Renaat S.A.R. van Rompaey

Forest gradients in West Africa
A spatial gradient analysis

Promotor:	dr.ir. R.A.A. Oldeman hoogleraar in de bosteelt en bosoecologie
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Proefschrift
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ABSTRACT

van Rompaey R.S.A.R. (1993). Forest gradients in West Africa : a spatial gradient analysis. Doctoral thesis, Wageningen Agricultural University, The Netherlands, xxii + 142 pp., 5 tables, 61 figs., 3 text boxes, 3 apps., 250 refs., 13 items in software list, 51 terms in glossary, Eng., French and Dutch summaries. ISBN 90-5485-120-1.

Forest gradients were studied at two levels of scale in West Africa, west of the Dahomey interval. At a regional scale, the forest gradient in SE Liberia and SW Côte d'Ivoire was analysed using forest inventory data from the pre-logging era. In total 22 000 ha of forest were fully inventoried. 53 large tree species were used for the ordination. Spatial gradient analysis was applied to the forest ordination scores and a gradient map was produced with isoscore lines. This forest gradient was related to climate, relief and lithology.

At a local scale, forest gradients were studied along three catenas in Taï National Park, SW Côte d'Ivoire. The sample plots of 22 to 25 ha were subdivided in contour sample plots, covering 2 ha each, using digital terrain models. The ordination of the trees above 70 cm diameter in these subplots allowed to conclude that the slope gradients are sliding gradients superimposed on the regional gradient and that moisture conditions are likely to control these gradients.

Forest management should take into account these forest gradients in forest inventory and adapt silvicultural methods and species choice to the position on the gradient. Conservation of biodiversity is needed over the entire gradient and a 'Green Sickle' is proposed to link National Parks and Forest Reserves from the savanna down to the Atlantic coast.

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

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Back cover: Soil peels from the soil catena of the Taï study site, units Ts1, Ts3, Ts4 and Tv. From ISRIC, Wageningen.
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Stellingen

1 De grote verscheidenheid aan bossen in West-Afrika rechtvaardigt het vervangen van de term "het tropisch regenwoud" door de meervoudsvorm "tropische regenbossen".

Dit proefschrift

2 De boomsoortensamenstelling in de Westafrikaanse regenbossen is niet chaotisch of toevallig bepaald, maar vertoont een duidelijke ordening langs gradiënten, bepaald door klimaat, moedergesteente en positie in het landschap.

Dit proefschrift

3 Steekproefmethoden volgens toeval, al dan niet na stratificering, benutten onvoldoende de ordening van natuurlijke vegetatie langs gradiënten.

Alder D. & Synnott T.J. (1992).
Permanent sample plot techniques for mixed tropical forest.
Tropical Forestry Papers 25, Oxford Forestry Inst.

4 Er bestaan geen homogene proefvlakken in tropische regenbossen, en ook geen herhalingen.

Dit proefschrift

5 Het nemen van onafhankelijke steekproeven binnen één en hetzelfde ekosysteem is een *contradictio in terminis*.

Dit proefschrift

6 Het uitblijven van overeenstemming over een wereldboskonventie tijdens de UNCED-konferentie in Rio wordt onder andere veroorzaakt door verschillen in kulturele grondhouding van mensen tegenover bossen.

7 Engels is geen bosbouwtaal en vormt dus een hindernis voor het wetenschappelijk denken over, en het publiceren van bosbouwwetenschap.

8 Rekenbladprogramma's laten toe, in tegenstelling tot databaseprogramma's, kreatief en soepel gegevens in de computer in te voeren en te verwerken omdat in elk hokje op het formulier de ruimte praktisch onbeperkt is.

9 In der Beschränkung wird man niemals Meister.

10 Indien men wetenschap ziet als vissen in open water, dan heeft beleidsondersteunend onderzoek meer weg van vissen naar de goudvis in het aquarium.

11 Een kathedraal met te veel stellingen is ook niet mooi meer.

Stellingen behorende bij het proefschrift:
"Forest gradients in West Africa : a spatial gradient analysis"

Renaat S.A.R. van Rompaey
Wageningen, 29 juni 1993

Aan mijn vader,
Prof.dr. Jan Van Rompaey

PREFACE

De natuur heeft me altijd al geboeid en mijn keuze voor de studie van bosbouwingenieur was dan ook ingegeven door het verlangen meer te leren over die natuur en hoe mensen ermee omgaan. Ik volgde het curriculum van de tropische bosbouw omdat dit een wijdere horizon bood en je er leerde over de grote verscheidenheid van mensen, dieren en planten over de gehele wereld. Het was Prof.dr.ir. J. Schalck die me stimuleerde om een afstudeervak in de tropen te doen, o.a. met zijn boeiende colleges over toegepaste tropische plantensystematiek. Het boek van Marius Jacobs (1982) over het tropisch regenwoud heb ik toen helemaal uitgelezen. Suriname werd mijn tropendoop. Ik bestudeerde er met ir. Jan Mallants als begeleider en Prof.dr.ir. M. Reynders als promotor de groei van bomen in natuurlijk bos in de uitgestrekte binnenlanden. Van op de Voltzberg keek ik voor het eerst in mijn leven uit op niets dan natuur, tot aan de horizon.

Deze Surinameavonturen brengen me bij dr.ir. Reitze de Graaf, aan wie ik te danken heb dat ik voor dit onderzoek werd aangesteld. Zijn enthoesiast vertelde ervaringen uit Suriname kwamen me later nog vaak van pas, en zijn begeleiding tijdens mijn AIO-schap, door dik en dun, hield me overeind.

Ir. Fred Vooren, directeur van het Centre Néerlandais bij Abidjan, was mijn bosbouwcollega overzee en bron van kennis van het Afrikaanse bos. Zijn prima ondersteuning tijdens het veldwerk in Ivoorkust heb ik zeer gewaardeerd.

Prof.dr.ir. R.A.A. Oldeman ontstak de lont van dit onderzoek en naar het eind toe was hij de motor was om de vele ideeën en ervaringen tot een gestroomlijnd proefschrift om te vormen. De vele gesprekken die we bij hem thuis voerden, zijn voor mij een blijvende bron van inspiratie en verdieping.

Je voudrais exprimer ma gratitude à M. le Ministre de la Recherche Scientifique en Côte d'Ivoire qui m'a offert une authorisation de recherche dans son pays. Aussi Théo de la Station Ecologique à Taï, Angelo Muchetti de BTA, et Claude Frischknecht de EFBA à Zagné, je vous remercie pour votre hospitalité et votre amitié. Bien sûr aussi Daouda Sidibé et Pierre Polé qui m'ont assisté en permanence en forêt et à Abidjan et tous les Africains dont je garde de bons souvenirs de notre coopération. Un grand merci sur le plan logistique, resp. mécanique pour Emmanuel et Abdoulaye du Centre Néerlandais et pour tous ceux qui ont rendu agréable mon séjour en Afrique.

Zelf eigenlijk nog een beetje student heb ik de compagnie van de Wageningse studenten erg geapprecieerd: Antoinette Stoffers, Pans Boddez, Ellen Schmidt, Paul Albers, Luc Jans, Lourens Poorter, Maarten de Klerk, Marc Parren, Kees Nooren, Frank Rademacher, Peter Sloot en de vele andere die steeds maar uit Nederland kwamen aanstromen. Mijn bijzondere dank gaat uit naar drs. Gerrit-Jan van Herwaarden die de bodemkartering van de drie onderzoeksgebiedjes verzorgde, samen met de studenten Kees Nooren en Frank Rademacher. Mijn collega's uit andere disciplines binnen het projekt in Ivoorkust (Léonie Bonnéhin, ir. Henk van Reuler, dr.ir. Anneke de Rouw, drs. Hans Vellema, ir. Joep Slaats, ir. Jetse Stoorvogel, dr.ir. Wouter Blokhuis, ir. Ellen Schmidt, ir. Peter Sloot, ir. Gerard Hazeu) maakten het onderzoek nog een stuk interessanter. Ik leerde in team te werken en de middenweg te zoeken tussen gezellig samen en kreatief alleen bezig zijn. De même pour mes collègues au DCGTx, à l'IGCI, au Centre Suisse et à l'IIRSDA et pour mes amis en Côte d'Ivoire. I would also like to thank Peter Weinstabel, Jochen Weingart and Reinhart Wolf from the German Forestry Mission to Liberia, for their kind reception in Monrovia in April 1990. They handed me over most of the information and data from Liberia used in this book.

In Wageningen is er tussentijds en vooral na terugkeer ook goed voor me gezorgd. De mensen op Bureau Buitenland, Hans, Eric, Philip en andere, en op de vakgroep Bosbouw, o.a. Marthy, Michael, Bert, Ed, Joke, Job, Annelies waren steeds voor me in de weer. Jullie hebben me steeds vooruitgeholpen en het was meestal nog gezellig ook. Niet te vergeten is ook de Werkgroep Ivoorkust die een team vormde over de grenzen van de vakgroepen heen.

Mijn dank ook aan de vrienden en collega's op de vakgroep Bosbouw en op andere vakgroepen, aan dr.ir. M.A.J. van Montfoort voor het statistisch advies en aan de teken- en de fotolokatie op de Biotechnion. Ir. Boudewijn de Roover van het Laboratorium voor Teledetektie en Bosbeheersregeling te Gent maakte het mooie plaatje op de voorkaft en wist me te interesseren voor satellietbeelden en landinformatiesystemen. Wout Bomer, fotograaf bij het ISRIC in Wageningen, maakte de opnamen van de lakprofielen op de achterkaft. Het LEB-Fonds ben ik erkentelijk voor de financiële steun bij de vierkleurendruk van de kaft.

My international colleagues Dr. Mike Swaine and Dr. Denis Alder are thanked for their enthusiasm. Et Dr. Henri-Félix Maître et Dr. Jean Maley pour leur encouragement lors de mes visites à Paris et à Montpellier.

De kritische lezers van de manuscripten, Prof.dr.ir. I.S. Zonneveld, Prof.dr. M.J.A. Werger, dr. Frans Bongers, dr.ir. Rob Peters, ir. Lourens Poorter, ir. Marc Parren, ir. Fred Vooren worden bedankt voor hun opmerkingen en suggesties. Het Engels in dit boek was nooit zo mooi geworden zonder de rode pen van Mevr. Joy Burrough-Boenisch. De prachtige kaarten zijn van de hand van Piet Versteeg van de tekenlokatie Biotechnion. The following authors are thanked for their permission to reproduce figures: A.G. Voorhoeve, J.L. Guillaumet, A.P. Vooren, M. Sachtler, and P. Bosman. Een aantal foto's werden me ter beschikking gesteld door P. Albers, H. Dop, M.P.E. Parren en A.P. Vooren. De overige foto's heb ik zelf genomen.

Niets van dit alles was gerealiseerd zonder de nooit aflatende zorg en liefde van Moeke, en van mijn allerliefste Sandra.

Wageningen, 31 maart 1993

Renaat van Rompaey

Renaat van Rompaey

CURRICULUM VITAE

Renaat Sylva Angèle Rosine van Rompaey werd geboren op 9 juni 1965 te Gent, België. Hij liep lagere school op de Gemeentelijke Jongensschool in De Pinte. Na het behalen van het Humanioradiploma in de richting Latijn-Wetenschappen aan het Sint-Barbaracollege te Gent in 1982, begon hij zijn studie aan de Fakulteit Landbouwwetenschappen van de Rijksuniversiteit te Gent met als studierichting 'Waters en Bossen', specialisatie Ontwikkelingslanden. Tijdens het laatste jaar van zijn studie schreef hij een afstudeerwerk met als titel: "Bosbouw in het tropisch regenwoud. Evaluatie van een vrijstellingsexperiment in Suriname". In 1987 behaalde hij zijn diploma met de grootste onderscheiding.

Eén maand na afstuderen trad hij in dienst van de Landbouwuniversiteit Wageningen als assistent in opleiding bij de vakgroep Bosteelt & Bosoecologie. Hij werd voor twee jaar uitgezonden naar het Steunpunt Ivoorkust van de Landbouwuniversiteit om onderzoek te verrichten naar de "Bostypologie en groeidynamiek van bos en bomen in het Taï Nationaal Park", in zuidwest-Ivoorkust. Nog één jaar na het aflopen van zijn aanstelling werkte hij verder aan de voltooiing van dit proefschrift, samen met zijn promotor Prof. R.A.A. Oldeman. Tussendoor was hij twee maand aangesteld voor het schrijven van een hoofdstuk over klimaatsonderzoek in zuidwest-Ivoorkust in opdracht van de Stichting Tropenbos.

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SUMMARY

The tropical rain forests of West Africa, west of the Dahomey interval, once covered some 40 million ha. Being on the western fringe of the African continent, they receive abundant rainfall from the SW monsoon. Further inland, rainfall gradually decreases and the forests give way to savanna and ultimately to the Sahara desert.

This Upper Guinea forest block used to cover most of Liberia and parts of Côte d'Ivoire and Ghana. Here, deforestation rates are among the fastest in the world. Humans have reduced the forest cover by some 80 %. Most of the forest has been converted to agricultural land. Fire and heavy timber mining have left the remaining forest in a poor state. Sustainable forest management has not yet been attained. A key prerequisite for achieving such management is more and better knowledge of the ecology of these complex and highly diverse ecosystems and of their species.

Gradients are gradual changes in space e.g. of species composition in the ecosystems. In this book forest gradients are studied at two levels of scale: the regional forest gradient from the coast to the forest-savanna boundary, and local gradients along slopes in the landscape. The species composition of the large forest trees with a diameter exceeding 70 cm was studied; this entailed adapting the existing methods used in vegetation science to cope with these huge subjects. In West African forest exploitation 70 cm diameter is a common limit for selective cutting of trees.

At the regional scale, the ***spatial gradient analysis*** consisted of a three-step approach:
1. ordination of forest areas and species; 2. spatial interpolation of the ordination scores of the forest areas; 3. relating spatial trends in species composition to trends in rainfall and patterns in lithology and relief.

Tree species composition in a forest area was determined by using forest inventory data from the pre-logging era in SE Liberia and SW Côte d'Ivoire. These data were ordinated together with data from three sample plots of 20 ha each established in Taï National Park. The old and new sample plots together covered 21 640 ha. Of the largest tree species, 53 were retained for the ordination.

The forest gradient was mapped by interpolating lines of equal ordination scores and plotting these on the map. The ordination table allowed these ordination scores to be translated into the corresponding species composition. Each tree species has an individual position along the gradient, given by its ordination score. The ecological range of the species is indicated by the range of sample scores in which it occurred. The gradient map with isoscore lines provides a valid alternative to mapping by types or classes and overcomes the problem of transitional types.

Over 400 km a pronounced regional forest gradient was found from the Liberian coast towards the forest-savanna boundary in Côte d'Ivoire. This gradient correlated well with the SW-oriented rainfall gradient. On part of the map the forest gradient showed an anomaly. The forests on a band of sericite-chlorite schist from Taï National Park towards the NE were ranked 'wetter' than expected from their position on the rainfall gradient. Apparently, the rainfall effect was compensated by the greater moisture content of the soils derived from sericite-chlorite schist. Furthermore, the rain shadow of Putu range (753 m above sea level) was reflected in the forest gradient by a zone of fast compositional change. These results are comparable with those of other studies on the regional forest gradients in Ghana, Côte d'Ivoire and Liberia.

Forest gradients along slopes spanning a 20 to 40 m elevation interval were studied in Taï National Park in sample plots at three locations: near Zagné in the drier north-west (plot size 23 ha), near Taï in the middle (25 ha) and near Para in the wetter south-west of the Park (22 ha).

All trees in these plots with a diameter larger than 70 cm were recorded and mapped. Swamp areas were excluded from these plots. A digital terrain model and a physiographic soil map were prepared for each site.

The approach used for the analysis of the slope gradient contained the same elements as for the regional gradient, but in reverse order: 1. the soil survey revealed that the spatial trend in environmental variation was related to local elevation; 2. thus, ***contour samples*** of trees growing within an elevation interval were composed. A series of 11 or 12 consecutive intervals was calculated at each site in such a way that each sample covered 2 ha. 3. Tree species composition was determined per sample and all samples of the three sites were ordinated together using Detrended Correspondence Analysis (DCA). The sample scores on the first ordination axis were plotted against elevation to check the hypothesis of elevational gradients. Tree density, species richness, basal area and stem biomass per contour sample were analysed in a similar way for elevational trends.

The ***contour sampling technique*** proved to be appropriate for the analysis of floristic slope gradients in large trees. The spatial autocorrelation of the contiguous samples is assumed to counterbalance the small number of trees per sample. The species order resulting from this ordination was similar to the one obtained in the regional gradient and hence, could be interpreted as a wet-dry axis. On the three sites species composition changed from "drier" species upslope to "wetter" downslope. The lower slope on a drier site was similar in species composition to the upper slopes of its wetter neighbour. Thus, slope gradients are sliding gradients on the regional forest gradient. The regional gradient was related to rainfall and lithology. These factors are largely expressed in soil moisture availability. Hence, gradients in moisture availability probably explain the forest gradients along slopes.

Tree density and species richness of the large trees decreased towards the wet end of the gradient, both between sites, e.g. from Zagné to Para, and within the Taï site, from upper slope to lower slope. This trend in species richness of the large trees contradicts one of the tenets of the Pleistocene forest refugia theory, namely that species richness increases towards the core area of a refugium. A Pleistocene refugium is hypothesized to have existed in the Grabo hills to the southwest of Taï National Park.

Basal area curves showed a peak in middle slope positions and declined towards both the upper and lower end of the catena. A general trend of increasing wood density of the large tree species was found towards the wet end of the gradient.

Some implications of the continuous variability model are evaluated as a scientific basis for forest management and conservation of biodiversity. At the regional scale, forest management should be adapted to the individual position of each forest area along the gradient. The tree species chosen and the forest land evaluation should both reflect this position. Catena plots are suggested as more appropriate for forest inventory than random sampling in areas with pronounced slope gradients.

Any conceivable strategy for conservation of biodiversity in West Africa must aim at protecting forests along the entire gradient, because at any point along the gradient different species attain their optimum. A "Green Sickle" is advocated which, if adopted and implemented, would link National Parks and forest reserves from the savanna down to the Atlantic coast.

In western Côte d'Ivoire there are two promising areas where conservation efforts could still produce worthwhile results: 1. the hills of Grabo, a hypothetical Pleistocene forest refugium with a high degree of endemism in Côte d'Ivoire, which merits the status of national park; 2. the semi-deciduous forests, which contain many species not found in wetter forests.

Regional and local gradients result in a great diversity of forests in West Africa. The satellite image on the front cover confirms this broad variation. Forests are not just hectares, trees not just cubic metres. Management of the most species-rich ecosystems on earth is a challenge for present and future generations. It will need international support and the efforts of all those fascinated by this pearl of our blue planet.

SAMENVATTING

Bosgradiënten in West-Afrika: een ruimtelijke gradiëntanalyse

In West Afrika ten westen van het Dahomey interval lagen vroeger 40 miljoen hectare tropische regenwouden. De vochtige zuidwest-moesson zorgt voor overvloedige regenval aan deze rand van het Afrikaanse continent. Dieper landinwaarts neemt de neerslag snel af en groeit er geen bos meer, maar savanne totdat uiteindelijk enkel nog woestijn rest.

Dit zogenaamde bosblok van Hoog-Guinea ligt voornamelijk in Liberia en in zuidelijke delen van Côte d'Ivoire en Ghana. Deze regio kent één van de hoogste ontbossingspercentages ter wereld. Door toedoen van de mens is het bosareaal er teruggebracht tot één vijfde van de oorspronkelijke bedekking. Het meeste bos werd tijdelijk of permanent omgezet in landbouwcultures. Het resterende bos is door vuur en "houtmijnbouw" zwaar toegetakeld. Duurzaam bosbeheer wordt nog weinig toegepast in deze landen. Zo'n beheer vergt goede kennis van de ekologie van deze complexe en hoogbiodiverse ekosystemen en van de dier- en plantesoorten die er leven.

Gradiënten zijn geleidelijke veranderingen in de ruimte in b.v. soortensamenstelling in de ekosystemen. In dit boek worden bosgradiënten geanalyseerd op twee schaalniveau's: de regionale bosgradiënt vanaf de kust, waar de hoogste neerslag valt, tot waar bos overgaat in savanne, en plaatselijke bosgradiënten langs hellingen in het landschap. De studie concentreert zich op de grote boomsoorten die dikker dan 70 cm worden, wat in West-Afrika een gebruikelijke diameterlimiet is voor selektieve kap. De bestaande methodieken uit de vegetatiekunde heb ik aangepast aan het groot formaat en het verspreide voorkomen van deze bomen.

Voor de ***ruimtelijke gradiëntanalyse*** in zuidoost-Liberia en zuidwest-Côte d'Ivoire hanteerde ik een aanpak in drie stappen: 1. ordinatie van bosgebieden en boomsoorten; 2. ruimtelijke interpolatie van de ordinatiescores van de bosgebieden; 3. het relateren van ruimtelijke trends in soortensamenstelling aan de neerslaggradiënt en aan patronen in moedergesteente en reliëf.

De boomsoortensamenstelling van de bosgebieden haalde ik uit de resultaten van bosinventarisaties die de grootschalige "houtmijnbouw" vooraf gingen. Deze gegevens werden geordineerd samen met gegevens van drie eigen proefperken in Taï Nationaal Park, elk tussen 22 en 25 ha groot. In totaal waren gegevens beschikbaar van 21 640 ha oude en nieuwe opnamen. De ordinatie is gebaseerd op 53 boomsoorten die de grootste bomen van het bos leveren.

De bosgradiënt werd in kaart gebracht door lijnen van gelijke ordinatiescore te interpoleren. Deze scores langs de eerste ordinatieas werden aan de hand van de ordinatietabel vertaald naar een bepaalde soortensamenstelling. Elke soort blijkt een individuele positie langs de gradiënt in te nemen. Haar ekologisch optimum wordt gegeven door de ordinatiescore en de ekologische amplitude van de soort is af te lezen aan het bereik aan opnamescores waarin de soort voorkomt. De gradiëntkaart met isoscore lijnen is een alternatief voor kartering aan de hand van types of klassen en lost het probleem op van de overgangstypes.

Uit de resultaten bleek dat er een uitgesproken bosgradiënt ligt over 400 km vanaf de Liberiaanse kust tot waar de savanne begint in Côte d'Ivoire. Deze gradiënt loopt grotendeels parallel met de ZW-NO georiënteerde neerslaggradiënt. Op een deel van de kaart wijkt de bosgradiënt af van de neerslaggradiënt. Dit blijkt te zijn op een band met sericiet-chloriet schist als moedergesteente die vanuit Taï Nationaal Park naar het NO loopt. De mindere neerslag wordt hier kennelijk gecompenseerd door meer bodemvocht in de kleiige bodems die uit de schist gevormd zijn. Een zone van snelle verandering in soortensamenstelling op de bosgradiëntkaart in Liberia is vermoedelijk te wijten aan de regenschaduw van de Putu berg (753 m boven zeeniveau) en het omliggend plateau. De resultaten zijn vergelijkbaar met die van andere bosgradiëntstudies in Ghana, Côte d'Ivoire en Liberia.

Bosgradiënten langs hellingen met een hoogteverschil van 20 tot 40 m werden onderzocht op drie plaatsen in Taï Nationaal Park: bij Zagné in het drogere NW, bij Taï in het midden en bij Para in het nattere ZW. Alle bomen dikker dan 70 cm werden opgenomen en gekarteerd binnen een proefperk van respectievelijk 23, 25 en 22 ha. Valleibos werd niet in het proefperk opgenomen. Van elke studiegebied werd een digitaal terreinmodel en fysiografische bodemkaart gemaakt.

De aanpak voor de analyse van de hellinggradiënten was analoog met die van de regionale gradiënt, maar de redenering werd in omgekeerde volgorde gevoerd: 1. de bodemkaart leerde dat de ruimtelijke trend in milieuvariatie afhing van de plaatselijke hoogteligging; 2. dus besloot ik, achteraf weliswaar, ***contouropnamen*** samen te stellen langs de hoogtegradiënt. In elk proefperk werd een reeks van 11 of 12 opeenvolgende hoogteïntervallen berekend met als randvoorwaarde dat elke contouropname 2 ha moest bestrijken. 3. De boomsoortensamenstelling binnen elke contouropname werd vastgesteld en alle opnamen van de drie gebieden samen werden geordineerd met correspondentieanalyse (DCA). De opnamescores langs de eerste ordinatieas werden uitgezet tegen hoogteligging om na te gaan of er een hellinggradiënt was. Ook boomdichtheid, soortenrijkdom, grondvlak en stambiomassa werden uitgezet tegen hoogteligging.

De ***contouropnametechniek*** bleek geschikt om floristische hellinggradiënten te onderzoeken van de grote bomen. De schijnbare nadelen verbonden aan het klein aantal bomen per opname worden ondervangen door de ruimtelijke autocorrelatie tussen aangrenzende opnamen. De soortsvolgorde bij deze ordinatie leek sterk op die van de regionale gradiënt en kon bijgevolg geïnterpreteerd worden als een droog-nat as. Naar beneden toe langs de helling kwamen in de drie studiegebieden steeds 'nattere' soorten voor. De soortensamenstelling beneden aan de helling bij Zagné sloot aan bij die bovenaan de helling in Taï en idem dito voor Taï en Para. Dit geeft aan dat de hellinggradiënten schuivende gradiënten zijn over de regionale bosgradiënt. Neerslag en moedergesteente bepaalden grotendeels de regionale gradiënt en beide faktoren komen tot uitdrukking in het beschikbaar vocht in de bodem. Het is dus aannemelijk dat hellinggradiënten in de boomsoortensamenstelling verklaard kunnen worden vanuit bodemvochtgradiënten langs die helling.

De dichtheid en soortenrijkdom van grote bomen nam af naar het natte uiteinde van de gradiënt; dit was het geval tussen studiegebieden, van Zagné naar Para, maar ook binnen het proefperk in Taï, van bovenaan de helling naar beneden toe. Deze trend in soortenrijkdom gaat in tegen één van de stellingen van de Pleistocene refugia theorie, namelijk dat de soortenrijkdom zou toenemen naar het kerngebied van een refugium toe. Er wordt een refugium verondersteld ten zuiden van Taï Nationaal Park bij de heuvels rond Grabo.

Het grondvlak bleek het hoogst op het midden van de helling en neemt af naar de top en naar de vallei toe. De gemiddelde dichtheid van het hout van de grote boomsoorten leek toe te nemen naar het nattere uiteinde van de gradiënt.

De continue verandering van de bossamenstelling heeft implikaties voor het bosbeheer en het natuurbehoud. Langs de regionale gradiënt moet het bosbeheer aangepast worden aan de individuele positie van elk bosgebied. Dit uit zich dan in een aangepaste boomsoortenkeuze en een individuele evaluatie van de standplaats. In de bosinventarisatie sluiten catena-opnamen beter aan bij de realiteit van de gradiënten langs hellingen dan willekeurig uitgelegde opnamen.

Natuurbehoud in West-Afrika moet zich richten op bescherming van bossen over de gehele gradiënt. Op elke positie van deze gradiënt zijn er weer andere soorten die hun optimum bereiken. Een 'Groene Sikkel' wordt voorgesteld om Nationale Parken en bosgebieden te verbinden vanaf de savanne tot aan de Atlantische kust in Liberia.

Binnen westelijk Côte d'Ivoire worden in het bijzonder twee gebieden genoemd waar natuurbescherming nog veel resultaat kan boeken: 1. de heuvelruggen van Grabo, een verondersteld Pleistoceen regenwoudrefugium met vele soorten die binnen Côte d'Ivoire enkel daar voorkomen. Dit gebied verdient de status van Nationaal Park; 2. de half-bladverliezende bossen die ook veel specifieke soorten herbergen.

De regionale en lokale bosgradiënten geven aanleiding tot een grote verscheidenheid aan bossen in West-Afrika. Het satellietbeeld op de kaft van dit boek staaft deze rijkdom. Bossen zijn meer dan hectares land en bomen meer dan kubieke meters hout. Een duurzaam beheer van de soortenrijkste ekosystemen op deze aarde vormt een uitdagende taak voor deze en volgende generaties. Die zal gedragen moeten worden door de hele internationale gemeenschap en door ieder die gefascineerd raakte door deze parel van onze blauwe planeet.

RÉSUMÉ

Gradients floristiques dans la forêt dense de l'Afrique de l'Ouest: une analyse spatiale

Il y un siècle et à l'Ouest de l'intervalle de Dahomey, l'Afrique était couverte de 40 millions hectares de forêt dense. Les pluies du mousson arrosaient abondamment cette bordure du continent africain. Plus à l'intérieur, la pluviosité diminuait et la savane et finalement le désert succéderaient à la végétation forestière.

Ce qui reste maintenant de ce bloc forestier, dite de "Haute Guinée", se trouve au Libéria et dans les parties méridionales de la Côte d'Ivoire et du Ghana. Cette région connaît un des plus forts taux de déboisement du monde. L'homme a réduit le couvert forestier jusqu'à un cinquième de l'original. La plupart de ces terrains ont été converti en terres agricoles. La reste de la forêt a été gravement détériorée par les feux de brousse et par l'exploitation 'minière' du bois. Les forêts n'y sont pas encore gérées de façon soutenu. Pour développer une gestion soutenue, il est indispensable de réunir au préalable des bonnes connaissances autant de l'écologie de ces écosystèmes complexes et hautement diverses, que des espèces végétales et animales qui les constituent.

Un gradient constitue une transition graduelle dans l'espace, par exemple, de la composition floristique. Dans ce livre j'ai analysé des gradients floristiques dans la forêt dense à deux niveaux d'intégration, respectivement le gradient régional climatique allant de la côte à la limite forêt-savane, et des gradients toposéquentiels. L'étude portait sur les grandes espèces arborescentes, pouvant atteindre un diamètre de 70 cm, limite habituelle de la coupe sélective en Afrique de l'Ouest. Les méthodes habituelles phytosociologiques ont donc été adaptées à la grande taille de ces arbres et à leur abondance souvent faible si l'on compte par hectare.

Pour l'***analyse spatiale du gradient*** régional dans le Sud-est du Libéria et dans le Sud-ouest de la Côte d'Ivoire j'ai procédé en trois étapes: 1. en appliquant l'analyse factorielle de correspondance aux forêts et aux espèces; 2. en calculant l'interpolation spatiale des scores des forêts; 3. en établissant les corrélations entre les tendances spatiales dans la composition d'espèces et le gradient climatique régional, la roche-mère et le relief respectivement.

Afin de caractériser la composition floristique des forêts, j'ai utilisé les données provenant des inventaires nationaux au Libéria et en Côte d'Ivoire. Ils décrivent la situation de ces forêts avant la grande vague d'exploitation forestière. En complément de ces anciennes données j'ai établi l'ordination des données prélevées dans ce but sur trois parcelles d'étude dans le Parc National de Taï, couvrant entre 22 et 25 ha chacune La surface totale des forêts inventoriées autrefois et plus récemment est de 21 640 ha. L'analyse de correspondance est basé sur 53 espèces de grands arbres.

Le gradient régional, allant de la forêt sempervirente à la forêt semi-décidue, a été visualisé en utilisant des courbes interpolées de score égal. Ces scores le long du premier axe sont liés à la composition floristique par le tableau de l'analyse de correspondance. Chaque espèce occupe une position individuelle le long du gradient. L'optimum écologique de l'espèce est donné par son score, et l'amplitude de l'espèce est proportionnelle à l'intervalle des scores des sites où l'espèce est présente. La carte du gradient avec des courbes d'isoscore fournit une alternative pour les cartes visualisant des types de forêt. Du coup, le problème des types transitionnels se trouve résolu.

Les résultats de l'analyse indiquent qu'il existe un gradient floristique prononcé sur les 400 km entre la côte libérienne et la limite forêt-savane en Côte d'Ivoire. Ce gradient suit largement le gradient pluviométrique orienté du SW au NE. Sur une partie de la carte, le gradient floristique semblait dévier du gradient pluviométrique. Cette déviation s'expliquait par une bande de schiste sériciteux qui se trouve dans une partie du Parc National de Taï et qui s'étend vers le nord-est. Apparemment, il existe une compensation entre une pluviosité moindre et une capacité plus grande de rétention d'eau des sols schisteux. Une zone de transition floristique plus rapide au Libéria se trouve à l'abri des pluies dû au Mont Putu (753 m) et son plateau. Les résultats se joignent à ceux d'autres études de gradients floristiques au Ghana, en Côte d'Ivoire et au Libéria.

A trois endroits dans le Parc National de Taï, j'ai étudié le gradient floristique le long d'une toposéquence. C'était près de Zagné dans une zone moins pluvieuse au nord-ouest du Parc, près de Taï au milieu et près de Para dans le sud-ouest du Parc où la forêt reçoit plus de pluviosité. Les pentes couvraient un intervalle de 20 à 40 m en altitude. Tout arbre de plus de 70 cm de diamètre a été inventorié et sa position portée sur la carte dans des parcelles de 23, 25 et 22 ha respectivement. Un modèle de terrain digital et une carte physiographique ont des sols été construits pour chaque périmètre de recherche.

L'approche suivie pour l'analyse des gradients toposéquentiels est analogue à celui du gradient régional, mais le raisonnement a été suivie en ordre inverse. 1. La carte des sols démontrait que la tendance spatiale dans les conditions environnementales dépendait de l'élévation. 2. Alors j'ai délimité, a posteriori, des sous-parcelles le long des courbes de niveau. De cette façon j'ai composé dans chaque site 11 ou 12 sous-parcelles, chacune couvrant 2 hectares. 3. La composition floristique des grands arbres a été calculé pour chaque sous-parcelle et une analyse de correspondance a été effectué avec ces ***relevés toposéquentiels***. La relation entre les scores le long du premier axe et l'élévation de chaque relevé a été étudiée. La densité d'arbres, la richesse en espèces, la surface terrière et la biomasse des troncs ont été analysé le long des toposéquences, eux, aussi.

La technique des relevés toposéquentiels s'est prouvé efficace pour l'analyse des gradients floristiques parmi les grands arbres. Le désavantage apparent du petit nombre d'arbres par relevé a été corrigé par l'autocorrélation spatiale entre relevés voisins. L'ordre des espèces le long du premier axe ressemblait beaucoup celui le long du gradient régional. Il fût donc interprété comme un axe indiquant l'humidité du milieu. Sur les trois périmètres, des espèces "humides" se trouvaient en bas de pente. La composition floristique en bas de pente à Zagné correspondait à celle de la haute pente à Taï. Il en était de même pour Taï et Para. Ceci montre que les gradients toposéquentiels sont des gradients "glissants superposés" sur le gradient régional. La pluviosité et la roche-mère déterminent largement le gradient régional. Tous deux s'expriment dans l'humidité du sol. Les gradients floristiques le long des toposéquences s'expliquent donc en majeure partie par des gradients d'humidité du sol dérivés.

La densité d'arbres et la richesse en espèces de grands arbres diminuaient tous les deux vers l'extrémité humide du gradient; ceci était le cas en allant de Zagné à Para, mais aussi à l'intérieur de la parcelle de Taï, suivant l'aval de la pente. Cette tendance de richesse floristique décroissante parmi les grands arbres contredit l'une des thèses de la théorie des refuges forestiers dans le Pléistocène, qui prétend que la richesse en espèces devrait augmenter vers le centre plus humide du refuge. Je suggère que les collines de Grabo, au sud du Parc National de Taï, faisaient partie d'un tel refuge parce que les espèces les plus "humides" y sont présentes.

La surface terrière culminait à mi-pente et diminuait aussi bien vers le sommet que vers le bas-fond. Par contre, la densité moyenne du bois des grands arbres augmentait vers l'extrémité humide du gradient.

Le changement continu et non pas discret de la composition floristique des forêts Ouest-africaines a des implications pour leur aménagement et pour la conservation de la biodiversité. Le long des gradients, les mesures sylvicoles doivent s'adapter à la position individuelle de chaque partie de forêt. Ceci s'exprime dans le choix d'espèces et dans l'évaluation individuelle de chaque site forestier. Dans la pratique de l'inventaire forestier, ce sont des parcelles couvrant une toposéquence entière qui correspondent au mieux à la réalité de gradients toposéquentiels, et non pas des parcelles choisies stochastiquement.

La conservation de la biodiversité en Afrique de l'Ouest devrait comprendre la protection de forêts tout le long du gradient régional. Chaque position sur ce gradient indique l'optimum écologique pour d'autres espèces. Un 'Croissant Vert' est proposé qui se fonde sur l'analyse des gradients et qui devrait lier entre eux les Parcs Nationaux et les Forêts Classées de la savane à la côte atlantique au Libéria.

Dans la partie ouest de la Côte d'Ivoire deux régions existent où la conservation de la nature peut encore espérer beaucoup de succès. 1. Les collines de Grabo sont un refuge forestier glacial supposé où poussent beaucoup d'espèces trouvées nulle part ailleurs en Côte d'Ivoire. Ces forêts méritent le statut de Parc National. 2. Les forêts semi-décidues qui à leur tour hébergent beaucoup d'espèces spécifiques, méritent d'être protégées au même titre.

Les gradients floristiques régionaux et locaux produisent une grande diversité de forêts dans l'Afrique de l'Ouest. L'image satellite sur la couverture de ce livre est une bonne illustration de cette richesse. Les forêts sont plus que des hectares de terrain vert, les arbres plus que des mètres cubes de bois. La gestion soutenue de ces écosystèmes les plus divers du monde forme un défi pour les générations actuelles et futures. Ceci demandera le soutien de la communauté internationale entière et de chacun qui se trouve à son tour fasciné par cette perle verte de notre planète bleue.

INTRODUCTION

A green ocean from a bird's eye view, but an ever changing kaleidoscope for the experienced observer; such are the forests of West Africa. It is all *forest but no two forests are the same. At first glance no order can be detected in this "green hell" (Oldeman 1983), but fairly quickly one learns to distinguish swamp forests from *upland forests. From the coast inland these upland forests change from evergreen to semi-deciduous. *Gradients, i.e. gradual changes in space, were the subject of this research. They were studied in the large forest trees, and therefore the existing methods used in vegetation science had to be adapted to cope with these huge subjects. These forest giants are the glory of the West African rain forests (Rollet 1974).

Spatial gradient analysis

Forest gradients are studied in the present book at two levels of scale: the regional forest gradient from the coast to the forest-savanna boundary, and local gradients along slopes in the landscape. On a vegetation map of the world (Walter 1979), West Africa and Russia are the classic examples of zonal vegetational change parallel to the equator. On these large, flat land masses this pattern is not disturbed by mountain ranges as in the Americas. So, it is not surprising that it was the Russian geobotanist L.G. Ramensky (1910 ex Sobolev and Utekhin 1973; 1924 ex Whittaker 1967) who first formulated the principles of species individuality, vegetation continuity and ecological series, and practised the method of *ordination of vegetation relevés.

Ordination, i.e. the arrangement of samples or species in a uni- or multi-dimensional order, was the translation by Goodall (1954) of the German "Ordnung" as used by Ramensky (1930). Curtis & McIntosh (1951) and Bray & Curtis (1957) applied ordination to relevés from an upland forest *continuum in Wisconsin (USA). They recognized that the position of a species on such a continuum is controlled by both the biotic and the physical environment. In the biotic control model, competition or predation between organisms is considered to be the primary *factor structuring the continuum, whereas in the environmental control model, factors from the abiotic environment are seen as determinants of the variations observed in the occurrence or abundance of organisms (Borcard et al. 1992). Hence, a species may be abundant in a relevé either because abiotic conditions are optimal for it, or because possible competitors are absent.

From this concept Bray & Curtis (1957) concluded that *patterns and gradients present in the vegetation itself should be made clear first, before searching to *explain* this variation. The explanation may lie in the vegetation itself and in its environment. They called their approach a 'direct ordination' of the vegetation data set. Whittaker (1967) termed it 'indirect gradient analysis' in opposition to his own approach in which compositional gradients are directly related to environmental gradients.

I agree with Hill (1973) that Whittaker's terminology of 'direct' and 'indirect' gradient analysis is confusing. Ordination is a method or technique and gradient analysis is the

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* Each term preceded by an asterisk, is defined in the Glossary.

field of research in which it is applied. In the same way, *clustering is a method and vegetation *classification and mapping is the field of research in which it is applied (Zonneveld 1988).

What is a *gradient? Literally, it means "stepping", from Latin gradi: to step, to stride. Whittaker (1967) applied the term to the gradual change in vegetation or environment when going up a mountain slope or, at the same elevation, when visiting slopes of varying exposure around a hill. Here the gradients have a spatial connotation and it is indeed possible to stride along them. In mathematics, the gradient vector, symbol $\nabla f(x,y,z)$, at a point has the direction of the greatest change at that point along a continuous line, surface or space and as magnitude the rate of change in this direction (Gillman & McDowell 1973). Thus, the gradient of a surface indicates the steepest slope at a point and the corresponding direction. For non-planar surfaces the gradient changes from point to point. No confusion should arise between the gradient and the surface itself, the former being determined by the directional derivatives of the latter. If the surface is meant, the term '*continuum' is to be preferred. If the direction and rate of change in a point are to be expressed, the term 'gradient' is appropriate.

The term 'gradient' has also been used in an abstract sense (Sobolev & Utekhin 1973; ter Braak & Prentice 1988), e.g. when samples from non-contiguous areas are compared and arranged to form an imaginary continuum, e.g. ranging from nutrient-rich to nutrient-poor. Here, the connection with physical space is lost. This leads me to distinguish spatial and imaginary gradients.

Concerning environmental variables Ramensky (ex Sobolev & Utekhin 1973) warned against confusing 'ecology' with, what he called '*topology' and insisted upon separating directly acting ecophysiological *factors like heat, light, water, nutrients, etc. from the condition of the locality described in terms of geomorphology, lithology, hydrology. The locality or site can be characterized by its elevation, slope position, soil and climate. Ramensky (1930) claimed that the former factors cannot easily be derived from the latter conditions. In field ecology the site conditions can be described visually but the factors acting directly can only be assessed by measurements (see also van Wirdum 1979).

Ter Braak & Looman (1987) analysed the supposed response of species and vegetation to each directly acting *factor* by regression and constrained correspondence analysis. For the study of patterns and spatial gradients in vegetation and their relation to *site conditions* and for the sake of clarity I propose the term '***spatial gradient analysis***', even although this might be a pleonasm in Whittaker's sense (see also ter Braak 1987b). A three-step approach is proposed: **first**, ordination of samples and species using detrended correspondence analysis (DCA), **second**, spatial analysis of the sample ordination scores using *kriging and cross-sections and **third**, relating this spatial compositional surface to spatial *trends in site conditions (e.g. altitude, distance to coast, rainfall at the regional level, and slope position, soil at the local level).

Forest gradients in West Africa

Since the beginning of this century botanists and foresters have tried to describe the regional forest gradient in West Africa (Chevalier 1909, Schnell 1950, Taylor 1952 & 1960, Mangenot 1955, Aubréville 1959, Voorhoeve 1965, Guillaumet 1967, Sachtler 1968, Guillaumet & Adjanohoun 1971). They delimited forest types or vegetation zones by listing characteristic plant and tree species for these types and mapping them. Only in recent decades have authors based their typologies on numerical clustering and ordination techniques (Hall & Swaine 1981 for Ghana, de Rouw 1991 for the Taï region).

The purpose of vegetation mapping in West Africa was mainly descriptive and sometimes explanatory. Biologists and ecologists wanted to better understand the change in plant and animal species composition of the forest ecosystems from the coastal areas with heavy year-round rainfall to the interior with its strongly seasonal rainfall regime (Hall & Swaine 1981, de Rouw 1991). Much attention was also paid to special types of vegetation on inselbergs, floodplains, coastal and montane vegetation types (Guillaumet & Adjanohoun 1971). Guillaumet (1967) was one of the first to describe forest variation along catenas. In his pioneering study of flora and vegetation of SW Côte d'Ivoire he mentioned some of the issues worked out in the present book, but, at that time, adequate computational techniques were not yet easily available and accessible.

Forest managers, in contrast, need to evaluate the position of a given forest reserve in a spatially varying environment, in terms of forest *dynamics, "growth and yield" and *sustainability per site. At the same time, the forest manager aims to obtain information on the ecology of large tree species, e.g. exceeding 70 cm diameter, many of which used to be considered as product carriers. Hence, his management decisions and options concerned large trees mainly during the long period when silviculture was identified with 'the commercial cultivation of trees for the production of timber' (James 1982, Glück 1987). In this context, foresters used to focus mainly on the commoner kinds of forests, as reservoirs of large, accessible quantities of standardized timber. They generally neglected the rarer forest types because these contained small quantities of wood per hectare and, furthermore, difficult access also hindered commercialization. So, swamps, inselbergs or mountain forests on steep slopes received less attention.

In the present book, the above forestry approach was the basic concept underlying the research. Building on this basically timber-oriented concept, improved management systems close to nature and the knowledge systems necessary for their design and development were sought and found. On the product and service side, the new concept now being developed is nested multiple use (Bonnéhin 1992, Oldeman 1992), in which timber does not rank higher than other products.

History of the project

In 1975 **MAB-Unesco** initiated the ***"Taï Project"*** on ***"Recherche et aménagement en milieu forestier tropical humide"***. Taï is the name of a small town along the Cavalla river which forms the border between Côte d'Ivoire and Liberia (Figure 1, p. 8). The IET (Institut d'Ecologie Tropicale, Abidjan) research station, 20 km south-east of Taï, was constructed in 1977 as the field base of this programme. To the east of Taï lies Taï National Park (446 000 ha) which is one of the last vast areas of unlogged forest left in

West Africa (Text box 3, p. 66). The interdisciplinary research programme focused on biotic and ecological aspects inside the Park and on the socio-economic setting around the Park (see Guillaumet et al. 1984 for a list of publications). From 1975 to 1983 field work was carried out by **ORSTOM, IET** and numerous other participants. **Wageningen Agricultural University** participated in this programme mainly with agricultural and forestry studies. Vooren (1985) found considerable local differences in tree species composition and forest dynamics along a catena near the IET field station. De Rouw (1991) compared plant associations in primary forest along a 50 km stretch of the climatic gradient between the coast and the drier interior (Figure 7) and on several bedrock types and concluded that climate and bedrock control the floristic composition to a great extent.

In 1985 the University set up the programme "***Analysis and design of land-use systems in the Taï region***", co-funded by the **Tropenbos Foundation**. Conservation of the National Park and management of its buffer zone were the major objectives the programme was to support with research. Forest and soil scientists, agronomists and rural health specialists did studies on the existing land-use systems in order to improve them and particularly to make them more *sustainable (WAU 1991). Within the research theme "***Silviculture and sustained timber production systems***" I was given the task to study the regional variation of the forests in 1987 in order to see to what extent the findings of Vooren (1985) could be extrapolated over a larger area, i.e. the entire National Park and surrounding forest reserves (Figure 28).

By the end of 1991, funding of the programme phased out and the University launched a new programme in Burkina Faso. The Tropenbos Foundation carried out an "***Etude de synthèse***" in 1992 which will result in a complete account of all the research carried out in SW Côte d'Ivoire. At the same time **GTZ** (German Technical Cooperation) is setting up a Park Management project which aims to implement the research findings. This project intends to ensure the sustained preservation of the Park by providing solutions to the land hunger problems caused by an ever-growing population around the Park. Since 1990 the immigration of Liberian war refugees has further intensified the pressure on the remaining forests.

Research objectives

The objectives of the research set out below were to describe and analyse forest gradients in West Africa both at a regional and a local scale, so as to contribute to the knowledge base needed for innovative multiple use forest management and nature conservation.

The following questions were tackled:

- How can sampling techniques be adapted to the large tree species, given their huge size and often low population density?
- What techniques can be used to map the vegetation as a continuum rather than as types or zones?
- How can the impact on species composition of both regional and local environmental gradients be analysed simultaneously at the level of a forest sample plot?

Methods of approach

Scope. The present book covers the forest areas of SE Liberia and SW Côte d'Ivoire in their pre-logging state. In both countries, these are the regions which are still the most densely forested (Sayer et al. 1992). The research programme of Wageningen University focused on the region around Taï, a town on the border between Côte d'Ivoire and Liberia. None of the earlier studies transgressed national borders. For a proper understanding of the forests around Taï, data from both sides of the border need to be integrated.

Regional forest gradient. I collected data on three sites (each circa 20 ha) in unlogged upland forest in Taï National Park and compared the species composition with the results of the pre-logging forest inventories in SE Liberia and SW Côte d'Ivoire covering a total area of 21 640 ha of sample plots.
The research strategy consisted of a three-step approach:

1) Ordination: to perform an ordination on relevés large enough to contain reliable information on 53 of the largest tree species;
2) Ordination → space: the sample scores on the first ordination axis, which describes most of the variation, were plotted on the map of the region. For the regional forest gradient, contours were interpolated using the *kriging method (Stein & Corsten 1991).
3) Space → environment: a cross-section through this interpolated compositional surface was compared with a similar cross-section through the rainfall gradient and plotted against elevation above sea level and distance to the coast. Explanation of deviations between vegetation and rainfall gradient were sought on the lithological map.

