain forest.

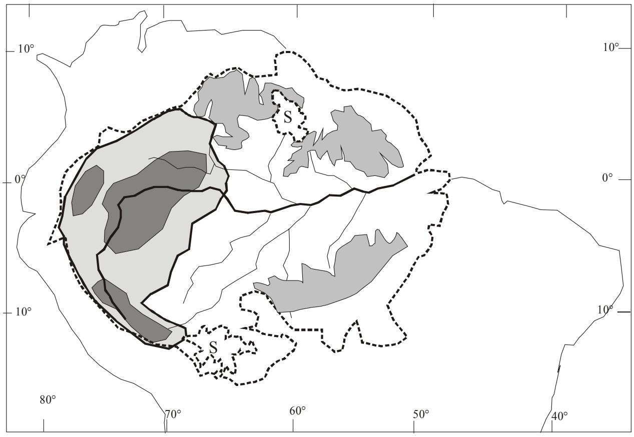


Fig. 6.5. A reconstruction of the Amazonian rain forest during the LGM according to the African approach. Dark grey: rainfall refugia, light grey: drier lowland refuge areas, intermediate grey: elevated refuge areas, lines: river refuge areas (i.e. gallery forest). S: savanna areas.

6.6 Conclusions

Palynological records showed that during the Last Glacial Maximum (LGM) the distribution of the lowland rain forests in Africa and South America was reduced due to the effects of climatic changes related to orbital forcing. This raises questions such as: what caused the change of climate?, what was the climate like?, and where were the forest refugia located? For the African lowland rain forest these questions can be most plausibly answered by assuming a climatic change related to increased upwelling causing a prolonged cool dry season. It may be questioned how far inland this impact of upwelling on the lowland rain forest would have continued. Therefore, the regions adjacent to the tropical Atlantic Ocean, i.e. Upper and Lower Guinea and Lower Amazonia will probably have been more affected by colder sea surface temperatures than regions further inland, i.e. Upper Amazonia and Congolia. Subsequently, refuge areas in the coastal regions were mainly located in the elevated areas and along rivers and in the wetter interior regions where presently drought stress is lowest during the dry seasons.

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Appendix 1

Species in the Lopé and Mitendi study site, their continental distribution and voucher material. L: Lopé, M: Mitendi, UG: Upper Guinea, LG: Lower Guinea, Con: Congolia. All vouchers collected by Leal are present in WAG.