Local catena gradients. A problem was immediately apparent: how should the samples to be used in the ordination be composed? In classical vegetation science, a 'site' or 'quadrat' is the basic sampling unit in the field to begin with (Mangenot 1955, ter Braak 1986). In contrast, Alder & Synnott (1992) recommended that the coordinates of each tree should be recorded for permanent sample plots in tropical rain forest. In the field and on the record sheets, the tree is the basic sampling unit. The problem of composing samples for ordination analysis only arises when one starts to process the data.

My approach had the same rationale as for the regional gradient, i.e. ordination ⇔ space ⇔ environment, but now I reasoned backwards in this three-step approach:

1) Environment → space: I knew from the soil survey that the soil variation was strictly related to the catena position and that the spatial trend in environmental variation is therefore related to local elevation.
2) Space → ordination: I composed samples in such a way that they were constrained to follow this same spatial trend. Trees were grouped along contour lines into samples covering 2 ha each, containing about 20 trees exceeding 70 cm diameter. I propose the name ***contour sampling*** for this technique. In this way, at least 10 samples were available per site for the ordination. Ninety-five tree species exceeding the lower diameter limit of 70 cm were used for the ordination.
3) Ordination of the contour samples of the three sites together to test two hypotheses:
    - Is compositional change related to catena position?
    - Does the catena gradient correspond with the regional gradient, and if so, might both be controlled by the same environmental factor or factors?

Fieldwork. The field work for the present study was carried out in Taï National Park during my sojourn in Côte d'Ivoire between September 1988 and April 1991. In 1989 I established two study plots of over 20 ha each in addition to the plot of 10 ha set out by Vooren in 1981 near Taï which was enlarged to 25 ha. All three plots were situated within Taï National Park and in unlogged forest (see Figure 28). One plot was near Zagné in the northwestern corner of the Park on ferrallitic soils developed from migmatitic bedrock, and where there is less rainfall than in Taï. The second plot lies near Para in the southwestern corner of the Park where rainfall is higher and where the sericite schist bedrock has weathered to yield soils with greater water retention capacity.

Outline of the book

In the first Chapter the general forest setting in West Africa is described. Here, West Africa is considered to be the coastal part of Africa west of the Dahomey (Bénin) interval. Relief and lithology are sketched as the spatial environment considered invariable with time. Throughout the book, both form the warp through which the weft of moisture conditions and tree species composition is woven.

In the second Chapter, I position my three study sites on the regional forest continuum by ordinating them together with data from pre-logging forest inventories, carried out in the sixties and seventies in SE Liberia and SW Côte d'Ivoire. Fifty-three of the largest tree species are used for this ordination. The regional forest gradient is mapped by plotting isoscore contours and related to maps of the SW-oriented rainfall gradient and of lithology.

In Chapter 3 the "catena position" is also taken into account by ordinating tree species composition between and within three forested catenas. The three sites are known from Chapter 2 to receive increasing amounts of rainfall from N to S. Gradients are also sought in tree species richness and total stem biomass. The ***contour sampling technique***, i.e. grouping trees along contour lines, is discussed in detail. Large tree species composition on these contour samples is ordinated and the scores are plotted against elevation and in this way related to soil characteristics. The correspondence between these local catena gradients and the regional climatic gradient is discussed.

In Chapter 4 the implications of this model of continuous forest variability are discussed for forest management and conservation of biodiversity. Recommendations are made to develop forestry on a more ecological basis and to extend conservation efforts in the region by interconnecting the remaining forest areas.

Several text boxes provide additional information on certain topics mentioned in the text. Conclusions are presented in the text, in italics, as they arise. Chapters 2 and 3 are set up in such a way that they can be read as independent parts of the book. The final Glossary contains definitions of the terms preceded by an asterisk in the text. In addition to the literature references, all software used is listed separately. Dutch readers should note that the reference list is arranged in international alphabetical order, i.e. names beginning with "de" or "van" are placed under D and V respectively.

1 FORESTS OF WEST AFRICA: SETTING THE SCENE

In this Chapter the physiographic setting of SE Liberia and SW Côte d'Ivoire is sketched and the development of the former into the actual forest cover is briefly recounted. Relief and lithology are considered as landscape constants, with negligible variation in time, and climatic or soil moisture and tree species composition will be related as variables to this fixed frame here and in succeeding Chapters.

1.1 The former extent of dense forests in West Africa

1.1.1 Forests on the fringe of a continent

West Africa, to the north of the coast from Conakry to Accra, was once covered by some 40 million ha of dense forest. The first European explorers might have thought that the entire continent was covered by the huge trees they saw along the coast and along the rivers they used to penetrate into the country (Martin 1989). This was not so. Only a fringe extending some hundreds of kilometres inland consisted of dense *rain forests. The interior soon became drier and the forests gave way to savanna and steppe vegetation. Such coastal fringes of forests are also known from the Atlantic coasts of Brazil and Mexico, from the western coast of India, from north-east Australia and east Madagascar (Whitmore 1990).

There is plenty of evidence that the extent of dense forests in West Africa has varied greatly during the last million years (Guillaumet 1967, Fritsch 1980, Maley 1991). The iron pans capping certain crests in SW Côte d'Ivoire were formed under a savanna climate (Ahn 1970, Fritsch 1980), so the entire forest must have expanded recently, i.e. since circa 10 000 years ago, from its Pleistocene refuges. On the other hand the present disjunct distribution of many species between Liberia-SW Côte d'Ivoire, SW Ghana and sometimes Cameroon-Gabon suggests that in the recent past, i.e. between 9000 and 4000 years BP (Maley 1991) those three ranges have sometimes been united in one vast forest about triple the area of today's (Guillaumet 1967; Hamilton & Taylor 1991).

Phytogeographers and bioclimatologists readily associated these areas with a climatic zone called after the forests themselves: "the tropical rain forest climate" (Köppen 1936, Walter & Box 1976). As will be shown in the next chapter, the climatic conditions change gradually from constantly humid on the coast to periodically dry further inland. It is possible to draw lines of equal climatic conditions (isolines) on the map of West Africa. These lines are not boundaries of climatic types, i.e. they are not markers of discontinuities in climate.

The physiographic map of West Africa, i.e. a map representing the natural appearance of the continent, is the starting point for this ecological study of the forests west of the Dahomey interval (Figure 1). However, I experienced the mapping of relief as compromising between scale and precision. Text box 1 goes into this matter further.

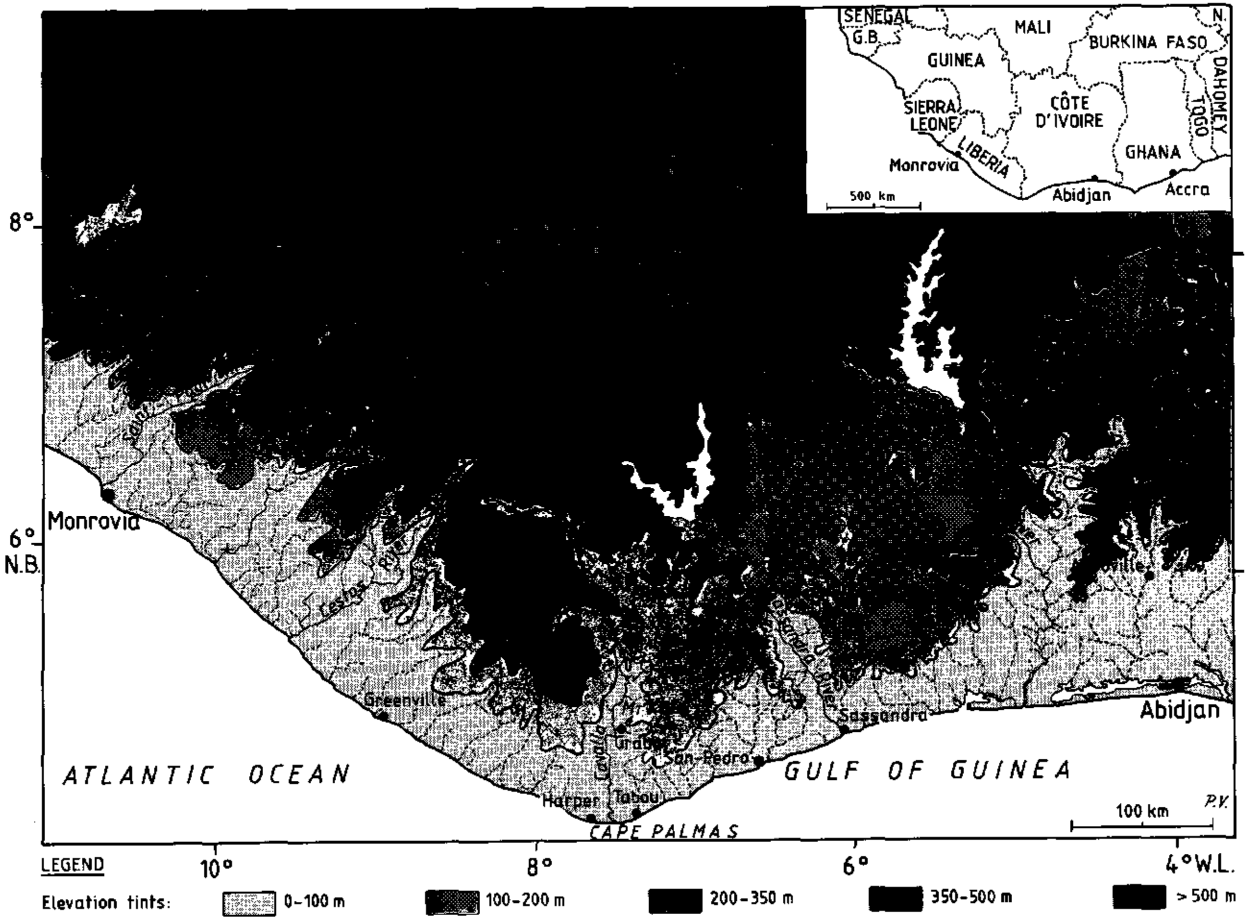

Figure 1 Relief and hydrography of Liberia and west Côte d'Ivoire. Contours are given at 100, 200, 350 and 500 m asl (Sources: IFAN 1968, elevation points in Liberia from MPEA 1983). Note that the Taï area does not directly face the coast.

In the present book "West Africa" does not include Nigeria, Cameroon nor Gabon, even though these lie on the west side of Africa. The "Upper Guinea" forest block (Hall & Swaine 1981) of Liberia, Côte d'Ivoire and Ghana forms a natural unit, especially apt for this study on relations between forest vegetation and the abiotic environment. I shall use the name "Côte d'Ivoire" instead of "Ivory Coast" as this is what the "Ivoiriens" wish their country to be called.

A mountain range, the Guinea Highland, spreads from the Fouta Djalon in Guinea to the 'Monts des Dans' in west Côte d'Ivoire with several summits exceeding 1000 m above sea level (asl). This mountain range certainly contains its own forest vegetation gradients and forest boundaries (Schnell 1950, Guillaumet & Adjanohoun 1971, Johansson 1974). The present book, however, only deals with lowland forest (below 500 m and generally between 100 and 300 m asl). The presence of these mountains also greatly influences the rainfall patterns, as will be discussed in Chapter 2. In the lowland forest only the Putu range in Liberia and the hills of Grabo cross the steadily increasing elevation of the landscape from the coast into the interior (see maps in IFAN 1968).

The old African *peneplain (Ahn 1970) that lies under the wet coastal fringe of forests, is intensely dissected by streams and rivers (see Figure 1). The Cavalla river, called 'Cavally' in Côte d'Ivoire, with the small town Taï on its border will remain in the centre of many maps throughout the present book.

Text box 1 Uncertainties and scales in natural history research

When preparing Figure 1 and further maps for the present book depicting physiographic features, I noticed that I almost automatically adjusted precision and detail to the scale of the map. However, the information content of the figure was not really reduced by these generalizations and smoothing. The following example taken from Mandelbrot (1977, ex Gleick 1991) brought an explanation of these phenomena.

How long is the coastline of England? On each map the outcome is different and the more detailed the map and its scale, the longer the coastline becomes. One could also measure it on a 1:1 scale in the field, but the more points used to pinpoint the coastline, the longer the coastline becomes. When using a measuring-rod instead of topographical instruments, the coastline becomes longer in a proportion inverse to the length of the rod. With an infinitesimally small rod, the coastline becomes infinitely long. The problem is that we are on the transition between the single (line) and double (surface) dimension, between the derivative and the integral function. The area of England does not increase to infinity when the fractal of its borderline increases in length. A fractal is defined as a figure with a broken dimension between 1 and 2 (e.g. 9/7, Gleick 1991).

The fractal nature of coastlines, streamlines and elevation contour lines causes difficulties when drawing them on a map. Details below drawing precision "fall off" and smoothing of lines often improves the readability of the map. Rivers have the peculiarity of branching quite often. To which branch order do we map rivers and creeks on a hydrographic map? In the present book I give more detail when the scale zooms in. Contour lines in Figure 1 have been deliberately smoothed in order not to draw attention to the effect of each river valley, but depict the rise of the landscape from the coast into the interior.

Other scale-detail relations can be seen on isohyet maps over a small creek basin (Audrénisrou, 3775 ha, Figure 30) near Taï where Casenave et al. (1984) found a range of 1500 to 1870 mm annual rainfall for the year 1981, which corresponds to the range of that year (1500 to 1900 mm) over the entire National Park (400 000 ha) (ANAM 1987).

1.1.2 The forest-savanna boundary and impacts of fire

The forest-savanna boundary is a striking discontinuity in the vegetation cover (see Figure 7). As shown by Swaine et al. (1976) and Gautier (1989) the boundary can easily be seen on satellite imagery. The annual impact of fire is often held responsible for the sharpness of the boundary (van Donselaar 1965, Devineau 1976; Figure 2). Less frequent fires would enable closed dry forest and dense woodland to develop and changes would be more gradual (Spichiger & Lasailly 1981). It comes as a shock to a forester or a conservationist that the entire savanna between Senegal in the west and Chad lake in the east is burnt annually, even National Parks as big as one million ha like the Comoé National Park in north-east Côte d'Ivoire. This frequent fire regime is likely to reduce biological and structural diversity, biomass reserves and soil fertility (Devineau et al. 1984). But a fire ban would drastically change the ecosystem (de Bie 1991), so a policy of what Connell (1978) called "intermediate disturbance level" and thus at present a reduced fire frequency is advisable in the case of active nature management.

Figure 2 Each year the savanna burns in West Africa. The fire often penetrates forest reserves and may cause severe damage (Bertault 1992, Hawthorne 1993).

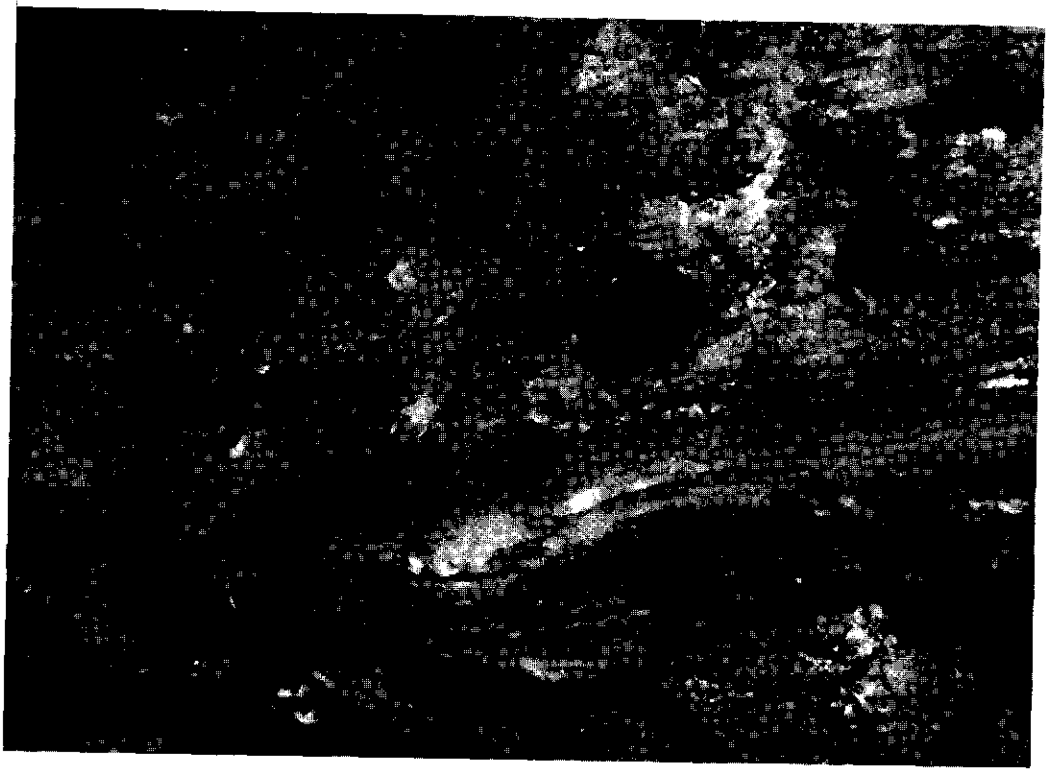

Figure 3 A close-up of weathered sericite-chlorite schist in a gully on the Para study site

1.2 Lithology of SE Liberia and SW Côte d'Ivoire

But there is more than fire and gradually decreasing rainfall (see Chapter 2) to determine the sharp boundary between forest and savanna. North of Abidjan, it coincides with a lithological boundary (Mangenot 1955, Rougerie 1960, Guillaumet & Adjanohoun 1971) between schist and granite, the former giving more clayey soils which better retain water during the dry season (Leneuf 1959). Five major rock types underlie the forests of SE Liberia and SW Côte d'Ivoire (Figure 4): sericite-chlorite schists (Figure 3), mica schists, gneisses and migmatites, two-mica granites and granites and granodiorites (Papon 1973, MPEA Ministry of Planning and Economic Affairs 1983). In this order, from low to high degree of metamorphism, they generally result in soils with a decreasing soil water retention capacity. Locally the soil formation processes and lateral and vertical transport of soil material may override this general rule (see Chapter 3).

Along the coast near Abidjan sandy Tertiary deposits bore a particular forest type now almost disappeared (Guillaumet & Adjanohoun 1971, de Koning 1983). The Volta sandstones in Ghana (Hall & Swaine 1976) may resemble granites in terms of moisture retention. The Nimba mountains owe their higher altitude to more resistant rock types, which include one of the richest iron ores in the world (MPEA 1983). Figure 4 shows

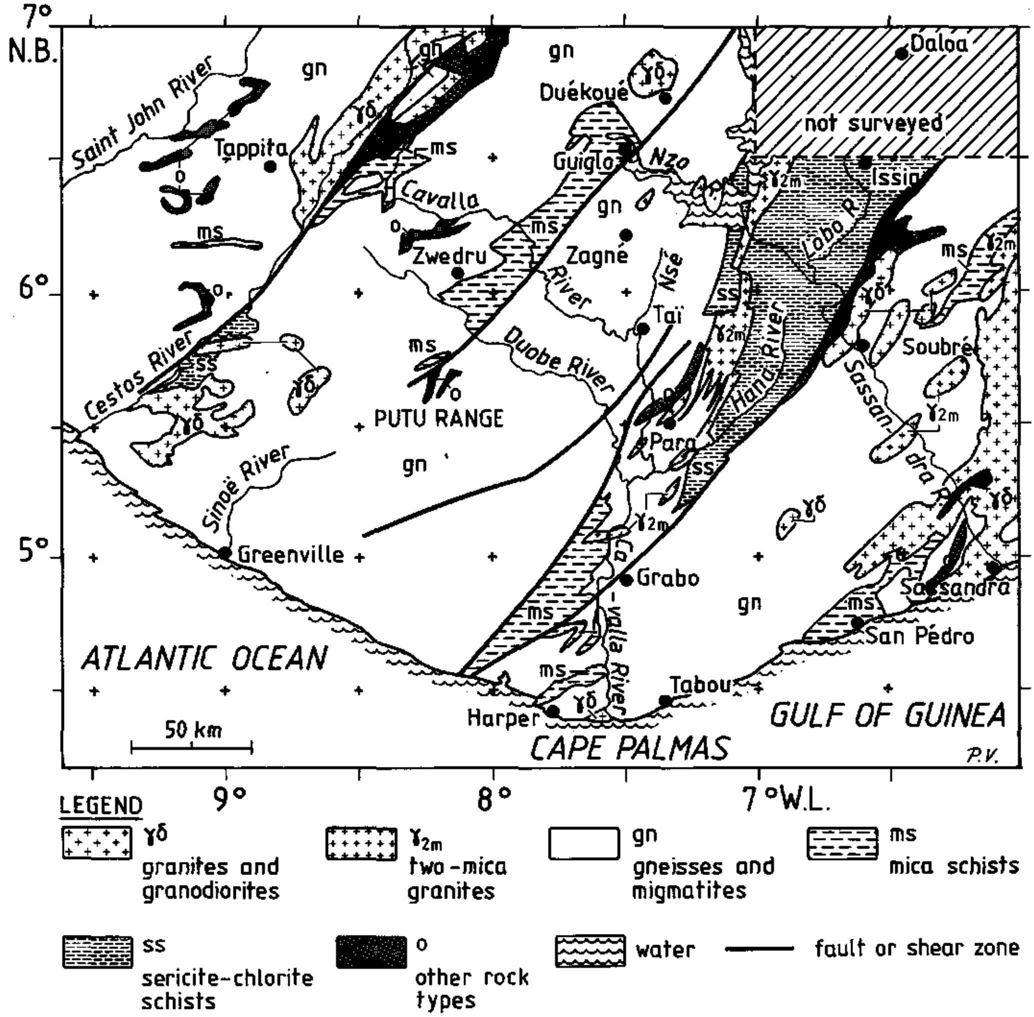

Figure 4 Lithology of SE Liberia and SW Côte d'Ivoire. Main rock types are gneisses, migmatites, two-mica granites, granodiorites, mica schists and sericite-chlorite schists. The major faults trend SW-NE. This lithological map is based on the most recent geological maps of the region. In Liberia a geological survey was carried out by the US Geological Survey (USGS) and the Liberian Geological Survey in the years 1965-1972 (Brock and Chidester 1977, Force and Beikman 1977, Tysdal 1977 and others). The final map was published by MPEA (1983) in the Planning and Development Atlas of Liberia. In SW Côte d'Ivoire a detailed geological survey was done by the Bureau de Recherches Géologiques et Minières (BRGM, Paris) and the Société pour le Développement Minier (SODEMI, Abidjan). Maps at a scale of 1:50 000 were prepared by Bos (1964), Jeambrun (1965; 1966), Letalenet (1965a,b) and others. The final report by Papon (1973) included a colour map at 1:500 000.

that most of the Liberian forest are underlain by gneisses, belonging to the Precambrian basement complex. Some of these gneisses are called migmatites (from the Greek *μῖγμα*: mixture) which is a metamorphic rock with granitic intrusions (Schumann 1979). The geological mapping of the gneisses done by the most recent geological surveys in Liberia (MPEA 1983) and Côte d'Ivoire (Papon 1973) is not consistent on both sides of Cavalla river. Furthermore, de Rouw et al. (1990) made no distinction between gneiss and migmatite to differentiate land units in their Land Unit Survey of the Taï region. So I grouped both rock types into one unit on Figure 4.

In the eastern half of Côte d'Ivoire (Bagarré et Tagini 1965) and in most of Ghana (Hall & Swaine 1981) schist is the dominant bedrock type, so a more northerly extension of wetter forest may be expected. Bedrock and rainfall gradient roughly coincide in Ghana (wetter climate on wettest bedrock, drier climate on drier bedrock), so that Hall & Swaine (1981) had a sufficient explanation for the vegetation gradient when considering climate alone. In Liberia bedrock never contradicts climate either, but in Côte d'Ivoire I confirm the findings of Guillaumet (1967) and de Rouw (1991) that a drier climate can be compensated for by a "wetter" bedrock (see Chapter 2).

1.3 Three man-made forest blocks

1.3.1 Actual forest cover

Only about 8 million ha of West African rain forest remained in the mid-eighties (Martin 1989, Sayer et al. 1992, Parren & de Graaf 1993 in prep.). This is some 20 % of the precolonial area. Enormous quantities of biomass ($400\ t\ ha^{-1} \cdot 32\ 10^6 ha = 13\ 10^9$ tonnes dry matter) have been burned and their combustion gases emitted into the atmosphere. Precise estimates of the actual forest cover only exist for Ghana (Ghartey 1989), where almost no forest remains outside the reserves but where the reserves are well protected and thus still under dense forest cover. In Côte d'Ivoire and Liberia both the forest area outside reserves and the state of conservation of the reserves are insufficiently documented (Vooren 1992b, Mayers 1992).

These forest relics in West Africa are divided over three major forest blocks, each centred on the border between two countries (Sayer et al. 1992):

1. east Sierra Leone & west Liberia: Gola and Kpelle National Forests (MPEA 1983, Hammermaster 1985)
2. east Liberia & south-west Côte d'Ivoire: Krahn-Bassa, Gbee, Gio and Grebo National Forests and Sapo and Taï National Park with surrounding forest reserves (see Figure 13)
3. east Côte d'Ivoire and south-west Ghana: Songan-Mabi forest reserve and Bia National Park, Nini-Suhien National Park and surrounding reserves (Hall & Swaine 1981)

My study focused on the second block, which is the largest one remaining (Sayer et al. 1992) and which contains the longest forest gradient (see Chapter 2). It is an ideal study area for *spatial gradient analysis.

1.3.2 Timber mining

Another difference between Ghana and its neighbouring countries is that the timber stocks in 1988 in the Ghanaian reserves were, on the average, 90 m^3 ha^{-1} (above 70 cm diameter, all species), and that more than 50 % were traditionally commercial species (Ghartey 1989; Figure 5). Almost all Ivorian reserves must be considered as depleted of commercial stock (e.g. Yapo forest with 9 m^3 ha^{-1}, Mengin-Lecreulx 1990), but no recent national inventory exists. In Liberia logging was much less intense in the past, but the natural stocks of commercial trees in these wet evergreen forests were smaller (Sachtler 1968).

? [illegible]

This book only presents data from unlogged forests, either from inventories before the logging era, or from the last 200 000 ha of unlogged forest in Côte d'Ivoire (Bousquet 1978) which are conserved within Taï National Park (see Text box 3, p. 66). I worked on a kind of "palaeotypology" of the forests. On the one hand, I considered how the composition was, not how it will, or should, or can become after effective conservation. But on the other hand, this study of the primeval forests of West Africa allows the initial conditions to be assessed, before the remaining forest has disappeared.

Figure 5 A Meliaceae trunk is transported to the sawmill in Ghana. The Ghanaian forest service has spared many of such large trees. In Côte d'Ivoire they have all been logged.

1.3.3 Forest management and conservation

In the land use plans of the three countries concerned, a number of forests have been designated as reserves, to remain closed forest. Eight of them have received the status of National Park (Sapo, Taï, Mt Péko, Maraoué, Azagny, Banco, Bia and Nini-Suhien; Martin 1989, Sayer et al. 1992). Stock management and natural regeneration silviculture have only occurred on a large scale in Ghana (Parren 1991). Extensive research plots were laid out by CTFT in Côte d'Ivoire (Bertault 1986, Maître 1991), but the results have only been applied in a pilot project in Yapo forest. Recent projects with British (ODA), French (CTFT) or German (GTZ) cooperation may result in sustainably managed forests in the future in Ghana, west and east Côte d'Ivoire respectively. Certain forests, like the Bosse-Matié forest in east Côte d'Ivoire, need rehabilitation management, so no timber will become available for the market in the first few decades. The civil war in Liberia since 1990 has stopped almost all economic activity in that country, and future management and conservation remain an open question.

However, a forest ecosystem is more than living timber. Wildlife protection is a problem in all three countries. Even in the large Taï National Park (446 000 ha, see Text box 3, p. 66) the survival of the forest elephant (*Loxodonta africana cyclotis* Matschie) is not guaranteed and hunting impact remains high (Figure 6). A tropical rain forest without animals is doomed (Alexandre 1978, Jacobs 1988) and forest managers should not content themselves with saving the trees.

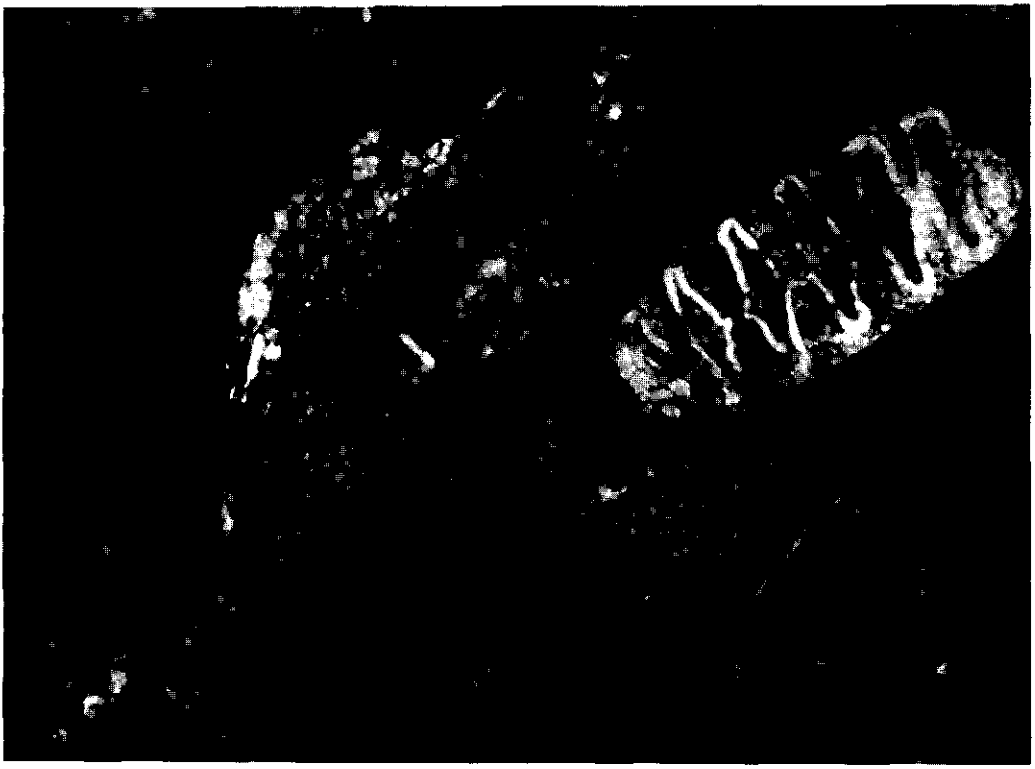

Figure 6 Remains of a forest elephant found in the Para study plot

2 THE REGIONAL FOREST GRADIENT IN SE LIBERIA AND SW CÔTE D'IVOIRE

In this Chapter, I will analyse the regional forest gradient using ordination and spatial interpolation techniques. As indicated in Chapter 1, I will concentrate on the middle forest block in West Africa in its pre-logging state (Figure 13), roughly between Cestos river (Liberia) in the west and Sassandra river (Côte d'Ivoire) in the east and North up to the forest-savanna boundary. The base for interpreting this gradient is the lithological map, (Chapter 1, Figure 4). However, first the rainfall gradient will be examined.

2.1 The SW-oriented rainfall gradient

These forests of the middle forest block lie on a climatic gradient which is described by Eldin (1971), DRC (1967a) and ASECNA (1979) for Côte d'Ivoire and by Voorhoeve (1965) and Sachtler (1968) for Liberia. The major components of this gradient are (see Griffiths 1972, Hayward and Oguntoyinbo 1987):

- the diminishing total amounts of rainfall from the Liberian coast into the interior: in the study region a NE-SW trend. Important factors here are the permanently warm waters off the Liberian coast and the upwelling of cold waters from July to October between Cape Palmas (Tabou) and Lagos;

- the change in the coefficient of variation of annual rainfall, which is high (20 to 25 %) along the coast, lower (15 to 20 %) in the forest zone and again increasing to 20 % and further even 50 % in the savanna and Sahel zones. This trend is related to distance inland;

- the change in seasonal distribution from bimodal along the coast to unimodal in the interior: a N-S trend resulting from the path of the zenithal sun;

- greater temperature fluctuations towards the interior, and higher diurnal temperatures towards the North, resulting in more evapotranspiration.

As rainfall totals are best documented for the region and show pronounced differences, I will concentrate on this component of the climatic gradient. Figure 7 shows the major rainfall stations in the region and the best estimate of their long-term average rainfall in dm y^{-1} or m $(10\ y)^{-1}$ (see Table 1 for the measuring period and sources of the data). When interpreting these rainfall data, spatial and temporal sources of variation need to be considered.

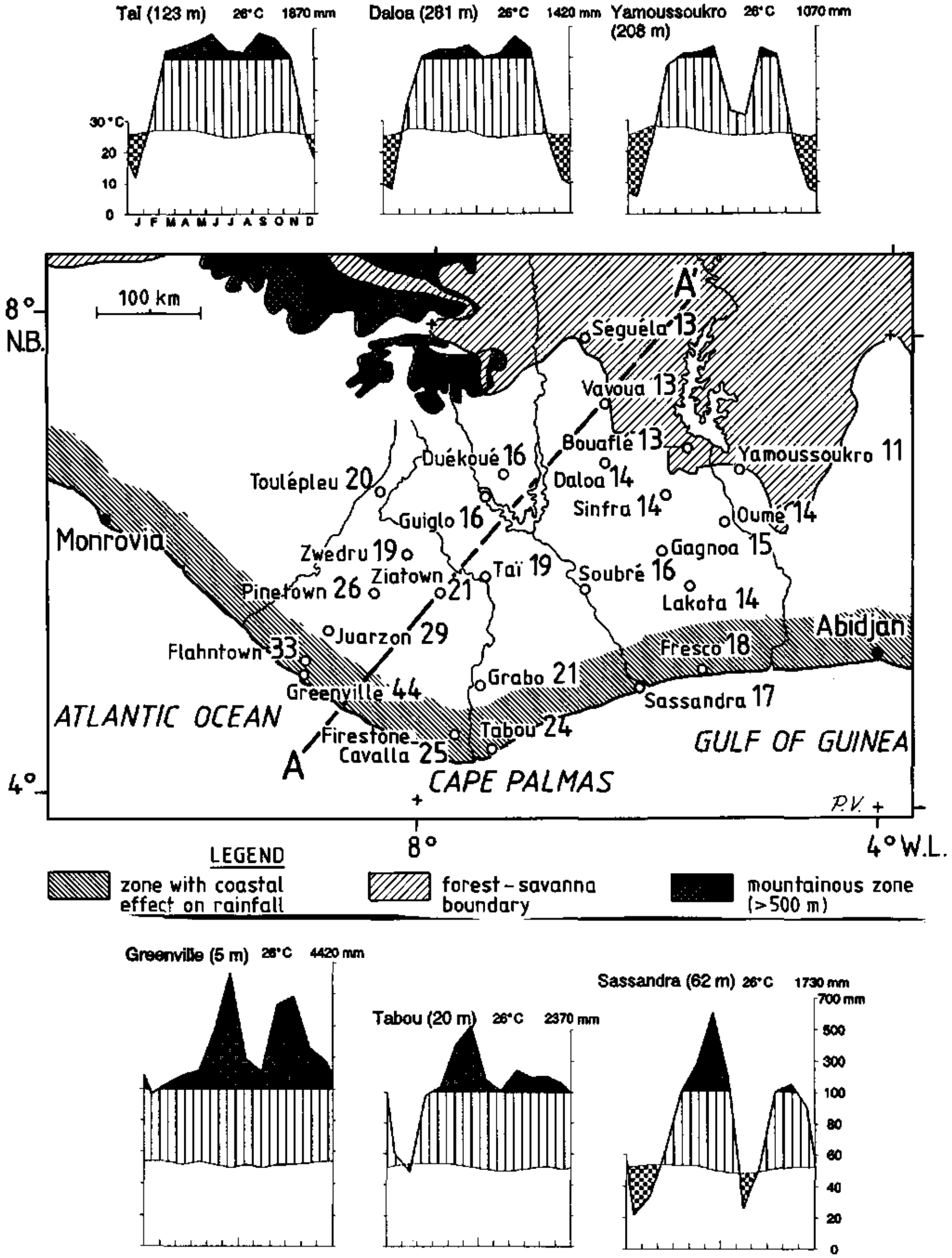

Figure 7 Rainfall map of SE Liberia and SW Côte d'Ivoire. Average precipitation figures per decade in m (10 y)$^{-1}$ on the map (sources see Table 1). Shaded line: forest boundaries with savanna (North) and Ocean (South), dark grey tone mountainous area (elevation above 500 m). The cross-section A-A' is given in Figure 10. Climate diagrams, originally called ombrothermograms by Gaussen (1954), were constructed following the procedure described in Walter (1979). The right-hand axis, indicating average monthly rainfall, is graded every 20 mm below 100 mm, and every 200 mm above 100 mm.

Table 1 Rainfall stations in SE Liberia and SW Côte d'Ivoire. Elevation above sea level given for all stations, distance from the coast for the Liberian ones. Rainfall is expressed as mean rainfall per decade in m (10 y)$^{-1}$. This latter dimension is considered more accurate, as the data are based on 10 years of measuring in Liberia and 30 years in Côte d'Ivoire. The common practice of expressing annual rainfall in mm y^{-1} has not been followed, because of the poor precision and the great variability of the averaged precipitation amounts and because of their limited spatial extrapolation value (see also Text box 1, p.9).

Rainfall stations	distance to Liberian coast (km)	elevation above sea level (m)	mean rainfall per decade (m (10 y)$^{-1}$)	measuring period	remark	source
Liberia						
Greenville	0	5	44.2	1951-'66	coastal	3
Flahntown (AFC)	7	20	32.8	1960-'66	coastal	3
Juarzon	50	100	28.9	1965-'66		3
Pinetown	110	230	25.5	1952-'66		2
Firestone Cavalla	30	50	24.9	1928-'81		1
Ziatown	144	160	20.6	1952-'61		2
Zwedru	160	215	19.3	1951-'73		1
Côte d'Ivoire						
Tabou		20	23.7	1951-'80	coastal	4
Grabo		78	21.1	1951-'80		4
Toulepleu		270	19.5	1951-'80		4
Taï		123	18.7	1951-'80		4
Fresco		5	18.0	1967-'80	coastal	4
Sassandra		62	17.3	1951-'80	coastal	4
Guiglo		217	16.4	1951-'80		4
Duékoué		245	16.3	1956-'80		4
Soubré		134	15.9	1951-'80		4
Gagnoa		205	14.8	1951-'80		4
Lakota		200	14.3	1951-'80		4
Daloa		281	14.2	1951-'80		4
Sinfra		273	13.9	1966-'80		4
Oumé		207	13.5	1951-'80		4
Séguéla		351	13.4	1951-'80		4
Bouaflé		187	13.2	1951-'80		4
Vavoua		260	12.9	1953-'80		4
Yamoussoukro		208	10.7	1964-'80		4

Sources:
1: Meijers and Saye (1983)
2: GFML (1967)
3: Sachtler and Hamer (1967)
4: ANAM (1987); for stations not covering 30 years, the mean has been constructed from neighbouring stations with complete series of data (see text)

2.1.1 Sources of spatial rainfall variation: about interpolation

The standard procedure in climatology for processing rainfall data on a map is by interpolating *isohyets using all data points. This descriptive procedure is based on the assumption that the variation is random and that no factors can be demonstrated to cause trends (Stein & Corsten 1991). A technique like cokriging (Krajewski 1987, Stein & Corsten 1991) uses observations of several co-variables in predicting e.g. rainfall. Gregory (1965, in Griffiths 1972) explained 75 % of the variation in annual rainfall in Sierra Leone by four factors: distance from the coast, longitude, latitude and elevation. A climatic predictive package BIOCLIM was developed for Australia by Busby (1986, ex Russell-Smith 1991). It is beyond the scope of this study to develop a similar model for West Africa but I will speculate on some possible sources of spatial variation.

The *mountain range* from west Côte d'Ivoire towards Guinea has a clear impact on rainfall amounts, distribution and variability (Eldin 1971). Records from rainfall stations within this range (e.g. city of Man) were omitted on Figure 7. The first 50 km from the coast inland also have high rainfall amounts and, importantly, a greater variability. This is caused by extremely intense heavy downpours (Sachtler 1968, Brunet-Moret 1976). These peak volumes contribute little to the soil moisture content. Because of this typical *coastal effect*, caution should be exercised when using data from gauges along the coast to interpolate isohyets; hence the shading in Figure 7. A third factor, somewhat related to the first, is *relief*. The position in the landscape of the rain gauge is a source of known variation which should be taken into account when interpolating. For instance, gauges placed in the valley near the river, as in Taï, Soubré and Guiglo, could possibly receive smaller quantities than gauges near the water divide and thus higher in the landscape like Pinetown and Ziatown. The maritime air masses might produce less rain when descending from the watershed than when ascending to it (ASECNA 1979).

The limited spatial interpolation value of the rainfall averages was illustrated by Casenave et al. (1980, 1981, 1984) in the Audrénisrou basin in Taï National Park. Fourteen rain gauges placed in a small river basin of 38 km^2 were recorded from 1979 to 1981. Within a few km, differences in rainfall of more than 0.3 m were found for the same year, but without consistent correlation with elevation. Clearly, more studies on small-scale rainfall variability are needed to obtain reliable interpolation estimates.

2.1.2 Temporal variation of rainfall: taking the mean?

Cyclic trends. Apart from obvious seasonal trends like wet and dry seasons, cyclic trends have been found in Côte d'Ivoire (Lhomme 1981; Snoeck 1975) and Nigeria (Adejuwon et al. 1990). One such cycle showed a period of 2 to 3 years, corresponding to the Quasi-Biannual Oscillation (QBO) known from meteorology (Lhomme 1981), others displayed periods of 11 and 30 years corresponding to the single and triple sun spot cycle. As an example the rainfall series of Daloa (central Côte d'Ivoire) is given in Figure 8. The decades 1925-1935 and 1955-1965 contained the maxima of the oscillation and rainfall was high. The minima were in 1940-1950 and in 1975-1985. If this oscillation, which corresponds to three times the sun spot cycle of 11 years, is really significant, another wet period may be expected in the period 1990-2000. Hayward and Oguntoyinbo (1987) predict a dry period starting about 2003, based on information from Nigeria. An

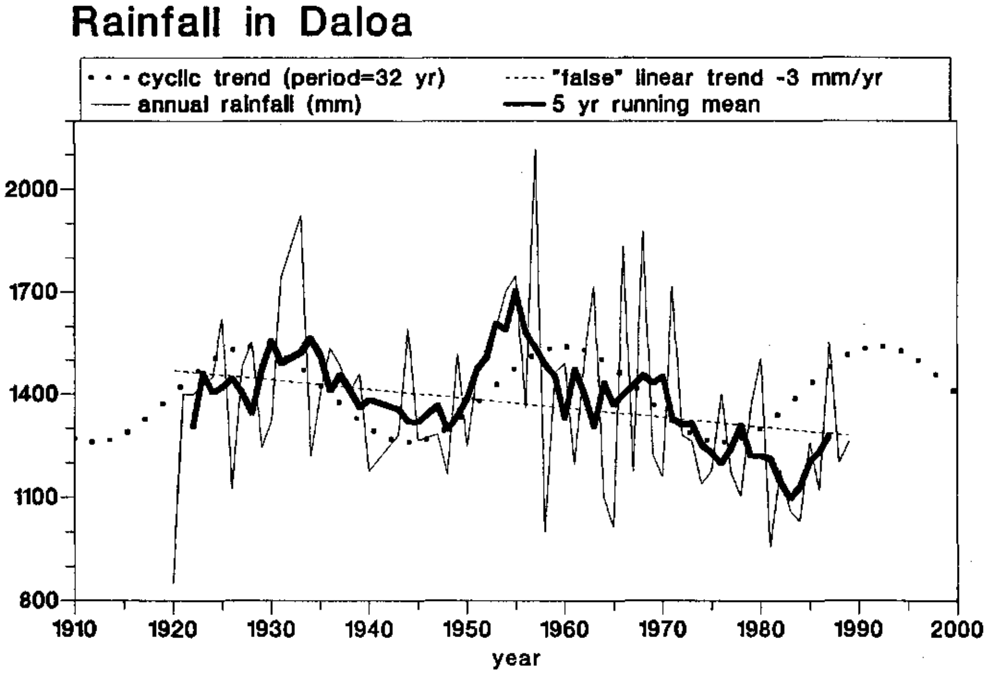

Figure 8 Temporal variation in annual rainfall, illustrated by the rainfall time series from Daloa (altitude 281 m asl), central Côte d'Ivoire (source of data: ORSTOM-CIEH 1973; Laboratoire d'Hydrologie, ORSTOM, Montpellier; Agence Nationale des Aérodromes et de la Météorologie (ANAM), Abidjan-Port Bouet). The five-year running mean is given by the bold line. The main cyclic trend as calculated with a periodogram (using Statgraphics, 1990 STSC), has a period of 32 years and is depicted by the dotted sine curve. The "false" negative linear trend can be entirely explained by the cyclic movement. Similar trends have been found for Bouna and Abengourou (Lhomme 1981) and in Nigeria (Adejuwon et al. 1990).

implication of this cyclic trend is that means calculated over different parts over the cycle are not directly comparable. Most of the rainfall data from Liberia were collected between 1950 and 1960 (Table 1), in a wetter part of the cycle with the five-year running average being 10 to 20 % higher than the mean over the whole cycle.

Linear trends. Adejuwon et al. (1990) reported significant negative trends (-3 to -8 mm y^{-1}) for annual rainfall at six rainfall stations in Nigeria between 1922 and 1985. They analysed the time series of 16 stations spread over the country. Only one station had a significant positive trend (+5 mm y^{-1}). A linear regression applied to the above-mentioned cyclic trend between 1922 and 1985 automatically resulted in the "false" negative trend shown in Figure 8, only because the sine curve starts with high values and ends with low ones. An appropriate regression model should contain both cyclic and linear terms (van Montfoort, pers. comm.). The time period considered, is also important. The curve of the five-year running mean in Figure 8 steeply declines between 1955 and 1982, as can be expected between the maximum and the next minimum of a sine curve. Given the evidence for a cyclic trend, the extrapolation of this negative trend beyond 1982 may be far from the truth.

If such trends also exist in Liberia and Côte d'Ivoire, the mean should lie on the base line of the sine curve. If this middle line is also declining, no overall mean can be calculated, i.e. the mean is time-dependent. The data for the Ivorian stations (ANAM 1987) as given in Table 1 and displayed in Figure 7 have been corrected by ANAM in a way which eliminates at least some problems of comparability. The mean for each station was calibrated for the period 1951-1980. If only a partial mean could be calculated, then this mean was corrected using the data from a nearby station with a complete record:

$$\overline{R_i} = \frac{\overline{R_i'}}{\overline{R_c'}} \cdot \overline{R_c}$$

in which:

$\overline{R_i}$ = adjusted mean for station with incomplete record

$\overline{R_{i,c}'}$ = partial mean over period with available data for station with incomplete record

$\overline{R_c}$ = mean annual rainfall 1951-1980 of station with complete record

It might be advisable to use several neighbouring stations for the calibration and to analyse the correlation of the stations first.

2.1.3 Description of the rainfall gradient: a cross-section

The forest-savanna boundary represented on Figure 7 corresponds to 11 to 13 m $(10\ y)^{-1}$ rainfall and runs parallel to the Liberian coastline. I therefore drew a cross-section through the region of interest (Figure 10) from Greenville on the Liberian coast, which is the only town in West Africa without a dry season, to Vavoua in central-west Côte d'Ivoire, which lies just in the savanna. Relief is given at the bottom as an independent and relatively constant factor. Mean 10-year rainfall in m $(10\ y)^{-1}$ is given in the middle and its first derivative, the rainfall gradient in m $(10\ y)^{-1}$ $(100\ km)^{-1}$ on top. The coastal effect is clearly visible on the very steep left-hand part of the rainfall curve. Both rainfall amount and rainfall gradient decrease gradually from the coast towards the savanna, which suggests an exponential path of the curve. Note that the rainfall decrease is not constant in space, but that rainfall zones become wider. A response of the same kind will be demonstrated in the vegetation gradient later in this Chapter. At some 150 km from the coast a striking discontinuity is found. It is apparently caused by the higher plateau around Putu Range (see Figure 1, Figure 9) and its rain shadow. Up to Putu Range the elevation rises steadily and further NE the relief becomes undulating and dissected by rivers flowing transversely to the gradient. The forests up to Putu Range directly face the SW monsoons, and Grebo National Forest and Taï National Park undoubtedly experience a rain shadow effect. The steep decrease in rainfall between Pinetown and Zwedru illustrates this rain shadow.

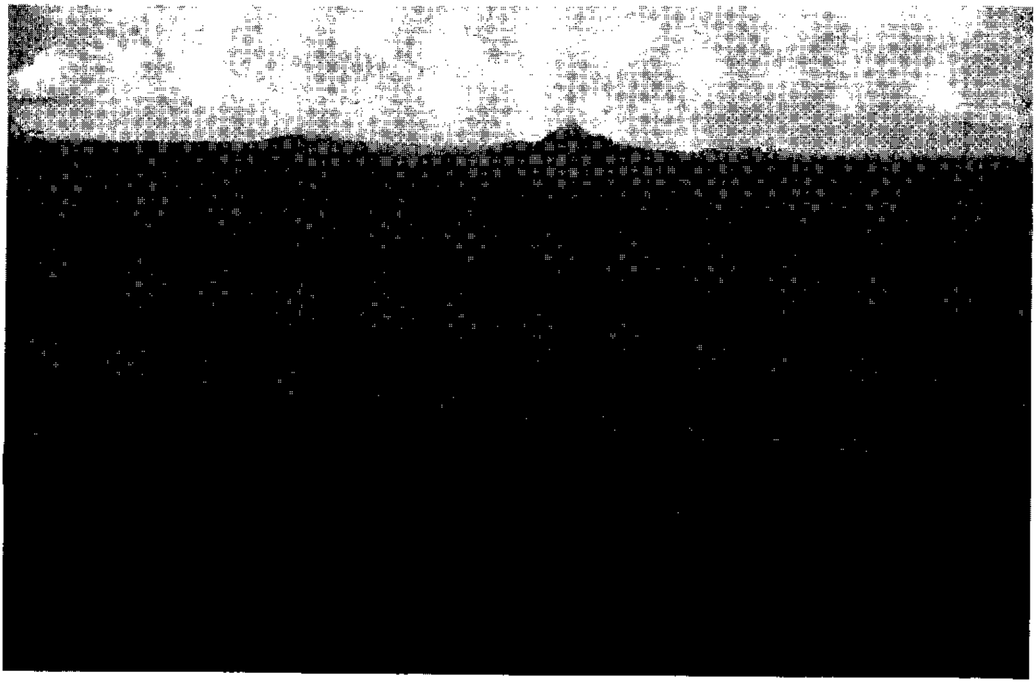

Figure 9 The everwet forests of Sapo National Park, looking towards Putu range (Liberia; Photo by H. Dop)

2.2 The regional forest gradient

For the analysis of the regional forest gradient I ordinated the tree species composition of several forests in SE Liberia and SW Côte d'Ivoire. Inventory data from the pre-logging era were analysed together with data from my three sample plots in Taï National Park. First I will explain why I chose the large tree species and why I considered the forest as a continuum. Both have consequences for the methods of sampling and data processing.

2.2.1 Large tree species

In this research I focused on large tree species that attain a diameter of 70 cm and more (Figure 12). Out of the total forest flora of at least 2000 species, i.e. the estimate for vascular plants in Ghana published by Hall & Swaine (1981), I used 53 of the largest tree species to describe the vegetation gradient from the coast to where the savanna begins. This subsample of the flora is of special interest to foresters and also forms the main structural element of the forest ecosystem (Albers 1990). The huge size of these trees when mature, and their often low population density demand an adapted sampling approach.

Former vegetation studies in SW Côte d'Ivoire used "complete" plant lists (Guillaumet 1967, de Rouw 1991). In Ghana, Hall & Swaine (1976) recorded 1248 vascular plant species and used 750 of these to describe the forest gradient there. In these data sets the

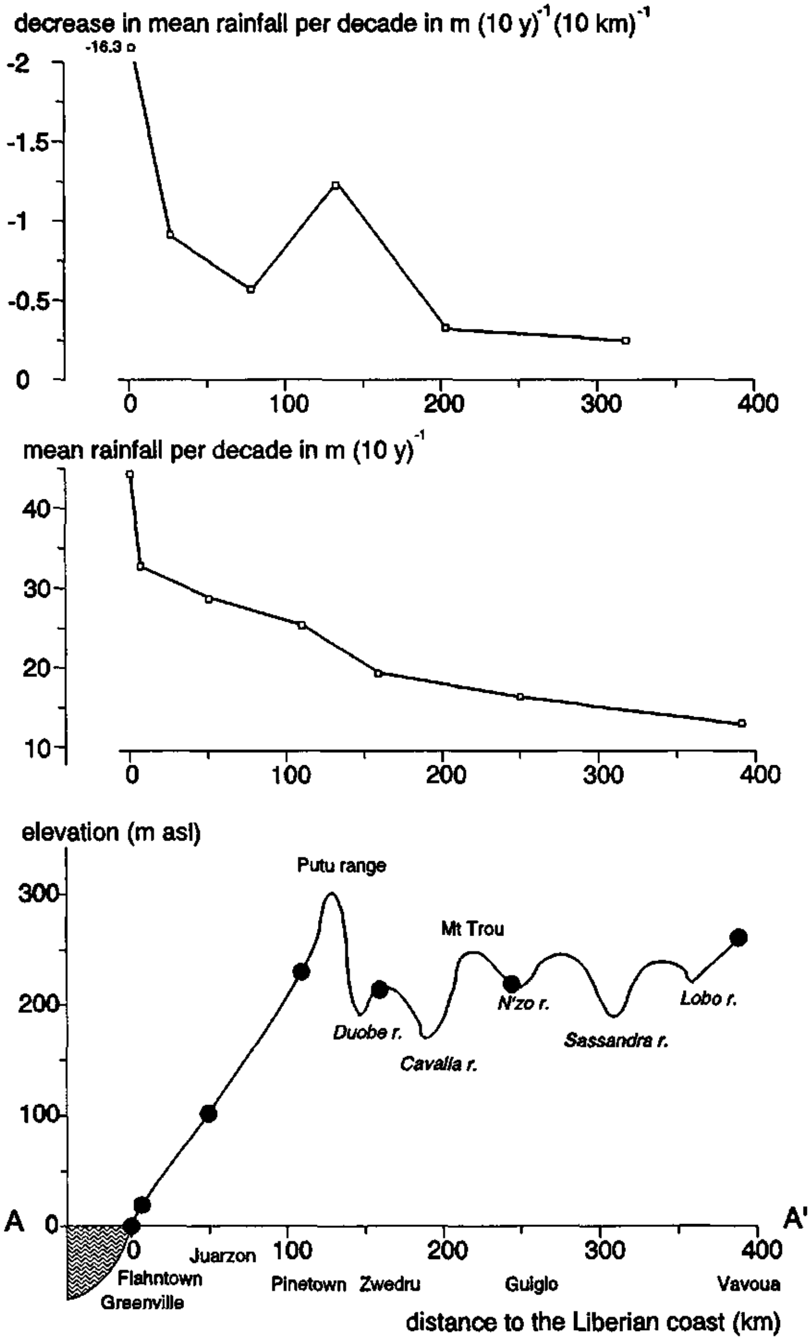

Figure 10 The rainfall gradient along cross-section AA' (see Figure 7) through SE Liberia and SW Côte d'Ivoire. The average elevation along the cross-section is given at the bottom. Source of rainfall data: see Table 1; source of elevation data: Sachtler (1968), IFAN 1968, MPEA 1983).

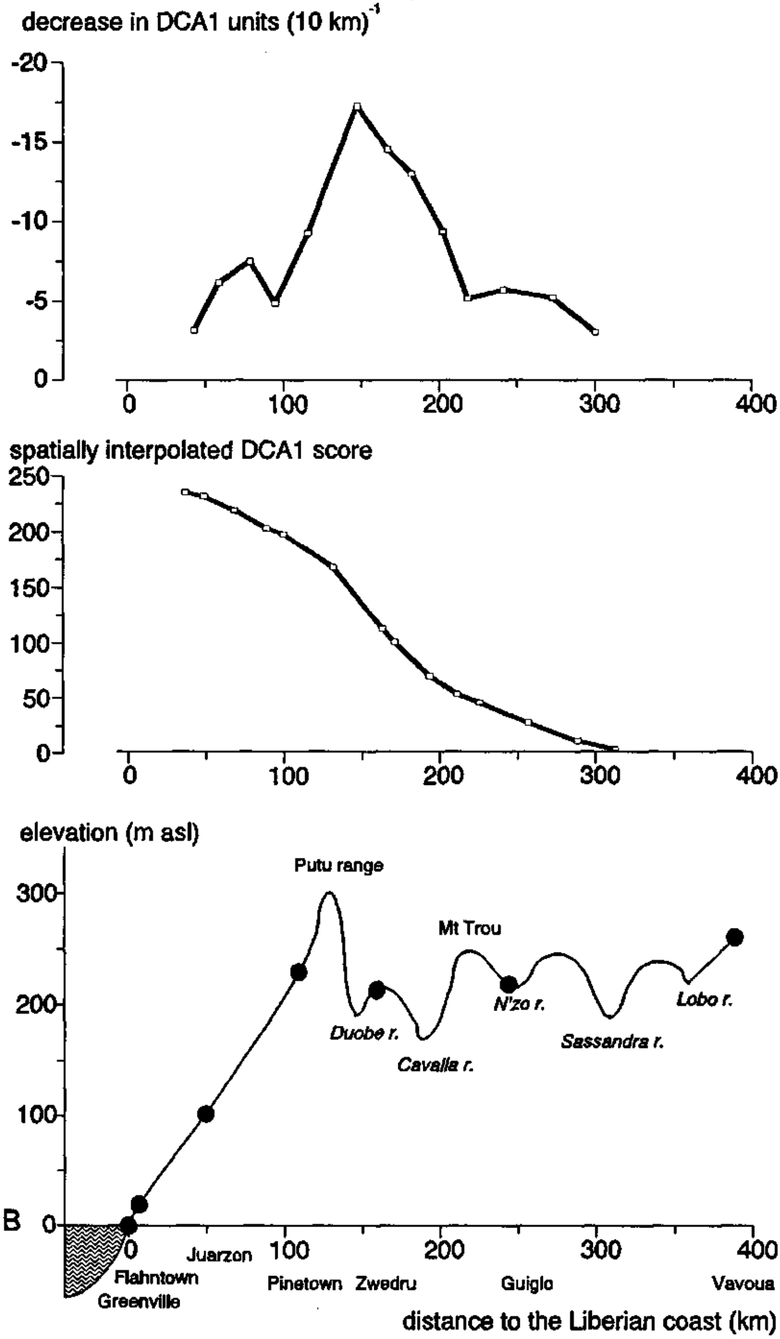

Figure 11 Cross-section BB' through relief, spatially interpolated DCA ordination score (Figure 14) and regional forest gradient in SE Liberia and SW Côte d'Ivoire

large trees species are often underrepresented and there are few distribution maps for Ghana of many of these species in the atlas by Hall & Swaine (1981) due to shortage of data. Their 155 sample plots (of 1/16 ha each) covered 10 ha in total (Hall & Swaine 1976). Hence, their conclusions were based on a 0.0005 % inventory, intended to be extrapolated over a total forest cover of about 2 million ha in Ghana. The power of their sampling method lay in regular distribution of the samples over southern Ghana and as a result, they sampled 3/4 of the total forest flora. Thus, the sampling intensity was sufficient to obtain a representative picture of the species distribution. For large trees, the scale of the inventory has to be adapted. In Chapter 3 I will show that in three areas of 20 ha each I found the major part of the total large tree flora of Taï National Park (446 000 ha), at a sampling intensity of 0.01 %. If in addition to the occurrence of a species, its abundance has to be estimated, sampling needs to be still more intense. Loetsch et al. (1973) advised a sampling intensity of 1 % to obtain reliable estimates of

Figure 12 A *Gymnostemon zaizou* tree (Simaroubaceae) at the Para study site. This large tree species is endemic to SW Côte d'Ivoire and Liberia. Photo by P. Albers.

timber volume, which also indicate the abundance of large tree species in forest compartments covering thousands of ha.

2.2.2 Forest inventories from the pre-logging era: a spatial gradient analysis

The botanical exploration of SE Liberia and of SW Côte d'Ivoire started in the 19th century. A extensive overview is given by Voorhoeve (1965) for Liberia and de Rouw (1991) for Côte d'Ivoire. The vegetation gradient was recognized by early botanist explorers (Chevalier 1909, Aubréville 1959). Vegetation scientists mapped the forest continuum by dividing it into forest types (Guillaumet & Adjanohoun 1971; Hall & Swaine 1976) or vegetation zones (Sachtler 1968, de Rouw 1991). Much valuable material was collected during timber inventories which were carried out with assistance from GTZ (German development aid) in the sixties in Liberia (Sachtler 1968) and with assistance from CTFT (the former Centre Technique Forestier Tropical, now CIRAD-Forêt) in the early seventies in Côte d'Ivoire (SODEFOR 1976a,b).

The continuous variability of the forest was illustrated by the ordination scatter diagrams on which some of these classifications are based and on which clustering of samples was seldom found. The approach of Hall & Swaine (1976) was to search for dividing lines in the ordination scatter diagram separating geographically contiguous zones on the map. They did this by trial and error. A further spatial analysis of this regional gradient is suggested in the present book using spatial interpolation techniques.

On the map, Hall & Swaine (1981) isolated a lower montane forest type, which they called 'upland evergreen forest', on hill ranges at 500 to 700 m elevation. The slope of these bauxite-capped hills was very steep, so there was no occasion to study the altitudinal gradient, as was done by Schnell (1952) and Adam (1983) for Nimba range at the point where Côte d'Ivoire, Liberia and Guinea touch. These 'upland evergreen forests' are an example of a cluster of samples that can be split off.

For lowland forests, the ordination scatter diagrams of Hall & Swaine 1976 and de Rouw 1991 were divided by vertical lines, based on the first ordination axis, which was indeed thought to explain the major part of the variation because it had the highest eigenvalue of all axes. The regional forest gradient apparently correlated well with the first ordination axis. The other axes remained largely unexplained. Hall & Swaine (1976) showed that the 6th axis of their RA ordination isolated the above-mentioned lower montane forests. So, gradients related to altitude may find their expression in higher axes. De Rouw (1991) ordinated "primary" and "secondary" forests together and found that the main floristic gradient, i.e. the first axis, was related to the degree of, or to the time since disturbance. Most of the forests I ordinated were unlogged, but disturbance by farming in certain parts and by large elephant populations was reported, e.g. in Krahn-Bassa forest (Sachtler 1968). These effects might show up in higher ordination axes.

Vegetational changes are gradual, especially when one is studying the large tree species with an ecological amplitude that allows them to cover a considerable part of the gradient. Even with a low abundance, such a species may remain present. It is rare to find large tree species that are unique to an area. Smaller plants more easily attain the status of uniqueness (Mangenot 1955, Guillaumet 1967, de Rouw 1991). This is partially caused by the size of the plants, which may be said to have a different "*eigenscale". Divisive *clustering methods such as Two Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979b) rely greatly on such indicator species. I tried out these methods on my data set and found that some divisions were placed at the edge of the range of distribution of rare species. For analysing a data set consisting of large tree species, DEtrended CORrespondence ANAlysis (DECORANA or DCA, Hill 1979a; Hill & Gauch 1980) provided better results. This ordination technique ranks the species according to the mode of their distribution, i.e. where each species attains its greatest abundance (ter Braak 1986).

The large number of "absence values", typical of species-sample matrices, have an important weight in the analysis. Samples with a small quadrat size, e.g. 625 m^2 (in Hall & Swaine 1976) and 36 m^2 plus a plotless sample of trees in the surroundings (in de Rouw 1991), never contain the complete list of the large tree species present in that forest, because these tree species have an irregular regeneration in time and rarely have seedlings and saplings permanently in the forest undergrowth. When surveying large plots for trees above a certain diameter limit, all smaller plants are disregarded and thus the species list is not complete, but samples in a small quadrat in which all plants are recorded are also incomplete, because they lack many irregularly regenerating large-sized species. In fact, this has to do with the question of the minimum area for a vegetation sample in tropical rain forests (Hommel 1991). On a 625 m^2 quadrat, Hall & Swaine (1976) only found 40 % of the vascular plants species present on 1 ha. This means that the other 60 % are marked "absent" in the data file but are present in the field, although maybe only at a density of less than 1 individual per 625 m^2 or with a clustered distribution. For large tree species the percentage of "**false absents**" may be even larger. TWINSPAN, however, relied both on the "presents" and on the "absents" in my data set, so it was probable that *Type II errors were made, in the form of artificial distinctions that did not correspond to forest reality. DCA seemed to be more robust to violation of the principle that all species in the vegetation must be listed (Hill & Gauch 1980, ter Braak 1986).

Besides its sensitivity to false absents, TWINSPAN splits a gradient even when it is completely linear. A theoretical linear spatial gradient on which change is constant, can be split into two, three or five equal parts, even if no information is added. The only information held in the data is that the line is straight and that it covers a certain range from starting to ending point. In many cases, however, the line is a curve and the steepness of the gradient changes along the range. Sometimes such curves show a point of inflection (Oldeman 1990b).

During the pre-logging forest inventories numerous individual sample plots or lines were laid out systematically in each inventory compartment to sample species composition and timber volume. In this Chapter, I will consider the composition of the sum of all these sample plots as representative of the species composition of the entire inventory compartment. However, neither such average compositions nor any single plot exemplifies how tree species grow together in these forests. The species composition was obtained from a mixture of several kinds of forests, valid for analyses at the level of means of species populations whose architecture is unknown because it has not been surveyed.

2.3 Study sites and methods

2.3.1 Study sites

The thirty *forest inventory compartments in SE Liberia and SW Côte d'Ivoire whose tree species composition was retrieved from inventory reports (Sachtler 1968, SODEFOR 1976a,b), are shown in Figure 13. Each inventory compartment covered quite a large area (on average 50 000 ha, see Table 2). They were part of *forest complexes, such as National Forests and National Parks. I ordinated my own three permanent sample plots of about 20 ha each within Taï National Park (see Chapter 3) together with the 30 inventory compartments using their large (d > 70 cm) tree composition.

All the forests are situated in the lowlands, below 400 m elevation. The lithology is mainly gneiss and migmatite, with small granitic areas in the south-western part of Krahn-Bassa forest (compartments K167, K69), in Taï National Park and in the lower valley of Sassandra river (Figure 4). A band of mica schist stretches from Zwedru to Guiglo (3NW) and a wedge of sericite-chlorite schist from Para north-eastward (1XV).

Three major rivers drain the area shown in Figure 13: Cestos, Cavalla and Sassandra rivers. The latter two have their valleys more or less perpendicular to the SW monsoon, resulting in the rolling landscape depicted in Figure 10 and Figure 11. Each successive ascent the air masses are forced to make might cause them to drop rain on the windward side, and rain shadows can be expected on the lee side. Cestos river runs NE-SW along a major geological fault and the maritime air masses can freely attain its upper stream basin.

2.3.2 Data collection methods

The sampling intensity in the inventories by Sachtler (1968) and SODEFOR (1976a,b) varied from 0.1% to 5% of the forest area (Table 2). Combined with the various sizes of the compartments, this resulted in a fully sampled area of 30 to 2600 ha per compartment. In comparison to these, the permanent sample plots in Taï National Park, each covering about 20 ha, were much smaller in area and moreover, they were contiguous and not a sum of small systematic sample plots. The inventory campaigns did not use the same lower diameter limit nor the same commercial species list. In some cases the inventory was stratified between swamp forest and upland forest. In other cases separate results were given for closed forest and degraded forest.

I combined data from four different inventories which each used a different method:

1) Côte d'Ivoire National Forest Inventory. The results of this inventory campaign were published in three volumes, covering the north-west, centre-south and centre-east region respectively. I used all 7 inventory compartments from the report on the *North-West region* (SODEFOR 1976b) for the ordination. I selected 2 of the 7 compartments from the report on the *Centre-South region* (SODEFOR 1976a).

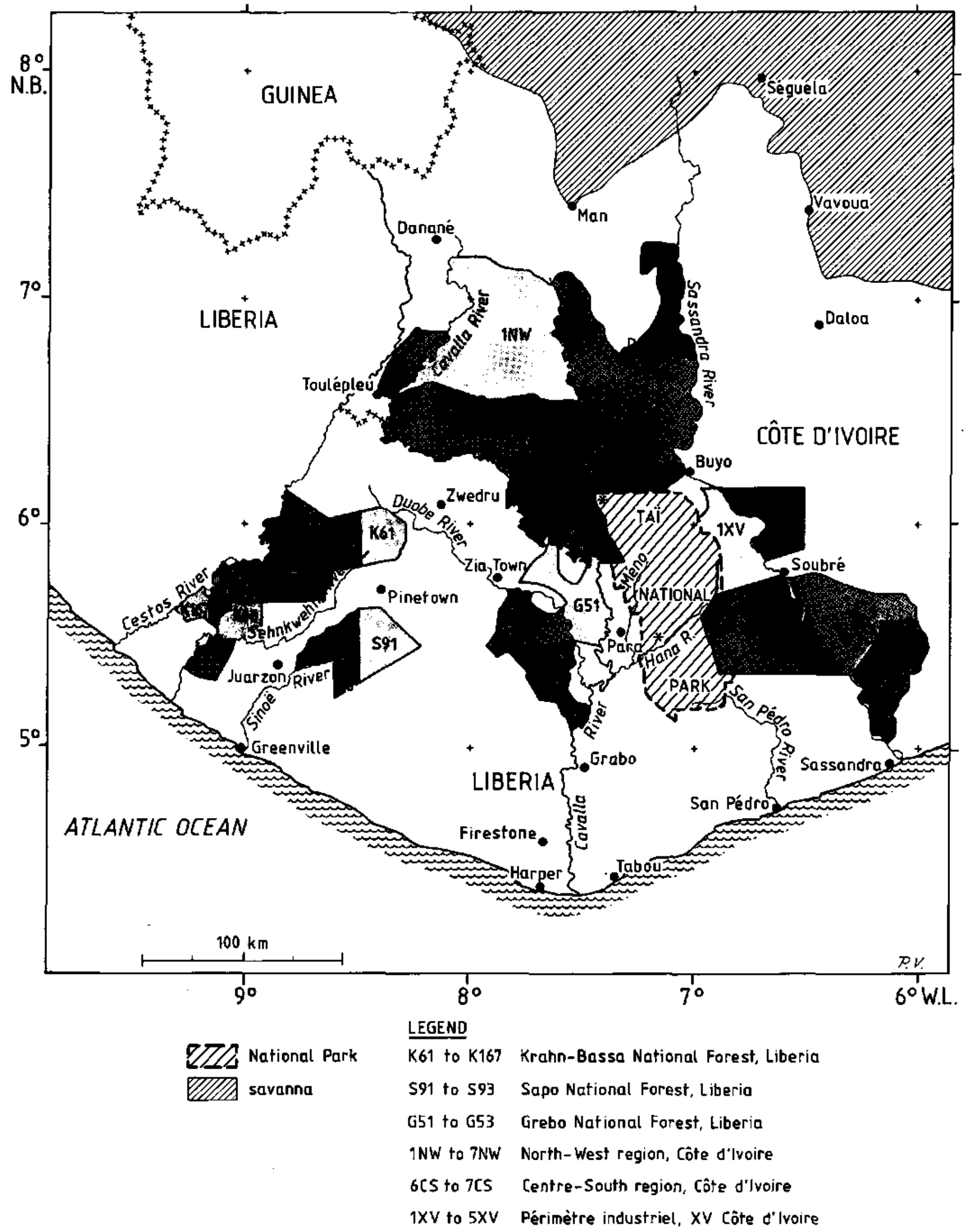

Figure 13 Forest inventory compartments in SE Liberia and SW Côte d'Ivoire used for the ordination described in Chapter 2. Note the different inventory methods as evidenced by the codes given to the compartments. For sources see Table 2. Different grey tones are only used to differentiate the compartments on the map.

Table 2 The forest inventory compartments used for the ordination described in Chapter 2 of the present book

	total area of the forest	sampling intensity	area of sample plot(s)	% swamp forest of total forest	% degraded forest of total forest
1) Côte d'Ivoire National Forest Inventory	(ha)	(%)	(ha)		
North-West region (SODEFOR 1976b)					
1NW F.Cl. du Scio	215000	n.a.	1000	n.a.	10 % (incl.)
2NW Biolékin-Toulépleu	145000	but	750	but	23 %
3NW F.Cl. du Goin	171000	probably	850	incl.	12 %
4NW F.Cl. du Haut Cavally	135000	0.5	650		5 %
5NW Réserve de faune du N'zo	140000	to	700		11 %
6NW F.Cl. de Duékoué	230000	1 %	1150		10 %
7NW between Mt Péko and Sass. river	91000		450		25 %
Centre-South region (SODEFOR 1976a)					
6CS F.Cl. de Niégré (northern part)	118000	n.a.	600	n.a. (incl.)	n.a. (incl.)
7CS F.Cl. de Niégré (southern part)	94000	n.a.	470	n.a.	n.a.
2) Côte d'Ivoire Inventory "Périmètre industriel XV"					
1XV east of Taï Nat. Park (Clément 1973)	71000	0.8 %	570	excluded	excluded
2XV "	88000	0.9 %	790	from	from
3XV "	19000	0.8 %	150	the sampled	the sampled
4XV "	6000	0.5 %	30	forest	forest
5XV east of Sassandra river	34000	0.8 %	270		
3) Liberia National Forest Inventory					
Grebo National Forest (250 000 ha) (GFML 1967)					
G51	95000	0.5 %	475	8 %	7 %
G52	81000	0.5 %	405	6 %	6 %
G53	75000	0.5 %	375	6 %	10 %
Krahn-Bassa National Forest (514 000 ha) (Sachtler & Hamer 1967)					
K61	46000	4 %	1840	14 %	1 %
K62	45000	5 %	2250	15 %	33 %
K63	45000	5 %	2250	16 %	10 %
K64	52000	5 %	2600	15 %	64 %
K65	48000	5 %	2400	27 %	27 %
K66	27000	<0.3 %	80	29 %	16 %
K67	26000	<0.3 %	80	25 %	0 %
K68	37000	<0.3 %	110	26 %	2 %
K69	31000	<0.3 %	90	33 %	2 %
K167	19000	<0.3 %	50	32 %	0 %
Sapo National Park (150 000 ha) (Sachtler & Hamer 1967)					
S91	55000	0.2 %	110	16 %	19 %
S92	40000	0.1 %	40	n.a.	n.a.
S93	26000	0.2 %	52	20 %	32 %
4) Côte d'Ivoire: my three sample plots in Taï National Park (see Chapter 3)					
Zagné			23	excluded	excluded
Taï			20		
Para			22		

n.a.: not available; incl.: included in the sampling; F.Cl.: Forêt classée (=forest reserve)

- The results were published for two strata:
  - forest (closed and degraded): used for the ordination
  - trees outside forest: not used
- 49 timber species were inventoried above 20 cm diameter; a 'minus' sign in Table 3 means absence of the species. The inventory report used vernacular names. As a result, I could specify six of these timber species only to genus level. Other tree species were inventoried above 60 cm diameter, but only the 20 most abundant species *in each inventory compartment* were listed in the reports, as well as the total volume for all species. The consequence of this way of reporting was that the presence or absence of the rarer species in a compartment could not be retrieved.
- To quantify the abundance of a species I selected the tables listing timber volume per species (in m^3 above 70 cm diameter), including all quality classes. These data are reproduced in Appendix 2. For use in the present ordination I rescaled the timber volume densities to abundance scores from 1 to 9 by calculating what percentage of total volume in the compartment consists of a given species. This percentage was rounded to the nearest integer and if less than 1, it was given the code 1, if more than 9, it was given the code 9.

2) **Côte d'Ivoire Inventory "Périmètre industriel XV"**. These forests, lying east of Taï National Park, were inventoried prior to the National Forest Inventory (Clément 1973). I used all 5 inventory compartments mentioned in the report.

- Results were specified according to three strata:
  - closed forest on well drained soils: used for the ordination
  - swamp forest: not used
  - degraded forest and shifting cultivation: not used
- 55 timber species (5 of which specified only to genus level) were inventoried above 20 cm diameter. No information was given on other species or on the total volume of all species.
- Timber volume above 70 cm diameter, all quality classes, was used to quantify a species. Rescaling as for 1).

3) **Liberia National Forest Inventory**. In cooperation with GTZ, the National Forests in Liberia were inventoried in the sixties (Sachtler 1968). I selected the three forests in SE Liberia for use in the ordination. Grebo National Forest, west of Taï National Park, was split into 3 inventory compartments (GFML 1967). Sapo National Forest, in the meanwhile designated a National Park (Mayers 1992), also contained 3 compartments (Sachtler & Hamer 1967) and Krahn-Bassa National Forest, the largest of all three, contained 10 compartments (Sachtler & Hamer 1967).

- In the reports no stratification was made within the compartments. Swamps and degraded forest were included in the results.
- 63 timber species were inventoried above 40 cm diameter. Smaller trees of those species, from 12 to 40 cm diameter, were counted in a subsample. Other species were grouped into a class "Miscellaneous" and the total volume was reported. 18 timber species could only be specified to genus level (e.g. *Uapaca* sp., *Parinari* sp., ...) (see Appendix 2).
- Timber volume per km^{-2} above 40 cm diameter, good quality, was used to quantify the species. Rescaling as 1).

4) **Côte d'Ivoire: my three sample plots in Taï National Park**

- Swamp forest was excluded.
- All species were inventoried above 70 cm diameter over 23, 20 and 22 ha in the Zagné, Taï and Para sample plots. The entire sample plot near Taï (see Chapter 3) covered 25 ha but the lowermost 5 ha were excluded.
- Stem number per 20 ha (all qualities) was used to quantify the species. These figures were rounded to the nearest integer to be used as abundance score. If more than 9 trees were counted in the sample plot, the abundance score '9' was given to the species. These data were extracted from the survey discussed in Chapter 3. See there for further information on these sites.

2.3.3 Methods for data processing

Ordination. The 33 samples were ordinated using the FORTRAN programme DECORANA (Hill 1979a) for detrended correspondence analysis (DCA). Two runs were done, one with the raw data set prepared as described above, a second retaining only the species common to all four inventory methods. In the first run, DCA was found to be sensitive to the incompleteness of the data. Quite a lot of ***false absents** occur because of the different methods of the inventories. *First*, the relevés were incomplete; they did not contain all plant species in a given forest, but only the tree species exceeding the indicated diameter limit and of actual or potential commercial interest. Certain tree species may be limited to young *cohorts and hence present below the diameter limit only. *Second*, the same species were not recorded consistently in all forests. This was partly because certain Liberian species do not even occur in Côte d'Ivoire and vice versa, but also because in the first method the non-commercial species were mentioned for compartments where they are abundant, but not for other compartments where they were rare, but may have been present. *Third*, the size of the sampling areas varied greatly, i.e. from 20 ha to more than 2000 ha. This certainly influenced the recording of the rarer species. The total number of species recorded for the relevés was 123 species. See Appendix 2 for a full listing.

A second run was made with a more consistent data set. Only those species common to the species lists of the four inventory methods, were retained. Where necessary, species were grouped to genus level to improve comparability. This yielded 53 timber species.

taxa

commercial [illegible] names?

Species and sample scores on the first DCA axis are given in Table 3. The species scores indicate the mode of the distribution of the species on the main vegetation gradient (ter Braak 1987a). The *ecological amplitude of the species can be read from the **range** of samples in which the species occurs. Note that this sample score axis, ranging from 0 to 243 units on axis 1 of DCA, henceforth called "u.DCA1", is not identical to the species score axis, ranging from -120 to 346 u.DCA1. Sample scores are weighted mean species scores (Hill & Gauch 1980).

Text box 2 **Problems with combining data sets of different origin and inventory method**

In the pioneer years of a science such as vegetation mapping scientists had to build up their own data sets from scratch. No previously collected data were available, or if they were, they contained far too little detail. The sampling methods, after fast initial development, were standardized from a certain moment on. In forest vegetation science many large data sets have been published, both for the tropics and for temperate countries (e.g. Hall & Swaine (1981) for Ghana, Vanclay (1989) for Queensland, Noirfalise (1984) for Belgium and van der Werf (1991) for Dutch forests).

Much new knowledge can be generated by combining existing data sets. This was attempted in the present Chapter. The inventory methods used in the different National Inventory Campaigns, show clear differences, as indicated in the text. *To what extent do these differences in methods influence the results?* (see also Ashton 1977). Each scientist prefers to analyse data that have been obtained by the same method, but in the present project it was impossible to re-examine the forests. Some forests have changed in the meantime as a result of logging and some have even disappeared.

Ordination analysis shows structure in data without human scientific bias. In the first DCA run on the crude data, the first axis ($\lambda=0.49$) reflected the main wet-dry gradient. The second axis ($\lambda=0.21$) separated the inventory methods. The third and fourth axes could not be attributed to any specific environmental variable. Along the second axis, my own sample plots (Zagné, Taï and Para) with complete species lists of trees exceeding 70 cm diameter were grouped at one end, followed by method 1, yielding most information on rarer species, and then methods 2 and 3, using only reduced species lists at the other end.

The sampling method therefore is seen to be part of the structure of a data set. In this case, DCA showed a difference in method on its second axis. The main effect, i.e. the wet-dry gradient, explained more variance in the data as it was related to the first ordination axis which had $\lambda=0.49$. This led me to continue the analysis after adjusting the data set by excluding the species not consistently surveyed under all methods. The second run showed that the methodological effect on the second axis had gone and its eigenvalue dropped below 0.10 ($\lambda_2=0.06$; $\lambda_3=0.04$; $\lambda_4=0.02$). The samples along the first axis were better ranked as to their position on the climate gradient.

Generally stated, analytic results reflect both the methods used and the reality they are applied to. Making comparable data sets is essential for the creation of integrated data systems. Sensitive tools must be developed to separate methodological structure from scientific information structure of data sets.

Spatial analysis. For spatial analysis, the sample scores (axis 1) were plotted on the map (Figure 14) and contour lines of the DCA1 surface were interpolated using the *kriging method, named after Krige (1951 ex Stein & Corsten 1991). This method interpolates DCA1 scores on a fixed grid, here 25 by 25 km, as a linear combination of up to 10 surrounding data points. The weights of these points depend on the degree of their spatial correlation (Stein & Corsten 1991). For the calculations I used the GIS software package Surfer 4.09 (© 1989 Golden Software).

A cross-section was made through the DCA1 surface in the SW-NE oriented part of the regional forest gradient, from Greenville to Vavoua (Figure 11). The decrease of the spatially interpolated DCA1 score was plotted against the distance from the Liberian coast. Above, the gradient is given, i.e. the rate of change of the DCA1 score with distance and thus of the tree species composition of the forests.

On the DCA1 surface, a line of maximal change, i.e. a "line" of inflection, can be drawn. It corresponds to a zone of quick vegetational change over a short distance, separating two areas with slower change. I analysed the ordination results to ascertain whether or not there were significant spatial trends and if so, whether they were linear or curved. If curved, I analysed the points of inflection, which are lines of inflection on the map. I looked to see whether there were spatial anomalies that could be related to the relief and thus the rainfall, and whether the trend had a consistent geographical orientation, in other words, whether the change in the vegetation corresponds to the SW-oriented rainfall gradient.

2.4 Results

The raw data run produced a first axis (*eigenvalue $\lambda = 0.49$) which roughly corresponded to the rainfall gradient, and a second axis ($\lambda=0.21$) which separated the samples by inventory method (see Text box 2). It was necessary to eliminate the differences caused by the inventory methods.

In the second run the first axis ($\lambda=0.41$) indicated the wet-dry gradient more closely and the second axis lost most of its significance ($\lambda=0.06$). In accordance with Hall & Swaine (1976) and de Rouw (1991) I continued the analysis with only the first axis. The species and sample ranking and axis 1 scores are given in Table 3, together with the species abundance in the samples.

2.4.1 Species ranking

In the upper left corner of Table 3, a number of typical wet evergreen tree species from Liberia formed a group. Some of these species do not occur in Côte d'Ivoire. Between these "everwets" and a number of *ubiquitous species, i.e. present everywhere but with a variable abundance, some typical swamp species were positioned by the ordination, which confirmed the findings of de Rouw (1991) that certain species that occur all over the catena in a wetter climate are restricted to the valley bottom in drier climates (e.g. *Heritiera utilis, Gilbertiodendron preussii* and *Sacoglottis gabonensis*). Other species like *Mitragyna ciliata* and *Loesenera kalantha* only occur in swamps (Voorhoeve 1965).

In the lower right corner of Table 3, tree species typical of the semi-deciduous forests were clustered, showing a linear response curve, or perhaps only the left-hand half of the supposedly unimodal curve of their distribution. Some of them, like *Ceiba pentandra, Terminalia superba* and to some extent *Triplochiton scleroxylon* extended quite a distance into the wet forests, probably because of their pioneer character (Aubréville 1959, Swaine & Whitmore 1988).

Several tree species showed a uniform distribution over the entire range of forests considered: *Canarium schweinfurthii, Lovoa trichiloides, Daniellia sp., Anopyxis klaineana, Afzelia bella, Amphimas pterocarpoides, Terminalia ivorensis, Tieghemella heckelii*. However, this may partly have been an artifact of the rescaling method used. The abundance score "1" was given to species present with one single tree, as well as to species present with a timber volume that was equal to 15 % of that of the most abundant species. This range is still quite large.

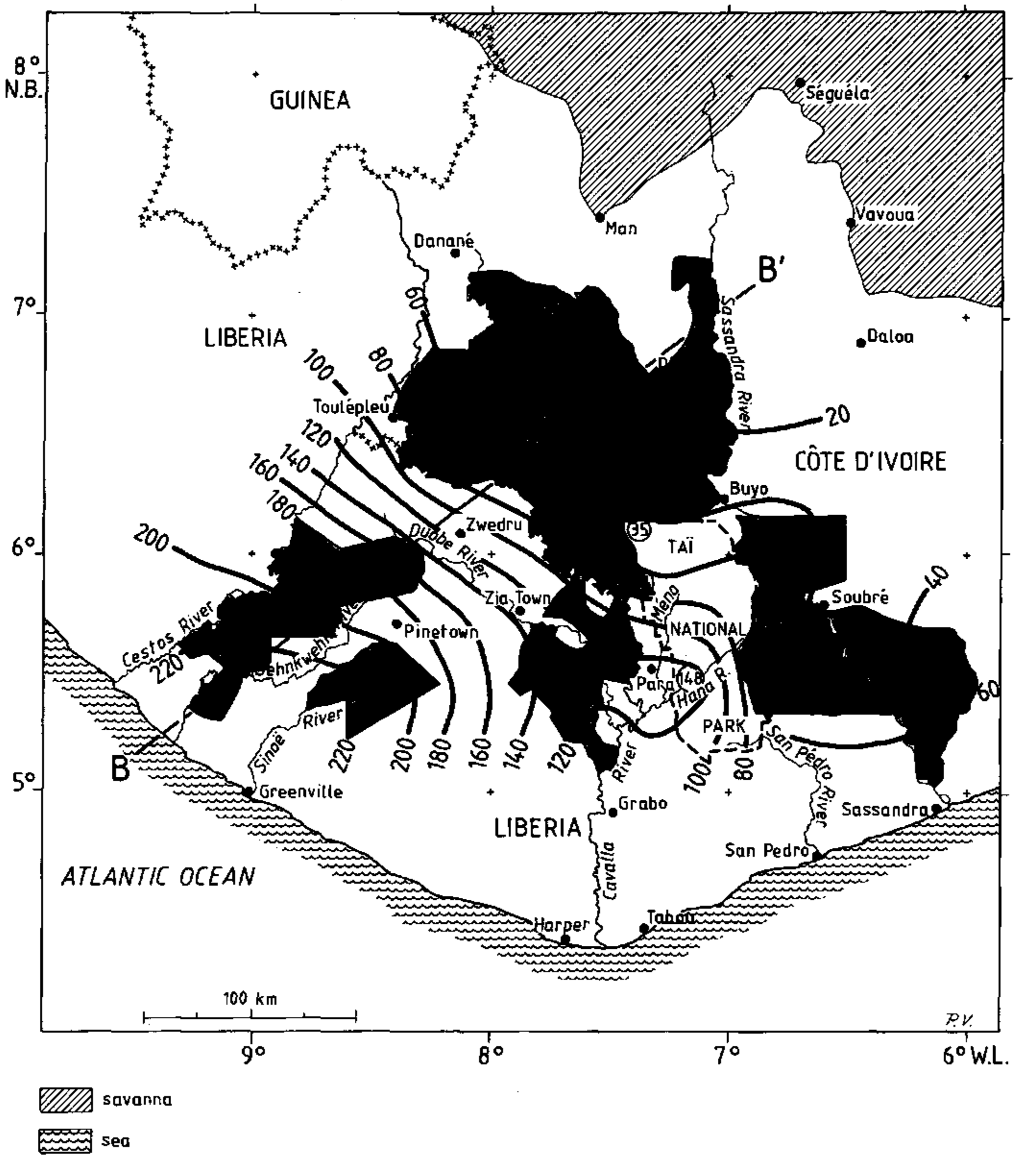

Figure 14 Spatial gradient analysis of the forests of SE Liberia and SW Côte d'Ivoire. The grey tone indicates the forest areas on which the ordination is based. The scores on the first DCA ordination axis are plotted in these forests. The three circled scores indicate my three sample plots in Taï National Park. The isolines join forest areas with the same DCA axis 1 score and thus with similar large tree species composition. The cross-section BB' is given in Figure 11. For sources of the data, see Table 2.

Table 3 DCA ordination table with 53 large tree species recorded consistently in 33 forest inventory compartments in SE Liberia and SW Côte d'Ivoire. Read plot numbers, u.DCA1 scores and number of species vertically. Species which are known to be briefly deciduous (Hall & Swaine 1981) are marked "(b)d".

			Z
			KKSKSKKSKKKKKPGGG a
			1 a 417T232565g14367
			6696966966666r555NXCaNNXXCNnNXXNN
			9826377153421a213WVSïWWVVSWéWVVWW
		u.DCA1	22222222211111111
			43311110099864320866655433333221
Large tree species			320653390716887168654770988548390
Didelotia brevipaniculata		346	25922--41-1----------------------
Loesenera kalantha		325	987959939979---------------------
Tetraberlinia tubmaniana		320	9999995999745-1-1----------------
Brachystegia leonensis		312	-12111-72-53---------------------
Cynometra ananta		305	32231612223-1-211----------------
Cassipourea spp.		296	--2-3--3111---1-1----------------
Monopetalanthus spp.		269	--1-1--114141-111----------------
Aralopsis soyauxii		268	-11-1--111111-111----------------
Heritiera utilis		248	996974165977945342612122111-11111
Didelotia idae		231	11-1-111111-1-1413---------------
Gilbertiodendron preussii		226	112222-328899-532114-31--21-1--1-
Sacoglottis gabonensis		224	154142224211192127-1-24--1--1----
Cryptosepalum tetraphyllum		223	---------1111-111----------------
Mitragyna ciliata		223	2531353431111-211211-111113-21111
Lophira alata	*bd*	216	2991979564346-642351-791115141211
Oldfieldia africana		212	1111111123123-6312--51-----1-----
Canarium schweinfurthii	*bd*	180	1-111232111111121111-111111111111
Lovoa trichilioides		163	111-1111111111121111-111111-11111
Daniellia spp.	*d*	156	-111111211111-111111-111211111111
Anopyxis klaineana		154	11211111111111111-11-113311111111
Nauclea diderrichii		149	121313211111223324423125211111111
Parinari/Maranthes spp.		145	11313213111229363734322334111211-
Afzelia bella	*d*	137	-11111-111-111111111-111111111111
Amphimas pterocarpoides	*d*	134	-11111-1111111111111111111111311-
Terminalia ivorensis	*d*	117	-111---1111111111111-11311111-111
Tieghemella heckelii		109	1--1---11111131111113111111-11111
Chlorophora spp.	*d*	95	--1-11-111111-111111-111111123111
Turraeanthus africanus	*d*	94	-------111111---11-1-11111--11-11
Distemonanthus benthamianus		87	----11-111111-111111-111111311111
Anthonotha fragrans		77	12111111111121222393312462311151-
Berlinia spp.		76	1111111111111-111162-112722-14311
Entandrophragma spp.	*d*	54	----1--11111115331119111111215111
Rhodognaphalon brevicuspe	*d*	51	---1---11111111111311113312111111
Khaya anthotheca	*bd*	48	--------11111-11111112111111-11111
Piptadeniastrum africanum	*d*	44	113123231154314567799979988189951
Erythrophleum ivorense		44	112111212211213223914348715633532
Pycnanthus angolensis		43	111112111122116675529556734143851
Antiaris toxicaria	*d*	35	-------11111111111111111111125111
Klainedoxa gabonensis		30	111111111211212124653238822115723
Petersianthus macrocarpus	*bd*	15	--111--11111112433242431552255241
Ricinodendron heudelotii	*d*	14	---1----1111-----1111111111112221
Guarea cedrata		7	---------1-11-111111-111111111111
Ceiba pentandra	*d*	-35	-1-111-111211-1123333655247293789
Terminalia superba	*d*	-35	---1-1-111111-1122412224343421559
Nesogordonia papaverifera		-36	----------1---1111111111111111111
Celtis spp.		-61	--------11-------111-111111-15211
Albizia ferruginea	*d*	-111	-----------------111-111211111111
Mansonia altissima	*d*	-112	-----------------11--111111-11111
Aningeria robusta		-114	-----------------1111111211112211
Triplochiton scleroxylon	*d*	-115	--------------1132321699679499999
Guibourtia ehie	*d*	-116	-----------------11--111211111111
Sterculia rhinopetala	*d*	-119	------------------11-111111-11111
Pterygota macrocarpa	*d*	-120	-----------------111-111111-1-113
Number of species:			223332244444324344442444444343343
			381239103330901922002320020028917

The unimodal response model (ter Braak 1986) was found for species like *Gilbertiodendron preussii, Anthonotha fragrans, Oldfieldia africana* and for the genera *Parinari* and/or *Maranthes*. They were present over the entire range of forests, which was 400 km wide, but each showed a clear optimum.

2.4.2 Sample ranking

It is striking that the forest inventory compartment furthest SW (code K69 on Figure 13) showed up in Table 3 at one end of the first ordination axis (243 u.DCA1) and the forest compartment furthest NE at the other end (0 u.DCA1), in perfect accordance with what we might expect from the rainfall gradient. The Krahn-Bassa and Sapo National Forests in Liberia are the wettest forests in this *forest block, varying from 243 down to 186 u.DCA1. They are characterized by the dominance of Caesalpiniaceae tree species in the forest canopy and contain several *endemic species (*Tetraberlinia tubmaniana, Didelotia brevipaniculata, Loesenera kalantha, Monopetalanthus compactus*). I could not study the extent of these forests in the extreme SW of Côte d'Ivoire (hinterland of Tabou, Grabo hills, Forêt classée de la Haute Dodo), as no forest inventory reports were available for this region, but Aubréville (1959) and Guillaumet (1967) report on the presence of numerous *endemic species in this SW corner where they located the "wettest" forests of Côte d'Ivoire.

The most north-eastern compartment of Krahn-Bassa forest K61 (168 u.DCA1) was already transitional in composition towards the Grebo National Forest. The wettest forest compartment studied in Côte d'Ivoire was the Forêt Classée du Haut-Cavally (code 4NW: 88 u.DCA1). It was the only inventory compartment in Côte d'Ivoire where the everwet tree *Didelotia idae* (broutou; Oldeman 1964) was found. This compartment, containing Mt Trou (Figure 11), lies on the windward side of the second major ridge which forms an obstacle to the maritime air masses drifting inland.

The three sample plots Zagné, Taï and Para had positions of respectively 35, 64 and 148 u.DCA1 on the first ordination axis. Whereas Zagné and Taï fitted quite well into the local gradient as plotted on the map (Figure 14), the Para plot was an outlier, which according to the ordination could have lain in Liberia. This may have been caused by the great abundance of *Sacoglottis gabonensis* on the Para site (Table 3, Figure 26). The Zagné plot is similar to the neighbouring Réserve de Faune du N'zo (code 5NW). The three sample plots were far from internally homogenous in tree species composition. The intra-sample variation will be analysed in Chapter 3.

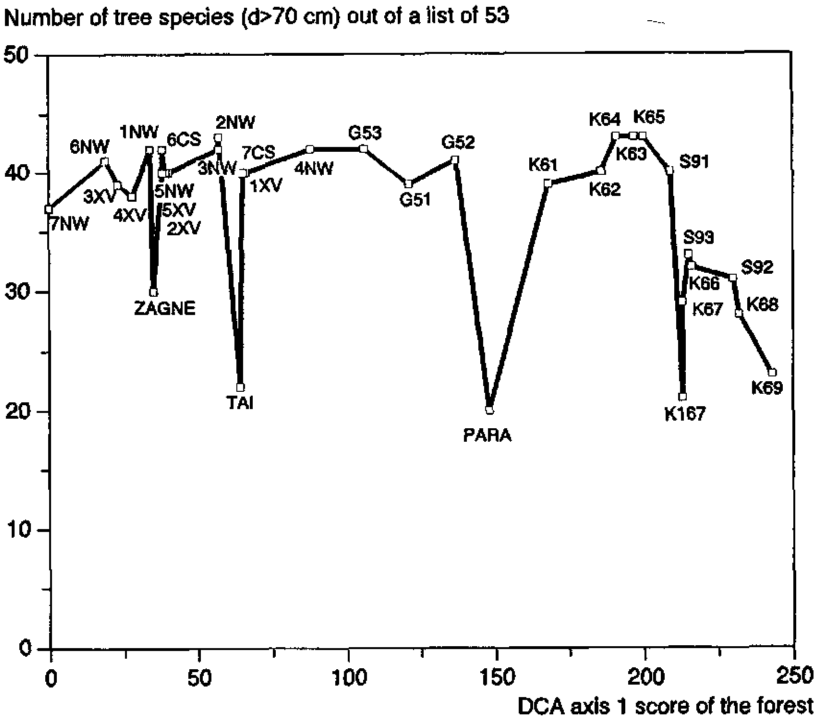

Figure 15 Number of timber species per forest inventory compartment out of a list of 53 large tree species, consistently recorded in all inventories. The x axis gives the DCA axis 1 scores of the samples. My sample plots near Zagné, Taï and Para each lacked certain species found in other samples on the same position of the gradient, partly because they covered a smaller area. Towards the wettest end (right) a drop in species richness was observed. These forests are rich in Caesalpiniaceae species which locally may dominate the vegetation (Voorhoeve 1965).