	sites		**abbrev.**	**regional centres**	**voucher**
Anthonotha macrophylla P.Beauv.	L	M	Ant mac	UG, LG, Con	Leal 178
Anthonotha triplomeris (Pellegr.) J.Léonard		M	Ant tri	LG, Endemic to Gabon	Doucet 285
Aphanocalyx djumensis (De Wild.) J.Léonard	L		Aph dju	LG, Con	Leal 180
Aphanocalyx heitzii (Pellegr.) Wieringa		M	Aph hei	LG, Endemic to Gabon	Leal 183
Aphanocalyx margininervatus J.Léonard		M	Aph mar	LG	Leal 75/203
Aphanocalyx microphyllus (Harms) Wieringa		M	Aph mic	UG, LG, Con	Leal 190
Augouardia letestui Pellegr.	L	M	Aug let	LG, Endemic to Gabon	Reitsma 2675
Baikiaea insignis Benth.	L		Bai ins	LG, Con	Leal 66
Baikiaea robynsii Ghesq.	L		Bai rob	LG, Con	Leal 69
Berlinia auriculata Benth.	L		Ber aur	LG	Leal 72
Berlinia bracteosa Benth.	L	M	Ber bra	LG, Con	Leal 65
Bikinia media Wieringa		M	Bik med	LG, Endemic to Gabon	Leal 192
Brachystegia mildbraedii Harms	L		Bra mil	LG	Leal 53
Crudia gabonensis Pierre ex Harms	L		Cru gab	UG, LG, Con	Leal 54
Crudia harmsiana De Wild.		M	Cru har	LG, Con	Leal 197
Cryptosepalum staudtii Harms	L		Cry sta	LG	Leal 49
Cynometra schlechteri Harms	L		Cyn sch	LG, Con	White 1015
Erythrophleum ivorense A.Chev.		M	Ery ivo	UG, LG	Leal 99
Eurypetalum batesii Baker f.	L	M	Eur bat	LG	Leal 196
Gilbertiodendron brachystegioides (Harms) J.Léonard		M	Gil bra	LG	Leal 187
Gilbertiodendron dewevrei (De Wild.) J.Léonard		M	Gil dew	LG, Con	Leal 198
Gilbertiodendron grandistipulatum (De Wild.) J.Léonard	L		Gil gra	LG, Con	White 1246
Gilbertiodendron ogoouense (Pellegr.) J.Léonard		M	Gil ogo	LG, Con	Leal 210
Gilbertiodendron preusii (Harms) J.Léonard		M	Gil pre	UG, LG, Con	Doucet 231
Gilletiodendron pierreanum (Harms) J.Léonard		M	Gil pie	LG	Leal 202
Guibourtia demeusii (Harms) J.Léonard	L		Gui dem	LG, Con	Leal 43
Hymenostegia felicis (A.Chev.) J.Léonard		M	Hym fel	LG	Leal 191
Hymenostegia klainei Pierre ex Pellegr.	L	M	Hym kla	LG, Endemic to Gabon	Leal 193
Hymenostegia pellegrinii (A.Chev.) J.Léonard	L	M	Hym pel	LG, Endemic to Gabon	Leal 194
Julbernardia brieyi (De Wild.) Troupin	L		Jul bri	LG, Con	Leal 50
Julbernardia pellegriniana Troupin	L	M	Jul pel	LG, Con	Leal 40
Julbernardia seretii (De Wild.) Troupin	L	M	Jul ser	LG, Con	Leal 169
Leonardoxa africana (Baill.) Aubrév.		M	Leo afr	LG	Leal 200
Librevillea klainei (Pierre ex Harms) Hoyle		M	Lib kla	LG	Leal 195
Neochevalierodendron stephanii (A.Chev.) J.Léonard	L	M	Neo ste	LG, Endemic to Gabon	White 0605
Oddoniodendron micranthum (Harms) Baker	L	M	Odd mic	LG, Con	Leal 146
Pellegriniodendron diphyllum (Harms) J.Léonard	L	M	Pel dip	UG, LG	Leal 205
Scorodophloeus zenkeri Harms	L	M	Sco zen	LG, Con	Leal 204
Sindoropsis letestui (Pellegr.) J.Léonard	L	M	Sin let	LG, Endemic to Gabon	Reitsma 2328
Tessmannia anomala (Micheli) Harms	L		Tes ano	LG, Con	Leal 147

Appendix 2

Synoptic table showing the presence of Caesalpinioideae in the three centres of species richness and endemism: Upper Guinea (UG), Lower Guinea (LG) and Congolia (C).

	UG	**LG**	**C**
Afzelia bella Harms	1	1	1
Anthonotha fragrans (Baker f.) Exell & Hillcoat	1	1	1
Anthonotha macrophylla P.Beauv.	1	1	1
Aphanocalyx microphyllus (Harms) Wieringa	1	1	1
Cassia mannii Oliv.	1	1	1
Didelotia unifoliolata J.Léonard	1	1	1
Pellegriniodendron diphyllum (Harms) J.Léonard	1	1	1
Berlinia grandiflora (Vahl) Hutch. & Dalziel	1	1	1
Erythrophleum suaveolens (Guill. & Perr.) Brenan	1	1	1
Paramacrolobium coeruleum (Taub.) J.Léonard	1		1
Afzelia africana Sm.	1	1	
Berlinia confusa Hoyle	1	1	
Crudia gabonensis Pierre ex Harms	1	1	
Crudia klainei Pierre ex De Wild.	1	1	
Cynometra megaphylla Harms	1	1	
Cynometra vogelii Hook.f.	1	1	
Daniellia ogea (Harms) Rolfe	1	1	
Dialium dinklagei Harms	1	1	
Dialium guineensis Willd.	1	1	
Distemonanthus benthamianus Baill.	1	1	
Erythrophleum ivorense A.Chev.	1	1	
Gilbertiodendron bilineatum (Hutch. & Dalziel) J.Léonard	1	1	
Gilbertiodendron preusii (Harms) J.Léonard	1	1	
Gilletiodendron kisantuense (De Wild.) J.Léonard	1	1	
Guibourtia ehie (A.Chev.) J.Léonard	1	1	
Hymenostegia afzelii (Oliv.) Harms	1	1	
Plagiosiphon emarginatus (Hutch. & Dalziel) J.Léonard	1	1	
Stemonocoleus micranthus Harms	1	1	
Afzelia bipendinsis Harms		1	1
Anthonotha accuminata (De Wild.) J.Léonard		1	1
Anthonotha pynaertii (De Wild.) Exell & Hillcoat		1	1
Aphanocalyx cynometriodes Oliv.		1	1
Aphanocalyx djumaensis (De Wild.) J.Léonard		1	1
Aphanocalyx ledermannii (Harms) Wieringa		1	1
Aphanocalyx obscurus Wieringa		1	1
Baikiaea insignis Benth.		1	1
Baikiaea robynsii Ghesq.		1	1
Bauhinia gossweileri Baker.f.		1	1
Berlinia bracteosa Benth.		1	1
Bikinia evrardii (Bamps) Wieringa		1	1
Copaifera mildbraedii Harms		1	1
Cryptosepalum congolanum (De Wild.) J.Léonard		1	1
Cryptosepalum pellegriniana (J.Léonard) J.Léonard		1	1
Cynometra hankei Harms		1	1
Cynometra schlechteri Harms		1	1
Daniellia pynaertii De Wild.		1	1
Dialium pachyphyllum Harms		1	1

Appendix 2 continued	**UG**	**LG**	**C**
Dialium zenkeri Harms		1	1
Gilbertiodendron dewevrei (De Wild.) J.Léonard		1	1
Gilbertiodendron ogoouense (Pellegr.) J.Léonard		1	1
Gilletiodendron mildbraedii (Harms) Vermoensen		1	1
Guibourtia demeusii (Harms) J.Léonard		1	1
Julbernardia seretii (De Wild.) Troupin		1	1
Lebruniodendron leptandrum (Harms) J.Léonard		1	1
Leonardoxa bequaertii (De Wild.) Aubrév.		1	1
Pachyelasma tessmannii (Harms) Harms		1	1
Prioria balsamifera (Harms) Breteler		1	1
Prioria bucholzii (Harms) Breteler		1	1
Prioria gilbertii (J.Léonard) Breteler		1	1
Prioria oxyphyllum (Harms) Breteler		1	1
Scorodophloeus zenkeri Harms		1	1
Stachyothyrsus staudtii Harms		1	1
Tessmannia africana Harms		1	1
Tessmannia anomala (Micheli) Harms		1	1
Tessmannia dewildemaniana Harms		1	1
Tessmannia lescrauwaetii (De Wild.) Harms		1	1
Anthonotha gilletii (De Wild.) J.Léonard			1
Anthonotha graciflorum (Harms) J.Léonard			1
Anthonotha lebrunii (J.Léonard) J.Léonard			1
Aphanocalyx jenseniae (Gram) Wieringa			1
Berlinia heudelotiana Baill.			1
Brachystegia laurentii (De Wild.) Hoyle			1
Crudia harmsiana De Wild.			1
Crudia laurentii De Wild.			1
Crudia michelsonii J.Léonard			1
Cynometra alexandri C.H. Wright			1
Cynometra michelsonii J.Léonard			1
Cynometra palustris J.Léonard			1
Cynometra pedicellata De Wild.			1
Cynometra sessiliflora Harms			1
Daniellia mortehanii De Wild.			1
Dialium corbisieri Staner			1
Dialium excelsum Stey.			1
Dialium graciliflorum Harms			1
Dialium hexasepalum Harms			1
Dialium pentandrum Louis ex Stey.			1
Dialium reygaertii De Wild.			1
Leonardoxa romii (De Wild.) Aubrév.			1
Michelsonia microphylla (Troupin) Hauman			1
Pseudomacrolobium mengei (De Wild.) Hauman			1
Tessmannia yangambiensis J.Léonard			1
Tetraberlinia baregarum Wieringa			1
Anthonotha crassiflora (Baill.) J.Léonard	1		
Anthonotha ernae (Dinkl.) J.Léonard	1		
Anthonotha explicans (Baill.) J.Léonard	1		
Anthonotha vignei (Hoyle) J.Léonard	1		
Aphanocalyx pteridophyllus (Harms) Wieringa	1		
Berlinia occidentalis Keay	1		
Berlinia tomentella Keay	1		