2.4.3 Species richness

The rather small plot size of my three sample plots (20 ha each) and the deliberate exclusion of swamps made them the samples poorest in species. Figure 15 gives the number of species per compartment out of the list of 53 consistently recorded ones. Compared with other forests on the same position of the gradient, they lacked a number of species that could have occurred when considering Table 3. Some of these "absent" species are typical swamp species, others are rarer ubiquitous ones. Concerning the Para site, Guillaumet (1967) already indicated that the forests on the sericite-chlorite schist band were poorer in evergreen species than the forests around Grabo. Perhaps since the last Ice Age certain species, e.g. Caesalpiniaceae with relatively heavy seeds, have not yet reached all the areas where they could ecologically occur (J.J.F.E. de Wilde, pers. comm.).

Among all forests there was a slight negative trend in species richness at the wetter end of the gradient. The incompleteness of the records, however, urges caution. In Chapter 3 these aspects of diversity will be discussed in more detail.

2.4.4 Spatial analysis

Plotted and interpolated on the map, the general direction of the gradient was SW-NE (Figure 14). A spatial anomaly occurred, from the Para study site up to Sassandra river. Three samples (Para, 1XV and 5XV) were ranked "wetter" than was to be expected from their geographical position. Comparing Figure 14 to the lithology of the area (Figure 4) revealed that all three of them lie on the band of sericite schist bedrock. The soils derived from sericite schist bedrock are known to be more clayey and have a better water retention capacity (Guillaumet 1967, DRC 1967b, van Herwaarden 1991a). In the extreme SE corner the inventory compartment coded 7CS, ranked out at 65 u.DCA1, which is again "wetter" than expected. Here the coastal effect of rainfall may intervene, but a comparison with neighbouring forests is needed to verify this.

2.4.5 Cross-section through the gradient

The SW-NE oriented part of the gradient was chosen to make a cross-section. On this cross-section (Figure 11) and also on the map it became clear that the gradient was not linear, but was sigmoidal with a point of inflection in the middle at about 140 u.DCA1. A zone of faster compositional change was found, more or less perpendicular to the SW-NE oriented gradient. This zone corresponds to a steeper part of the rainfall gradient which I detected in the rain shadow from Putu range. In the literature on Liberia (Voorhoeve 1965, Sachtler 1968) this zone has been recognized as the transition between evergreen and semi-deciduous forest and as the southernmost position of the Intertropical Front (see Figure 21). The rest of the gradient has a rate of change of about 5 u.DCA1 per 10 km.

2.4.6 Coverage of the vegetation gradient by the National Parks

The position of Taï National Park on the gradient is between 40 and 150 u.DEC1. The Park does not even cover half the length of the entire gradient, i.e. 240 u.DCA1. Sapo National Park covers an even less diverse stretch on the wettest side of the gradient (210-230 u.DCA1).

2.5 Discussion

2.5.1 Comparison with the forest gradient in southern Ghana

Hall & Swaine (1976; 1981; Swaine & Hall 1976) analysed and described the forest vegetation gradient in Ghana, which is largely similar to the gradient in SE Liberia and SW Côte d'Ivoire. They used the ordination technique of reciprocal averaging (RA, Hill 1973), as DCA (Hill 1979a) had not yet been invented. The species scores of the Ghanaian ordination correlate quite well with the scores of my ordination ($R=-0.75$, $p<0.01$, see Figure 16). The species that are ranked differently in both ordinations often have a uniform distribution without a clear optimum and the minimal abundance score of 1, and include *Canarium schweinfurthii, Chlorophora spp., Aningeria robusta, Guibourtia ehie*. Species with the same abundance have no influence on the ordination and may be eliminated from the data set. These rare "wandering" species, however, are typical of tropical rain forest, and it is merely the rescaling method which is not sensitive enough to identify their optimal conditions. Hall & Swaine (1981) described a gradient that extended much further into the drier forests.

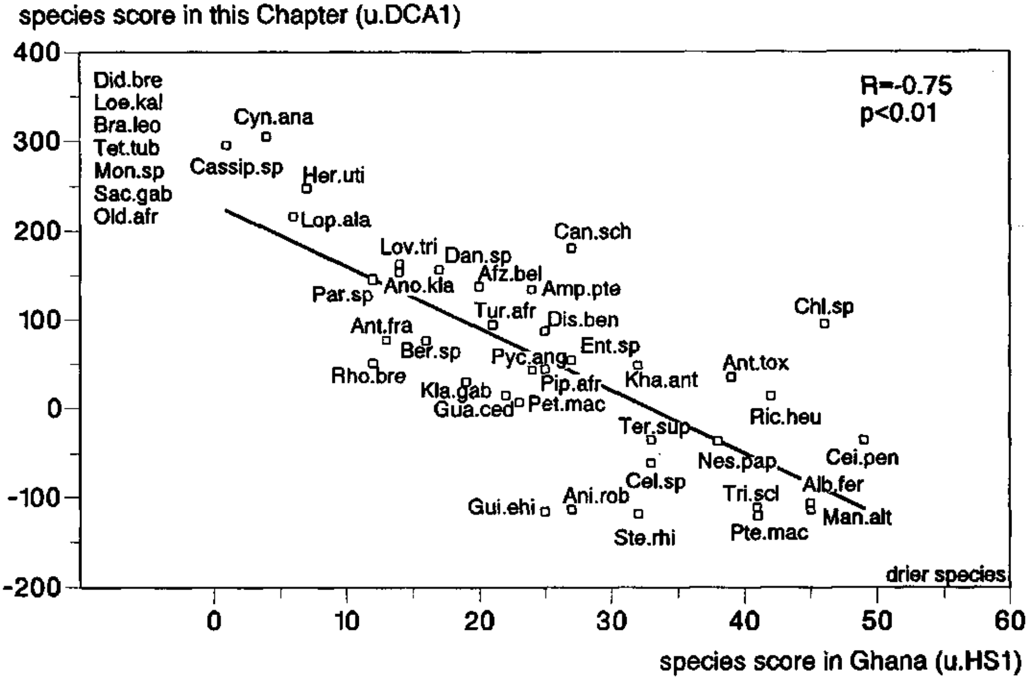

Figure 16 Correlation of my species scores (u.DCA1) with those found by Hall & Swaine (1981) (u.HS1). Beside the species common to both data sets, a number of "everwet" species are listed in the upper left corner. Hall & Swaine's (1981) ordination extended much farther in the dry forests.

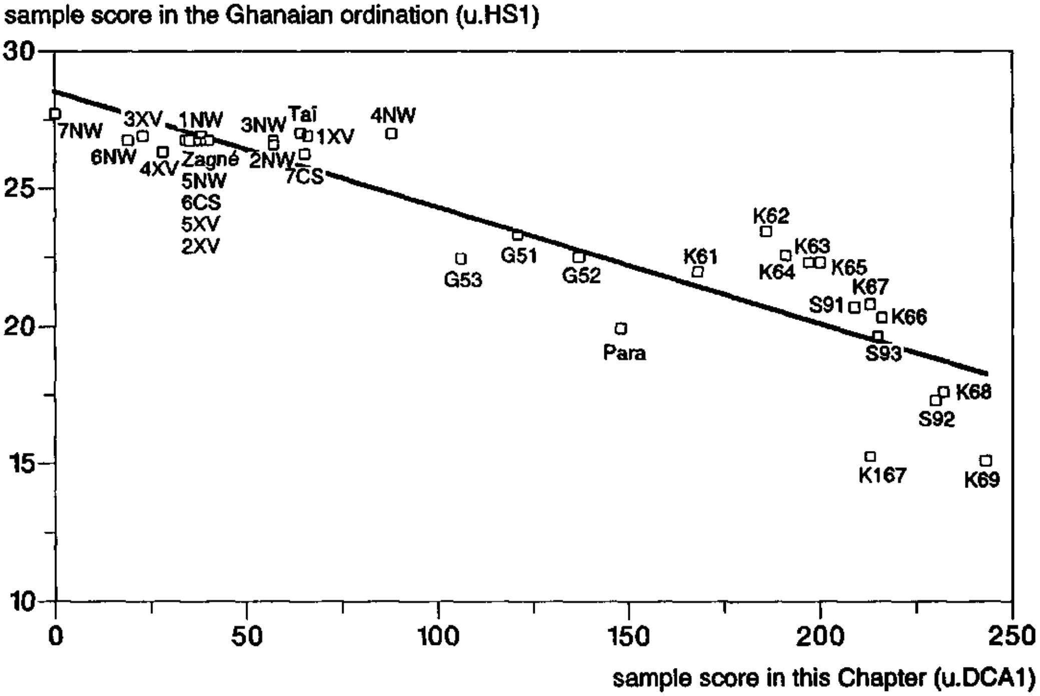

Figure 17 Correlation of my sample scores (u.DCA1) with scores calculated after the species scores given by Hall & Swaine (1981) (u.HS1). On the y axis the Ghanaian forest types are indicated.

I applied the method of identification by 'coordinate estimation' (Swaine & Hall 1976) to my samples, i.e. I calculated the average species scores of my samples using the Ghanaian species scores and found that the forests I considered fell within a range of 15 to 28 Hall & Swaine (1981) axis 1 units (u.HS1; see Figure 18). The correlation with my own sample scores is good ($R=-0.91$, $p<0.01$, see Figure 17). However, on the HS1 axis my samples formed two clusters: all Ivorian forests except Para at 27 u.HS1 and the Liberian forests plus Para at 20-24 u.HS1, the wettest forest going down to 15 u.HS1. The presence of the first cluster is an indication that the Ghanaian ordination did not reveal the differences between the Ivorian forests because only a limited list of large tree species was considered.

In Ghana only my wettest forests would be classified as wet evergreen (15-20 u.HS1), the other ones as moist evergreen/moist semi-deciduous (20-33 u.HS1). No dry semi-deciduous forests were represented among the forests I studied. The distinction between moist evergreen and moist semi-deciduous forest in Ghana was based on axis 6 of Hall & Swaine's ordination with an eigenvalue of 0.13 and thus explaining little of the variation. My 'moist' forests, i.e. with Hall & Swaine axis 1 values above 20 u.HS1, have axis 6 values between 37 and 42 u.HS6, which would indicate that they are *transitional* between the moist evergreen (35-40 u.HS6) and the moist semi-deciduous (40-44 u.HS6) forests of these authors (Figure 18).

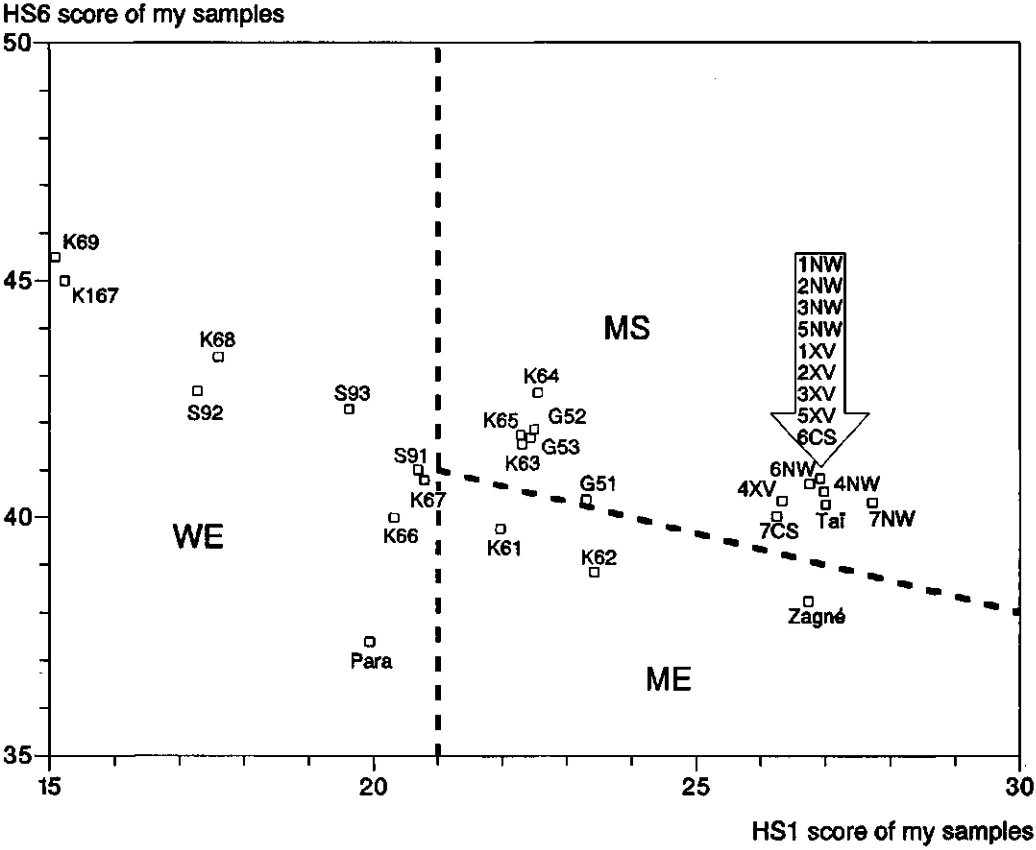

Figure 18 My samples placed in the Ghanaian ordination diagram by 'coordinate estimation', i.e. the coordinates of a sample as given by the mean species scores, taken from ordination axis 1 and 6 of Hall & Swaine (1981). The interrupted lines indicate the division in forest types as made by Hall & Swaine (1981); WE: wet evergreen forests; ME: moist evergreen forests; MS: moist semi-deciduous forests.

It would be interesting to see the outcome of a detrended correspondence analysis (DCA) on the Ghanaian data to complement the reciprocal averaging practised by Hall & Swaine (1976).

De Rouw (1991) used this technique of coordinate estimation to position the relevés of Guillaumet (1967) in her ordination diagram. All Guillaumet's relevés fell within her driest forest type, even if they originated from wetter forest. De Rouw (1991) argued that this was caused by the sampling method used by Guillaumet (1967) with which he undersampled the ground flora and the understorey tree species. Coordinate estimation seemed to work well only if the same life forms were recorded and thus the same inventory criteria were applied both in the original survey and in the new relevés.

At the wet end of my gradient four "everwet" and very abundant tree species were ranked beyond the wettest Ghanaian species, *Cynometra ananta*, that both sets have in common. This means that in Liberia there are wetter forests than in Ghana. *Tetraberlinia tubmaniana, Loesenera kalantha* and *Didelotia brevipaniculata* were very abundant in these forests, and the *Brachystegia leonensis* trees occurring there are among the tallest trees in Liberian forest. Sachtler (1968) and Voorhoeve (1964) even report on single-dominant forest with *Tetraberlinia tubmaniana* in all height levels of the forest canopy (Figure 22; see also Hart (1990) and White (1983) on single-dominant forests).

2.5.2 Vegetation studies in SW Côte d'Ivoire

Guillaumet (1967) published a thorough *study on the vegetation and the flora of SW Côte d'Ivoire*. He made relevés of all vascular plants on 21 plots, covering from 150 to 1000 m^2 each, and described soil-vegetation catenas on different bedrock types. He classified the plant and tree species according to three criteria: position in the forest canopy at maturity (herbs and shrubs, lower, middle and upper canopy species and epiphytes), light intensity needed when young, and water retention capacity of the soil in which they grow. Based on the last criterion he distinguished *psammophilous species and *pelophilous species (the former grow on sandy soil and the latter on clayey soil) plus a category of indifferent species.

On his vegetation map of SW Côte d'Ivoire (Figure 19), he indicated a predominance of pelophilous species in all topographical positions in the extreme SW corner of Côte d'Ivoire: from Guiroutou over Grabo to Tabou. On the sericite schist bedrock these pelophilous species are still dominant but fewer species occur. In the rest of SW Côte d'Ivoire pelophilous species are restricted to lower slopes. Psammophilous species are only dominant on a narrow band of Tertiary sands starting east of San Pédro and extending east up to the Ghanaian border.

In the extreme SW-corner of Côte d'Ivoire, "Liberian" high rainfall conditions overruled the influence of soil texture (Guillaumet 1967). Pelophilous plant species do grow there not because the soil is so clayey, but because of optimal moisture conditions. Drought stress is a combined effect of climate and soil. With respect to this it may be better to use the terms "*drought stress tolerant or intolerant species*" (see further Chapter 3).

My results confirm the findings of Guillaumet (1967) that "wetter" forests exist on sericite schist bedrock. A direct comparison is difficult, as his data on absence or presence of large tree species are much less complete than mine, because he sampled a much smaller area. On the other hand, most of Guillaumet's and de Rouw's (1991) discriminatory species are lower canopy species, herbs, lianas and shrubs. Both studies have only limited comparability because of this profound difference in criteria.

The presence of species from the semi-deciduous forests and the absence of pelophilous species in a rather large area west of Sassandra river and south of the town Soubré (forests coded 3XV and 4XV; Figure 13) was also confirmed. Guillaumet (1967) did not relate the presence of these drier forests to different bedrock but simply to a drier climate and a longer dry season. Here again, the problem of interpolation of the climatic data from the weather stations appeared (see subsection 2.1.1). Rainfall stations are scarce and therefore neither the existence of a possible rain shadow of the hills of Grabo, nor of the effect of the general descent of elevation towards Sassandra river could be proved. The southern inventory compartment of Grebo National Forest (G53) in Liberia also lay windward of a large river and in the same way was the driest forest in its region.

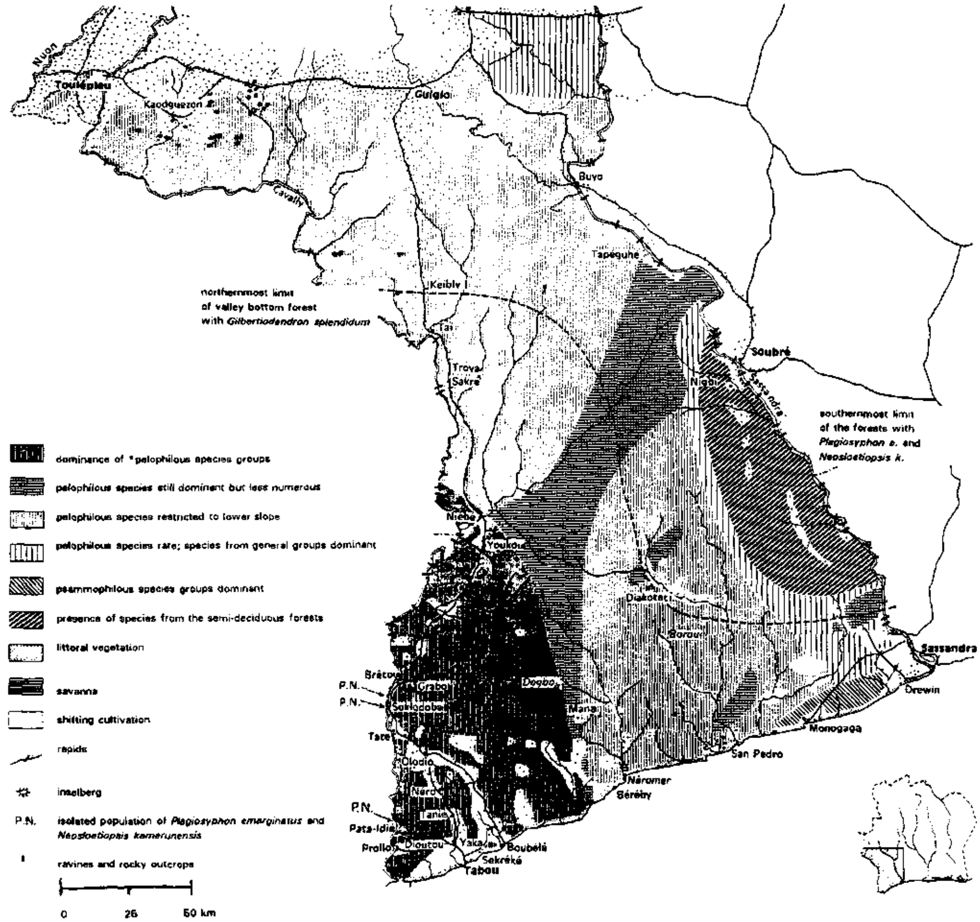

Figure 19 Vegetation map of SW Côte d'Ivoire as drawn by Guillaumet (1967)

Guillaumet & Adjanohoun (1971) published a *vegetation map of Côte d'Ivoire* at a scale of 1:500 000. They lumped the wet evergreen forests of Grabo and the impoverished ones on the band of sericite schist bedrock together into one evergreen forest type: "the *Diospyros-Mapania spp.* evergreen forest". On this new vegetation map it was striking to note that the border of this wettest type, especially within the Taï National Park, was placed considerably northwards by comparison with its position on the map in Guillaumet (1967; Figure 19).

The only characteristic *tree* species for this type, mentioned by Guillaumet & Adjanohoun (1971), is *Heritiera utilis*, which in my data set is ubiquitous with a clear maximum of abundance in the wettest forests of Liberia. Under its trade name "Niangon" it is the most important commercial species in Liberia. It represents 27 % of the felled wood and 36 % of the timber value exported from Liberia in 1989 (FDA 1990). *H. utilis* also occurs in the other evergreen forest types, so it is the association of herbs, lianas and small tree species that yields characteristic species for this forest type. The forest tree association of *Cynometra ananta, Brachystegia leonensis, Didelotia brevipaniculata, Cassipourea nialatou* and others which is called the mixed evergreen forest in Liberia (Sachtler 1968, Voorhoeve 1965), does indeed occur on the hills of Grabo, but not on the sericite schist band in Taï National Park. I suggest separating these forests as distinct types on vegetation maps. The map by Guillaumet & Adjanohoun (1971) suggests that the same forests are found around Grabo and in the major part of Taï National Park. This could be used as an argument against a special protection of the forests around Grabo.

> ***However, the Forêt classée de la Haute Dodo and the hill ridge from Mont Kopé to Mont Kédio and Mont Bodelé do contain numerous tree species found neither in Taï National Park, nor anywhere else in Côte d'Ivoire (Aubréville 1959, Guillaumet 1967). Hence they merit special protection and conservation management (Vooren 1992b).***

North of the road Guiglo-Toulepleu Guillaumet & Adjanohoun (1971) distinguished a separate climatic forest type, considered to be transitional between evergreen and semi-deciduous forest: "the forest with *Uapaca corbisieri* (syn.: *U. esculenta*), *Uapaca guineensis* and *Chidlowia sanguinea*". The inventory compartment 1NW, Forêt classée du Scio, lay in this forest type and had a u.DCA1 score of 34, thus indeed transitional. In composition it is similar to the Réserve du N'zo (5NW), the Zagné sample plot and the inventory compartments 5XV and 6CS (Forêt classée de Niégré, just east of Sassandra river).

The Forêt classée de Duékoué (6NW, 19 u.DCA1) and the forests east of Mont Péko (7NW, 0 u.DCA1) are drier than the Scio forest and were classified by Guillaumet & Adjanohoun (1971) as semi-deciduous forests with *Celtis spp.* and *Triplochiton scleroxylon.*

Further, there is the issue of transitional types and the transition between types which posed problems for vegetation mapping. It is illustrative to see how Guillaumet & Adjanohoun (1971) depicted the transition of evergreen to semi-deciduous forest in three different ways on their map: 1) by a colour code specific to a transitional type; 2) by alternating light and dark green bars, i.e. a mixture of their two neighbouring forest types, and 3) by light green (semi-deciduous) dots in a dark green (evergreen) matrix, i.e. another kind of mixture.

Faced with these transitional forests, it is convenient to pass from mapping types at an *ordinal scale, to mapping isolines, corresponding to an interval scale. When mapping a continuous gradient by e.g. three types, both the extreme types are well characterized, but often the middle one is not (I.S. Zonneveld, pers. comm.). The clearest proof of this is the forest type that Guillaumet & Adjanohoun (1971) called "evergreen forest with *Eremospatha macrocarpa* and *Diospyros mannii*", which is "essentially based on negative characteristics, namely the absence of species typical of other forest types." (Guillaumet & Adjanohoun 1971, p. 171). The same weak characterization was used by Hall & Swaine (1981) for their "Moist semi-deciduous forest type", lying in the middle of the gradient. Very few species were found to be confined to this type and, at the same time, it is the most extensive forest type in Ghana. Hall & Swaine (1981, p. 37), using an example of *Diospyros* species in Ghana, showed that there is no geographical coincidence of ranges of species to support these forest types.

> ***From this, I conclude that mapping a spatial gradient using isoscore lines resolved the problem of transitional types.***

2.5.3 Forest zonation in Liberia

The German Forestry Mission to Liberia, a project of the German Gesellschaft für Technische Zusammenarbeit GTZ, carried out a National Forest Inventory in Liberia during the sixties (Sachtler 1968). I abstracted climate and vegetation data from their reports. Sachtler (1968) distinguished two major vegetation zones in Liberia: "the evergreen forests" and "the moist semi-deciduous forests". He considered the December position of the Intertropical front as the boundary between the two zones (Figure 21). On Figure 14 Sachtler's line followed my 120 u.DCA1 contour line through Zwedru and along the Duobe river. This line also followed the northern limit of the distribution of *Didelotia idae* (Figure 20). When extrapolated into Côte d'Ivoire, the 120 u.DCA1 line would coincide with the northern limit near Guiroutou of the wet evergreen forest as distinguished by Guillaumet (1967; Figure 19).

Throughout Liberia this boundary line was not congruent with any isohyet. In NW Liberia it would be at 2800 mm rainfall, in SE Liberia at 2000 mm. This boundary line also corresponded to the line of inflection, i.e. the greatest rate of compositional change, of the forest gradient found in Figure 11. If the forests were to be divided into two groups, then this line where the gradient is steepest, would be the most appropriate limit.

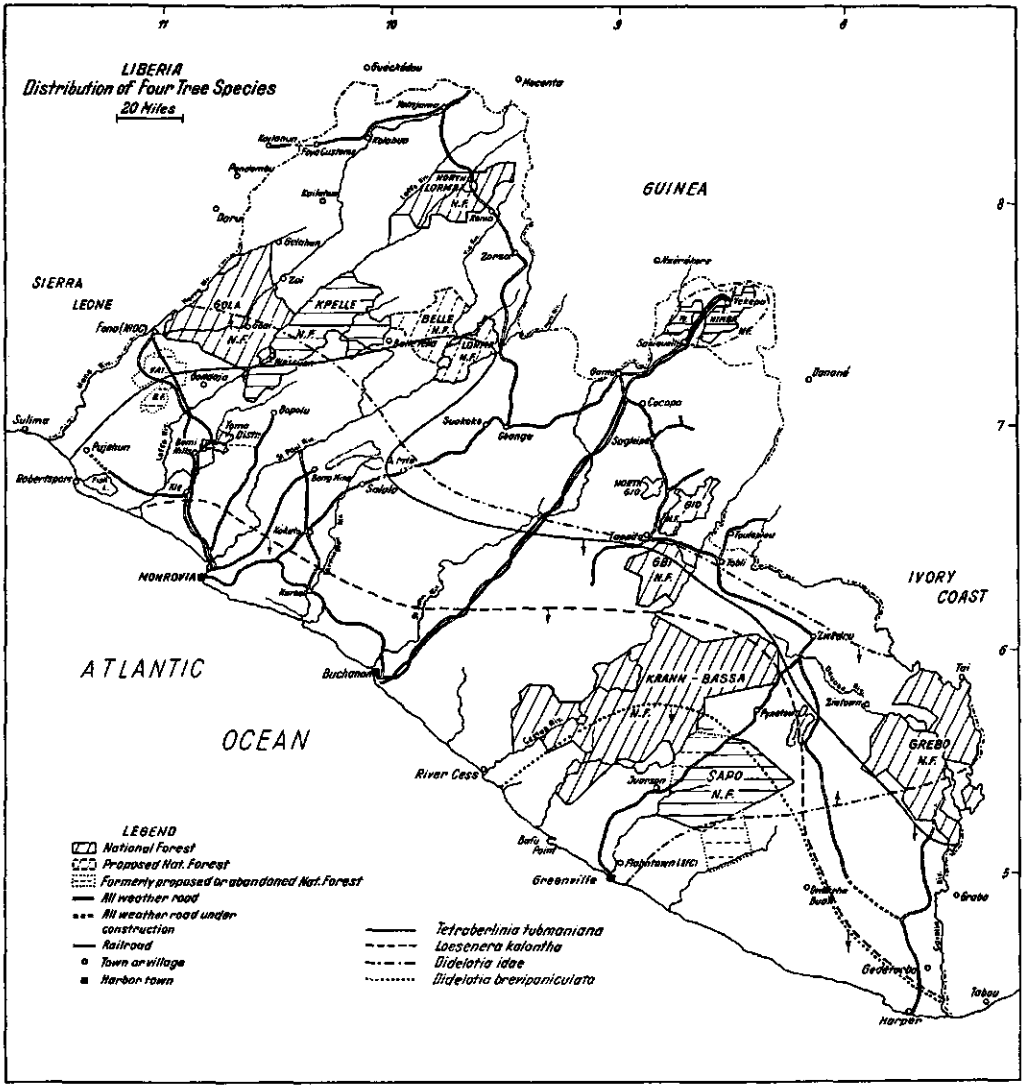

Figure 20 Distribution of four Caesalpiniaceae tree species, characteristic of the wet coastal forest in Liberia (from Sachtler 1968)

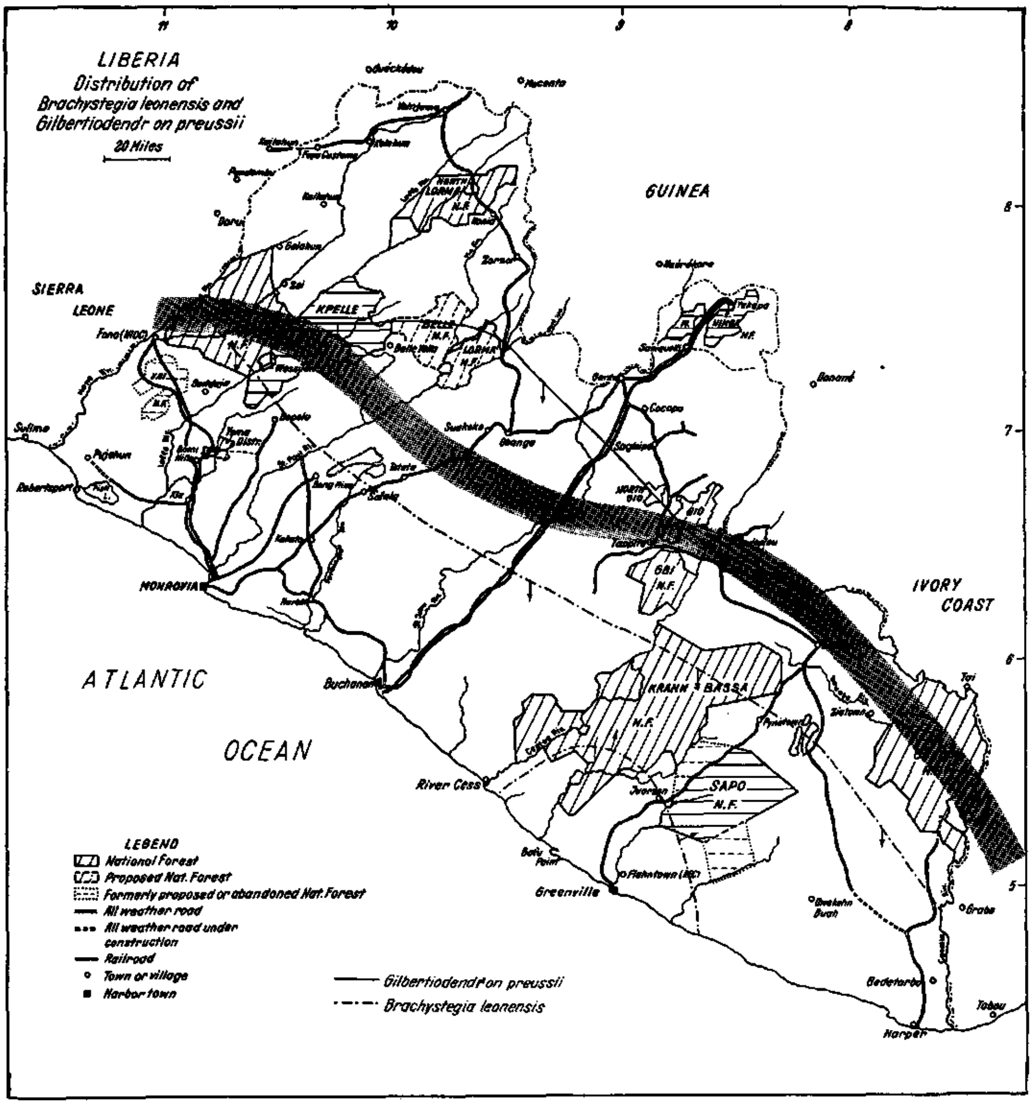

Figure 21 Distribution of two Caesalpiniaceae tree species typical of the mixed evergreen rain forest in Liberia (from Sachtler 1968). The grey band indicates where Sachtler (1968) positioned the boundary between evergreen and moist semi-deciduous forest and, at the same time, the southernmost position of the Intertropical Front.

Large tree species list in Yoma-Gola forest (Voorhoeve 1964). Only species from Table 3 are listed.

Afzelia bella
Amphimas pterocarpoides
Anopyxis klaineana
Anthonotha fragrans
Araliopsis soyauxii
Berlinia confusa
Brachystegia leonensis
Canarium schweinfurthii
Chlorophora regia
Cryptosepalum tetraphyllum
Daniellia thurifera
Didelotia idae
Erythrophleum ivorense
Gilbertiodendron preussii
Heritiera utilis
Klainedoxa gabonensis
Lophira alata
Maranthes aubrevillei
Maranthes glabra
Mitragyna ciliata
Monopetalanthus compactus
Nauclea diderrichii
Oldfieldia africana
Parinari excelsa
Piptadeniastrum africanum
Pycnanthus angolensis
Ricinodendron heudelotii
Sacoglottis gabonensis
Tetraberlinia tubmaniana

Figure 22 Profile diagram of a single dominant forest of *Tetraberlinia tubmaniana* J. Léonard in Yoma-Gola National Forest near Bomi Hills, Liberia, 1962. The diagram represents a strip of forest 61 m long and 7.6 m wide. *Tetraberlinia* trees are shaded and marked with a "T" in the ground-plan, a single *Treculia africana* tree with a "Tr". Reproduced from Voorhoeve (1964).

Figure 23 Evergreen rain forest along Lofa river in west Liberia (Photo by H. Dop)

1. Within the "**evergreen *forest zone**" (Figure 23), Sachtler (1968) distinguished two sub-zones.

1a. ***The wet coastal rain forest***, ranging along the coast between River Cess and Harper in a belt of maximally 80 km wide (see the distribution of *Didelotia brevipaniculata* on Figure 20). The wetter compartments of Sapo and Krahn-Bassa Forest fell within this sub-zone (more than 200 u.DCA1 on Figure 14). According to Sachtler (1968), these forests were characterized by the occurrence of single-dominant forests of *Tetraberlinia tubmaniana*, by the occurrence of *Didelotia brevipaniculata* and by a large proportion of swamps (20 to 30 %) covered with very dense stands of *Loesenera kalantha* (see Figure 20 for distribution maps of these species). *Gilbertiodendron preussii* and *Monopetalanthus spp.*, typical of "mixed evergreen forest", the second sub-zone, were rare, and of all Meliaceae only *Lovoa trichiloides* was found.

The same combination of *Tetraberlinia, Didelotia* and *Loesenera* seems to exist in the wet coastal forests of West Cameroon, in Korup National Park and near Kribi (Letouzey 1968, White 1983). These forests in Korup National Park are associated with soils displaying little available phosphorus (Gartlan et al. 1986). Their Caesalpiniaceae tree species live in symbiosis with ectomycorrhizal fungi (Newbery et al. 1988) which, according to these authors, may explain their often gregarious habit.

1b. ***The mixed evergreen rain forest***, its most frequent species being *Gilbertiodendron preussii* (see Figure 21 for a distribution map) and *Monopetalanthus compactus*. Patches of *Tetraberlinia tubmaniana* still exist, but the forest is essentially mixed, there are twice as many species as in the wet coastal forest and single-dominant stands are rare (Sachtler 1968).

2. In the "**moist semi-deciduous forests**" *Gilbertiodendron preussii, Monopetalanthus* spp., *Sacoglottis gabonensis, Didelotia* and *Cassipourea spp.* become increasingly rare and are replaced by large numbers of shade intolerant species which shed their leaves in the dry season (Figure 24): *Entandrophragma* spp., *Khaya anthotheca, Piptadeniastrum africanum, Triplochiton scleroxylon* and others.

Sachtler (1968) reserved the term "forest types" for the *inventory strata he distinguished locally in the inventory compartments:

- forests on uplands, in swamps, on river banks and on steep slopes;
- three regeneration stages after shifting cultivation;
- forest damaged by elephants;
- monospecific *Tetraberlinia* high forest;
- natural low bush or extensive areas of windbroken forest.

This physiognomic nomenclature is essentially different from the two vegetation zones mentioned above.

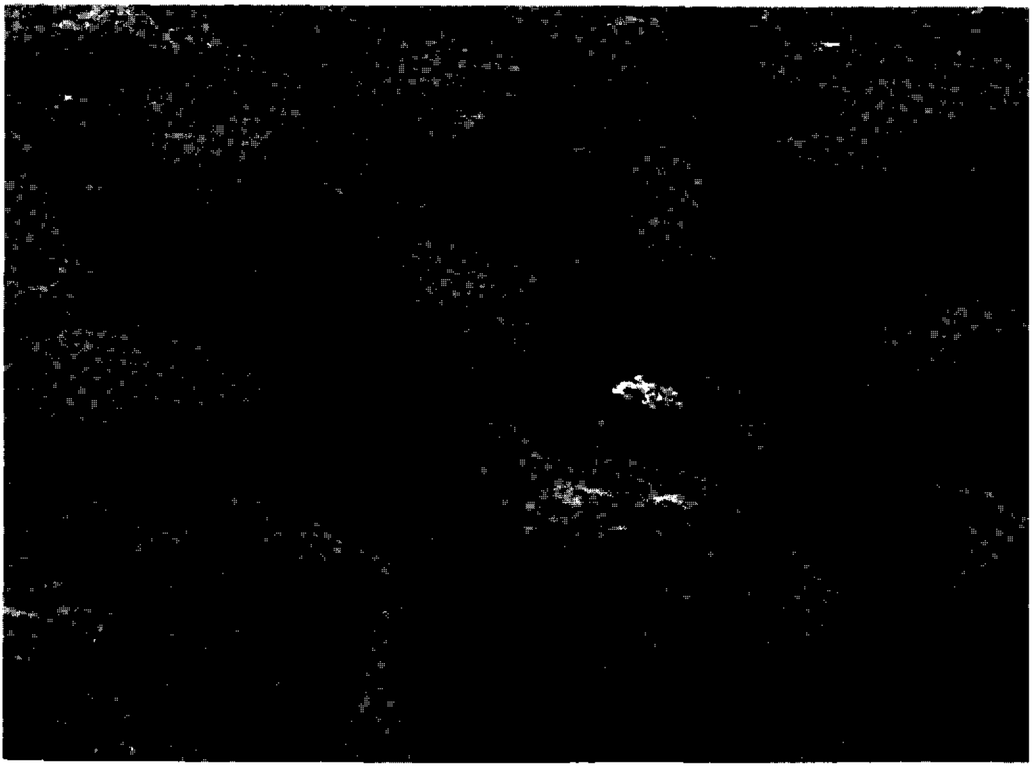

Figure 24 Semi-deciduous forest in north-west Liberia upstream Lofa river (Photo by H. Dop). Note the numerous trees that are leafless. This photo was taken on the same day in February as Figure 23.

2.5.4 The exclusion of swamp forests

The forest gradient, described in this Chapter, only applied to non-degraded 'high forest' on upland soils, to use the terminology of Sachtler (1968). The variety of landforms, however, is great and the transition between them is gradual. In most cases, swamps can be excluded easily, but lower slopes and river banks, which are assumed to be fed by groundwater as well, are more difficult to distinguish from upland forest. In my data set, which mainly comprises systematic inventory samples, swamps were included in Liberia and in the inventories of Northwest and Centre-South Côte d'Ivoire (see Table 2). They were excluded, however, from the "Périmètre industriel XV" and from my three permanent sample plots. When verifying the occurrence of the swamp specialist tree *Mitragyna ciliata* in Table 3, I found it was only absent in my sample plots, although it grew in swamps near all three of them. In the data set of the "Périmètre industriel XV" this species was still recorded. This shows that in large inventories the exclusion of swamps was not completely "waterproof".

2.5.5 The issue of "primary" and "secondary" forest

Even more complex is the desired exclusion of forest degraded by farming. Sachtler (1968) considered most of the Liberian forests as 'secondary high forest' and even single-dominant forests were said to have originated after farming (Voorhoeve 1965, Hart 1990). Indeed, on all three study sites I sampled within Taï National Park pottery shards and charcoal were found when digging the soil profile pits. Humans have been present in Africa since time immemorial and they have been practising shifting cultivation for thousands of years. The debate about "primary" and "secondary" forest in West Africa has always been very lively (Chevalier 1948, Aubréville 1949, Schnell 1950, Mangenot 1955, Aubréville 1959, Voorhoeve 1965, de Namur et Guillaumet 1978, Guillaumet & Adjanohoun 1971, Hall & Swaine 1981).

For the interpretation of forest gradients it is important to know whether or not tree species which occur naturally in drier forests are able to colonize former farmland in a wetter forest zone (e.g. *Ceiba pentandra, Terminalia superba, Pycnanthus angolensis, Canarium schweinfurthii, Triplochiton scleroxylon, Chlorophora spp., Piptadeniastrum africanum* on Figure 25, etc.). This would rank the resulting forests on a drier position along the gradient and hence mask zonal effects. On the other hand, a species can never be typical of secondary forest alone, it must have a natural habitat, e.g. steep slopes, rock outcrops or other sites unfavourable to typical "primary" species. These special sites may be located within large areas more hospitable to forests, and a systematic sampling design may include some plots in such special forests. This is in agreement with ***Budowski's rule (1965; amend. Oldeman 1990b) that any plant species which plays a pioneering role in hospitable environments has a geographical distribution which includes less hospitable environments.***

Figure 25 A large *Piptadeniastrum africanum* crown in a field south of Taï. The tree was not felled because of its huge buttresses and very hard wood. This species may profit from its position and regenerate in the abandoned fields.

2.6 Conclusions

The regional forest gradient presented in this Chapter was extracted from large samples covering 20 to 2000 ha each. This was necessary to obtain reliable data on the occurrence and abundance of the large tree species. The resulting species composition was a ***spatial average*** over the area. Thus the entire gradient also reflected the average species composition.

The compositional trend correlated well with the SW-oriented rainfall gradient. In part of the map the forest gradient showed an anomaly. The forests on a band of sericite-chlorite schist from Taï National Park towards the NE were ranked 'wetter' than expected from their position on the rainfall gradient. Apparently, the rainfall effect was compensated by the greater moisture content of the soils derived from sericite-chlorite schist.

The gradient cannot be divided in an *objective way. Its best representation is that of a DCA1 or compositional surface that covers the continent like a continuous blanket with different local patterns and built by the complete set of species. Its major driving force is found to be the moisture conditions determined by rainfall and lithology.

In this way the natural vegetation provides a more detailed map of these conditions than the rainfall records or geological surveys can provide. But the vegetation also has a memory in which its history can be read far beyond the start of scientific research in the region. Complex systems require powerful approaches that are scale sensitive and that safeguard the detail.

Individual sample plots of e.g. 20 ha may show up much wetter or drier on this gradient than the inventory compartment they lie in, because of the effect of spatial averaging that results from grouping the data from all sample plots within an inventory compartment. When we zoom in and the area covered by a pixel becomes smaller, the gradient will show more and more "noise" and the regional trend will become more and more vague and overruled by local lithology and catena effects. At a certain pixel size, forest dynamics and gap formation processes will also influence tree species composition.

In the next Chapter I take up the challenge and test the robustness of the approach after changing the scale and zooming in into more detail. The once so smooth vegetation surface will become more "hairy" and new techniques will be needed to adapt the degree of spatial averaging. Lithological maps are replaced by soil maps, but topography and relief still hold the key to understanding vegetation variability.

Figure 26 A *Sacoglottis gabonensis* tree at the Para site. Here this species was found all over the toposequence, whereas near Taï it occurred only on lower slopes and in valley bottoms. Near Zagné it was absent from all slope positions.

3 FOREST GRADIENTS ALONG SLOPES IN TAÏ NATIONAL PARK

I concluded from Chapter 2 that on a regional scale the tree species composition in forest areas changed gradually along the rainfall gradient in West Africa. Species composition was averaged over large areas of about 50 000 ha, as a result of which local variation due to landscape diversity was ignored. However, many large tree species not found in upland forests occur over the landscape in valley bottoms and along rivers. Within the upland forests, forest gradients are found along slopes. These are the subject of this Chapter.

Forest gradients along slopes have been studied in temperate (Whittaker 1956 and 1967, Bormann et al. 1970) and in tropical climates (Schnell 1952, Whitmore 1984, Ohsawa et al. 1985, Nakashizuka et al. 1991). Most of these studies focused on mountain slopes spanning altitudinal intervals of hundreds or even thousands of metres. Temperature, cloudiness and rainfall change considerably along such elevation transects. These altitudinal gradients are related to a change in climate as was the regional forest gradient described in Chapter 2.

3.1 Local forest gradients

Slopes in Taï National Park are not mountain slopes. Taï National Park is on a dissected *peneplain (see Chapter 1). The highest terrain positions, the crests, are remnants of extensive ironstone sheets that covered the Tertiary peneplain and probably developed during drier periods in the geological past (Tagini 1972). The valleys that dissected this peneplain are 20 to 50 m deep, and a typical *sequence of soils (*catena) has developed from the valley bottom up to the ironstone crest (see Figure 27).

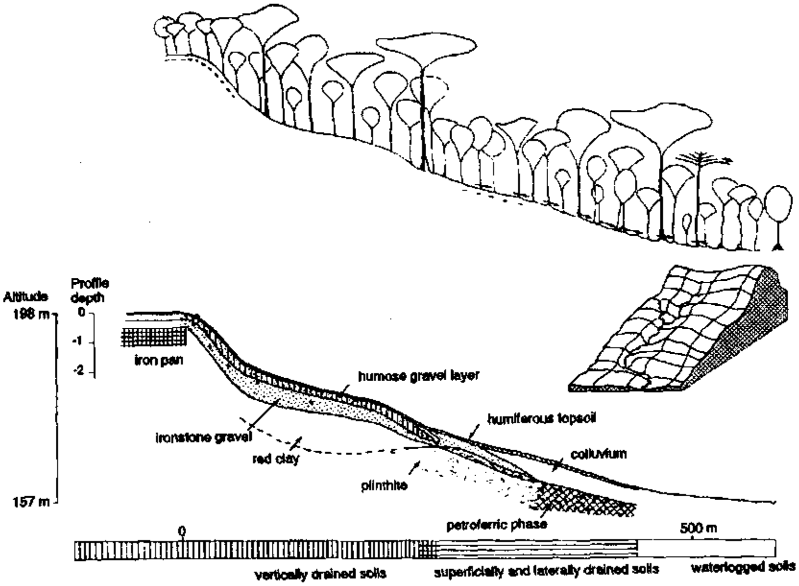

Figure 27 Example of a soil and vegetation catena in the Taï study area (modified after Vooren 1985)

3.1.1 Sequential models

One way of describing such a landscape is to make point observations at regular intervals from the summit to the valley bottom. Typically, five physiographic positions are chosen: summit, upper slope, middle slope, lower slope and valley bottom (de Rouw, Vellema & Blokhuis 1990). The observations form a sequence related to topography: a **topo-sequence*.

In soil science, such a sequence of soils is called a **soil catena*, if all the soils are underlain by the same rock type and occur under similar climate (Ahn 1970). In West Africa soils frequently occur in such sequences (Nye 1954, DRC 1967b, Ahn 1970, Lawson et al. 1970, Fritsch 1980, de Rouw et al. 1990).

This model has been used as a basis for physiographic soil maps (Lawson et al. 1970, van Herwaarden 1991a). Most of the lines in these maps do not represent ecological boundaries, but connect points somewhere half-way between two physiographic positions. The extent of alluvial soils in the valley bottom and of the iron pan on the crest can, in most cases, be mapped objectively. Along the slope, changes in gravelliness, colour and texture occur gradually, so subdivisions are drawn arbitrarily. Most authors stress the fact that in reality there is a continuum (de Rouw et al. 1990).