Appendix 2 continued	**UG**	**LG**	**C**
Brachystegia leonensis Burtt, Davy & Hutch.	1		
Bussea occidentalis Hutch.	1		
Copaifera salokounda Heckel	1		
Cryptosepalum minutifolium (A.Chev.) Hutch. & Dalziel	1		
Cryptosepalum tetraphyllum (Hook.f.) Benth.	1		
Cynometra anata Hutch. & Dalziel	1		
Cynometra leonensis Hutch. & Dalziel	1		
Daniellia thurifera Bennett	1		
Dialium aubrevillei Pellegr.	1		
Dialium pobequinii Pellegr.	1		
Didelotia afzelii Taub.	1		
Didelotia engleri Dinkl. & Harms	1		
Gilbertiodendron aylmeri (Hutch. & Dalziel) J.Léonard	1		
Gilbertiodendron ivorense (A.Chev.) J.Léonard	1		
Gilbertiodendron limba (Scott Elliot) J.Léonard	1		
Gilbertiodendron oblijugum (Stapf) J.Léonard	1		
Gilbertiodendron splendidum (Hutch. & Dalziel) J.Léonard	1		
Gilletiodendron glandulosum (Portères) J.Léonard	1		
Guibourtia copaifera Bennet	1		
Guibourtia dinklagei (Harms) J.Léonard	1		
Guibourtia leonensis J.Léonard	1		
Hymenostegia aubrevillei Pellegr.	1		
Hymenostegia gracilipes Hutch. & Dalziel	1		
Loesenera kalantha Harms	1		
Polystemonanthus dinklagei Harms	1		
Stachyothyrsus stapfiana (A.Chev.) J.Léonard ex Voorh.	1		
Talbotiella gentii Hutch. & Greenway	1		
Tessmannia baikiaeoides Hutch. & Dalziel	1		
Tetrabelinia tubmaniana J.Léonard	1		
Afzelia pachyloba Harms		1	
Anthonotha conchyliophora (Pellegr.) J.Léonard		1	
Anthonotha ferruginea (Harms) J.Léonard		1	
Anthonotha gabunensis J.Léonard		1	
Anthonotha isopetala (Harms) J.Léonard		1	
Anthonotha lamprophylla (Harms) J.Léonard		1	
Anthonotha leptorrhachis (Harms) J.Léonard		1	
Anthonotha obanensis (Baker f.) J.Léonard		1	
Anthonotha pellegrinii Aubrév.		1	
Anthonotha stipulacea (Benth.) J.Léonard		1	
Anthonotha triplomeris (Pellegr.) J.Léonard		1	
Anthonotha trunciflora (Pellegr.) J.Léonard		1	
Aphanocalyx hedinii (A.Chev.) Wieringa		1	
Aphanocalyx heitzi (Pellegr.) Wieringa		1	
Aphanocalyx margininervatus J.Léonard		1	
Aphanocalyx pectinatus (A.Chev.) Wieringa		1	
Augouardia letestui Pellegr.		1	
Berlinia auriculata Benth.		1	
Berlinia congolensis (Baker f.) Keay		1	
Berlinia coriacea Keay		1	
Berlinia craibiana Baker f.		1	
Berlinia hollandii Hutch. & Dalziel		1	