In vegetation science, the distinction between riverine, swamp and *upland forest is based on comparison of similar point observations (Lindeman and Moolenaar 1959, Schulz 1960, Guillaumet 1967, Hubbell & Foster 1983 and 1986). Using physiographic soil maps as a base, Lawson et al (1970), Huttel (1977) and Jonkers (1987) made vegetation relevés on each physiographic position. Swamp forest appeared to be the most distinct, but some indication of compositional change along the upper parts of these *vegetation catenas* was found (see also Hall & Swaine 1981; Longman and Jeník 1987, Boddez 1989). Methodological problems were encountered when analysing this directional variation. Unlike the soil surveys for which a standard methodology is available (FAO 1977, Touber et al. 1989), the vegetation surveys struggle with the huge size that trees can attain, the wide range in tree sizes and life forms to be sampled, the great species diversity and the forest dynamics which mean that the species composition in a plot is permanently changing. Apparently, the vegetation has to be considered at different scale levels than the one determined by soil, and, moreover, it is made up of living components (Oldeman 1990b), making it more dynamic. It is not as self-evident to make point observations, as it is in soil survey.

3.1.2 Gradient models

The gradual change in soil and vegetation along slopes can also be studied using a continuous model of variation. Soil characteristics like gravelliness, clay content or even available water can be presented as contour maps (Stein & Corsten 1991), or, more simply, they can be plotted against elevation (see also Lescure & Boulet 1985). Lieberman et al. (1985) plotted the ordination scores of contiguous sample plots against elevation.

In a landscape, there is a slight scale-dependent difference between *elevation belts* and slope positions. The altitude of the valley bottom decreases gradually downstream because of the river gradient, e.g. 5 m per km at the Taï study site (Casenave et al. 1980). For instance, at a certain place the valley bottom may be included in the 150-160 m elevation belt, but some kilometres downstream the same swamp forests and soils are found in the 130-140 m elevation belt, whereas at that location middle slope soils and forests are found in the 150-160 m elevation belt. If the river gradient is not too steep and the study site is reasonably compact, the *elevational gradient model* can be considered to approximate the *toposequential model*. The continuous elevation variable has considerable computational advantages to the discontinuous slope classes. The elevation scale is an *interval scale, i.e. differences can be computed quantitatively between any two sites by taking the difference in elevation. This is not possible with the *ordinal scale of slope position.

3.1.3 How to sample the large tree species

The soil can be described at a given point by taking a soil core or digging a soil pit. To sample the tree species composition "at that point", a plot around it must be inventoried and the tree species listed and their abundance estimated. The size and shape of such plots differ in each study, as does the subset of life forms studied.

The size of such a plot depends on the life forms considered. The fewer individuals available per unit area, the larger the plot needs to be. Large trees ($d > 70$ cm) occur at densities of 10 to 20 trees per ha. With a species pool of 50 tree species that can attain such large diameters, the plot must be at least a few hectares large to obtain a reliable species list. For maximal homogeneity, the shape of the plot should be close to circular if no spatial trend is discernible in species composition. However, such a trend *is* expected along the slope, so the plot must be laid out as much as possible on the same slope position, or, by approximation, within the same elevation belt.

Here, I propose the **contour sampling technique* which fulfils three requirements:
1. the samples are large enough to include numerous big trees;
2. each sample is as close as possible to the same contour line;
3. the samples occupy equal areas.

Grouping trees according to soil types would have been an alternative, but then the samples would have covered areas very different in size which are not directly comparable in terms of species richness, and both species composition and tree density would have been known with unequal precision in all samples.

The vegetation samples obtained with this technique were used to analyse the local forest gradients and to answer the following questions:
1. Can the local forest gradient be accurately described by ordinating these contour samples?
2. Do these local gradients indeed reflect the same change in species composition as the regional gradient?
3. Do the densities, or biomass, or species richness of large trees display trends linked to elevation and if so, how do both trends compare?

3.2 Description of the study sites

3.2.1 Location

Three study plots of 23, 25 and 22 ha respectively were laid out near the villages Zagné, Taï and Para (see Figure 28), and within the border of Taï National Park in southwest Côte d'Ivoire. Taï National Park (446 000 ha) is covered by *tropical rain forests within the stream basin of Cavalla river (Text box 3). In these sample plots there was no evidence of former logging activities. These forests belong to the last "virgin" forests of Côte d'Ivoire (see Text box 3).

Table 4 Geographical position and area (ha) of the soil and tree surveys at the three study sites

Study site	Geographical coordinates	Area of soil survey (ha)	Area (ha) surveyed for trees with d ≥		
			70 cm	50 cm	30 cm
Zagné	6°07' N and 7°24' W	145	23	10	5
Taï	5°53' N and 7°20' W	133	25	13	9
Para	5°28' N and 7°10' W	72	22	10	6
All sites		350	70	33	20

Table 4 gives the geographical position of the three plots, the area of soil surveys and area of tree surveys. The study site near Taï was selected in 1981 by Vooren (1985, 1986) for a study of catena effects on tree and branch fall. I selected the other sites in 1989, one as far as possible from Taï in the northern direction but within Taï National Park, towards a drier climate, and one as far as possible to the south, under a wetter climate. The part of Taï National Park south of Hana river was logged before 1973, so no sites were selected there.

The distance between the Taï and the Zagné sample plots is 25 km; between the Taï and the Para plots 55 km. For the soil surveys the entire toposequence was considered, but tree surveys were mainly restricted to upper catena positions (see also Figure 38, Figure 40 and Figure 42). Figure 29 to Figure 31 display the position of the survey areas in the landscape. They are centred on water divides and delimited by water courses. The access road or track is also shown.

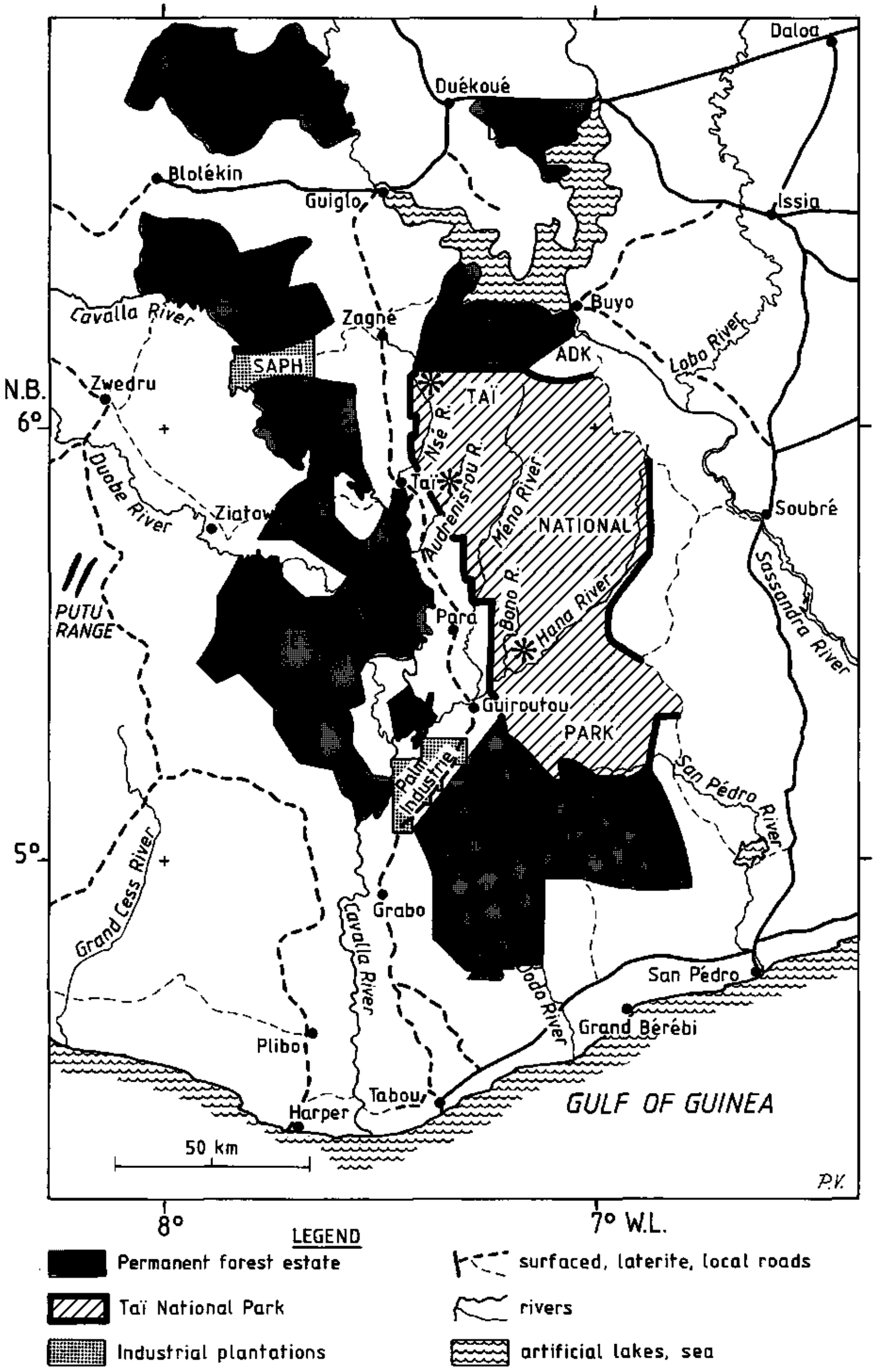

Figure 28 Map of Taï National Park and surrounding forest reserves. Asterisks: three study sites close to Zagné, Taï and Para villages. Sources: SODEFOR map (1975) of the "Domaine forestier", MPEA (1983), LANDSAT MSS image from 1986.

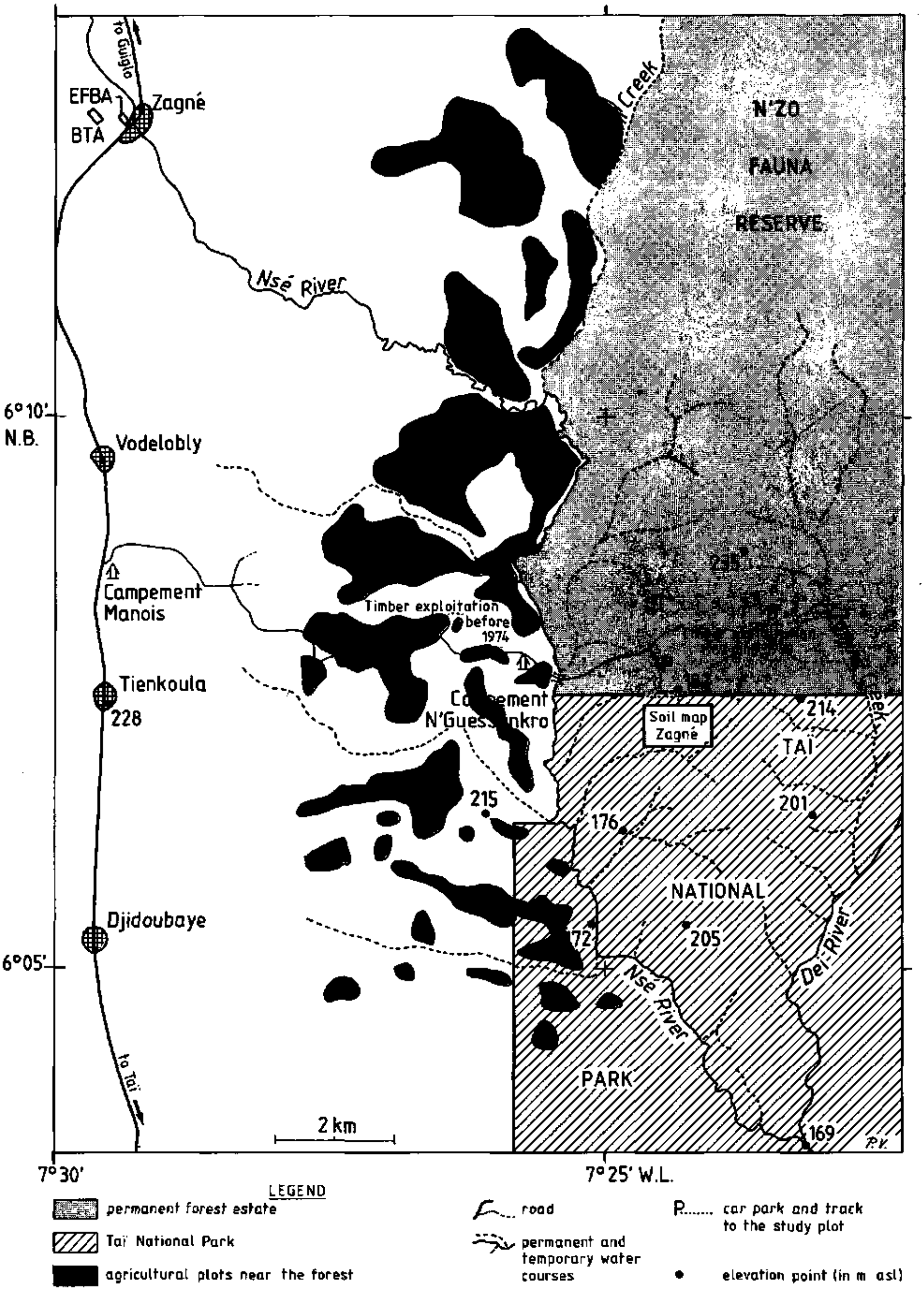

Figure 29 Topographical map of Zagné survey area in its landscape. Sources: 1:50 000 topographical map by IGN (1966), sheet Guiglo 2a; SPOT multispectral satellite image dd. 14/2/88, scene 45-338.

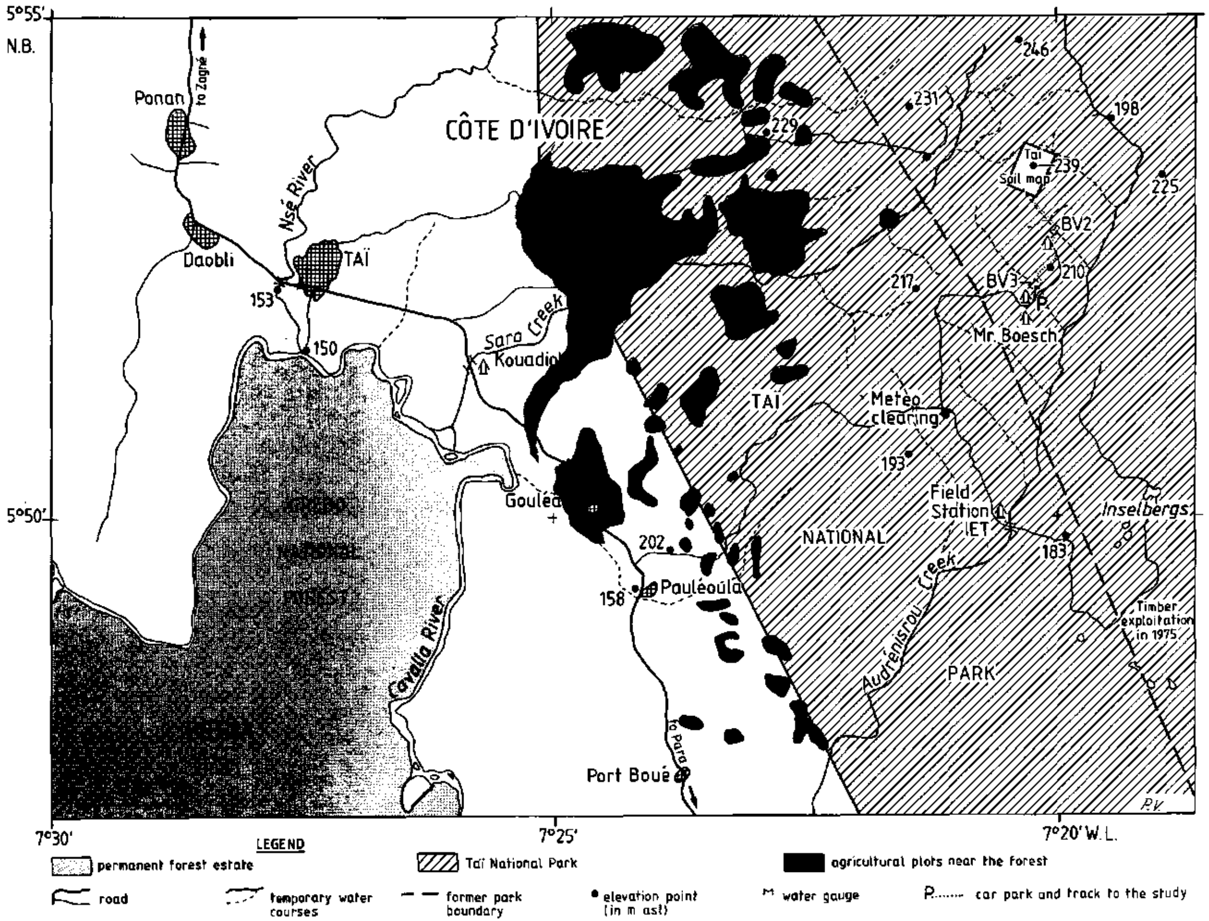

Figure 30 Topographical map of Taï survey area in its landscape. Sources: 1:50 000 topographical map by IGN (1966), sheet Taï 4c; Schmidt (1990), SPOT image dd. 14/2/88, scene 45-338.

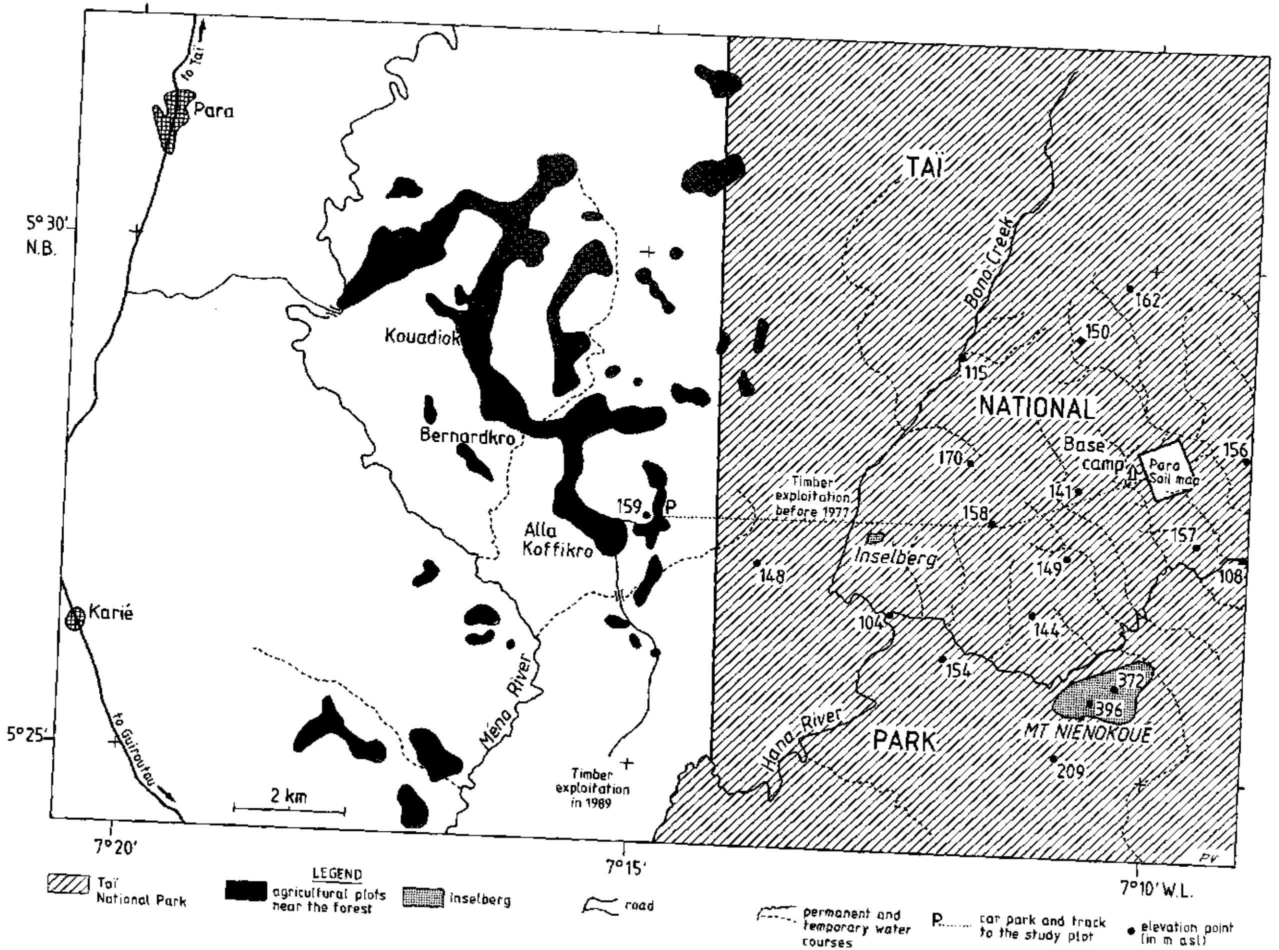

Figure 31 Topographical map of Para survey area in its landscape. Sources: 1:50 000 topographical map by IGN (1961), sheets Taï 2c,2d,4a,4b; SPOT satellite image dd. 14/2/88, scene 45-339

Figure 32 All limits around Taï National Park have been marked by signs. Photo by M.P.E. Parren

3.2.2 Climate

All three sites lie on a rainfall gradient with decreasing rainfall from south-west to north-east (see Chapter 2). Mean rainfall per decade for the sample plots Zagné, Taï and Para can be estimated at 17, 19 and 20 m (10 y)$^{-1}$ respectively. Rainfall distribution goes from clearly bimodal in the south to unimodal in the north (see Figure 7). Typically, diurnal temperature variation is greater than seasonal variation (Eldin 1971), and hardly any difference in average temperature can be found between the climatic stations. But the difference between the extreme temperatures does increase from south to north. The lowest absolute temperatures are recorded in the early mornings at the beginning of the dry season when the "Harmattan" blows (end December-January). The highest temperatures occur after midday in full dry season (February-March; ASECNA 1979).

Text box 3 Facts and figures about Taï National Park

On the first maps of south-west Côte d'Ivoire the Taï Forest is marked as "No man's land" (Bouys 1933, ex de Rouw 1991). Chevalier (1909) visited the region in the early 1900s and described the interfluvium between Sassandra and Cavalla rivers as covered by "vast, primary forests".

1926: the colonial administration created the "Parc refuge de la région forestière" (960 000 ha) with the status of a Forest reserve and a Fauna reserve (Bousquet 1978)

1956: it was renamed "Réserve de Faune de Taï" and "Forêt classée de Taï" and its limits modified (431 000 ha; DRC 1967a), including the present N'zo Fauna Reserve.

1972: transformation into **Taï National Park** (350 000 ha; Bousquet 1978; Décret 72-544, 28 August 1972); creation of the "Réserve partielle du N'zo" (73 000 ha) in the north, where timber mining was allowed.

1973: A 5 km band (20 000 ha) along the northern border of Taï National Park was transferred to the Réserve du N'zo and hence to timber mining (Décret no. 73-132, 21 March 1973). Timber concessions ("chantiers") cover 5 by 5 km in Côte d'Ivoire. The remaining Park now covers 330 000 ha.

1975: enlargement of the Forêt Classée de la Haute Dodo, south of Taï National Park, so that it extends up to the Park.

1977: creation of a "Zone périphérique de protection" with the status of "réserve partielle de faune" around Taï National Park (Décret no. 77-348 of 3 June 1977). This zone covered 66 000 ha. No protection zone was foreseen in the north where the Réserve du N'zo assured protection, or in the south-east where a large pulpwood plantation was projected (Périmètre papetier, now Forêt classée de Rapide Grah).

1978: registration of Taï National Park by MAB-UNESCO as Biosphere Reserve, i.e. an inviolate pristine core surrounded by a buffer zone of forest managed for sustainable production (Whitmore 1990). The protection zone around Taï National Park has been created in accordance with the World Conservation Strategy concept of sustainable utilization with the maintenance of full diversity and species richness: man living in balance with nature (Man And Biosphere).

1978: construction of the "Station écologique de Taï" (see Figure 30), a research fieldwork station near Taï village, under the aegis of IET (Institut d'Ecologie Tropicale, office at Abidjan)

1981: start of the inundation of Buyo lake behind a barrage on Sassandra river. The northern part of the Réserve du N'zo and the southern part of the Forêt Classée de Duékoué were transformed into a periodically flooded grassy plain with dead standing trees.

1982: Taï National Park added to the World Heritage List of UNESCO, i.e. qualified as an area of acknowledged universal value (Whitmore 1990).

1983: creation of a "Zone de protection" between Taï National Park and this Périmètre papetier, (Arrête ministeriel no 09 of 11 May 1983).

The area figures above are taken from the decrees. E. Schmidt (WAU) digitized the map of Taï National Park prepared by the National Parks Service, Abidjan (1989) and obtained the following area estimates. Taï National Park consists of a core area of 320 000 ha surrounded by a protection zone of 126 000 ha. In total, 446 000 ha are well protected. Adjacent to the Park are the Réserve du N'zo (79 500 ha) in the north, and the Forêt Classée de la Haute Dodo in the south (76 000 ha of which are still covered by forest; Marchesi et al. 1990). Thus, on the interfluvium between Sassandra and Cavalla river a continuous area of about 600 000 ha of forest is left, which is about one-third of Côte d'Ivoire's remaining rain forests. At the beginning of the 20th century there were still 14 500 000 ha of rain forest in Côte d'Ivoire (Gornitz & NASA 1985). Some 200 000 ha of this elongated area were never logged but almost certainly no "unpoached" forest remains.

3.2.3 Lithology

The Zagné and Taï sample plots are underlain by migmatites, and the Para plot by sericite schists (Papon 1973). Figure 4 shows that granite outcrops occur in considerable parts of the Park. Along the track towards the Para plot such forests on granite were encountered close to the river Bono. Mount Niénokoué (Figure 28) is also a granitic inselberg rising

Figure 33 The field team consisting of soil and vegetation scientists crossing the Bono river to reach the Para study site. Photo by M.P.E. Parren

300 m above the surrounding forests. These forests on granite contained more species typical of drier forests (e.g. *Triplochiton scleroxylon, Terminalia superba, Alstonia boonei, Chlorophora regia*) than sample plots on schists like "Para" (personal observation). Guillaumet (1967) also found these species in old secondary forests near Tabou in a wetter climate. This was to be expected according to *Budowski's rule (1965; see p.53). In this case, both soil and climate determine site hospitality.

3.2.4 Relief

The basement complex of Pre-Cambrian rocks in West Africa has a long erosional history (van Herwaarden 1991a). The continent has been worn down to an almost flat surface or *peneplain at least twice (Ahn 1970). The younger of these is associated with iron pans, remnants of which were found on the hill tops at the Para and Taï plots. At the Zagné site no continuous pan was found but only some ironstone boulders. This could be the reason why the difference in altitude between valley bottom and crest is less than 20 m in the Zagné survey area, whereas it is 40 to 50 m in the Taï and Para survey areas. The relief is undulating in Zagné and rolling in the Taï and Para plots (van Herwaarden 1991a).

Preparation of the digital terrain model. General topographical data could be read from the 1:50 000 topographical maps (IGN 1965), based on 1:50 000 aerial photocover from 1956-1957. From both sources I selected an interfluvium large enough for my purposes (20 to 50 ha). A straight access track was cut through the forest and along this track I assessed traces of logging and searched for the highest point in the landscape. From this point a base line was cut down the slope into the valleys on either side of the crest. Starting from this line a grid was laid out, resulting in twenty to twenty-five square one ha plots, but avoiding lower slope and valley bottom forest.

The inclination of the slope at 25 to 50 m intervals along all lines was measured using a Silva clinometer. These data were converted to altitudinal differences and adjusted for discrepancies using the spreadsheet package Supercalc (**© 1991 Computer Associates). Irregular terrain characteristics like water courses, ravines and the edge of ironstone capping were mapped separately. The hypsometrical data (x,y and z coordinates) were transferred to the Surfer package (© 1989 Golden software) to produce detailed ***elevation contour maps***. Relative elevation in metres above the lowest valley bottom point was transformed into absolute elevation in metres above sea level by adding the estimated absolute elevation of the valley bottom. The latter was deduced from elevation points on the topographical maps at scale 1:50 000. However, along the road to the IET research station (the field station of the Institut d'Ecologie Tropicale from Abidjan; see Introduction) south of Taï, a topographical survey (Casenave et al. 1980) had shown that the elevation points indicating hill summits on those topographical maps include the 30 to 40 m high forest vegetation, whereas points along roads and rivers correspond to ground level. This resulted in an exaggerated relief in areas on the map where both types of measures coincide.

Preliminary interpretation maps showing possible physiographic units for use during the fieldwork of the soil survey were made on the basis of these maps. Detailed soil maps were subsequently drawn at a scale of 1:5000 and cross-sections were prepared to visualize the relation between soil layers and slope position, as will be explained in subsection 3.2.6. The digital terrain models of the sites allowed the calculation of the z coordinate of the position of each tree. This z coordinate was used to group trees into contour samples, see subsection 3.3.3.

3.2.5 Hydrology

The Zagné survey area belongs to the catchment area of Nsé river, the Taï area lies in the Audrénisrou basin and the Para area in the Hana basin. All three rivers are first order tributaries of Cavalla river, which forms the border between Côte d'Ivoire and Liberia.

On the higher convex geomorphological units of the survey areas (crests, shoulders, upper and middle slopes) drainage is predominantly vertical (Fritsch 1980; van Herwaarden 1991a) and soils are well drained in terms of the FAO (1977) classification. On the lower slopes there is an important lateral drainage component and soils are moderately well drained. Gullies occur downslope and become larger as they descend. At a certain point, the water which flows after heavy rains may form a waterfall when it breaks through a resistant petroferric layer present in the subsoil on lower slopes. Under the waterfall a permanent pool may be excavated (Figure 34). From this point on a deep ravine is formed with 2 to 5 m high walls. Soils in these concave ravines are imperfectly drained. The wettest parts are the stream valleys where ponding occurs and the water table is often

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**The full reference can be found in the Software list at the end of this book.

near the surface. This is more pronounced (very poorly drained soils) downstream than upstream (poorly drained soils).

3.2.6 Soils

A physiographic soil survey was carried out on each site by van Herwaarden (1991a), additional work having been done by Rademacher (1992) and Nooren (1992). The Tropenbos guidelines for a common methodology for inventory and evaluation of tropical forest land by Touber et al. (1989) were used for the survey. The approach, followed for the soil survey, relied much on the physiography of the terrain. For that purpose a detailed relief map was made first (see subsection 3.2.4; Figure 39, Figure 41 and Figure 43). Mapping units were named after, and mainly follow the physiographic pattern. More details about the survey procedure and a description of the physiographic units on each site are given in Appendix 3.

Pisolithic ironstone gravel is abundant in upper slope positions and is derived from the physical disintegration of the ironstone sheets (Figure 35) and subsequent partial transportation of the ironstone fragments (Perraud 1971, de Rouw et al. 1990). Its content and the range in depth in which it occurs, change gradually on upper and middle slopes. In the subsoil on lower slope positions, the formation of plinthite is characteristic, i.e. an iron-rich, humus-poor mixture of clay with quartz commonly occurring as dark red mottles in

Figure 34 Erosion gully on the lower slope in the Taï study area. At this point the water breaks though a resistant petroferric layer. A permanent pool has been excavated under the waterfall. Photo by A.P. Vooren

Figure 35 Ironstone boulders that broke off an iron hardpan, here on the beach near Fresco. Exactly the same kind of boulders are found just below the crests with iron pan at the Taï site. They disintegrate into ironstone gravel.

a pale yellow matrix. Both the depth and the consistence of the plinthite layer on lower slopes vary along the slope.

Drainage is also clearly related to topography (Lescure & Boulet 1985, Fritsch 1992). The increasing moisture availability downslope, both from lateral drainage and from finer texture, may be a major factor influencing tree species composition along a catena. Rooting conditions in the soil are also linked to catena position. An iron pan occurs at shallow depth in Taï and Para, and a petroferric layer (FAO 1988), also called petroplinthite, is found at the three sites, typically on lower slope positions. A permanent water table in the valley bottom soils may also form a root floor.

Figure 38, Figure 40 and Figure 42 show the physiographic soil maps for each site. The map units, documented in the legends, correspond to physiographic positions. The soils on a given physiographic position may differ from one site to another. The typical crests with iron pan are only found in Taï and Para, not in Zagné. Lower crests without iron pan are described in Para. These also exist in the Taï landscape (Fritsch 1980).

3.3 Methods of data collection and analysis

3.3.1 Exclusion of swamp forests

Swamp forests and upland forests are very different in species composition, physiognomy and ecology (Guillaumet & Adjanohoun 1971, Hall & Swaine 1981, Lieberman et al. 1985), the former with a variable but permanent water table whereas the latter are rain-fed and so are subject to climatic drought stress. The swamp forests in Taï National Park contain specialist tree species like *Mitragyna ciliata, Uapaca paludosa* and *Gilbertiodendron splendidum* as well as tree species which are often abundant in swamps but can also occur in higher catena positions, e.g. *Heritiera utilis, Sacoglottis gabonensis* and *Gilbertiodendron preussii* (Huttel 1977, Bech 1983, de Rouw 1991)

Although the inventory reports used in Chapter 2 pooled information from swamp and upland forests, I wish to exclude the swamp forest from the analysis in this Chapter, in order to obtain a clearer picture of local variation of forests along slopes superimposed on the effect of the rainfall gradient. I excluded swamp forest when establishing my sample plots in Zagné and Para. In Taï, the lowermost ha contained some swamp and was excluded when delimiting the contour sample plots.

Swamp specialist trees will not be discussed further, but the facultative swamp species will be taken into account to some extent. The great abundance of these species does indeed influence the neighbouring lower slope forests on better drained land, and the swamp-lower slope boundary is once again a fuzzy forest limit. I thus expect the slope gradient to be complicated by a "swamp effect", especially on lower slopes.

3.3.2 Tree recording in nested plots

Large trees. Trees with a diameter exceeding 70 cm were identified in the entire sample plot (see Table 4), were mapped and had their diameter measured as precisely as possible. A glass-fibre tape and if necessary a ladder were used to measure the girth of the tree. If buttresses exceeded the height of the ladder, the diameter was measured with a 2 m ruler as described by Cailliez and Alder (1980). The height at which the measurement was taken, was also noted. Tree numbers were painted in white on the bark together with a ring at the height of measurement.

Smaller trees. These were sampled in half (diameter 50 to 70 cm) and a quarter (diameter 30 to 50 cm) of the entire 20 ha sample plot (see nested plots in Figure 38, Figure 40 and Figure 42). At the Para site, the hectare plots to be subsampled for smaller trees were chosen in such a way that all slope positions were represented but in a contiguous layout for later studies of species populations (de Klerk 1991) and forest dynamics (Jans et al. 1993 in press, Poorter et al. 1993 in prep). In Taï, existing sample plots were included and in Zagné, the plot was consecutively enlarged from 5 to 10 and to 23 ha, raising the lower diameter limit by 20 cm each time. This layout in Zagné showed to be not optimal for the analysis, as will be explained in 3.3.4.

Figure 36 The diameter of large trees was measured with a 2 m ruler as described by Cailliez and Alder (1980). On the photograph a *Sacoglottis gabonensis* of about 70 cm diameter is being measured in the Para plot.

Species identification. Trees were identified using the characteristics of their leaves, fruits and trunks. Most of the identification work was done by the Ivorian botanists Pierre Polé and Henri Téhé using Aubréville (1959). The former had collaborated with Vooren (1985) and de Rouw (1991). De Rouw deposited many specimens in the herbarium at Wageningen (WAG). The latter had worked for many years for ORSTOM in Abidjan and contributed largely to the ORSTOM herbarium (ABI) which contains duplicates from WAG and was recently transferred to the Centre National de Floristique (UCJ) in Abidjan. At the Taï site I continued working in the sample plot established by A.P. Vooren (1985), where trees had been identified by Vooren (Wageningen Agricultural University) and C. de Namur (ORSTOM).

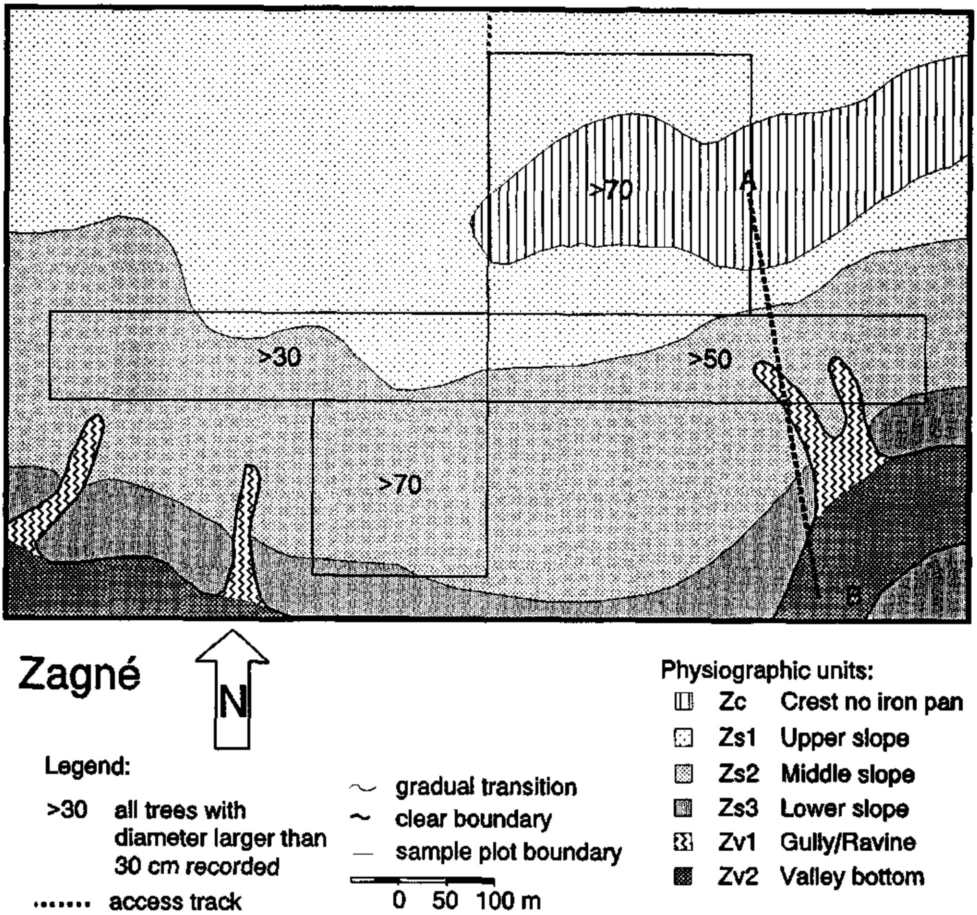
The nomenclature in the present book follows Hall & Swaine (1981), Voorhoeve (1965), Aubréville (1959) or Hutchinson & Dalziel (1954-1972), in that order (i.e. if a species was not in the most recent publication, the next older one was consulted). In Appendix I the list of tree species found in the three sample plots, is given, including authors, sources and synonyms of species according to the four above references.

3.3.3 Definition of the contour samples

Samples for *ordination analysis must be homogeneous and complete with regard to species composition of the life forms considered. I define *contour samples, intentionally with low precision, as "samples along the same contour line". Such samples should be sufficiently large to contain enough trees, and that the sample plots should be of the same area. A mathematical line of course does not fulfil these conditions. Hence, I proceeded as follows to obtain belt-like contour sample plots of 2 ha each. The digital terrain model that resulted from the topographical survey (see subsection 3.2.4) was used to interpolate the elevation of each 10 by 10 m square in the sample plot grid. Trees were assigned the z coordinate of the square they were standing in. The ZCOORD programme was written in Turbo Pascal (© 1990 Borland) by J.J. Stoorvogel to perform the calculations.

The squares were arranged along descending z coordinate and were then grouped into 2 ha contour sample plots (Figure 39 to Figure 43) by taking the first 200 cells, the second 200, and so on. The contour lines which delimited the belt-like sample plots corresponded to the z coordinate of the 200th, 400th, etc. square (see Figure 39 to Figure 43). These levels were used to take the trees together into contour samples. Notice that the contour levels separating these samples are not equidistant. In Figure 39 to Figure 43 the

Figure 37 A *Canarium schweinfurthii* tree of 130 cm diameter is being measured over the white paint ring. Left, tree spotter Pierre Polé, right Dr N.R. de Graaf (WAU). Photo by M.P.E. Parren



Soil legend of the physiographic units of the Zagné survey area (Rademacher 1992, van Herwaarden 1991a)

Unit	Physiography	Drainage	Depth of rotten rock/ petroplinthite	Altitude in m asl	Parent material	Slope form	Slope degree	Colour	Soil texture	FAO-UNESCO classification
Zc	Crest	well drained	> 150 cm no iron pan	203-205	Migmatite	straight to convex	gently sloping	strong brown over red	gravelly sandy (clay) loam over sandy clay	Ferric Acrisol
Zs1	Upper slope	well drained	> 150 cm	199-203	Migmatite	convex	gently sloping	strong brown	slightly gravelly sandy (clay) loam over gravelly clay	Haplic Ferralsol
Zs2	Middle slope	moderately well drained	> 150 cm	190-201	Colluvium/ Migmatite	straight	gently sloping	yellowish brown	non-gravelly sandy (clay) loam over gravelly clay loam	Plinthic Acrisol
Zs3	*Lower slope*	*imperfectly drained*	*100-130 cm rotten rock*	*187-197*	*Colluvium*	*concave*	*gently sloping*	*yellowish brown*	*non-gravelly sandy clay loam*	*Haplic Acrisol*
Zv1	Ravine/gully	poorly drained	0- 80 cm petroplinthite	187-199	Alluvium/ Migmatite	concave	gently sloping	yellow-brown to grey	non-gravelly to very gravelly coarse sand to sandy clay	Ferralic Cambisol
Zv2	Valley bottom	very poorly drained	100-150 cm rotten rock	< 195	Alluvium/ Migmatite	concave	almost flat	light gray to greenish gray	non-gravelly coarse sand to sandy clay	Dystric Fluvisol

Figure 38 Physiographic map of the Zagné study area. Grey tones correspond to physiographic units. The soil in these units is described in the soil legend. Straight lines delimit the sample plot and the figures indicate the tree sampling intensity. From van Herwaarden (1991a), Rademacher (1992).

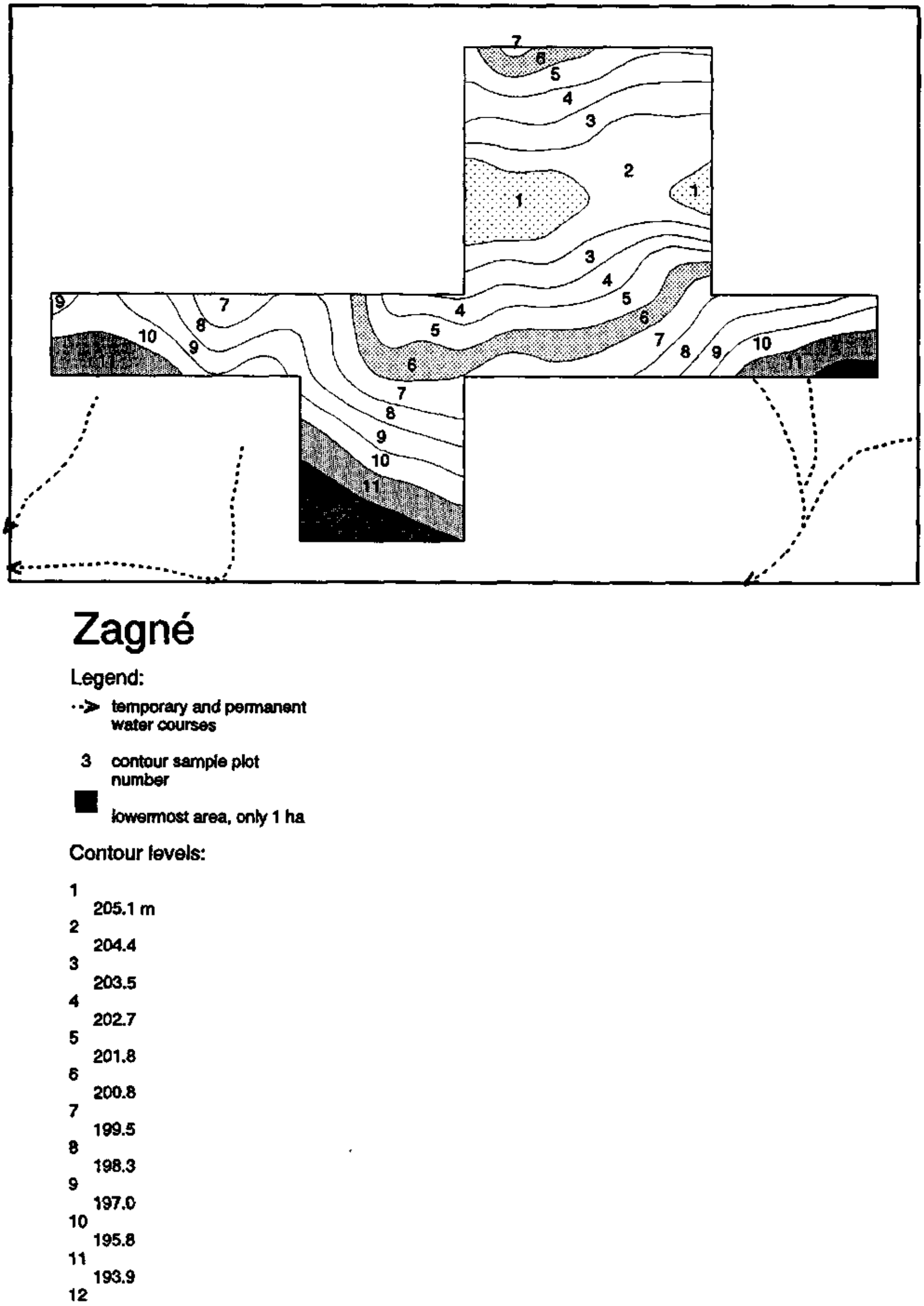
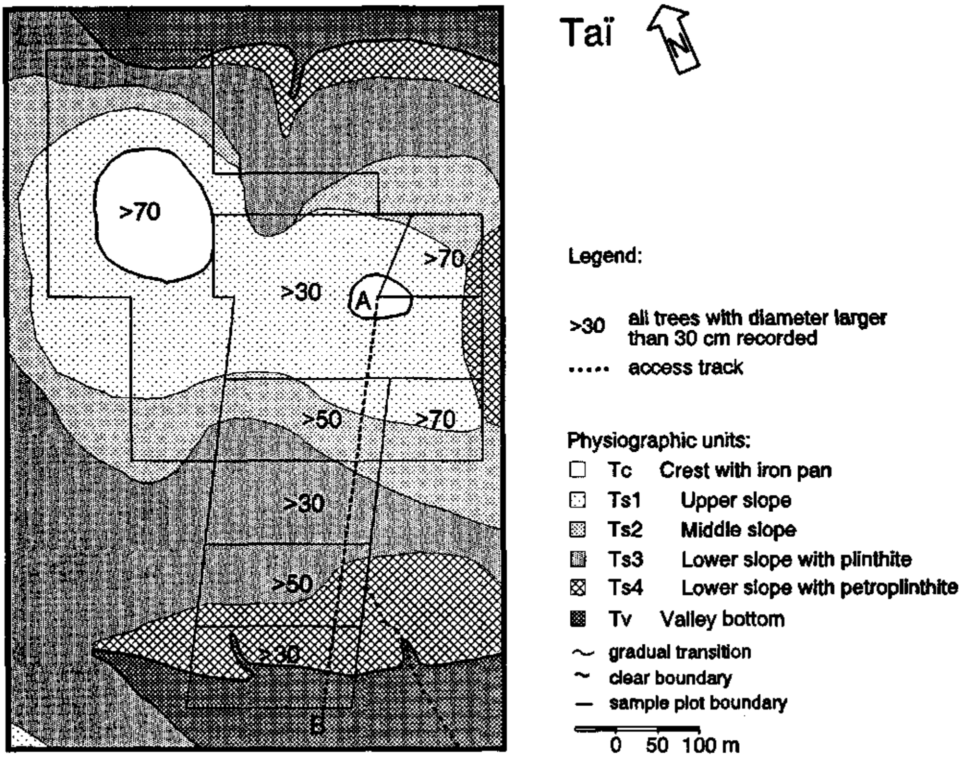


Figure 39 Contour sample plots at the Zagné study site. Contour levels are not equidistant, but each contour sample plot covers each 2 ha (except no. 12: 1 ha), even when the plot is split up into five parts.