Appendix 2 continued

	UG	LG	C
Bikinia aciculifera Wieringa		1	
Bikinia breynei (Bamps) Wieringa		1	
Bikinia coriacea (Aubrév.) Wieringa		1	
Bikinia durandii (F.Hallé & Normand) Wieringa		1	
Bikinia grisea Wieringa		1	
Bikinia letestui (Pellegr.) Wieringa		1	
Bikinia media Wieringa		1	
Bikinia pellegrinii (A.Chev.) Wieringa		1	
Brachystegia cynometroides Harms		1	
Brachystegia eurycoma Harms		1	
Brachystegia kennedyi Hoyle		1	
Brachystegia mildbraedii Harms		1	
Brachystegia nigerica Hoyle & A.Jones		1	
Brachystegia zenkeri Harms		1	
Bussea gossweileri Baker f.		1	
Caesalpinia welwitschia (Oliv.) Brenan		1	
Copaifera religiosa J.Léonard		1	
Cryptosepalum diphyllum Duvign.		1	
Cryptosepalum staudtii Harms		1	
Cynometra letestui (Pellegr.) J.Léonard		1	
Cynometra lujae De Wild.		1	
Cynometra mannii Oliv.		1	
Cynometra nyangensis Pellegr.		1	
Cynometra oddonii De Wild.		1	
Cynometra sanagaensis Aubrév.		1	
Daniellia klainei A.Chev.		1	
Daniellia oblonga Oliv.		1	
Daniellia soyauxii (Harms) Rolfe		1	
Detarium macrocarpum Harms		1	
Dialium bipindense Harms		1	
Dialium densiflorum Harms		1	
Dialium eurypetalum Harms		1	
Dialium lopense Breteler		1	
Dialium soyauxii Harms		1	
Didelotia africana Baill.		1	
Didelotia brevipaniculata J.Léonard		1	
Didelotia letouzeyi Pellegr.		1	
Didelotia minutiflora (A.Chev.) J.Léonard		1	
Didelotia morelii Aubrév.		1	
Erypetalum batesii Baker f.		1	
Erypetalum tessmannii Harms		1	
Erypetalum unijugum Harms		1	
Gilbertiodendron barbulatum (Pellegr.) J.Léonard		1	
Gilbertiodendron brachystegioides (Harms) J.Léonard		1	
Gilbertiodendron demonstrans (Baillon) J.Léonard		1	
Gilbertiodendron grandiflorum (De Wild.) J.Léonard		1	
Gilbertiodendron grandistipulatum (De Wild.) J.Léonard		1	
Gilbertiodendron imenoense (Pellegr.) J.Léonard		1	
Gilbertiodendron klainei (Pellegr.) J.Léonard		1	
Gilbertiodendron limosum (Pellegr.) J.Léonard		1	
Gilbertiodendron mayombense (Pellegr.) J.Léonard		1	
Gilbertiodendron ngounyense (Pellegr.) J.Léonard		1	

Appendix 2 continued

	UG	LG	C
Gilbertiodendron pachyanthum (Harms) J.Léonard		1	
Gilbertiodendron stipulaceum (Benth.) J.Léonard		1	
Gilbertiodendron unijugum (Pellegr.) J.Léonard		1	
Gilbertiodendron zenkeri (Harms) J.Léonard		1	
Gilletiodendron pierreanum (Harms) J.Léonard		1	
Guibourtia arnoldiana (De Wild. & T.Durand) J.Léonard		1	
Guibourtia pellegriniana J.Léonard		1	
Guibourtia tessmannii (Harms) J.Léonard		1	
Hylodendron gabunense Taub.		1	
Hymenostegia bakeriana Hutch. & Dalziel		1	
Hymenostegia brachyura (Harms) J.Léonard		1	
Hymenostegia breteleri Aubrév.		1	
Hymenostegia felicis (A.Chev.) J.Léonard		1	
Hymenostegia floribunda (Benth.) Harms		1	
Hymenostegia klainei Pellegr.		1	
Hymenostegia mundungu (Pellegr.) J.Léonard		1	
Hymenostegia neoaubrevillei J.Léonard		1	
Hymenostegia ngounyensis Pellegr.		1	
Hymenostegia normandii Pellegr.		1	
Hymenostegia pellegrinii (A.Chev.) J.Léonard		1	
Hymenostegia talbotii Baker f.		1	
Julbernardia brieyi (De Wild.) Troupin		1	
Julbernardia hochreutineri Pellegr.		1	
Julbernardia pellegriniana Troupin		1	
Leonardoxa africana (Baill.) Aubrév.		1	
Librevillea klainei (Harms) Hoyle		1	
Loesenera gabonensis Pellegr.		1	
Loesenera talbotii Baker f.		1	
Loesenera walkeri (A.Chev.) J.Léonard		1	
Microberlinia bisulcata A.Chev.		1	
Microberlinia brazzavillensis A.Chev.		1	
Neochevalierodendron stephanii (A.Chev.) J.Léonard		1	
Oddoniodendron micranthum (Harms) Baker f.		1	
Oddoniodendron normandii Aubrév.		1	
Plagiosiphon discifer Harms		1	
Plagiosiphon gabonensis (A.Chev.) J.Léonard		1	
Plagiosiphon longitubus (Harms) J.Léonard		1	
Plagiosiphon multijugus (Harms) J.Léonard		1	
Prioria joveri (Normand ex Aubrév.) Breteler		1	
Prioria mannii (Baill.) Breteler		1	
Sindora klaineana Pellegr.		1	
Sindoropsis letestui (Pellegr.) J.Léonard		1	
Talbotiella batesii Baker f.		1	
Talbotiella eketensis Baker f.		1	
Tetraberlinia bifoliolata (Harms) Hauman		1	
Tetraberlinia korupensis Wieringa		1	
Tetraberlinia longiracemosa (A.Chev.) Wieringa		1	
Tetraberlinia moreliana Aubrév.		1	
Tetraberlinia polyphylla (Harms) J.Léonard ex Voorh.		1	
Zenkerella citrina Taub.		1	