Soil legend of the physiographic units of the Taï survey area (Nooren 1992, van Herwaarden 1991a)

Unit	Physiography	Drainage	Depth iron pan / petroplinthite	Altitude in m asl	Parent material	Slope form	Slope degree	Colour	Soil texture	FAO-UNESCO classification
Tc	Crest	well drained	70 cm iron pan	185-198	Migmatite	convex	flat to gently sloping	red	very gravelly clay	Ferric Acrisol
Ts1	Upper slope	well drained	> 150 cm	180-192	Migmatite	straight to convex	sloping	red	very gravelly sandy clay loam over non-gravelly clay	Ferric Acrisol
Ts2	Middle slope	well drained	> 150 cm	170-180	Migmatite	straight	gently sloping	strong brown to red	very gravelly sandy clay loam over non-gravelly clay	Ferric Acrisol
Ts3	Lower slope	moderately well drained	> 150 cm	160-175	Colluvium	straight	gently sloping	yellowish brown	very gravelly sandy loam over non-gravelly clay	Plinthic Acrisol
Ts4	Lower slope	moderately well drained	70-90 cm petroplinthite	160-170	Colluvium	concave	gently sloping	yellowish brown	non-gravelly sandy loam over very gravelly clay	Xanthic Ferralsol
Tv	Valley bottom	poorly drained	> 150 cm	< 160	Alluvium	concave	almost flat	light gray to brown	non-gravelly sandy loam	Dystric Gleysol

Figure 40 Physiographic map of the Taï study area. From Herwaarden (1991a), Nooren (1992).

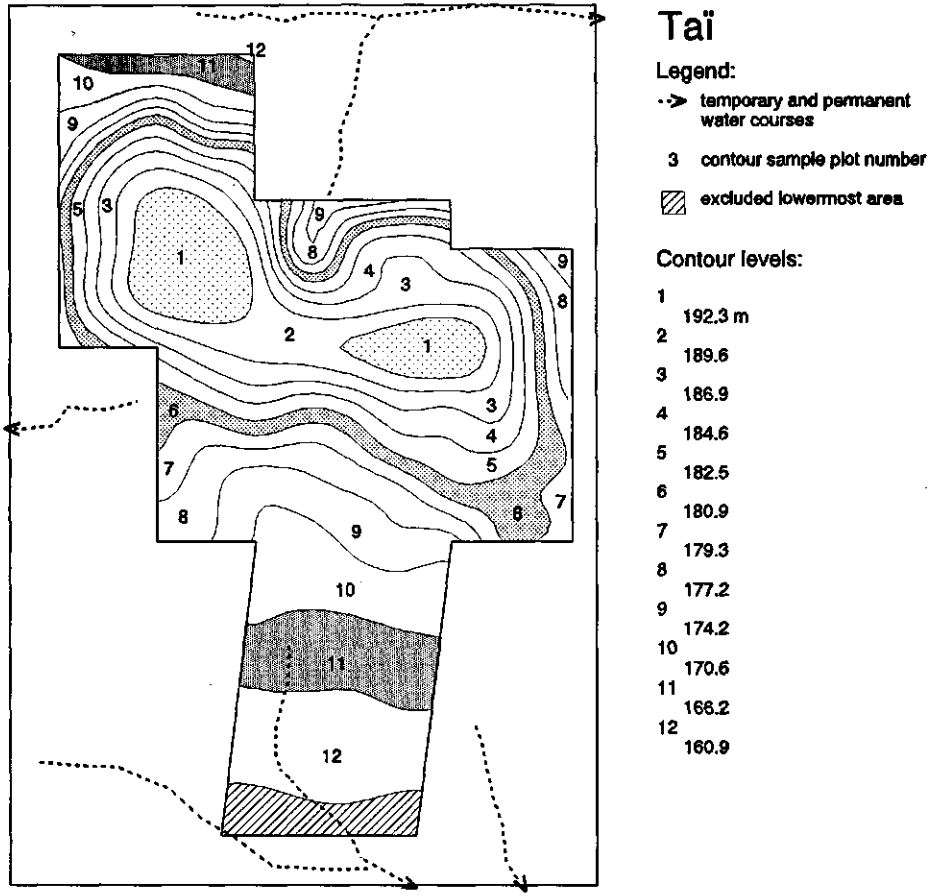
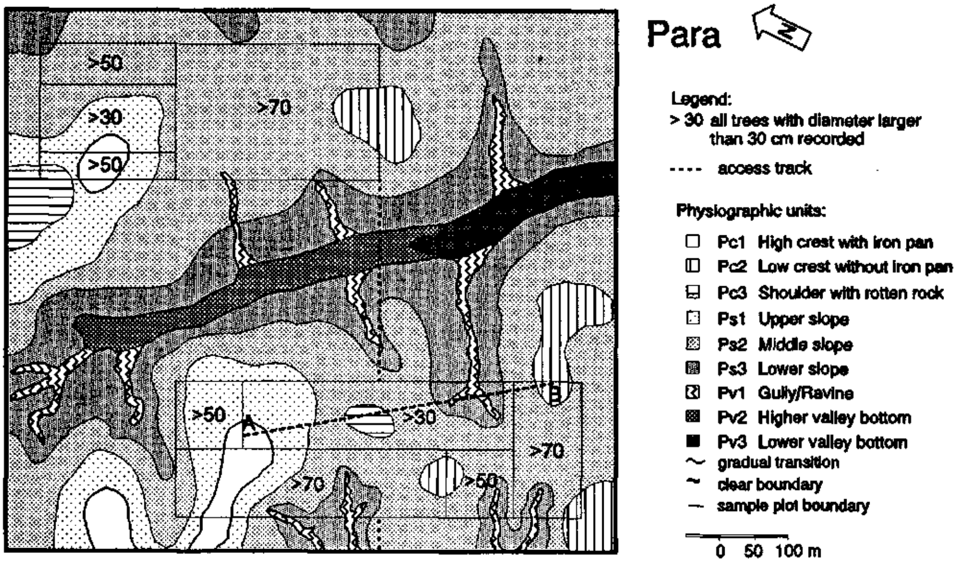


Figure 41 Contour sample plots at the Taï study site. For explanation see also Figure 39.



Soil legend of the physiographic units of the Para survey area (van Herwaarden 1991a)

Unit	Physiography	Drainage	Depth of rotten rock /iron pan /petroplinthite	Altitude in m asl	Parent material	Slope form	Slope degree	Colour	Soil texture	FAO-UNESCO classification
Pc1	High crest	well drained	125-150 cm iron pan	143-155	Schist	convex	gently sloping	red	(very) gravelly clay loam over clay	Haplic Ferralsol
Pc2	Low crest	well drained	110-150 cm rotten rock	128-133	Schist	convex	gently sloping	strong brown	gravelly to very gravelly clay loam to clay	Haplic Acrisol
Pc3	Shoulder	well drained	10-100 cm rotten rock	131-148	Schist	convex	gently sloping	reddish yellow	non-gravelly clay loam to clay	Ferralic Cambisol
Ps1	Upper slope	well drained	125-150 cm rotten rock	133-153	Colluvium/ Schist	straight	moderately steep	yellowish red	gravelly loam over clay loam	Haplic Ferralsol
Ps2	Middle slope	well drained	> 150 cm	119-141	Colluvium	straight to convex	sloping	yellowish brown	slightly gravelly clay loam	Xanthic Ferralsol
Ps3	Lower slope	moderately well drained	70-150 cm (petro)plinthite	115-135	Colluvium	concave	sloping	brownish yellow	slightly gravelly clay loam over clay	Plinthic Ferralsol
Pv1	Gully/Ravine	imperfectly drained	0-50 cm rotten rock	115-127	Schist	concave	gently sloping	variegated	slightly gravelly clay loam	Ferralic Cambisol
Pv2	Higher valley bottom	poorly drained	80 cm rotten rock	115-123	Alluvium/ Schist	concave	almost flat	gray over variegated	non gravelly to gravelly coarse sand to clay	Dystric Fluvisol
Pv3	Lower valley bottom	very poorly drained	> 150 cm	< 115	Alluvium	concave	almost flat	gray	non gravelly loamy sand	Dystric Gleysol

Figure 42 Physiographic map of the Para study area. From van Herwaarden (1991a).

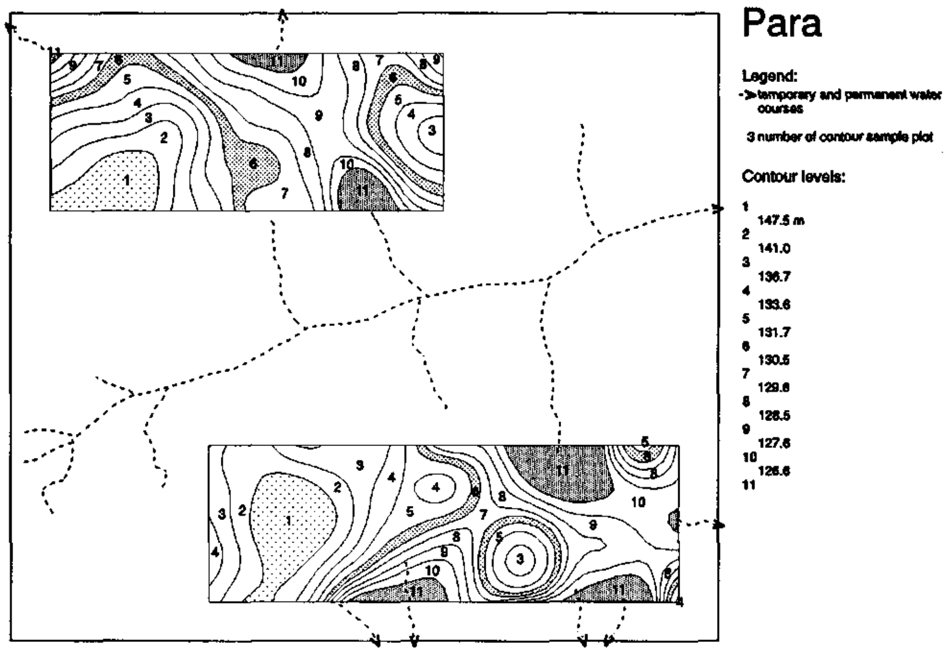


Figure 43 Contour sample plots at the Para study site. For explanation see also Figure 39.

stepped lines separating the squares of the contour samples, have been smoothed into curvilinear lines.

This method of a posteriori resampling of the trees has three advantages:

1. within a sample all trees grow in the same slope position;
2. the sample plots all have the same size (here 2 ha), so species richness and density figures such as basal area are comparable;
3. for ordination purposes 11 or 12 samples are available per site, which is more than the 4 soil types within the sample plot.

Distribution of the physiographic units over the contour samples. The contour samples with a fixed area of two ha always span several physiographic units (Figure 44). However, soils along the slope form a continuum from one physiographic unit to the next (see Figure 45). In Para, only the lower crest (Pc2) and the ravine (Pv1) unit have a wide elevation range, because of their geomorphology. Lower crests do not have a protective iron pan and are thus steadily lowered by erosion. Ravines pass through all elevations starting from their origin on the middle slope. The digital terrain model with a 10 by 10 m precision does not take into account the locally lower relief in the ravines, which is permissible because these account for less than 2 % of the area of the sample plots. For Taï the lower slope soils (Ts4) show a disjunct distribution, by the higher elevation of the northern valley which lies upstream from the southern valley. Both are tributaries of Audrénisrou river, which flows southwards. The contour line of the source of a stream

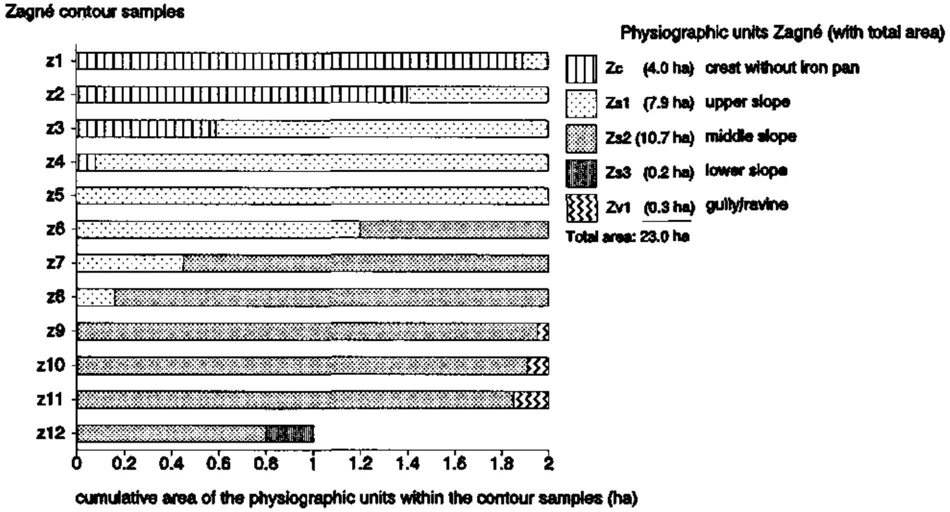
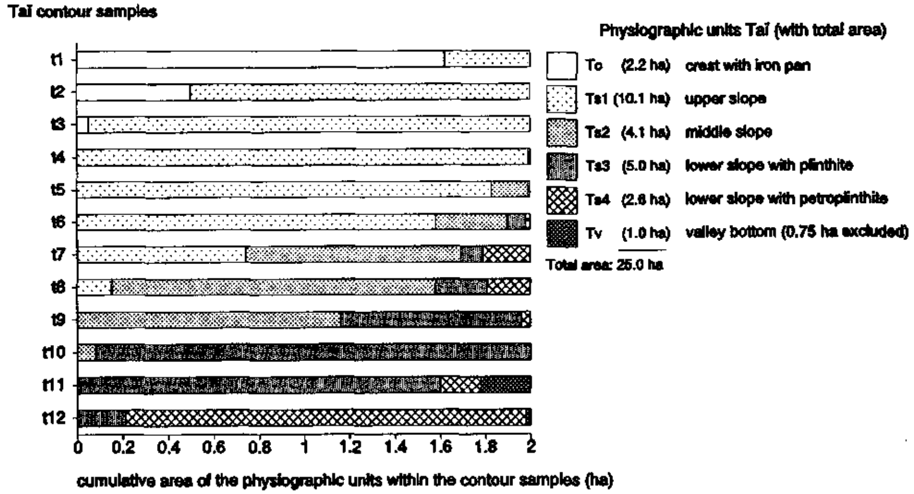


Figure 44 Distribution of the physiographic units over the contour samples in Zagné, Taï and Para. In the legend the total cover (in ha) of each physiographic unit within the entire sample plot is given. For explanation of the codes of the units see the legends in Figure 38, Figure 40 and Figure 42.



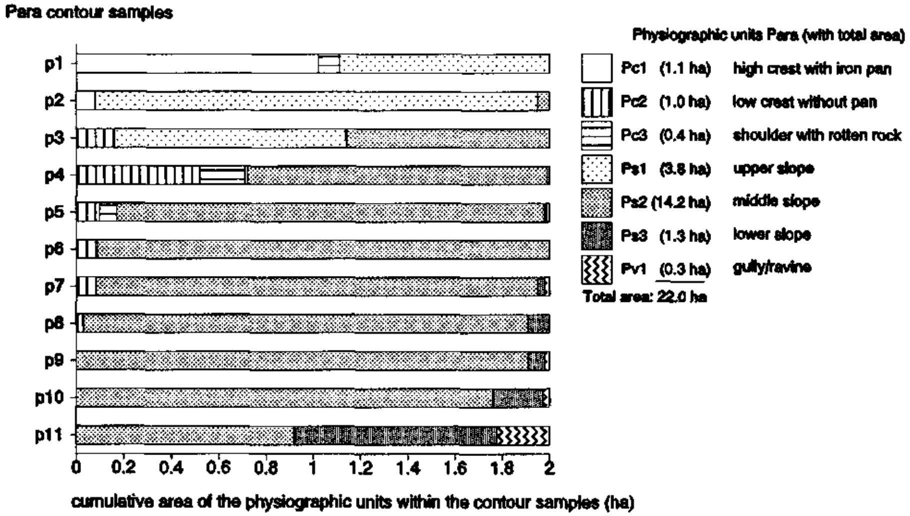


Figure 44 (continued)

cuts through all slope positions when it is followed downstream, therefore the fall of the water courses is a drawback to *contour sampling.

The middle slope unit is by far the most common physiographic unit in the Para plot (65 %) and the Zagné plot (50 %). In the Taï plot the upper slope unit is the most common (40 %). Three cross-sections are displayed in Figure 45 representing the typical sequence of soil characteristics at the three sites.

3.3.4 Ordination and comparison of the contour samples

An indirect approach was followed to relate species composition and other forest characteristics to soil. Both vegetation and soil were first related to topography, which is invariable at the time scale used and can be precisely measured. The relation between soil and elevation is shown in Figure 45. To analyse the response of the vegetation I plotted the compositional gradient and other forest characteristics against elevation.

Species composition was determined for each contour sample. In a first run I only considered the large trees (d > 70 cm). The abundance of a species was expressed on a scale of 1 to 9. It corresponds to the basal area of the species in the 2 ha contour plot, rounded to the nearest integer. Species with basal area less than 1 m² per 2 ha were given the code 1, those with basal area more than 9 m² per 2 ha the code 9.

The correspondence between these samples was analysed with Detrended Correspondence Analysis (DCA, Hill & Gauch 1980). As I found out that after the first run the vegetation table was rather incomplete with regard to the presence or absence of certain species, I decided to search the data set of the smaller trees (30 < d < 70 cm) for trees belonging to the 95 large tree species found in the first run. I *fine-tuned* the vegetation table, especially for the species that only rarely attain 70 cm diameter, but that are more abundant in the smaller diameters. If present below but not above 70 cm diameter, the abundance code 1 was given to the species, regardless of its basal area below 70 cm. The vegetation table resulting from this second run is shown in Table 5. Fine-tuning was not possible in all plots, however. In the crest sample plots z1 to z3 in Zagné smaller trees were not recorded because recording was done before contour sampling was conceived, as can be seen by superimposing Figure 39 on Figure 38 (see 3.3.2). Hence, these samples are not fine-tuned and caution is needed when comparing them with the other samples in Zagné. For the same reason the area of forest surveyed for smaller trees in the other contour samples was variable, as contour sample plots were designed for the entire 22 to 24 ha and not for the 10 or 5 ha surveyed in more detail. In the present Chapter these aspects are always taken into account.

The sample scores on the first DCA axis were plotted against the elevation midpoints of the contour intervals of the samples.

Tree species richness and population density of all trees over 70 cm diameter were calculated per contour sample and plotted against elevation. Basal area and biomass were analysed in the same way. Biomass per contour sample was calculated by multiplying basal area per species by the wood density of each species (see Appendix I for densities; from Bolza & Keating 1972, Dudek et al. 1981, Durand 1985, Vivien et Faure 1985).

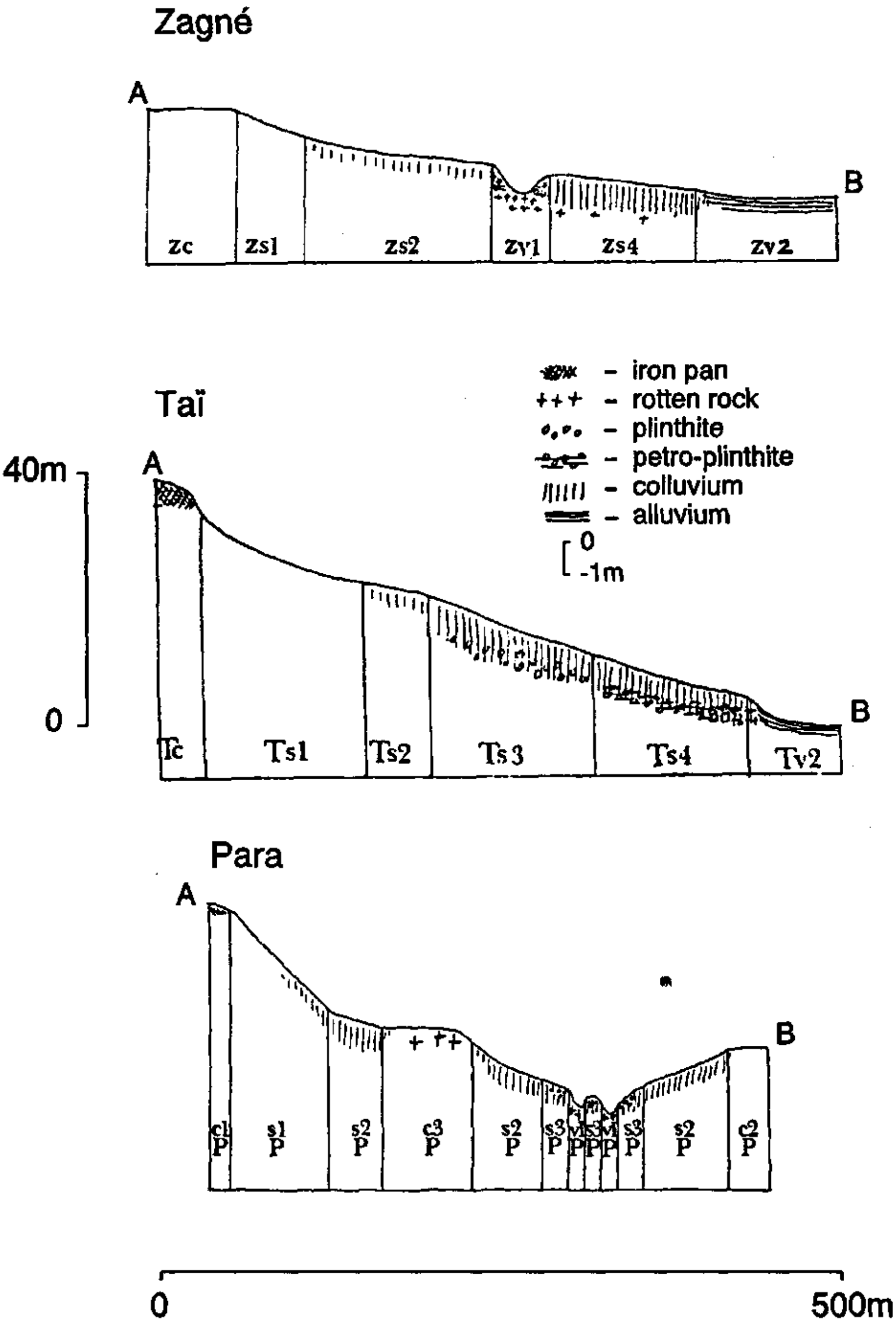


Figure 45 Three soil catenas in Taï National Park (Zagné and Taï on migmatite; Para on sericite schist; from van Herwaarden 1991a) indicating the origin of boundary lines (iron pans, alluvium) and other soil characteristics whose importance changes gradually along the slope. For a description of the physiographic units see Appendix III.

3.4 Results: vegetation response to slope position

3.4.1 Large tree species composition

In 35 contour sampling plots covering a total of 69 ha of upland forest, 894 trees were found to have a diameter exceeding 70 cm. They belonged to 95 species. The lowermost contour sample in Zagné (z12) covered only 1 ha, so it was only accessorily considered when comparing species composition. The ordination results from the second run are given in Table 5. For this run the abundance scores of the species were fine-tuned by including occurrence information from 1474 smaller trees, i.e. with a diameter between 30 and 70 cm. Downweighting of rare species was applied as an option within DCA. The first axis had an eigenvalue λ of 0.55 and separated the three study sites. The other axes had eigenvalues of 0.13, 0.10 and 0.07, mixed up the sites and, at first sight, could not be related to any spatial trend.

Figure 46 shows the relation between the ordination of the samples along DCA1 and the altitude of each sample in m above sea level. From Zagné towards Para altitude decreases and rainfall increases. Para is closer to the Liberian coast than Zagné. The catenas in Zagné and Taï overlap in absolute altitude. Taï and Para are disjunct with respect to altitude. Soil conditions show pronounced differences within each catena (see Figure 45), but in general, more moisture is available in the lower slope positions.

Sample ranking. The first DCA axis ranked the study sites in the same order as in Chapter 2, along the regional gradient. In Chapter 2 it was shown that the change in species composition between the sites correlates with an increase in rainfall. There is considerable variation within the sites. The Taï samples show the clearest trend within the site.

> ***The compositional change in the downslope direction is similar to the change of forest composition which occurs in directions towards areas with wetter climate.***

In other words, **compensation* occurs between the ecological factors "climate" and "catena position" (see also de Rouw 1991). This compensation is also found at Zagné from z5 to z12 and in Para from p1 to p10. The samples z1 to z4 and p11 do not follow this trend in Figure 46.

Separate ordination on each site. The outlying position of z1, the crest forest at Zagné, became even more pronounced (Figure 47). As mentioned in the methods section (3.3.4) the samples z1 to z3 were not fine-tuned, so their composition is less precisely known than that of the other samples. When considering all samples in Zagné, no correlation was found with altitude (R= 0.06, p=0.85), when z1 was omitted the correlation became significant (R= -0.77, p=0.006). Statistically significant correlations were also found for Taï (R= -0.81, p=0.002) and Para (R= -0.82, p=0.002). Notice how DCA inverted the gradient's direction for the Para site, wet having a low score, dry a high one.

Table 5 DCA ordination table of 95 large (d > 70 cm) trees species in 35 contour samples, each covering 2 ha. Read plot numbers, DCA1 scores and number of species vertically.

	Contour sample plots:	ppppppppppptttttttttttttzzzzzzzzzzzz
		1 1111 1 1 1
		80657924311120895427613223049711658
	DCA1 score	33322222222111111111
		110997766549766422109997654333211
Large tree species		82276847311413053059941419264249840
Sacoglottis gabonensis	385	99999854511------------------------
Protomegabaria stapfiana	369	11111111111------------------------
Anthocleista nobilis	356	1111111--12--1---------------------
Maranthes glabra	348	2111-142131-11---------------------
Pentadesma butyracea	325	---1--1-11----1--------------------
Afzelia bella	316	-1--1--1-------------------1-------
Uapaca guineensis	308	2-112-12111-11----------1--1-----1-
Uapaca corbisieri	305	1--1--1-11-3----------1------------
Antiaris toxicaria wel. wel.	295	--------1--1-----------------------
Scytopetalum tieghemii	294	11--1111111111-11--11--------------
Heritiera utilis	287	11-11-1311-11111-1-1-11------------
Dacryodes klaineana	285	------111111-----1-1---------------
Coula edulis	273	11-1111111111111-1111-1----1-------
Canarium schweinfurthii	272	--11----1--------------1---------1-
Dialium aubrevillei	271	111-1-1111112---111---1-----1-----1
Anthonotha macrophylla	267	----1---1-1-111---1----------------
Nauclea diderrichii	256	1-1-211-1-11-12111---1---1------2--
Tieghemella heckelii	253	--2----2--------5-----1------------
Amphimas pterocarpoides	248	--11----1-------1--11-----1--------
Trichoscypha arborea	247	---1--111--111-1111---1------------
Irvingia gabonensis	245	11---------1--1-----------1------1-
Rhodognaphalon brevicuspe	243	11--1-2-1--11-11-11------111-1-----
Parinari excelsa	242	---1321----111----11-11--111------1
Parkia bicolor	241	1-1---1111131-1111-11--1-----2-----
Pentaclethra macrophylla	201	-------------1---------------------
Lovoa trichilioides	194	------11----1---1-----------11-----
Detarium senegalense	191	--------1---------------------1----
Samanea dinklagei	177	-----------111-1----1--------------
Entandrophragma angolense	173	------1------12-1-11-1-------------
Strombosia glaucescens	169	-1111-11111-111111111-1111111111111
Newtonia duparquetiana	166	------------11-----1---------------
Klainedoxa gabonensis	165	------1--2--1-11-211-11--1-1-------
Pachypodanthium staudtii	156	---1--1--1--1--11111-11---11--1----
Copaifera salikounda	154	-------------1--1------------------
Spathodea campanulata	149	---------------1-------------------
Scottellia klaineana	148	-1-1--111111111--1---11111111111111
Maranthes aubrevillei	143	-------------1-----1---------------
Ficus spp.	137	-------------1-1----1--------------
Placodiscus boya	128	--------------1-11-----------------
Beilschmiedia mannii	126	-------------11-11---1-------------
Pycnanthus angolensis	121	---1----1--212211121191-1---1---1--
Trichilia splendida	117	--------1-----------------1--1-----
Chrysophyllum taiense	104	----1------1121312111111-11-11-1---
Piptadeniastrum africanum	102	-----1----1212-33411121--11-12----2
Ricinodendron heudelotii	101	------------1-----1----1-----------
Discoglypremna caloneura	98	-----11-1--------11--1-1--1-111-11-
Terminalia ivorensis	98	----------1---------------1-1------
Oldfieldia africana	97	-----------2211-11114-1---1--11----
Anopyxis klaineana	91	---1---111--------------11111111-11
Calpocalyx aubrevillei	91	-1---11---2-------------11123-3-1-1
Stereospermum acuminatissimum	82	---------------1-11--11------------
Corynanthe pachyceras	78	-------111-111111321111111111111111
Lannea welwitschii	77	---------1------1-11111----1--1----
Lophira alata	76	------------4------------1-12------
Nesogordonia papaverifera	73	-------------1-1-1-1111-----1------
Gymnostemon zaizou	67	--------------1-2---1-1-----1------
Aubregrinia taiensis	59	----------------1---111------------
Entandrophragma candollei	58	----------------2--------1---------
Aubrevillea platycarpa	54	--------------------2--------------
Anthonotha fragrans	51	-----1------11--2111-11-1111-11--11
Khaya anthotheca	51	------------------1-221------------
Erythroxylum mannii	47	--1-----------1-1-1-1111--11111-1--
Antiaris toxicaria wel. afr.	36	-------------1-------1--1----1-----
Erythrophleum ivorense	35	1-1-11----1111-1-11211331515242-56-
Petersianthus macrocarpus	26	-------1----11111-11-11-21121112-11
Entandrophragma utile	23	----------------13--2241--------111
Ficus elasticoides	22	------------------1--1----1--------
Aningeria robusta	20	----------------11-1111--2---2-----
Entandrophragma cylindricum	-1	----------------1--------------1---
Guarea cedrata	-1	----------------1--------------1---
Sterculia oblonga	-5	-----------11----------11-1---1-111
Ceiba pentandra	-15	----------------21--1-2---217------
Duboscia viridiflora	-19	--------------1-----------------1-1
Canthium arnoldianum	-21	-------------1----1-------1---1--11
Balanites wilsoniana	-36	-------------------1----------2----
Bombax buonopozense	-38	----------------------1--2-1-----1-
Keayodendron bridelioides	-39	------------------11-11---11111-111
Zanthoxylum gilletii	-40	--------------------1-------------1
Terminalia superba	-57	---------------1-1---21--2111111234
Albizia ferruginea	-60	---------------------------2-------
Chidlowia sanguinea	-64	--------------1-11-41-1121574761698
Xylia evansii	-69	-----------------------11111131-111
Albizia zygia	-74	-------------------------1---1---1-
Daniellia thurifera	-74	---------------------------2-1--1--
Triplochiton scleroxylon	-82	------------------1-------35221-153
Alstonia boonei	-87	--------------------------11----1-1
Chlorophora regia	-91	--------------------------1-1--1--1
Distemonanthus benthamianus	-92	-------------------------1--1--1111
Blighia welwitschii	-93	------------------------------1----
Chlorophora excelsa	-97	------------------------------11---
Sapium aubrevillei	-100	-----------------------------1-1-1-
Guibourtia ehie	-101	-------------------------------11--
Bridelia grandis	-102	-------------------------------1---
Albizia glaberrima	-133	----------------------------------1
Aubrevillea kerstingii	-133	----------------------------------1
Number of species		11111121221223223222223112322221222
		54486359708291322987574443186646135

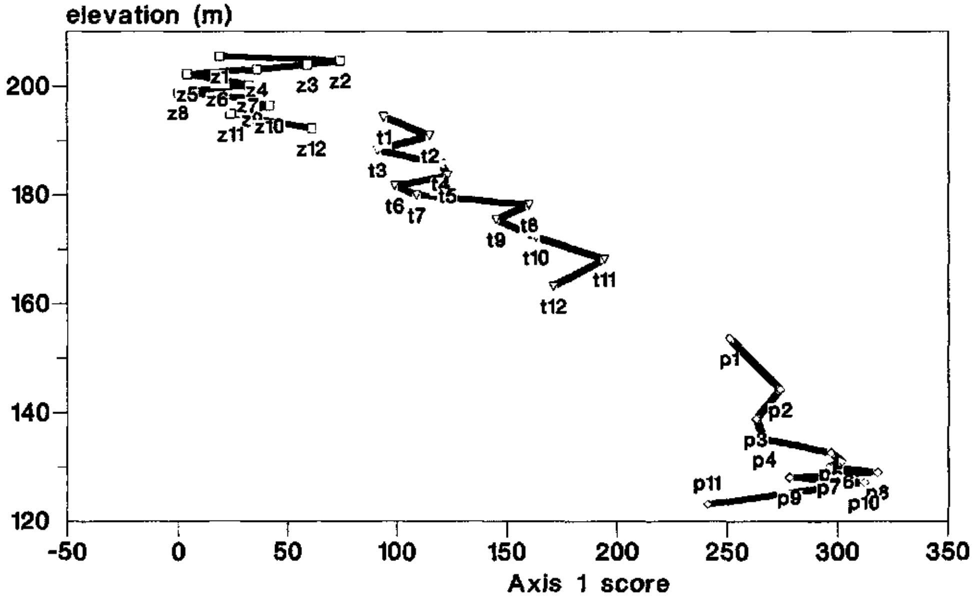
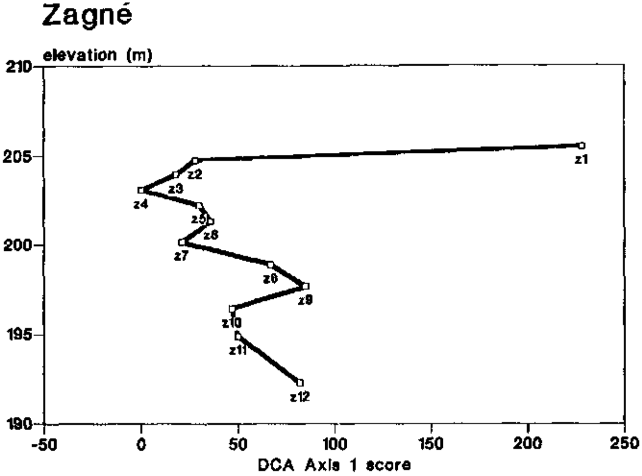


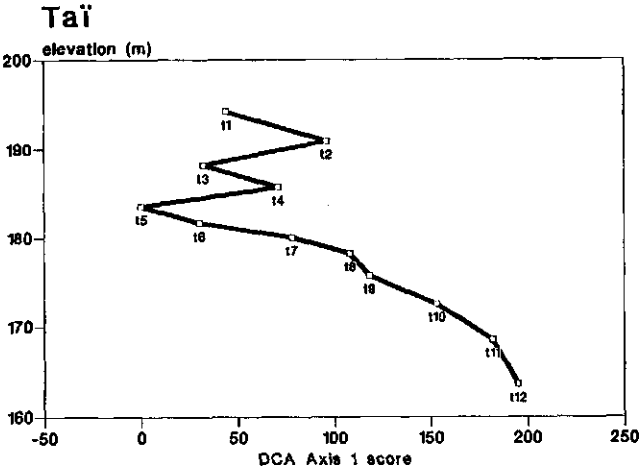
Figure 46 Relation between altitude and the DCA1 scores of the contour samples. The point label indicates the site (z=Zagné, t=Taï, p=Para) and position of the contour sample plot, "1" is the highest, "11" or "12" the lowest plot. Elevation in m above sea level.

By comparing the overall ordination (Figure 46) with the separate ones (Figure 47) an "attractive" or "repulsive" effect of the presence of other sites on the within-site-ranking may be observed; z1 is skewed left by the Taï samples, t12 by the Para samples; p11 seems to be "attracted" by the Taï samples. All this results from the fact that sample scores are derived from the same species ordination shown in Figure 46. In the separate ordination the information of the other sites is not used to rank the species, so certain species may end up in a central, undetermined position, although they can be precisely positioned with the help of information from the other sites. When using correspondence analysis the composition of the data set seems to influence the results of the ordination.

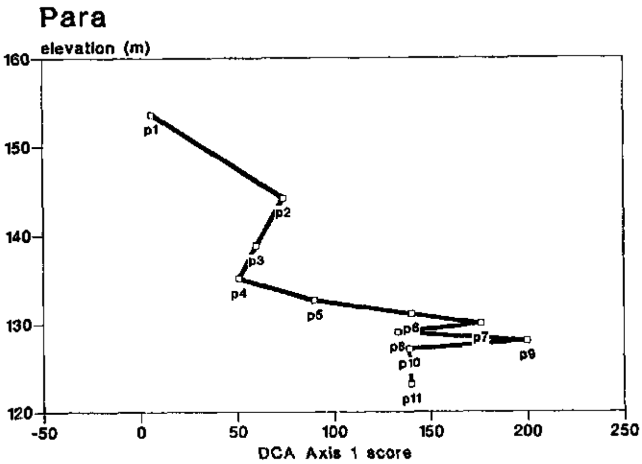
Nevertheless, I conclude that the catena, although a distinct cause, has a similar effect on tree species composition as climatic variation. The length of a catena gradient (e.g. Taï: 100 u.DCA1-Chapter 3) corresponds to a piece of the gradient induced by climate about 46 u.DCA1-Chapter 2 long. The latter figure is an estimate derived from the DCA1-Chapter 2 scores of the three sites: Zagné 35, Taï 64 and Para 148. From Figure 46 we read that the driest contour samples lie at two-fifths of the distance from the *centroid of Taï (2/5 of (64-35=29) is 12 u.DCA1-Chapter 2) towards the centroid of Zagné, and the wettest samples lie at two-fifths from the centroid of Taï (2/5 of (148-64=84) is 34 u.DCA1-Chapter 2) towards the centroid of Para, bringing the length of the gradient to 46 u.DCA1-Chapter 2. On the regional gradient the rate of compositional change is 5 u.DCA1-Chapter 2 per 10 km, so this distance (see Figure 11) is some 90 km long and



Zagné		Aub.ker	125	Xyl.eva	-14
		Zan.gil	125	Als.boo	-17
$\lambda_1=0.23$		Ter.ivo	118	Tri.scl	-28
$\lambda_2=0.15$		Ter.sup	118	Nau.did	-33
68 species		Bal.wil	78	Tri.spl	-33
Bri.gra	459	Bli.wel	78	Uap.gui	-37
Ent.cyl	459	Det.sen	78	Pac.sta	-39
Gua.ced	459	Dub.vir	64	Par.exc	-50
Chl.exc	328	Lov.tri	50	Ery.ivo	-54
Gui.ehi	324	Cal.aub	41	Can.sch	-69
Sap.aub	270	Can.arn	41	Lan.wel	-71
Chl.reg	267	Ste.obl	33	Alb.zyg	-86
Dis.ben	235	Ant.toa	29	Par.bic	-90
Chr.tai	228	Chi.san	26	Ric.heu	-90
Pet.mac	227	Amp.pte	23	Rho.bre	-101
Gym.zai	197	Fic.ela	23	Ani.rob	-106
Nes.pap	197	Pip.afr	18	Ent.can	-122
Ano.kla	193	Dis.cal	9	Bom.buo	-127
Dia.aub	170	Lop.ala	9	Dan.thu	-127
Cor.pac	164	Kea.bri	6	Kla.gab	-168
Sco.kla	164	Old.afr	2	Afz.bel	-215
Str.gla	164	Ent.uti	-4	Alb.fer	-215
Pyc.ang	131	Irv.gab	-12	Cou.edu	-215
Cei.pen	130	Ant.fra	-14		
Alb.gla	125	Ery.man	-14		



Taï		Her.uti	189	Dis.cal	17
		Dia.aub	186	Ste.acu	15
$\lambda_1=0.28$		Dub.vir	181	Ant.fra	13
$\lambda_2=0.14$		Pen.but	181	Cop.sal	6
72 species		Cou.edu	177	Kea.bri	-9
Lop.ala	451	Scy.tie	175	Fic.ela	-10
Ste.obl	421	Tri.arb	172	Ter.sup	-11
Ant.tow	392	Ant.toa	165	Chi.san	-21
Mar.gla	388	Tri.scl	153	Pla.boy	-31
Uap.gui	388	Ficus sp	145	Ery.man	-45
Ant.nob	324	Chr.tai	139	Kha.ant	-54
Pen.mac	324	Nau.did	135	Lan.wel	-56
Ric.heu	306	Lov.tri	108	Ani.rob	-67
New.dup	293	Kla.gab	105	Ent.uti	-70
Irv.gab	287	Pet.mac	103	Amp.pte	-91
Uap.cor	281	Old.afr	102	Bom.buo	-95
Ant.mac	280	Cor.pac	90	Gym.zai	-99
Sam.din	263	Ery.ivo	79	Aub.pla	-108
Rho.bre	247	Str.gla	75	Zan.gil	-108
Can.arn	243	Pip.afr	68	Aub.tai	-109
Spa.cam	216	Pyc.ang	64	Cei.pen	-112
Mar.aub	213	Ent.ang	58	Tie.hec	-175
Par.exc	199	Bal.wil	39	Ent.can	-191
Sco.kla	199	Pac.sta	35	Ent.cyl	-191
Par.bic	196	Nes.pap	20	Gua.ced	-191
Dac.kla	191	Bei.man	17		



ra		Tri.arb	233	Rho.bre	94
		Uap.cor	223	Dis.cal	93
1=0.26		Ent.ang	216	Afz.bel	32
2=0.15		Pyc.ang	215	Ant.nob	28
45 species		Sco.kla	198	Ant.mac	21
Lan.wel	445	Her.uti	187	Sac.gab	14
Kla.gab	369	Mar.gla	182	Nau.did	-34
Cor.pac	331	Par.bic	177	Irv.gab	-38
Ano.kla	290	Tie.hec	142	Cal.aub	-40
Pet.mac	286	Amp.pte	141	Ter.ivo	-47
Pac.sta	277	Can.sch	141	Ery.man	-54
Pen.but	273	Str.gla	140	Par.exc	-112
Ant.tow	261	Dia.aub	123	Ery.ivo	-127
Det.sen	261	Uap.gui	122	Pip.afr	-175
Tri.spl	261	Cou.edu	108	Chr.tai	-205
Lov.tri	251	Scy.tie	101	Ant.fra	-303
Dac.kla	243	Pro.sta	95		

Figure 47 Separate ordination of the study sites: DCA axis 1 scores of the contour samples against the middle contour line of each contour sample, respectively for Zagné, Taï and Para.

reflects a rainfall increase of 3.5 m $(10\ y)^{-1}$ (350 mm y^{-1}). In other words, ***the wettest and the driest forests on the catena with an elevation interval of about 30 m differ as much in composition as forests lying 90 km apart on the rainfall gradient,*** when comparing a spatially averaged composition of the latter forests with the composition of contour samples.

3.4.2 Tree *species richness and tree density

A general trend of *decrease* of large tree species richness is found from Zagné towards Para, i.e. with *increasing* rainfall (Figure 48). Among the sample plots covering a fixed area of 2 ha, most species are found in Zagné and least in Para. Within the catenas a decrease is found in Taï down the slope and an optimum in Para in upper slope, shoulder and lower crest positions. Tree density shows even more variation: decrease from crest to lower slope in Taï, and a maximum in upper and middle positions in Zagné and Para. This might be related to the steepness of the terrain. On the latter sites crests and lower slopes are less densely populated by trees. The number of species is a *tree population* characteristic rather than a *forest* characteristic, it should be compared for equal numbers

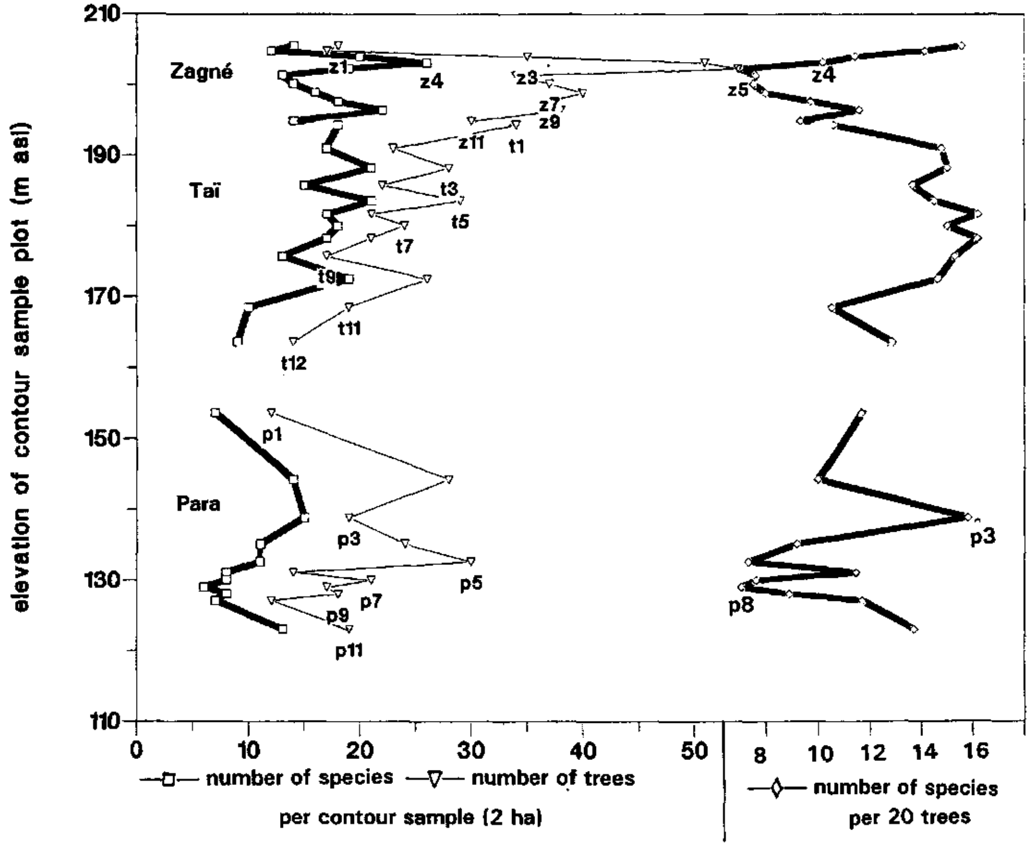


Figure 48 Tree species richness (bold line) and tree density (thin line) per two ha contour plot, plotted against altitude. On the right the quotient of both variables is given, expressed as the number of species per 20 trees.

of trees, and not for equal areas of forest. ***So, I calculated the number of species per 20 trees as a measure of diversity of the tree population.*** High and low diversity now occur both in Zagné and Para. ***Variation in large tree species richness within sites is greater than variation between sites.*** At the Taï site a maximum diversity is found on upper and middle slopes. The samples with low diversity are often dominated by abundant species like *Chidlowia sanguinea* in Zagné z5, *Pycnanthus angolensis* in Taï t1, and *Sacoglottis gabonensis* in Para p5, p7 and p8.

3.4.3 Biomass and basal area

Basal area peaks in middle slope positions and is small at both ends of the catena. Here the influence of the very big trees is felt (Figure 53). In Taï huge *Entandrophragma spp.* (wood density d=0.6) and *Tieghemella heckelii* (d=0.7) trees occur as a corona around the ironstone cap (see Figure 50 and also Oldeman 1974, Vooren 1985). In Zagné *Triplochiton scleroxylon* (d=0.4), *Erythrophleum ivorense* (d=0.9) and *Ceiba pentandra* (d=0.3) trees grow very large, up to 240 cm diameter, with a preference for the middle and upper slope position (Figure 51). In Para numerous very big but relatively short-boled *Sacoglottis gabonensis* (d=0.9) trees were present (Figure 52)

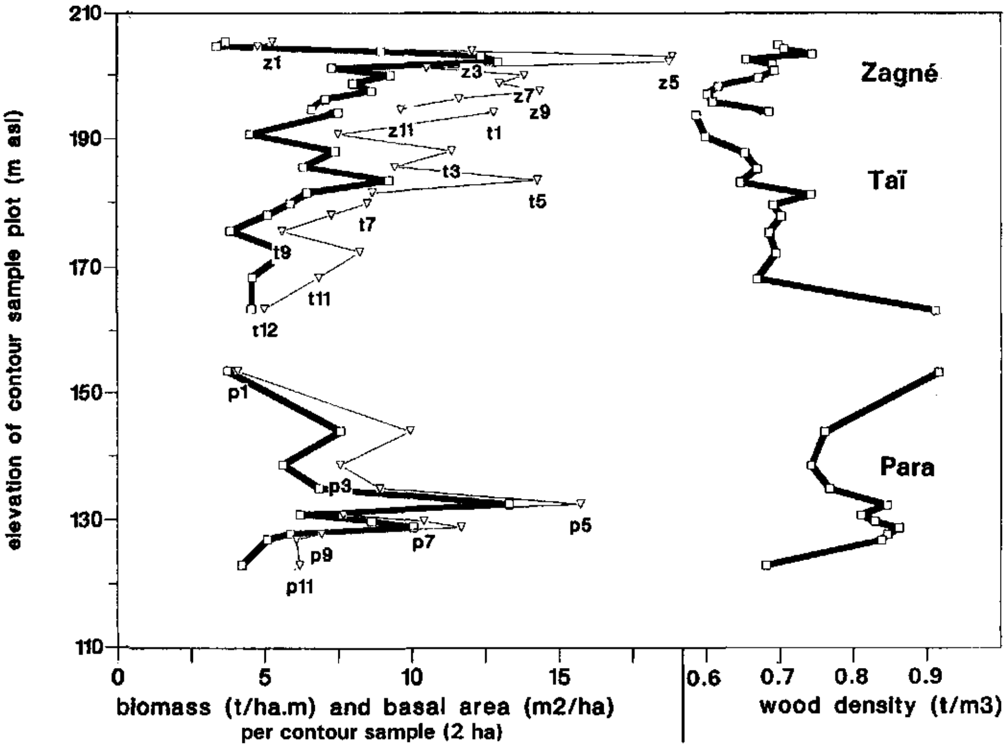


Figure 49 Biomass in t ha^{-1} m^{-1} and basal area in m^2 ha^{-1} per contour sample, plotted against altitude. Biomass is calculated as the sum of the basal area per species weighted by the species' wood density. On the right the average wood density in t m^{-3} of the large trees within a contour sample is given.

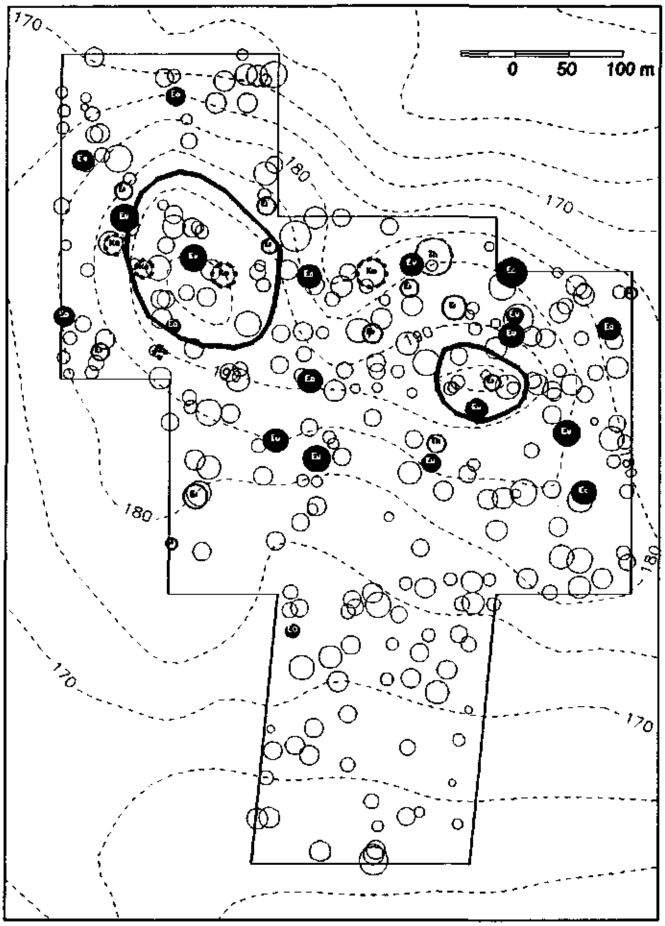


Figure 50 A corona of large trees around the crest at the Taï site. The bold line indicates the extent of the iron pan. All large trees (d > 70 cm) are plotted as open circles. The solid circles indicate the position of 20 *Entandrophragma spp.* trees, 11 *Erythrophleum ivorense* trees, 5 *Khaya anthotheca* trees and 2 *Tieghemella heckelii* trees. The diameter of the circles is square-root proportional to the diameter of the tree, the smallest circles are trees of 70 cm d, the largest circle a tree of 240 cm d. Elevation contours, in m above sea level, are given every 5 metres.

Biomass was calculated as the sum of the basal area per species weighted by the species' wood density. The high basal areas in Zagné consisted mainly of wood of relatively low density, although heavy species also occurred. In Para the dominant large tree species had very dense wood. The quotient of biomass and basal area is given on the right in Figure 49, being the average wood density of the large trees. *An increase in average wood density from 0.7 in Zagné and Taï to 0.8 in Para is found with increasing rainfall.* A similar trend can be discerned in the data published by Whitmore and Silva (1990) for Amazonian forests.

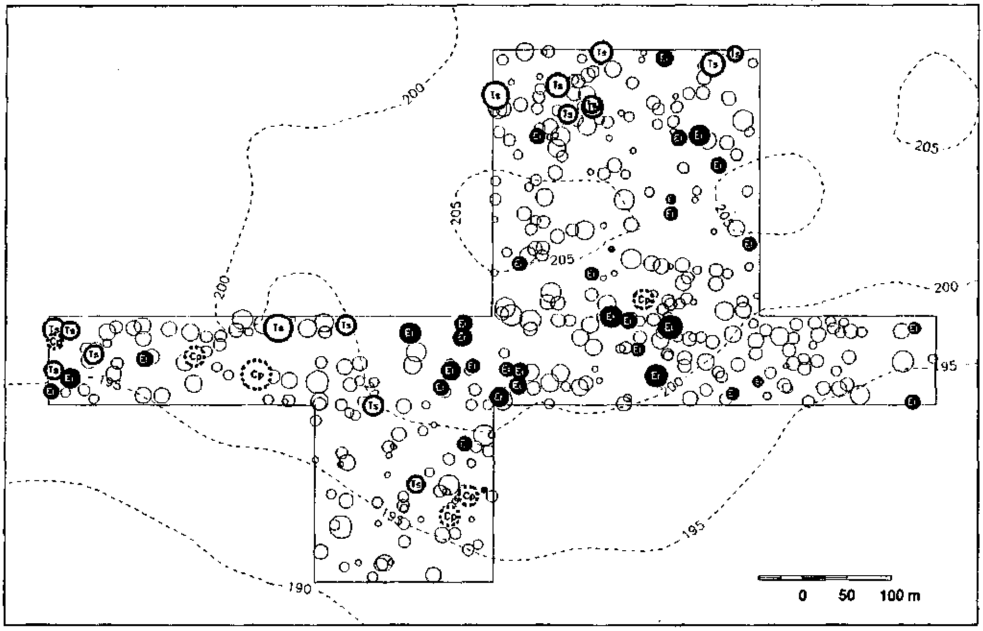


Figure 51 *Triplochiton scleroxylon* (16 ex.), *Erythrophleum ivorense* (35 ex.) and *Ceiba pentandra* (6 ex.) trees growing preferentially on upper and middle slope positions at the Zagné site. Drawing conventions as in Figure 50.

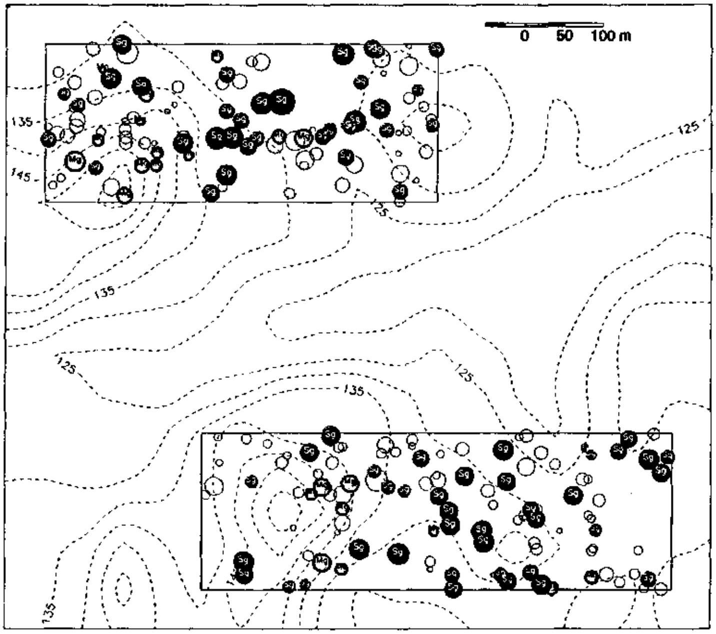


Figure 52 The distribution of *Sacoglottis gabonensis* (74 ex.) and *Maranthes glabra* (23 ex.) trees at the Para site. *S. gabonensis* seems to avoid the high crest with iron pan, where *M. glabra* prefers the steep and gravelly upper slopes.

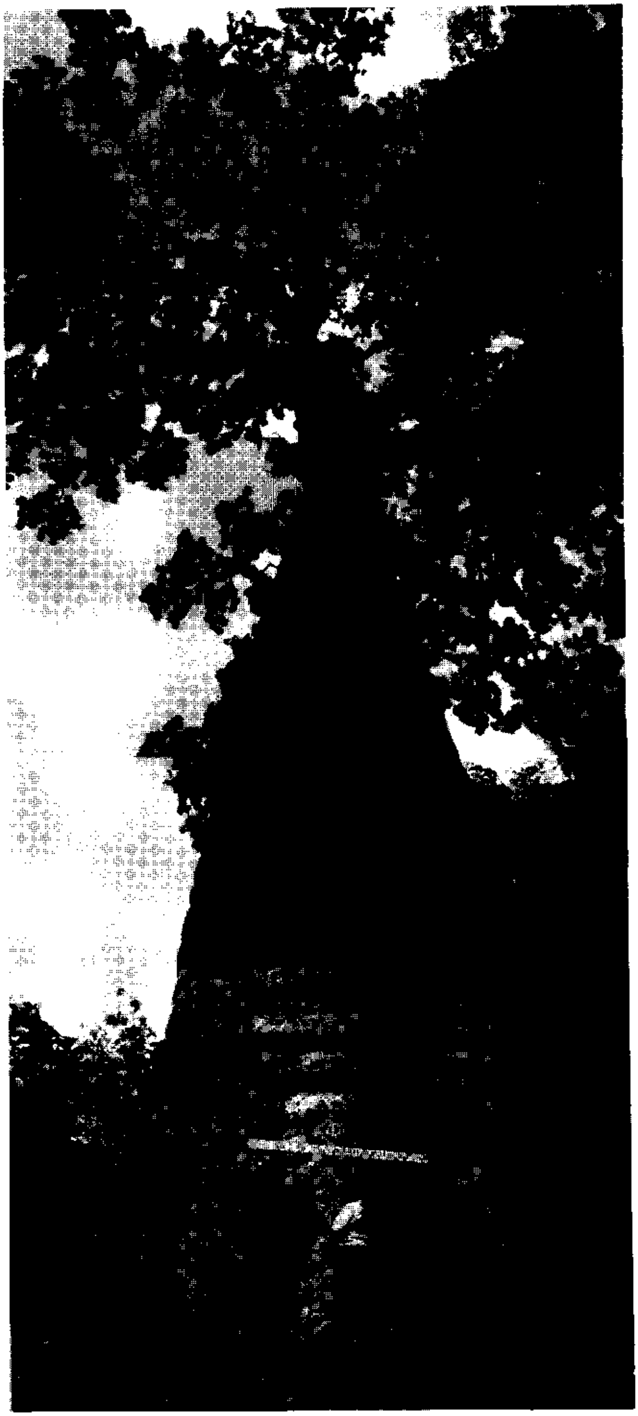


Figure 53 The biggest tree of western Côte d'Ivoire. An *Entandrophragma candollei* tree in the Forêt classée du Haut-Sassandra with a swollen base, 6 metres diameter at the height of the ruler, held by Sormongar S. Zwuen, a Liberian forest researcher. The ruler itself measures 2 m.

3.4.4 Comparison of the local and regional ordination

Correlation analysis of the species scores of the ordinations of Chapters 2 and 3 shows the *similarity between the regional and the local forest gradient. 38 tree species were represented in both ordination tables (Table 3 and Table 5). Their correlation is plotted in Figure 54 ($R = 0.59$, $p < 0.001$). 'Wet' species are grouped in the upper right corner, 'dry' species in the lower left. The further away the species lay from the regression line, the more their position differed in both ordinations. Both ordinations are subject to error resulting from the varying sample size per species, and thus the varying precision of the species' score. The ordination from Chapter 2 has a wider scope in terms of the wet-dry gradient and is based on a larger data set containing many more trees, and thus its species ranking is judged more reliable.

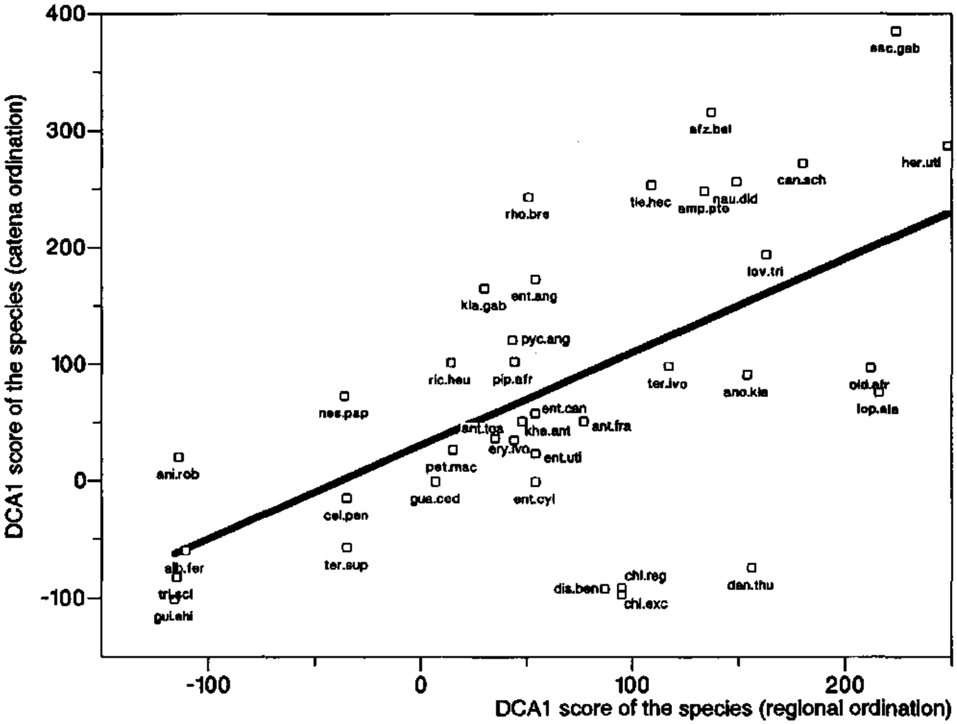


Figure 54 Correlation of the species scores from the slope gradient ordination with those of the regional ordination. $R = 0.59$, $p < 0.001$. There were 38 large tree species common to both ordinations.

Correlation of the slope ordination with the regional gradient described for Ghana (Hall & Swaine 1981) is of the same statistical significance. This time 67 species could be compared and $R = -0.64$, $p < 0.001$. Some of the outliers are rather rare but ubiquitous species like *Afzelia bella, Canarium schweinfurthii, Irvingia gabonensis* and *Daniellia thurifera*. DCA1 species scores estimate where the species attain their maximum abundance along the gradient (ter Braak 1987a). The confidence limits of this estimate are larger for species with a rather flat response curve than for species with a narrower ecological range and a peaked response curve.

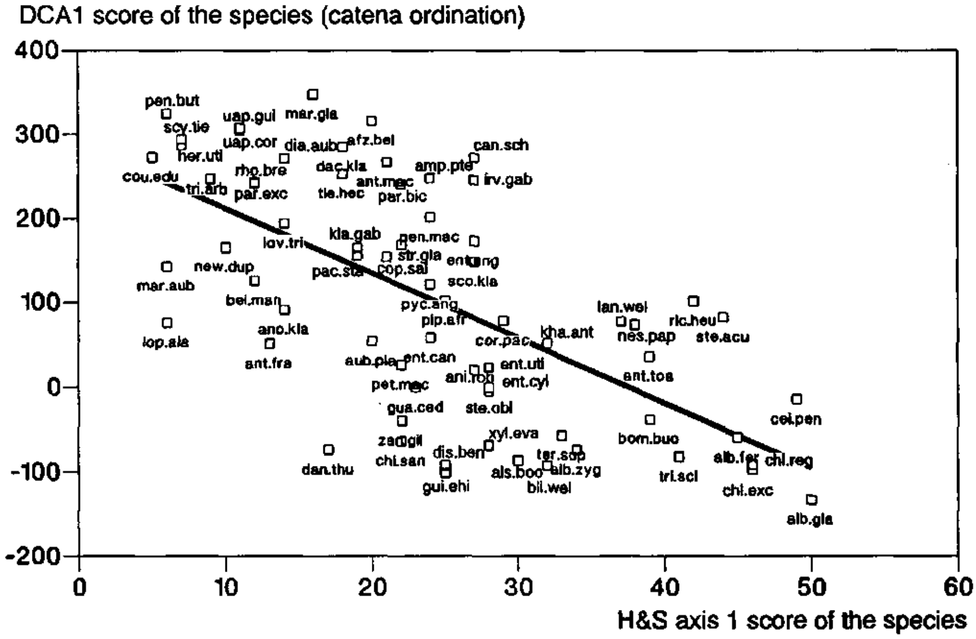


Figure 55 Correlation of the species scores of the catena ordination with the scores of Hall & Swaine (1981). R= -0.65, p<0.001. There were 67 tree species common to both ordinations. The further a species is situated from the regression line, the more differently it was ranked in both ordinations. For species codes, see Appendix I.

3.5 Discussion

3.5.1 Compositional gradients along slopes

Slope gradients in tropical forest were described by Davis & Richards (1933) in Guyana, by Lawson et al. (1970) in Ghana, by Lieberman et al. (1985) in Costa Rica and by Jonkers (1987) in Suriname. In each study, a different lower diameter limit and a different plot size were used to study the gradient in species composition. As in tropical rain forests many large tree species do not have an exponential but rather a bell-shaped diameter distribution curve (Rollet 1974, Bongers et al. 1988) and each have a different maximal size (Poker 1992), different species are abundant in different diameter intervals. Thus, the species pool considered to describe the slope gradient depends on the diameter interval chosen for study. The list of 95 species found at the three sites contains most of the large tree species known from the region between Zagné and Para (Guillaumet 1967, Huttel 1977, Alexandre 1980, de Rouw 1991. Not found but present at low density in the region are *Kantou guereensis, Pericopsis elata, Hannoa klaineana* and *Okoubaka aubrevillei. Gilbertiodendron preussii* was found in the valley bottom at the Taï site (Bech 1983); de Rouw (1991) found it in association with *Heritiera utilis* over the entire catena in forests half-way between Taï and Para.

In forest close to my Taï site, Huttel (1977) studied the slope gradient considering mostly smaller tree species, like *Diospyros mannii*, most abundant in the diameter class 3.5 to 13 cm, and *Corynanthe pachyceras*, most abundant above 13 cm diameter (see also Vooren 1979, Bech 1983). I considered trees above 70 cm diameter and found *Pycnanthus angolensis* most prominent on the crest and *Piptadeniastrum africanum* on the slope. Depending on the size class studied, different tree species are prominent, but the changing abundance of any of these along the slope can express the slope gradient.

Large tree species often cover a broad interval along the slope gradient, so the gradient analysis relies on differences in abundance of the species, rather than on presence or absence data alone. A more intensive sampling is necessary to obtain relevant quantitative data per species. I admit that the abundance scores and absence data in Table 5 can be interpreted neither with high precision nor in an absolute sense because of the limited number of trees per sample (13 to 50 trees above 70 cm diameter per 2 ha). Hardly any individuals of *Piptadeniastrum africanum, Sacoglottis gabonensis* or *Triplochiton scleroxylon* were found in the data set on smaller trees ($30 < d < 70$ cm), so a reduction of the diameter limit provided no additional information on their distribution.

Contour samples are spatially contiguous, e.g. t7 touches both t6 and t8, and species composition is a spatially *autocorrelated attribute (Hubbell & Foster 1983). Hence, t7 is supposed to have a composition intermediate to that of t6 and t8. As a result, it is permissible to spatially interpolate the ordination scores of the contour samples, so t6 and t8 also provide indirect information on the species composition of t7. The weight of the neighbouring samples is inversely related to the distance (elevation interval) to these samples. The spatial correlation of the sample with its neighbours compensates to some extent the limited precision of the species composition of the sample itself.

Besides the analysis of individual slope gradients, the results prove the *similarity between the local forest gradients determined by slope and the regional forest gradient induced by climate. Slope gradients are ***sliding gradients*** superimposed on the regional forest gradients, as shown by Figure 46. When analysing four soil-vegetation catenas in SW Côte d'Ivoire, Guillaumet (1967) already found this compensation effect of rainfall by slope position. De Rouw (1991) found that valley bottom species near Taï, like *Gilbertiodendron preussii* and *Heritiera utilis*, "climbed up" the slope under wetter climate more to the south. My results substantiate these findings and yield a beginning of explanation.

3.5.2 The method of contour sampling

A strong point of the method is the constant area of each sample. Jonkers (1987) for instance compared samples with areas varying from 740 to 1600 m² and so introduced differences between samples which indeed reflect the sampling method rather than forest reality (see also Text box 2, p. 34).

On the contrary, a small methodological discrepancy between *absolute* elevation contour lines and relative lines of equal slope position does not affect the results. However, within larger plots, e.g. 50 ha instead of 20 ha, this will probably present a problem. Its solution lies in correcting the digital terrain model for the river gradient. In this way, a continuous variable would be created, indicating the *relative* catena position for each point in the forest. In their study in Costa Rica Lieberman et al. (1985) also directly compared plots with the same absolute elevation, although one plot was close to the main river and the other two were situated further upstream in the tributary water basins.

> ***When comparing contour samples it is advisable to check the altitude levels of the valley bottoms where they occur within a plot, and to examine the need for a correction. The relative altitude above the valley bottom level should be assessed for any permanent sample plot in tropical rain forest*** (see also Alder & Synnott 1992).

Species composition on a slope position could be assessed more precisely by increasing the size of the contour samples to e.g. 3 or 4 ha, and thus the number of trees in the sample. Within the same sample plot, this would enlarge the elevation intervals and so increase the likelihood of including different catena positions in one sample.

The contour levels separating the samples are not equidistant. This is a consequence of the choice of constant area of the samples. My method automatically adjusted the elevation interval to the steepness of the terrain. In Para, for instance, contour sample 2 on steep upper slopes covered an elevation interval of 6.5 m whereas samples 7 and 9 on gently sloping lower slopes only covered 0.9 m (Figure 43). Soil variation may be greater in samples with a wider elevation interval.

Constant area and equidistance of the contour lines are not necessarily conflicting restrictions. If I had had a much larger plot, I could have taken 2 ha subsamples from fixed elevation intervals, e.g. 2 m. Inevitably, less of the information contained in the data set would be used in this way. However, certain intervals would be so large that two or more subsamples would be available. Then also the within-sample variance for the same catena position could be assessed. In Figure 46 and Figure 47 this unexplained variance can only be roughly guessed from the oscillation of the curve around the linear trend, although this residual variance is interesting because it may reflect patterns resulting from forest dynamics and seed dispersal that are independent of environmental conditions.

A point of debate might be the homogeneity within the contour samples. When designing them, I assumed that the within-sample variation would be smaller than variation in rigid square subplots of the same size. The shape of some, however, became very elongated. Some other contour plots on lower positions were composed of subplots dispersed on the outskirts of the plot. Given the spatial *autocorrelation character of species composition, this design therefore may have lumped heterogeneous parts of the forest into the same contour plot.

Moreover, from a theoretical point of view, species richness may be expected to be greater in an elongated plot or in a set of distant subplots than in a square or circular plot (Begon et al. 1986). However, the presence of a strong slope gradient means that samples of the same *dissimilarity are found much farther along the contour line than down the slope, so the 'ideal' plot shape would amount to a very elongated ellipse, of which my contour samples are an acceptable approximation.

3.5.3 Tree density and biomass along the slope

Large tree density was found to be greatest in Zagné. This probably is caused by the abundant occurrence of *Chidlowia sanguinea* with many individuals just exceeding the 70 cm diameter limit. The great height of the emergent trees and their long boles also leave more space for the canopy trees. In Para, *Sacoglottis gabonensis* trees had broad crowns and short boles and so occupied large crown volumes, filling most of the canopy.

In Taï, Bech (1983) found that more emergent trees (h> 45 m) grew on the upper slope than in other slope positions. This was confirmed by my results. In the same forest Huttel (1977) found more trees above 13 cm diameter but fewer large trees (d>40 cm) on summit sites with iron pans. Rollet (1974) stated that the absence of larger trees generally coincides with a greater density of smaller trees. The scarcity of large trees on crests might be related to the iron pan, impeding deep rooting. Another aspect is that summit sites are more exposed to strong winds (Williams et al. 1969, Vooren 1985), so that uprooting and gap formation may be more frequent (see also Bonnis 1980, Poorter et al. 1993 in prep.).

3.5.4 Species richness gradients

***Species diversity**, which is a characteristic of a population of trees, not of an area of forest, was expressed as the number of species per 20 trees. The essential difference between ***species richness**, a plot-related characteristic, and species diversity, a population-related one, clearly emerged from Figure 48. In grassland vegetation such a distinction is uncommon, because it is not individual plants but species that are recorded. The fact that perennial phanerophytes constitute most of the life form spectrum in tropical rain forests (Guillaumet 1967), requires that the researcher makes much more detailed inventories by recording the complete spatial setting (x, y and z coordinates) of each individual.

This greater precision of rain forest relevés inspired Oldeman (1974; 1990b) in developing his forest architecture analysis. He noted that by discarding the spatial setting of the data one ascended to a level of abstraction at which much essential information on the ecosystem and its functioning was lost, e.g. by extracting average species lists and diameter distributions, by summarizing tree data in averaged basal area or stem volume figures and by averaging diameter increment figures or tree mortality data. Abstraction is part of the knowledge acquisition process, but should be done in prudent steps, as suggested by Koop (1989) or Leersnijder & Boeijink (1990). Oldeman (1974) plotted total tree height against trunk diameter, neither in order to calculate the average h/d ratio nor to fit an average h/d curve, but in order to rank the individuals and to distinguish their affinity to a reference value. Deviation is then not considered as statistical noise but as information (also cf. Hoekman 1985, for signals obtained by radar remote sensing).

Hamilton (1982) suggested that species richness increased towards **Pleistocene forest refugia**. Species richness gradients might thus be expected to be oriented towards the core areas of Pleistocene refugia. This orientation is often parallel to the actual rainfall gradient. On a 100 by 100 m plot, Faber-Langendoen & Gentry (1991) found over 250 tree species above 10 cm diameter in the very wet Chocó region in Colombia, receiving over 7 m rainfall per year. They ranked these forests among the most species-rich forests in the world and concluded that great species richness is correlated with high rainfall and with low nutrient levels (see also Bongers et al. (1988) and Hall & Swaine (1976) for further discussion of the relation between diversity and soil fertility).

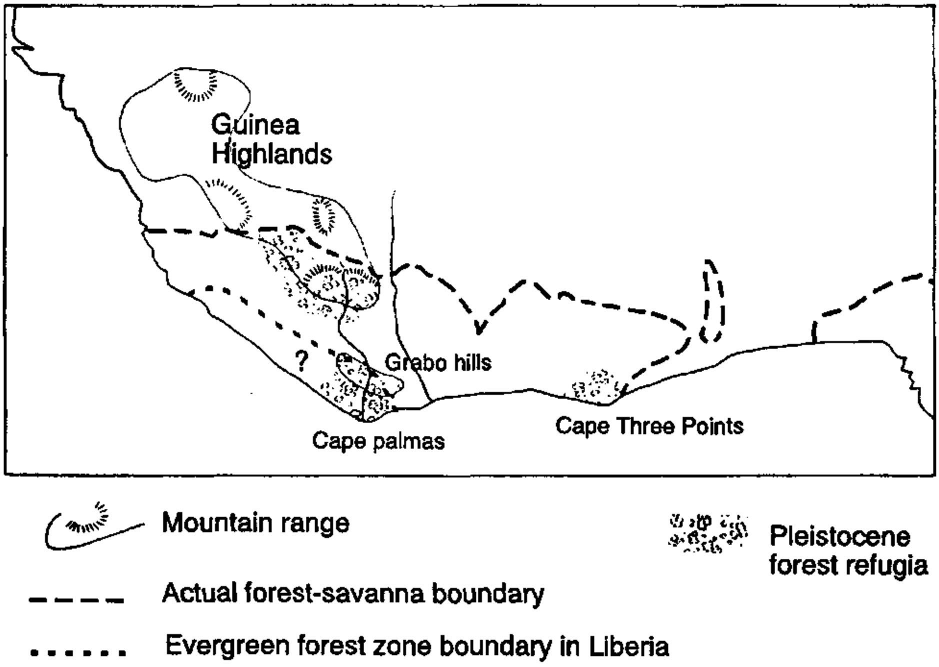


Figure 56 The hypothetical positions of the Pleistocene forest refuges in West Africa according to Guillaumet (1967). The western extent of the refuge on the hills of Grabo remains unknown (question mark on the map).

However, Maley (1987, 1991) pointed out that in West Africa refugia were not located near the coast, where nowadays the highest rainfall is recorded, but in mountainous areas. He believed that the stratiform cloud cover, generated by the upwelling of cold sea water in the Gulf of Guinea at glacial times, only produced much rain when rising over mountain ranges. He therefore doubted the existence of Pleistocene forest refugia near Cape Palmas in Côte d'Ivoire and near Cape Three Points in Ghana as suggested by Aubréville (1962) and Guillaumet (1967) and admitted only one refuge towards the Guinea Highlands. However, the region of Cape Palmas contains hills up to 750 m in Liberia (Putu range) and up to 475 m in Côte d'Ivoire and thus cannot be considered as being flat (Figure 1, Figure 56). Moreover, the sea level was up to 110 m lower than today at the time of glacial maximum (Martin 1972), so coastal relief was much more pronounced than it is now.

Based on bird distribution maps of Hall & Moreau (1970), Hamilton & Taylor (1991) supported the location of a core refugial area in SE Côte d'Ivoire and SW Ghana (Cape Three Points) but not the one near Cape Palmas in SE Liberia and SW Côte d'Ivoire. They situated another refugium core area along the coast in Sierra Leone and western

Liberia (see also Endler 1982, Mayr and O'Hara 1986). However, the sampling intensity in Hall & Moreau (1970) was much higher in Sierra Leone and western Liberia and in Ghana than it was in east Liberia and Côte d'Ivoire, so the gradients of declining species diversity pointing towards Côte d'Ivoire, as interpreted by Hamilton (1982) and Hamilton & Taylor (1991), may be a result of this sampling pattern.

Within Côte d'Ivoire plant species richness was found to be greatest in the SW and SE corners (Aubréville 1959, Guillaumet 1967) and decreases towards the centre region where the savanna comes close to the coast, called the V-Baoulé. Within Liberia, the wettest forests are centred on Greenville with endemic large tree species like *Didelotia brevipaniculata* and *Loesenera kalantha* (Figure 20). New evidence concerning narrowly endemic *Begonia* spp. again pointed at refugia in SW Côte d'Ivoire and SW Ghana (Sosef 1993 in press; see also Hall & Swaine (1981) for a discussion of the SW Ghana refugium). It is possible that the entire evergreen forest zone, sensu Sachtler (1968; see Figure 21) constituted a lowland forest refugium in glacial times, including the extreme SW corner of Côte d'Ivoire and the SE corner of Sierra Leone.

> ***The hill ridges around Grabo with summits attaining 475 m at some 50 km from the coast should be investigated further, preferably including palynological studies, to confirm the position of the hypothetical Pleistocene refugia. Special attention should be paid to the westward extent of this refugium, namely to see whether the Grabo forests have either a biogeographically unique position or are merely the easternmost part of forests found under similar climatic conditions throughout Liberia.***

Figure 57 Mount Kopé (412 m asl) is one of the summits of the hill ridges around Grabo, a hypothetical glacial forest refuge. At present, it does not yet have a protected status and is threatened by conversion to cocoa plantations and by logging.

The continuous model of rain forest variability, as presented here, brings a new dimension to the refuge theory, namely that of the "compressing" and "stretching" of such gradients under long-term oscillation of climatic conditions. Maps of a reconstruction of the vegetation cover at glacial maximum (18 000 years BP), should not only distinguish savanna from dense forest, but also indicate the gradient from evergreen to semi-deciduous forest within the whole forested zone.

I suggest that the everwet Caesalpiniaceae species from the wettest forests in Liberia might have a evolutionary migration history differing from the "normal" wet species also found in Ghana. The everwet coastal forests of Liberia may have been separated from similar forests in Cameroon for much longer than the wet evergreen forests, sensu Hall & Swaine (1981), in Côte d'Ivoire, Ghana and Nigeria. Among the original species of the everwet forests in Liberia and Cameroon, I therefore expect much more speciation to have occurred than among those of the wet evergreen forests in Côte d'Ivoire, Ghana and Nigeria.

As to the large tree species, my data showed a *decrease* in species richness from Zagné towards Para, this is in the direction of *increasing* rainfall. I also showed that this trend is related to a decrease in tree density from Zagné to Para. During a visit to the forests on Mount Kopé near Grabo several large tree species belonging to everwet environments were found which were absent from the Para study site, e.g. *Brachystegia leonensis, Cynometra ananta, Didelotia spp.*. It should be investigated whether these forests are richer in species than the Para forests. From Figure 15 in Chapter 2 no trend in species richness on a regional scale could be detected, except from a drop in species richness in the wettest forests in Liberia. Hall & Swaine (1976; 1981) found a clear species richness gradient in Ghana's forests when considering all vascular plants: high moisture was correlated with high species richness. When considering only tree species (large and small), they found no trend below 35 u.HS1 (Hall & Swaine 1976), i.e. for the wet and moist evergreen forests. All the forests I studied were wetter than this limit (see Figure 17). Gentry (1982) also found a positive correlation between species richness and rainfall for trees with a diameter above 2.5 cm, but no correlation for trees above 10 cm diameter. This means that on wetter sites the diversity of biological plant types other than trees increases markedly, which was also found by Guillaumet (1967) and de Rouw et al. (1990).

> ***The species richness of the large trees within the West African tropical rain forests does not increase with higher rainfall. On the contrary, in very wet conditions with rainfall above 30 m per ten years the diversity in large tree species is often seen to decrease. As discussed in Chapter 2, certain Caesalpiniaceae species then become single-dominant in these forests.***

With some caution I conclude that the regional maximum of tree species richness is achieved at sites with intermediate rainfall conditions, where the tree species areas of the evergreen and the semi-deciduous forests overlap. The local slope gradient found at the Taï site also provides an example of such a combination: tree species typical of semi-deciduous forests grow on the upper slope and on the crest, whereas the tree species on the lower slope are typical of evergreen forests. The entire Taï plot is therefore richer in species, but given the trend in species composition along the slope, this is ß rather than α diversity, i.e. diversity related to kinds of forests occurring besides each other, rather than species diversity within one single kind of forest.

The α-diversity, i.e. diversity per slope position, was greatest on the middle to upper slopes near Taï (Figure 48). This was also found by Huttel (1977). It might be caused by the fact that the two species groups, evergreen and deciduous, overlap in this intermediate slope position.

3.5.5 Moisture indicator values for the large tree species

DCA proved successful in extracting one single axis pinpointing vegetation composition out of a multivariate data set of up to 100 tree species. So it finally became possible to describe more precisely the ecological optima and ranges of large trees in the West African tropical rain forests, without being forced to use rather vague descriptive terms like wet or moist evergreen, semi-deciduous, transitional, etc. The ecological optimum of a species can be read from its position on the first ordination axis (see Table 3 and Table 5). Variation along this axis is apparently related to moisture, so the species scores can be used as moisture indicator values. The ecological range of the species can be read from the range of samples in which the species occurred. Adding more observations to the data set would increase the reliability of these estimates and might result in a set of more or less absolute environmental parameters of each species, similar to the indicator values Ellenberg (1979) gave to the plants of Central Europe.

To make this possible, a West African data base would have to be created including as many methodologically comparable or translatable sample plots as possible all over the Upper Guinea forest block: data collected by GTZ in Liberia (Sachtler 1968, Wöll 1981, Poker 1989 and 1992), and many herbarium specimens available in the Wageningen herbarium (Voorhoeve 1965), existing data sets from Côte d'Ivoire (Aubréville 1959, SODEFOR 1976a and 1976b, Bertault 1986, Vooren 1979 and 1985, Huttel 1977, Maître 1991, de Rouw 1991, Aké Assi & Pfeffer 1975, Aké Assi 1984 and new inventory data which are being collected at the moment by SODEFOR); and last but not least the recent Ghanaian forest inventory (Ghartey 1989, Alder 1990, Hawthorne & Juam Musah 1993) as well as the Hall & Swaine (1976, 1981) data set and the Kade data (Swaine et al. 1987). Such a project with both European and African partners would fit well into the objectives of the development programmes of the European Community.

3.5.6 Moisture availability as a site hospitality factor

I showed that vegetation composition changes along soil catenas in a similar way as along the rainfall gradient (see also de Rouw 1991). I therefore linked both gradients to the moisture available in the ecosystem. Van Herwaarden (1991b) found no difference in available moisture contents between gravelly crest and upper slope soils and non-gravelly lower slope soils (Figure 45). He found that the water contents at saturation of the ironstone nodules was up to 35 vol %, whereas quartz gravel only contained 3 vol.%. How can we then explain the wetter forests on lower slopes? Lateral drainage from uphill may be one factor (Lescure & Boulet 1985, Bruijnzeel 1990, Fritsch 1992), the groundwater level in the valley bottom may be another. All slope positions receive the same amount of rainfall, but lateral distribution and also availability of water are different.

Figure 58 Inundation of the Nsé valley bottom near the Zagné study site in September 1990. Most of the year this road can be used without any problem. These peak flow also have a great impact on the forest vegetation.

So the *hierarchy of forest gradients can be formulated as follows:

1. **a major gradient correlated with the rainfall gradient;**
2. **compensation or enhancing of the rainfall effect by bedrock at a meso-scale level.** On the one hand, under less rainfall, wetter forests are still found on sericite schist bedrock, weathered to more clayey soils, rich in ironstone gravel in the upper catena positions and with high water capacity. On the other hand, under higher rainfall, drier forests are found on granite bedrock, because the soils are sandier, the gravel is quartz and often the soil is shallow with low water capacity and frequent rock outcrops.
3. **small-scale slope gradients sliding on the regional gradient.** Summits carry rather dry forests because an iron pan in the subsoil hampers the roots from reaching the underlying clayey rotten rock. Lower down the slope, the rainfall water is augmented by lateral seepage and flow.

The two sources of rainfall compensation, i.e. bedrock and slope position, are strong enough to induce differences in forest composition which would otherwise be found 50 or 100 km further away on the main rainfall gradient. This means that the species composition of a random sample of forest for which two of the three sources of forest variation are unknown, remains highly unpredictable. Careful assessment of all three sources allows the moisture in a forest's environment to be predicted and the corresponding tree species composition derived.

The calculation of the compensation factors as part of an algebraic explanatory model was beyond the scope of this study. However, I indicated that schist bedrock resulted in a rise of about 30 u.DCA1 of Chapter 2 in Figure 13. On granite bedrock near Para I found forests containing numerous tree species also found in Zagné, which is some 70 u.DCA1 of Chapter 2 drier on the regional gradient. Along the Taï catena the forests on the crest are some 50 u.DCA1 of Chapter 2 away from the lower slope forests. The axes, provided by DCA, compress species information into a single dimension which can be further used in algebraic modelling.

As shown in Chapter 2, it is difficult to quantify climate and bedrock. Furthermore, along the soil catena rooting depth as well as the processes involved in lateral internal drainage remain largely unknown. The interdisciplinary terminology developed by Beaudou et al. (1978) and Richard (1989) can be used to describe and analyse these "layered" abiotic and biotic phenomena.

3.6 Conclusions

A series of two hectare *contour samples allowed compositional gradients of large trees to be analysed along slopes. The ordination of the contour samples clearly demonstrated that tree species composition was strongly determined by slope position.

The simultaneous ordination of the three sites showed that these local slope gradients were sliding gradients superimposed on the regional gradient. The regional gradient was related to rainfall and lithology. These factors were largely expressed in soil moisture availability. Gradients in moisture availability hence are expected to explain the slope gradients too.

So, I conclude that moisture correlates well with tree species composition in West African rain forests. For a given forest, moisture conditions are a function of climate (rainfall, temperature, air humidity), lithology (determining essential characteristics of the soil catena) and slope position (local hydrology, presence of a hardpan).

As to large tree species richness, no positive correlation was found with moisture conditions. On the contrary, a decrease in large tree density and species richness was found towards the wettest study site. This supports the hypothesis that maximal tree species richness is related to intermediate rainfall conditions.

Having studied the great variability of tropical rain forests at several scale levels, I warn against the artless use of averaging and mixing techniques in rain forest studies, which are based on over-simplified models of forest reality. The patterns in the three-dimensional settings in natural forest ecosystems must be respected. I created the contour sampling technique to provide a sensitive tool for this purpose.

4 IMPLICATIONS OF THE CONTINUOUS VARIABILITY MODEL FOR FOREST MANAGEMENT AND CONSERVATION OF BIODIVERSITY

In this Chapter, some implications of the continuous variability model are evaluated. What can forest managers and conservationists do with the results from the present study? This Chapter suggests ways of using this model, after confronting it with the practice of forest management and nature conservation in West Africa.

4.1 Forest management

Sustainable forest management has not yet been attained in West Africa (Parren & de Graaf 1993 in prep.). Timber mining companies have been profitably managed, not the forests. Future management should focus first on conservation of remaining forest areas and of nature and timber and other "values" in these forests. Another important task for forestry will be the rehabilitation of overexploited and depleted forests and of degraded agricultural land (WRR 1992). The present book depicts the forest wealth before exploitation, but additional research must be done on the numerous problems encountered in such rehabilitation.

4.1.1 Forest inventory

The classic methods used for timber inventory Côte d'Ivoire and Ghana were based on systematic line-sampling with a high sampling intensity in the line and a large distance between lines (DRC 1967a, SODEFOR 1976a and 1976b, Ghartey 1989). For the Liberian inventory, the area under investigation was divided into blocks of 8 km² each, within which the location of tracks (lines or squares) was determined at random (Sachtler 1968). The use of blocks introduced a systematic element into the inventory method.

An alternative method that involuntarily profited by the slope gradients present in the forests was used in the soil survey of SW Côte d'Ivoire (DRC 1967b, see also Gillison & Bremer 1985). Large rectangular blocks of 50 ha each which included all topographical positions were delimited. Both soil and trees were studied within these blocks. Unfortunately, I did not manage to retrieve the original tree data but the three-dimensional representations of these landscapes are included in the report of DRC (1967b). Some of these have been reproduced by de Rouw et al. (1990).

A parallel can be drawn with two existing approaches to soil survey (Blokhuis 1993). Either a regular grid is laid over the landscape and at each grid node the soil is described, or the surveyor first studies intensively a number of representative catenas and tries to understand the pedogenetic processes that lead to the present situation (cf. Fritsch 1980). Special attention is paid to lateral relations between slope positions as induced by drainage, transport of soil material and erosion.

I believe that the latter approach can be much more informative in matters of forest ecology, forest architecture analysis and the study of forest dynamics. Narrow strips of forest may be sufficient for the timber miner to calculate the richness of his wooden ore, but for the forest manager who wants to intervene in the forest ecosystem in an ecologically sound way, the relation between forest composition and geomorphology of the terrain is of major importance (van Miegroet 1976, Mayer 1981, Fanta 1985, Oldeman 1991).

The species DCA scores presented by Hall & Swaine (1981) and in the present study provide a helpful framework to precisely determine the position of any newly sampled West African forest area on the regional gradient. The impact of lithology can be assessed on the forest gradient map by comparing the score of this sample with nearby samples underlain by different bedrock. In addition, the degree of compensation on a particular site as a result of catena position can be evaluated from the correlation of local gradients with the regional gradient. To increase the reliability of species and sample scores, all existing and newly gathered information should be compiled into an integrated interactive data system.

4.1.2 Assessment of forest productivity

Besides an inventory of the existing stock, a forest manager needs information on forest dynamics and productivity (de Graaf 1986). As the present forest is the result of its growth in the past, the evaluation of the productive quality of a site will rely heavily on our knowledge about the vegetation catenas. The method proposed by Alder & Synnott (1992) to install permanent sample plots of 1 ha, randomly distributed over the forests, again disregards the landscape coherence of these forests. Therefore, information on mortality, regeneration and increment of the 100 largest tree species in West African forests, should be collected in much larger plots, covering at least one complete catena. Forest dynamics are driven by the mortality of the very big trees (Vooren 1992c) and value increment is realized by their diameter growth (Stoffers 1989). Only 5 to 10 such trees occur on a 1 ha plot. So, *catena plots* of 50 ha as used by DRC (1967b) are definitely more appropriate in these specific forests than 1 ha permanent sample plots.

Regeneration surveys should be oriented to entire populations of a species, instead of applying 'standard' systematic subsampling of the smaller diameter or height classes (Swaine & Hall 1988; de Klerk 1991). Phenology, seed production, seedling establishment and juvenile growth should be studied species by species. Otherwise there is a risk of gathering vast amounts of largely useless data. Here also the knowledge of the existence of catena gradients should be used.

4.1.3 Forest sensitivity to climatic change

The strong dependence of tree species on moisture conditions, as demonstrated in Chapters 2 and 3, implies that they are sensitive to climatic change. Climatic change may or may not be induced by large-scale deforestation. But climate is known to be dynamic and forests migrated over considerable distance to adapt to such changes in Pleistocene times (Hamilton 1992). There was, however, great stress and many species became extinct; this accounts for the relative actual poverty of the West African forest flora and fauna (Hamilton 1976, Hall & Swaine 1981). Forest managers wish to arm the forests against future modifications by controlling the hydrological cycles (Monteny & Casenave 1989) and by ensuring that the moisture does not leave the ecosystem too quickly. In the

Figure 59 Excessively logged forest in N'zo fauna reserve north of Taï National Park. The canopy has been opened up completely and the control of the forest ecosystem on moisture conditions severely weakened.

event of climatic change, species composition will change too. Stability, if it ever existed, is lost. This may explain the lack of regeneration of certain emergent tree species as found by Aubréville (1938) and de Klerk (1991) and as discussed by Swaine & Hall (1988).

Excessive opening up of the forest canopy by timber exploitation weakens the forest ecosystem's ability to control moisture conditions (Figure 59) and so induces a shift in species composition towards drier conditions. It is to be expected that timber production forests under sustained management will occupy a drier position on the vegetation gradient than the pristine forest that once existed on that spot. As mentioned in Chapter 3, *Budowski's (1965) rule says that "secondary" tree species in wetter forests which are likely to profit from canopy openings, are also characteristic of drier forests (Guillaumet 1967). Forest exploitation may therefore result in a "drier" forest composition.

- verschil! G - vri!

4.1.4 Forest harvesting systems

Several cycles of logging most often preceded forest management. The state in which the forest is left by the loggers largely determines which silvicultural techniques can be applied afterwards. However, measures will be more effective if the forest manager does not wait until the logging dragon has appeased his hunger but starts right away with the domestication of the loggers (de Graaf 1986) and tries to get their harvesting habits under his control (Vooren 1992c). Ultimately, tree spotting, i.e. the selection of the trees to be harvested, is the responsibility of the Forest Service. This has been practised in Ghana for decades (Parren & de Graaf 1993 in prep.).

Hendrison (1990) studied actual and improved logging systems in Suriname. He stressed the importance of a careful design of the skidding pattern to reduce damage to the remaining stand. In Côte d'Ivoire, forest roads are preferentially constructed on the water divides on crest soils. The forests richest in timber are often located besides the crests on upper and middle slopes (Vooren 1985). Excessive felling and damage in these most valuable forests is like pulling the heart out of the future timber production forest. If these parts of the forests crucial for timber production are severely damaged, future production will be late and poor, even if the rest of the forest landscape remains untouched. In other words, the yield, calculated over an entire landscape but taken from the richest parts of the forest, is not a sustainable yield. *Average damage* might be slight, but *local devastation* of the most productive parts is complete.

It is a common mistake to consider the entire forested area in a forest reserve as productive forest (see also Vanclay 1989). Real value production can only be assured in that part of the landscape where soil conditions are optimal for forest growth. Swamps, ravines, rocky outcrops and iron pans reduce the proportion of really useful forest land. In industrial plantations of rubber trees (*Hevea brasiliensis*), the SAPH (Société Africaine pour les Plantations d'Hévéa, west of Zagné) only planted trees on this more suitable half of their concession. I advise forest managers to apply this also to their forests, as was the practice in Queensland (Vanclay 1989). Productivity figures of 2 m^3 ha^{-1} y^{-1} obtained from sample plots on fertile soil (Maître 1991) should not be expected from the entire forest estate (Ministère des Eaux et Forêts 1988), but maximally from half of it, and then only if not all highly productive large trees in these forests have been logged or destroyed.

4.2 Conservation of biodiversity

4.2.1 Land use planning: conservation over the entire gradient

Chapter 2 showed a continuous change of tree species composition from the Liberian coast towards the forest-savanna boundary. Each part of the gradient has its proper species that attain their optimum there. As a consequence, species conservation areas should extend along the entire gradient. But how can we find a compromise between conservation along the entire gradient, and the designation of reserves large enough to attain the minimum area needed by large mammals to survive? In any case, there are no forests left in West Africa covering areas so large that poachers are unable to affect the mammal populations. Large mammals like elephants or buffaloes manage to survive in secondary forests as well (Hoppe-Dominik 1989), in even larger densities than in pristine forests.