Curriculum vitae

Miguel Esteban Leal was born on the 4th of July 1967 in Bogota, Colombia. He started secondary school in the Netherlands at the Jacoba College in Enschede (1980). His family moved to Mozambique in 1981, where he first started the LOI-secondary school written course and later went to the International School in Maputo. In 1983 he went back to the Netherlands and stayed at a boarding school in Bosch en Duin where he attended school in Bilthoven at the Nieuwe Lyceum. In 1984 he went to Ede and graduated from the Marnix College in 1989. In that same year he started to study biology at the university in Utrecht (RUU). Half-way he switched to the University of Amsterdam (UvA), where in 1994 he obtained his doctorandus title (M.Sc.). During this study he investigated the leaf morphology in a cloud forest in Costa Rica and the dispersal and pollination ecology of climbers in the lowland rain forest of Colombia. In between he had an ERASMUS grant to study in Århus, Denmark. After his graduation he worked as an honorary staff member at the Biosystematics Group, where in 1997 he was selected for the PhD-position related to the present work. In 2004 he finished his thesis in Wageningen and started inventorying protected areas in Gabon employed by Missouri Botanical Garden, St. Louis.

Publications

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Popular papers and interviews

Interview by Noorderlicht Dutch Radio 2003

Geografica Dutch National Geographic June 2003

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I ascribe this to my parents who after being born at almost 3000 m took me below sea level, and within a period of six months exposed me to extremes such as earthquakes, tropical lowland rain forest, wooden shoes, windmills and tulips.

The completion of my thesis would not have been possible without the help and support of many. The Netherlands Foundation for the Advancement of Tropical Research (WOTRO) financed this research project. The Gabonese Ministère des Eaux et Forêts gave me permission to work in the Lopé Reserve. For their hospitality, logistics and pleasant company I am indebted to the staff of the Lopé research station (Station d'Etude des Gorilles et Chimpansés, SEGC) of the Centre International pour la Recherche Médicale à Franceville / World Conservation Society (CIRMF / WCS). The Programme de Conservation et Utilisation des Ecosyst-èmes Forestiers en Afrique Centrale (ECOFAC), and the logging company National Societé Gabonese (NSG) also provided logistics and accommodation. I am grateful to the Eaux et Forêts Brigade, and the Herbier National du Gabon / CENAREST (Centre National de Recherche de Science Technologique) in Libreville. I thank my supervisors Hans de Wilde, Jos van der Maesen, Toine Cleef and Marc Sosef, and I appreciate the help of Jean Maley, Ton van der Wal, Henry Hooghiemstra, Frans Bongers, and Hans ter Steege for their inputs and discussions and Fred de Boer who backed up my statistics. I thank the people of the Biosystematics Group in Wageningen for their support and companionship, the Research School Biodiversity, the Nationaal Herbarium Nederland, Lee White in Lopé; Tom van der Hammen in Amsterdam who fed my scientific interest at an early age, and Helene Bernink who allowed me to wander through her museum in Denekamp after closing hours, and last but not least my family.

Miguel

Wageningen 2004

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