4.2.2 Corridor establishment: the Green Sickle

The problem of isolated populations could be partially solved by installing corridors. Would it be feasible to make a linked natural infrastructure from the semi-deciduous forests in Forêt Classée du Haut-Sassandra and the Mount Péko National Park, over the Réserve de faune du N'zo, Taï National Park and Grebo National Forest towards Sapo National Park, Krahn-Bassa National Forest and ending near the mouth of Cestos River (Figure 60)? Such a "Green Sickle" would not necessitate the removal of all human settlements in the corridors, but these regions could be given a "greener" appearance, with permanently protected patches and belts of forests along water courses. It must be explained to local people that the 100 % exploitation of landscape and wildlife will not bring salvation to their children. In western Europe, private forestry is subsidized to provide recreation, timber, wildlife habitats and landscape scenery. To some extent these forest functions are also valid in the villages and towns in West Africa (Vooren 1987, 1992a).

4.2.3 Urgent conservation priorities

From a biodiversity point of view the attention of conservation agencies and Ministries should be drawn to two promising areas within Côte d'Ivoire where many results could still be obtained:

- *the semi-deciduous forests*, which contain their proper biodiversity. To date, conservation efforts in these formerly timber-rich forests have lagged behind, both in Ghana and in Côte d'Ivoire. I suggest improved protection plans for Marahoué National Park in central Côte d'Ivoire and e.g. the Forêt Classée du Haut-Sassandra.

- *the wettest forests of Côte d'Ivoire*. The hypothetical Pleistocene forest refuge on the hills of Grabo merits the status of National Park. No foreign aid programme has yet focused on these forests, which Guillaumet (1967, p. 72) praised as "C'est du Sud-Ouest, la forêt la plus riche et la plus belle que nous connaissions".

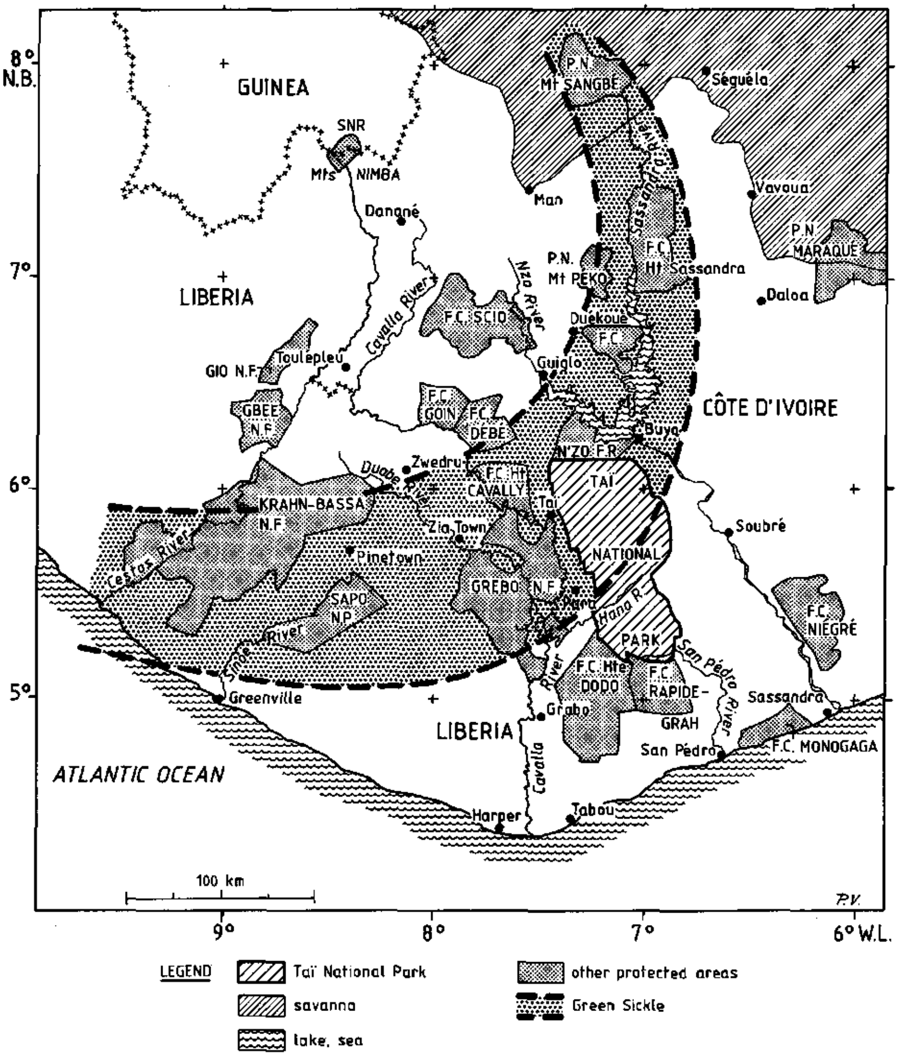


Figure 60 The Green Sickle, a green zone stretching from Mount Sangbé National Park in savanna over Taï National Park towards the Atlantic Ocean. The installation of corridors between existing reserves can guarantee the conservation of biodiversity over the entire gradient.

Other core areas in Liberia should receive all necessary protection. Further research could clarify the issue of diversity centres in the region. Near the mouth of Cestos river, between River Cess and Bafu Bay, the rain forest still borders the Atlantic Ocean for long stretches, an ideal place to preserve all natural ecosystems from the beach and the lagoons near the river's mouth up to the everwet rain forests inland (Figure 61).

4.3 Epilogue

Forest gradients on regional and local scale explain a considerable part of the forest variability in West Africa. A forest gradient is essentially an ecosystem gradient. The large tree species I studied are only one set of forest organisms, albeit impressive ones and the pillars of forest architecture. Gradient studies on other sets of organisms and at other levels of scale will provide additional insight into the functioning of tropical forest ecosystems. The faunal aspect has been neglected in this book, but is of paramount importance in rain forest ecology. Koptur (1985), for instance, studied plant-animal relations along an elevational gradient in Costa Rica and demonstrated alternative defences of trees against herbivores along the gradient.

On a more general level, I hope that gradient approaches may find further acceptance among ecologists and other scientists. Since the 18th century people have been at great pains to classify all kinds of phenomena in this world. Now a promising path is to focus on transitions and fuzzy limits and to redefine and reappreciate the variability of nature. At the beginning of this study I abandoned existing classifications and this seemed to be a step back into uncertainty, but in the end it yielded a cleared and quantified picture of the ever changing rain forest kaleidoscope.

Forests are not just hectares, trees not just cubic metres. The management of the most species-rich ecosystems on earth is a challenge for present and future generations. It will need international support and the efforts of all those fascinated by this pearl of our blue planet.

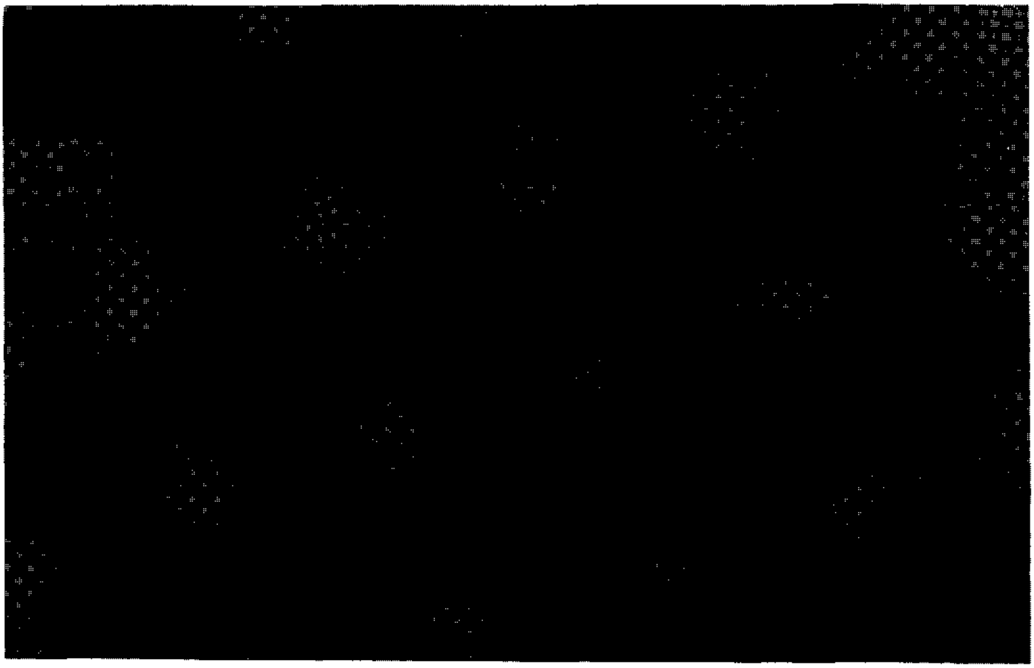


Figure 61 A mother elephant bathing her young in the Atlantic Ocean. Based on sightings in Gabon, reproduced from Bosman & Hall-Martin (1986). An image for the future in West Africa?

GLOSSARY

autocorrelation: (spatial -) an attribute is said to be spatially autocorrelated when sample points close together tend to be more similar than points further apart, but often without easy, direct relation between sample site location and the value of the attribute (Burrough 1987)

Budowski's rule: Budowski (1965) stated that pioneer or secondary woody species of the humid tropics generally have a geographical area that includes drier regions. Oldeman (1990b) amended its formulation, so that it may be applied world-wide: any plant species which plays a pioneering role in hospitable environments has a geographical distribution which includes less hospitable environments.

catena: (< Latin, chain) a connected series of related things; e.g. a *soil catena (see there)

centroid: centre of mass, e.g. from a cloud of points in two- or three-dimensional space

classification: (vegetation -): the modelling in discrete units of vegetation by identifying sociological or ecological species groups after first arranging species and samples and then clustering them. Combinations of these groups define community types, each with characteristic species combination (after Zonneveld 1988).

clustering: methods for grouping species and samples. There are agglomerative and divisive clustering methods (van Tongeren 1987).

compensation: (of ecological factors) interaction between factors in such a way that they may counterbalance each other's effects (e.g. soil moisture and climatic moisture)

continuum: something that is continuous, e.g. a forest continuum. The term 'continuum' applies to the spatial variable itself and not to the direction or rate of change of the variable (cf. *gradient).

contour sampling: combining a vegetation sample for gradient analysis by selecting trees growing between two elevation contour lines. Coordinates of the trees must be known and a digital terrain model of the plot available.

cohort: (in forest ecosystem analysis) contains all individuals of one species within one ecosystem that are of the same age (Oldeman 1990b)

dissimilarity: the degree of ecological difference between vegetation samples or species, sometimes expressed as a distance function (see van Tongeren 1987)

diversity: see species diversity

dynamics (forest -): all processes of growth, death and species reproduction taking place during *silvigenesis

ecological amplitude: (of a species) indicates the range of the environmental variables within which the species occurs, e.g. temperature range, range in rainfall conditions, etc.

eigenscale: (by analogy with *eigenvalue) term indicating that objects (such as trees) of different size that are studied together, are to be considered each at their proper (in German and Dutch: eigen) scale in matters of area of distribution and of dispersion. See also Walter (1974) who discussed different scales for different plant sizes.

eigenvalue (of an *ordination axis): a value, proper to the *eigenvector of the axis, indicating the dispersion of the species scores on the *ordination axis. In this way it is a measure of the importance of the axis (ter Braak 1987a).

eigenvector: the vector characterizing an *ordination axis. If an extra iteration cycle is carried out, the scores remain the same, so the vector is transformed into itself (ter Braak 1987a).

endemic (species): restricted to a particular geographical area or country (Webster's Dictionary 1976)

factor (environmental - ; < Latin, maker): something that actively contributes to the production of a result, e.g. plant growth (Webster's 1976)

false absent: a species not found in a certain sample and thus falsely considered to be absent if it does occur but is not detected because of the inventory method used, e.g. because sample plots were too small, because only trees above a certain diameter limit were considered, or because only commercial trees species were recorded.

forest: 1. (uncountable noun) land including a tree cover; 2. (countable noun) a plant and animal community in a given abiotic environment

forest architecture: spatio-temporal structure linked to a well-defined hierarchical level (Oldeman 1990b), here the forest ecosystem levels

forest complex: a large forested area, like a National Forest or a National Park, which for an inventory needs to be split up into inventory compartments

forest block: a geographically more or less contiguous group of forests, covering e.g. 500 000 to 1 000 000 ha. Typically, the West African forests can be grouped into three such blocks separated by deforested areas.

forest dynamics: see dynamics

forest inventory compartment: area of forest for which the inventory results are given separately in the reports. Such an area generally covers 20 000 to 50 000 ha.

forest sample plot: a contiguous area of forest for which the data are recorded in one set of files during the fieldwork. Such plots can be 1 ha, 20 ha as in Chapter 2, or 2 ha as in Chapter 3.

forest structure: the mathematical expression of structure of the trees in a forest sample plot, e.g. as expressed by size (diameter or height) class distributions (cf. Rollet 1974)

forest zone: a living, forested vegetation zone, corresponding to a certain abiotic climatic zone. The concept of zonation implies large geographical areas and a more gradual change between zones than between e.g. types (Sachtler 1968).

gradient: 1. change in the value of a quantity per unit of distance in the direction of greatest change, mathematically expressed as a vector (Webster's Dictionary 1976, Gillman & McDowell 1973), e.g. a river gradient: the degree of slope of the river in m per km. For non-linear or non-planar continua the gradient vector differs from point to point. 2. a regularly increasing or decreasing change in a factor, e.g. temperature (Lincoln et al. 1982) 3. a character gradient, also called 'cline', e.g. when samples from areas not in contact, are compared and arranged according to this character to form an imaginary continuum (Sobolev & Utekhin 1973)

hierarchy: a system organized in levels from lowest to highest in which one higher-level system adds coherence to several subsystems one level lower. In ecology: a series of levels in which each lower level consists of smaller subsystems of the higher level (e.g. forest-organisms-organs-cells, Oldeman 1990b).

interval scale: a scale which possesses a constant unit of measurement. The differences between values can be compared with each other, e.g. temperature in degrees centigrade (Jager & Looman 1987).

inventory strata: distinguished in the inventory method "Stratified sampling". Strata (like swamp forest, rocky outcrops, natural low bush, etc.) are often distinguished by aerial photo-interpretation.

isohyet: line on a map joining places receiving the same amount of rainfall

kriging: a spatial interpolation technique, developed by Krige (1951), that calculates the interpolated value of a spatial variable as a linear combination of the values from several nearby observations. The weight of these observations depends on the degree of spatial *autocorrelation of the variable (Stein & Corsten 1991)

objective: adj. 1. dealing with outward things, actual facts, etc. uninfluenced by personal feelings or opinions (Hornby et al. 1974); 2. (of a choice or a method) accompanied by a user's guide so that it can be checked or repeated in the same way, i.e. independently of the researcher (subject) (Oldeman 1990b)

ordinal scale: a scale of measurement that implies a rank order between the values of classes, e.g. the Braun-Blanquet scale for measuring abundances of plants (Jager & Looman 1987).

ordination: a technique used in vegetation science by which vegetation samples and species are arranged in a uni- or multidimensional order (Goodall 1954)

pattern: (originally: visible organization of a woven tissue) spatial configuration (Webster's Dictionary 1976); see also Grace (1989)

pelophilous species: species growing on clayey soils with a high water retention capacity (Mangenot 1955, Guillaumet 1967)

peneplain: ('pene'(Latin)=almost) a flattish plain resulting from erosion (in geomorphology; Ahn 1970)

psammophilous species: species growing on sandy soil with a small water retention capacity (Mangenot 1955, Guillaumet 1967)

rain forest: see tropical rain forest

sequence: a continuous or connected series of discrete units or events

scale: see interval, ordinal scale

silvigenesis: the process containing and organising all processes making a forest, e.g. forest dynamics, succession, pollination, dispersal, etc. (Oldeman 1990b)

similarity: expresses their ecological resemblance of two sites or species. Several indices of similarity exist (see van Tongeren 1987; see also dissimilarity).

soil catena: a sequence of soils underlain by similar bedrock and occurring under similar climatic conditions, but having different characteristics due to variation in relief, in natural drainage and in position in relation to other soils (Ahn 1970)

spatial gradient analysis: an analysis of the gradual change of e.g. the species composition of the forest vegetation, but taking full account of the spatial setting of the samples. After ordination of the samples, contours of the gradient are drawn on the map using spatial interpolation techniques (see also ter Braak 1987b).

species diversity: the diversity of species within a given number of organisms. Several indices exist, each taking into account the number of individuals per species (see e.g. Krebs 1985).

species richness: the number of species on a sample plot (Krebs 1985, Begon et al. 1986)

structure: see forest structure

subjective: (of a method or choice) the grounds for the choice are not or cannot be fully explained and so cannot be divorced from the person who made the choice.

sustainability: the capability to supply services and products at one and the same fixed level and/or rate over an undefined but long time span

topology: 1. topographical study of a particular place; in this sense used by Ramensky (ex Sobolev & Utekhin 1973). 2. a branch of mathematics that investigates the properties of a geometric configuration (as a point set) that are unaltered if the configuration is subjected to a one-to-one continuous transformation (Webster's 1976)

toposequence: a sequence of topographical positions; e.g. from the lowest point (valley) to the highest point (hill summit) in a landscape

trend: general direction of change, in space or time (Webster's 1976)

tropical rain forest: in the present book, I use this term in its broadest sense to indicate the closed-canopy forests south of the savanna region in West Africa.

Type II error: is made when a null hypothesis is falsely accepted (Sokal & Rohlf 1969)

ubiquitous: omnipresent

upland: in the present book: referring to the upper part of the *catena; oppos.: swamp and lower slope forests at the lower part of the catena

vegetation classification: see classification

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APPENDICES

Appendix I List of large tree species occurring in SE Liberia and SW Côte d'Ivoire, including synonyms

All species from the forest inventories in Chapter 2 are listed, as well as those found in my three sample plots in Taï National Park (Chapter 3). Nomenclature follows Hall & Swaine (1981, H), Voorhoeve (1965, V), Aubréville (1959, A) or Hutchinson & Dalziel (1954-1972) D, in that order. Synonyms have no code (colomn 1) before the scientific name (2) and in column (3) there is referred to the name used in this book. The source of the scientific name is given in column (4); "-" means: not mentioned in this reference; "." means: mentioned with another name. Column (5) gives a reference that mentiones the species for SE Liberia or SW Côte d'Ivoire (Guillaumet 1967, G; Sachtler 1968, S; de Rouw et al. 1990, R; de Rouw 1991, R91;).

Columns (6) to (11) give the number of trees in the size classes >70 cm diameter (Z,T,P) and 30<d<70 cm (z,t,p) in the sample plots Zagné (23 ha for >70 cm, 10 ha 50-70 cm, 5 ha 30-50 cm), Taï (24 ha for >70cm, 12 ha 50-70 cm, 8 ha for 30-50 cm) and Para (22 ha for >70 cm, 10 ha 50-70 cm, 6 ha 30-50 cm). The maximal diameter found is given in column (12); the air-dry wood density in g per dm^3 in column (13), sources: Bolza & Keating 1972, Dudek et al. 1981, Durand 1985, Vivien et Faure 1985).

					occurrence							
					Zagne		Taï		Para			wood
code (1)	scientific name (2)	family (3)	source (4)	(5)	Z (6)	z (7)	T (8)	t (9)	P (10)	p (11)	dmax (12)	density (13)
Aci.bar	Acioa barteri (Hook.f. ex Oliv.) Engl.	Chrysobal .	HVA			1					38	
	Afrormosia elata Harms	=Per.ela	..A									
Afr.afz	Afrosersalisia afzelii (Engl.) A.Chev.	Sapotacea .	HVA					1			50	980
Afz.bel	Afzelia bella Harms var.gracilior Keay	Caesalpin .	HVA		1				2	1	83	700
Afz.bra	Afzelia bracteata T.Vogel ex Benth.	Caesalpin .	-VA	G,V								
Alb.adi	Albizia adianthifolia (Schumach.) W.F.Wight	Mimosacea .	HVA	R								
Alb.fer	Albizia ferruginea (Guill. & Perr.) Benth.	Mimosacea .	HVA		1						141	600
Alb.gla	Albizia glaberrima (Schumach. & Thonn.) Benth.	Mimosacea .	HVA		1						100	670
Alb.zyg	Albizia zygia (DC.) J.F.Macbr.	Mimosacea .	HVA		3						105	500
Als.boo	Alstonia boonei De Wild.	Apocynace .	HV.		3	1					120	360
	Alstonia congensis Engl.	=Als.boo	..A									
Amp.pte	Amphimas pterocarpoides Harms	Caesalpin .	HVA		1		3		2	2	100	750
Ani.rob	Aningeria robusta (A.Chev.) Aubrév. & Pellegr.	Sapotacea .	HVA		3		4	2			140	500
Ano.kla	Anopyxis klaineana (Pierre) Engl.	Rhizophor .	HVA		8	3			4		100	880
Ant.nob	Anthocleista nobilis G. Don	Loganiace .	H-A				1		8	16	94	550
Ant.cra	Anthonotha crassifolia (Baill.) J.Léonard	Caesalpin .	--A					2			44	
Ant.fra	Anthonotha fragrans (Bak.f.) Exell & Hillcoat	Caesalpin .	HVA		8	1	8	2	1		130	750
Ant.mac	Anthonotha macrophylla P.Beauv.	Caesalpin .	HVA				1	10		3	115	910
	Antiaris africana Engl.	=Ant.toa	.VA									
Ant.toa	Antiaris toxicaria Leschenault subsp. welwitschii (Engl.) C.C.Berg, var. africana	Moraceae .	H..		2		2				115	430
Ant.tow	Antiaris t. subsp. w., var. welwitschii	Moraceae .	H..				1		1		135	430
	Antiaris welwitschii Engl.	=Ant.tow	..A									
Ant.mic	Antrocaryon micraster A.Chev. et Guillaum.	Anacardia .	HVA	R								
Ara.soy	Araliopsis soyauxii Engl.	Rutaceae .	H..									720
	Araliopsis tabouensis Aubrév. & Pellegr.	=Ara.soy	.VA									
Aub.tai	Aubregrinia taiensis (Aubrév. & Pellegr.) Heine	Sapotacea .	HV.				2	2			100	600
Aub.ker	Aubrevillea kerstingii (Harms) Pellegr.	Mimosacea .	HVA		1						83	850
Aub.pla	Aubrevillea platycarpa Pellegr.	Mimosacea .	HVA				1				150	850
Bal.wil	Balanites wilsoniana Dawe & Sprague	Balanitac .	HVA		1	1	1				140	500
Bei.bit	Beilschmiedia bitehi Aubrév.	Lauraceae .	-VA	R								
Bei.man	Beilschmiedia mannii (Meisn.) Benth. & Hook.f.	Lauraceae .	HVA				4	2			83	710
Ber.con	Berlinia confusa Hoyle	Caesalpin .	HVA									
Ber.occ	Berlinia occidentalis Keay	Caesalpin .	HVA	R								
Bli.wel	Blighia welwitschii (Hiern) Radlk.	Sapindace .	HVA		2						81	900
	Bombax brevicuspe Sprague	=Rho.bre	H.A									
Bom.buo	Bombax buonopozense P.Beauv.	Bombacace .	HVA		5		1				120	380
	Bosquiea phoberos Baill.	=Tri.mad	.-A									
Bra.leo	Brachystegia leonensis Hutch. & B.Davy	Caesalpin .	-VA	G								

code (1)	scientific name (2)	family (3)	source (4)	 (5)	Z (6)	z (7)	T (8)	t (9)	P (10)	p (11)	dmax (12)	density (13)
Bre.lep	Breviea leptosperma (Baehni) Heine	Sapotacea .	HV.			1					52	600
	Breviea sericea Aubrév. et Pellegr.	=Bre.lep	..A									
	Bridelia aubrevillei Pellegr.	=Bri.gra	..A									
Bri.gra	Bridelia grandis Pierre ex Hutch.	Euphorbia .	HV.		1						80	590
	Brieya fasciculata De Wild.	=Pip.fas	.-A									
Buc.cor	Buchholzia coriacea Engl.	Capparace .	H-A	R								
Bus.occ	Bussea occidentalis Hutch.	Caesalpin .	HVA			10		1			62	1010
Cac.bre	Caloncoba brevipes (Stapf) Gilg.	Flacourti .	--A					2		4	40	
Cal.aub	Calpocalyx aubrevillei Pellegr.	Mimosacea .	-VA		24	2			7	6	130	470
Cal.bre	Calpocalyx brevibracteatus Harms	Mimosacea .	HVA			50		46		3	65	
Can.sch	Canarium schweinfurthii Engl.	Burserace .	HVA		2				2	1	130	530
Can.arn	Canthium arnoldianum (De Wild.& Th.Dur.) Hepper	Rubiaceae .	H-.		2	4		2			89	
Can.man	Canthium manense Aubrév. & Pellegr.	Rubiaceae .	--A			1					52	
	Canthium tekbe Aubrév. & Pellegr.	=Can.arn	.-A									
Car.pro	Carapa procera DC.	Meliaceae .	HVA	R								
Cas.aub	Cassia aubrevillei Pellegr.	Caesalpin .	--A			1		2			64	
Cas.fik	Cassia fikifiki Aubrév. & Pellegr.	Caesalpin .	--A					2			47	
Cas.nia	Cassipourea nialatou Aubrév. & Pellegr.	Rhizophor .	-VA	V								
Cei.pen	Ceiba pentandra (Linn.) Gaertn.	Bombacace .	HVA		6		4				230	320
Cel.ado	Celtis adolfi-friderici Engl.	Ulmaceae .	HVA			1					64	740
Cel.mil	Celtis mildbraedii Engl.	Ulmaceae .	HVA	R91								
Chi.san	Chidlowia sanguinea Hoyle	Caeselpin .	HVA		109	174	12	15			117	950
Chl.exc	Chlorophora excelsa (Welw.) Benth.	Moraceae .	HVA		2						95	640
Chl.reg	Chlorophora regia A.Chev.	Moraceae .	HVA		4						120	640
	Chrysophyllum africanum DC.	=Chr.del	..A									
Chr.alb	Chrysophyllum albidum G.Don	Sapotacea .	HVA	V								
Chr.del	Chrysophyllum delevoyi De Wild.	Sapotacea .	HV.									
Chr.per	Chrysophyllum perpulchrum Mildbr. ex Hutch. & Dalz.	Sapotacea .	HVA	V								
Chr.pru	Chrysophyllum pruniforme Pierre ex Engl.	Sapotacea .	HVA					1			38	
Chr.tai	Chrysophyllum taiense Aubrév. & Pellegr.	Sapotacea .	--A		3	5	3	60		1	84	740
Coe.oxy	Coelocaryon oxycarpum Stapf	Myristica .	HVA									650
Col.cor	Cola lateritia K. Schum	Sterculia .	HVA			2					34	610
Col.nit	Cola nitida (Vent.) Schott & Endl.	Sterculia .	HVA					1			32	
	Combretodendron africanum (Welw. ex Benth. & Hook.f.) Exell	=Pet.mac	..A									
	Combretodendron macrocarpum (P.Beauv.) Keay	=Pet.mac	.V.									
Cop.sal	Copaifera salikounda Heckel	Caesalpin .	HVA				1	1			100	780
Cor.pla	Cordia platythyrsa Bak.	Boraginac .	H-A									500
Cor.pac	Corynanthe pachyceras K.Schum.	Rubiaceae .	H-A		4	19	4	119		3	96	760
Cou.edu	Coula edulis Baill.	Olacaceae .	HVA			1		27	3	67	80	990
Cru.gab	Crudia gabonensis Pierre ex Harms	Caesalpin .	HVA	V,G								
Cru.kla	Crudia klainei Pierre ex De Wild.	Caesalpin .	-VA	R								
Cry.min	Cryptosepalum minutifolium Hutch. & Dalz.	Caesalpin .	-VA	G								
Cry.tet	Cryptosepalum tetraphyllum (Hook.f.) Benth.	Caesalpin .	HVA	V,S								
Cyn.ana	Cynometra ananta Hutch. & Dalz.	Caesalpin .	HVA	R								
Cyn.meg	Cynometra megalophylla Harms	Caesalpin .	HVA	R								
Dac.kla	Dacryodes klaineana (Pierre) H.J.Lam	Burserace .	HVA				2	1	3	4	100	610
Dan.oge	Daniellia ogea (Harms) Rolfe ex Holl.	Caesalpin .	HVA	V								
Dan.thu	Daniellia thurifera Benn.	Caesalpin .	HVA		2	1					143	550
Det.sen	Detarium senegalense J.F.Gmel.	Caesalpin .	HVA		1				1		123	730
Dia.aub	Dialium aubrevillei Pellegr.	Caesalpin .	HVA		1	1	2	17	5	13	119	970
Dia.din	Dialium dinklagei Harms	Caesalpin .	HVA	R								
Dia.gui	Dialium guineense Willd.	Caesalpin .	HVA									
Did.bre	Didelotia brevipaniculata J.Léonard	Caesalpin .	-V.	G								
Did.ida	Didelotia idae Oldeman, De Wit & Léonard	Caesalpin .	-V.	G								
	Didelotia unifoliolata Oldeman, De Wit & Léonard	=Did.ida	-.A									
	Diospyros ivorensis Aubrév. & Pellegr.	=Dio.man	.-A									
Dio.man	Diospyros mannii Hiern	Ebenaceae .	H-A					1			36	960
Dio.san	Diospyros sanza-minika A.Chev.	Ebenaceae .	H-A					3		14	53	860
Dio.sou	Diospyros soubreana F.White	Ebenaceae .	H--					1			32	
Dis.cal	Discoglypremna caloneura (Pax) Prain	Euphorbia .	HVA		3	30	4	3	1	6	85	400

code	scientific name	family	source		Z	z	T	t	P	p	dmax	density
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
Dis.ben	Distemonanthus benthamianus Baill.	Caesalpin .	HVA		7						105	670
Dry.aub	Drypetes aubrevillei Léandri	Euphorbia .	HVA							16	50	
Dry.ayl	Drypetes aylmeri Hutch. & Dalz.	Euphorbia .	H-A					1			35	
Dry.kla	Drypetes klainei Pierre ex Pax.	Euphorbia .	-VA			1					33	
Dry.pel	Drypetes pellegrinii Léandri	Euphorbia .	H-A					1			41	700
Dub.vir	Duboscia viridiflora (K.Schum.) Mildbr.	Tiliaceae .	HVA		1	1	1				91	550
	Dumoria heckelii A.Chev.	=Tie.hec	..A									
Ehr.tra	Ehretia trachyphylla C.H.Wright	Boraginac .	H-A			1					37	
Ela.gui	Elaies guineensis Jacq.	Palmae .	H-A					1			42	
Ena.pol	Enantia polycarpa (DC.) Engl. & Diels	Annonacea .	HVA			2		1		1	33	540
	Endotricha taiensis Aubrév. & Pellegr.	=Aub.tai	..A									
Ent.ang	Entandrophragma angolense (Welw.) DC.	Meliaceae .	HVA				8	1	1		130	540
Ent.can	Entandrophragma candollei Harms	Meliaceae .	HVA		1		1				165	690
Ent.cyl	Entandrophragma cylindricum (Sprague) Sprague	Meliaceae .	HVA		1		1				125	620
Ent.uti	Entandrophragma utile (Dawe & Sprague) Sprague	Meliaceae .	HVA		2	2	10				150	660
Ery.ivo	Erythrophleum ivorense A.Chev.	Caesalpin .	HVA		35	4	11	7	2	4	182	950
Ery.man	Erythroxylum mannii Oliv.	Erythroxy .	HVA		4	6	3	9		1	88	660
	Fagara macrophylla (Oliv.) Engl.	=Zan.gil	.VA									
Fag.tes	Fagara tessmannii Engl.	Rutaceae .	-V-	V								
Fic.ela	Ficus elasticoides De Wild.	Moraceae .	H-A		1		2				120	
Fun.afr	Funtumia africana (Benth.) Stapf	Apocynace .	HVA					4			56	480
Fun.ela	Funtumia elastica (Preuss) Stapf	Apocynace .	HVA			11					56	500
Gil.bil	Gilbertiodendron bilineatum (Hutch. & Dalz.) J.Léonard	Caesalpin .	HVA	G								
Gil.ivo	Gilbertiodendron ivorense (A.Chev.) J.Léonard	Caesalpin .	-VA	G								
Gil.pre	Gilbertiodendron preussii (Harms) J. Léonard	Caesalpin .	HV.									810
Gil.spl	Gilbertiodendron splendidum (A.Chev. ex Hutch. & Dalz.) J.Léonard	Caesalpin .	HVA									680
	Gilbertiodendron taiense Aubrév.	=Gil.pre	..A									
Glu.ivo	Gluema ivorensis Aubrév. & Pellegr.	Sapotacea .	HVA	R								
Gua.ced	Guarea cedrata (A.Chev.) Pellegr.	Meliaceae .	HVA		1			1			75	580
Gua.tho	Guarea thompsonii Sprague et Hutch.	Meliaceae .	HVA	A								
Gui.ehi	Guibourtia ehie (A.Chev.) J.Léonard	Caesalpin .	HVA		2						80	800
Gym.zai	Gymnostemon zaizou Aubrév. & Pellegr.	Simarouba .	HVA		1		6				109	500
Han.kla	Hannoa klaineana Pierre & Engl.	Simarouba .	H.A	G,V								
Hap.mon	Haplormosia monophylla (Harms) Harms	Papiliona .	-VA	V								
Her.uti	Heritiera utilis (Sprague) Sprague	Sterculia .	HV.				8	18	15	23	110	620
	Hirtella butayei (De Wild.) Brenan.	=Mag.but	.-A									
Hol.gra	Holoptelea grandis (Hutch.) Mildbr.	Ulmaceae .	H-A									
Hom.let	Homalium letestui Pellegr.	Flacourti .	H-A									
Hun.ebu	Hunteria eburnea Pichon	Apocynace .	H-A	R								
Irv.gab	Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill	Irvingiac .	HVA		2		1	1	2		100	910
Kan.gue	Kantou guereensis Aubrév. & Pellegr.	Sapotacea .	-VA	R								
	Kaoue stapfiana (A.Chev.) Pellegr.	=Sta.sta	-.A									
Kea.bri	Keayodendron bridelioides (Mildbr. ex Hutch. et Dalz.) Léandri	Euphorbia .	H-A		9	20		6			80	900
Kha.ant	Khaya anthotheca (Welw.) C.DC.	Meliaceae .	HVA				5				160	500
Kig.afr	Kigelia africana (Lam.) Benth.	Bignoniac .	H-A	R								
Kla.gab	Klainedoxa gabonensis Pierre ex Engl.	Irvingiac .	HVA		2		7	5	2	1	145	1060
Lan.wel	Lannea welwitschii (Hiern) Engl.	Anacardia .	HVA		2		6	3	1		89	500
Loe.kal	Loesenera kalantha Harms	Caesalpin .	-V-	V,$								
Lop.ala	Lophira alata Banks ex Geartn.f.	Ochnaceae .	HVA		3		3				160	1060
Lov.tri	Lovoa trichilioides Harms	Meliaceae .	HVA			2	2	3	1	1	92	490
Mac.bar	Macaranga barteri Muell. Arg.	Euphorbia .	HVA							1	35	
Mag.but	Magnistipula butayei subsp. sargosii De Wild.	Chrysobal .	H..					2		2	38	930
Mam.afr	Mammea africana Sabine	Guttifera .	HVA					2			53	740
	Manilkara multinervis (Bak.) Dubard	=Man.obo	.-A									
Man.obo	Manilkara obovata (Sabine & G.Don) J.H.Hemsley	Sapotacea .	HV.					1			32	1050
	Manilkara sylvestris Aubrév. & Pellegr.	=Man.obo	-.A									
Man.alt	Mansonia altissima (A.Chev.) A.Chev.	Sterculia .	HVA			3					65	650
Mar.aub	Maranthes aubrevillei (Pellegr.) Prance	Chrysobal .	H..				2	2			79	
Mar.chr	Maranthes chrysophylla (Oliv.) Prance	Chrysobal .	H..	G								

code (1)	scientific name (2)	family (3)	source (4)	 (5)	Z (6)	z (7)	T (8)	t (9)	P (10)	p (11)	dmax (12)	density (13)
Mar.gla	Maranthes glabra (Oliv.) Prance	Chrysobal .	H..				1	3	23	5	140	980
Mar.rob	Maranthes robusta (Oliv.) Prance	Chrysobal .	H-.	D,G								
Mar.mic	Mareya micrantha (Benth.) Muell. Arg.	Euphorbia .	H-A			1					32	
Mem.lat	Memecylon lateriflorum (G.Don) Bremek.	Melastoma .	H-A									
Mit.cil	Mitragyna ciliata Aubrév. & Pellegr.	Rubiaceae .	HVA									580
Mit.sti	Mitragyna stipulosa (DC.) O.Ktze	Rubiaceae .	HVA	D								
Mon.com	Monopetalanthus compactus Hutch. & Dalz.	Caesalpin .	-V-	V,S								
Mor.sen	Morelia senegalensis A.Rich.	Rubiaceae .	--A							1	32	
Mor.mes	Morus mesozygia Stapf	Moraceae .	HVA									
Nau.afv	Nauclea aff. vanderguchtii (De Wild.) Petit	Rubiaceae .	-V-					2			31	
Nau.did	Nauclea diderrichii (De Wild. & Th.Dur.) Merrill	Rubiaceae .	HV.		3		9	2	7	2	125	740
Nau.pob	Nauclea pobeguinii (Pobéguin ex Pellegr.) Petit	Rubiaceae .	HVA	R								
	Nauclea trillesii (Pierre) Merrill	*=Nau.did*	..A									
Nau.xan	Nauclea xanthoxylon (A.Chev.) Aubrév.	Rubiaceae .	-VA	R								
Nes.pap	Nesogordonia papaverifera (A.Chev.) R.Capuron	Sterculia .	HVA		1	2	1	9			100	740
New.aub	Newtonia aubrevillei (Pellegr.) Keay	Mimosacea .	HVA									730
New.dup	Newtonia duparquetiana (Baill.) Keay	Mimosacea .	HVA				2	1			90	730
	Ochthocosmus africanus Hook.f.	=Phy.afr	.VA									
Oct.bor	Octoknema borealis Hutch. & Dalz.	Olacaceae .	HVA					12		9	43	
Oko.aub	Okoubaka aubrevillei Pellegr. & Normand	Santalace .	HVA	A								
Old.afr	Oldfieldia africana Benth. & Hook.f.	Euphorbia .	-VA		1	2	13	2			135	970
Omp.ahi	Omphalocarpum ahia A.Chev.	Sapotacea .	HVA	R								
Ong.gor	*Ongokea gore (Hua) Pierre*	Olacaceae .	HVA			1		3		3	63	810
Pac.sta	Pachypodanthium staudtii Engl. & Diels	Annonacea .	HVA			3	4	6		3	90	720
Pac.bre	Pachystela brevipes (Bak.) Baill. ex Engl.	Sapotacea .	H-A	R								
Pan.ole	Panda oleosa Pierre	Pandaceae .	HVA					5		1	62	670
	Parinari aubrevillei Pellegr.	=Mar.aub	.VA									
	Parinari chrysophylla Oliv.	=Mar.chr	.VA									
Par.con	Parinari congensis F. Didr.	Chrysobal .	HVA	R								
Par.exc	Parinari excelsa Sabine	Chrysobal .	HVA		2	2	7	5	7		140	900
	Parinari glabra Oliv.	=Mar.gla	.VA									
	Parinari robusta Oliv.	=Mar.rob	.-A									
Par.bic	Parkia bicolor A.Chev.	Mimosacea .	HVA		3		8	4	7	1	140	470
Pav.cor	Pavetta corymbosa (D.C.) F.N.Williams	Rubiaceae .	H--			1					37	
	Pavetta nitida (Schum.& Thon.) Hutch. & Dalz.	=Pav.cor	.--Rouw91									
Pen.mac	Pentaclethra macrophylla Benth.	Mimosacea .	HVA				1	2			90	950
Pen.but	Pentadesma butyracea Sabine	Guttifera .	HVA				1		3	6	90	850
Per.ela	Pericopsis elata (Harms) van Meeuwen	Papiliona .	HV.	G								
Pet.mac	Petersianthus macrocarpus (P.Beauv.) Liben	Lecythida .	H..		14	6	7	9	1		150	810
Phy.afr	Phyllocosmus africanus (Hook.f.) Klotzsch	Ixonantha .	H..					3		1	60	
Pip.afr	Piptadeniastrum africanum (Hook.f.) Brenan	Mimosacea .	HVA		7	1	21	3	2		148	690
Pip.fas	Piptostigma fasciculatum (De Wild.) Paiva	Annonacea .	H-.			1		3			59	
Pla.boy	Placodiscus boya Aubrév. & Pellegr.	Sapindace .	H-A				1	2		1	76	
Pla.pse	Placodiscus pseudostipularis Radlk.	Sapindace .	H-A					1			69	
Pla.ema	Plagiosyphon emarginatus (Hutch. & Dalz.) J.Léonard	Caesalpin .	-VA	R								
Pro.sta	Protomegabaria stapfiana (Beille) Hutch.	Euphorbia .	HVA						1	36	72	550
Pte.hyl	Pteleopsis hylodendron Mildbr.	Combretac .	HVA									
Pte.san	Pterocarpus santaloides L'Her. ex DC.	Papiliona .	HVA	R								
Pte.beq	Pterygota bequaertii De Wild.	Sterculia .	H-A	A, R91								
Pte.mac	Pterygota macrocarpa K.Schum.	Sterculia .	HVA									610
Pyc.ang	Pycnanthus angolensis (Welw.) Warb.	Myristica .	HV.		3		34	3	1	1	137	470
	Pycnanthus kombo Warb.	=Pyc.ang	..A									
	Quassia undulata (Guill. & Perr.) D.Dietr.	=Han.kla	.V.									
Rho.bre	Rhodognaphalon brevicuspe (Sprague) Roberty	Bombacace .	.V.		3	2	4	5	4	2	110	460
Ric.heu	Ricinodendron heudelotii (Baill.) Pierre ex Pax	Euphorbia .	HVA		1		1	1			111	350
Sac.gab	Sacoglottis gabonensis (Baill.) Urb.	Humiriace .	HVA						74	3	240	880
Sam.din	Samanea dinklagei (Harms) Keay	Mimosacea .	HVA				5				108	900
Sap.aub	Sapium aubrevillei Léandri	Euphorbia .	HVA		4	1					95	650
Sch.arb	Schrebera arborea A.Chev.	Oleaceae .	H-A									
	Scotellia chevalieri Chipp.	=Sco.kla	.-A									
	Scotellia coriacea A.Chev. ex Hutch. & Dalz.	=Sco.kla	.VA									

code (1)	scientific name (2)	family (3)	source (4)	(5)	Z (6)	z (7)	T (8)	t (9)	P (10)	p (11)	dmax (12)	density (13)
Sco.kla	Scottellia klaineana Pierre	Flacourti .	H..		5	26		10	1	17	90	660
Scy.tie	Scytopetalum tieghemii (A.Chev.) Hutch. & Dalz.	Scytopeta .	HVA					9	1	28	72	700
Spa.cam	Spathodea campanulata P.Beauv.	Bignoniac .	HVA				1				77	300
Spo.pre	Spondianthus preussii Engl.	Euphorbia .	HVA							1	30	
Sta.sta	Stachyothyrsus stapfiana (A.Chev.) J.Léonard & Voorhoeve	Caesalpin .	-V.	G,V								
Ste.obl	Sterculia oblonga Mast.	Sterculia .	HVA		2	8		2			90	780
Ste.rhi	Sterculia rhinopetala K.Schum.	Sterculia .	H-A			1		1			69	840
Ste.tra	Sterculia tragacantha Lindl.	Sterculia .	HVA					1			36	380
Ste.acu	Stereospermum acuminatissimum K.Schum.	Bignoniac .	HVA				3	8			106	
Str.pse	Strephonema pseudocola A.Chev.	Combretac .	HVA	R								
Str.gla	Strombosia glaucescens Engl.	Olacaceae .	HVA		2	26	1	41		26	74	900
Sym.glo	Symphonia globulifera L.f.	Guttifera .	HVA	G								
	Tarrietia utilis (Sprague) Sprague	=Her.uti	..A									
Ter.ivo	Terminalia ivorensis A.Chev.	Combretac .	HVA		2				1		120	540
Ter.sup	Terminalia superba Engl. & Diels	Combretac .	HVA		29	12	7	1			95	550
Tet.tub	Tetraberlinia tubmaniana J.Léonard	Caesalpin .	-V-	V,S								
Tet.tet	Tetrapleura tetraptera (Schum. & Thonn.) Taub.	Mimosacea .	HVA			1		1			65	610
Tie.hec	Tieghemella heckelii Pierre ex A.Chev.	Sapotacea .	HV.				2		2		247	670
	Toubaouate brevipaniculata (J.Léonard) Aubr. et Pellegr.	=Did.bre	-.A									
Tre.afr	Treculia africana Decne	Moraceae .	HVA									
	Trichilia heudelotii Oliv.	=Tri.mon	.VA									
	Trichilia lanata A.Chev.	=Tri.tes	.VA									
Tri.meg	Trichilia megalantha Harms	Meliaceae .	H-A					1			39	
Tri.mon	Trichilia monadelpha (Thonn.) J.J. De Wilde	Meliaceae .	H..					1			51	
Tri.spl	Trichilia splendida A.Chev.	Meliaceae .	--A		1	1				1	83	600
Tri.tes	Trichilia tesmannii Harms	Meliaceae .	H..					1			31	550
Tri.arb	Trichoscypha arborea (A.Chev.) A.Chev.	Anacardia .	H-A				1	13		5	76	780
Tri.mad	Trilepisium madagascariense DC.	Moraceae .	H-.	O								
Tri.scl	Triplochiton scleroxylon K.Schum.	Sterculia .	HVA		16		1				205	390
Tur.afr	Turraeanthus africanus (Welw. ex C.DC.) Pellegr.	Meliaceae .	HVA	R								
Uap.cor	Uapaca corbisieri De Wild.	Euphorbia .	HV.				1	1	3	6	90	720
	Uapaca esculenta Aubrév. & Léandri.	=Uap.cor	..A									
Uap.gui	Uapaca guineensis Muell. Arg.	Euphorbia .	HVA		3		1	1	11	9	125	710
Uap.heu	Uapaca heudelotii Baill.	Euphorbia .	HVA	R								
Uap.pal	Uapaca paludosa Aubrév. & Léandri	Euphorbia .	HVA									750
Vit.fer	Vitex ferruginea Schum. & Thonn.	Verbenace .	H-.					1			40	
	Vitex fosteri C.H. Wright	=Vit.fer	.-A									
Vit.mic	Vitex micrantha Gürke	Verbenace .	HVA					1		1	55	530
Vit.riv	Vitex rivularis Gürke	Verbenace .	H-A					1			38	
Xyl.eva	Xylia evansii Hutch.	Mimosacea .	HVA		21	46					110	800
Xyl.aet	Xylopia aethiopica (Dunal) A.Rich.	Annonacea .	H-A					5			47	610
Xyl.ell	Xylopia elliotii Engl. & Diels	Annonacea .	H-A					1			42	
Xyl.par	Xylopia parviflora (A.Rich.) Benth.	Annonacea .	H-A									
Xyl.qui	Xylopia quintasii Engl. & Diels	Annonacea .	H-A			2		8		2	43	850
Xyl.sta	Xylopia staudtii Engl. & Diels	Annonacea .	HVA			1		1		2	52	420
Xyl.vil	Xylopia villosa Chipp	Annonacea .	H-.					1		2	40	
	Xylopiastrum villosum (Chipp) Aubr.	=Xyl.vil	.-A									
Zan.gil	Zanthoxylum gilletii (De Wild.) Waterman	Rutaceae .	H..			1	1				80	810
	Total number of trees:				401	511	277	592	213	368		

Appendix II Forest inventory data from SE Liberia and SW Côte d'Ivoire

From the SODEFOR (1976a,b) inventory reports I used the figures of total volume per inventory compartment of trees exceeding 70 cm diameter. The first table gives the first class species, and the second table the non-commercial species. The latter were not exhaustively inventoried.

Commercial species

SODEFOR (1976a,b) National Forest Inventory: timber volumes above 70 cm d in m3 per inventory compartment

		North-West region							Centre-South region	
species	vern. name	1NW	2NW	3NW	4NW	5NW	6NW	7NW	6CS	7CS
afz.bel	Azodau-Lingue	47	25	25	33	46	35	24	19	7
alb.fer	Iatandza	170	45	118	35	103	198	14	40	27
als.boo	Emien	273	151	217	106	104	186	237	154	81
ani.rob	Aniegre blanc	227	36	66	19	54	99	11	117	44
ant.tox	Ako	301	43	55	51	59	229	42	67	30
ber.con	Melegba	2	16	8	50	2	10	1	64	72
ber.occ	Pocouli	23	1	17	38	182	94	34	158	125
can.sch	Aiele	224	102	161	123	74	81	3	82	46
cei.pen	Fromager	1693	505	695	289	622	1394	772	367	196
cel.ado	Lohonfe	132	18	34	1	20	94	22	37	11
cel.mil	Ba	114	17	15	5	44	81	30	32	14
chlor sp	Iroko	299	84	104	24	73	239	24	55	15
chr.gig	Aniegre rouge	52	23	47	1	1	12	1	22	43
dan.thu	Faro	223	106	106	97	69	195	22	53	40
dis.ben	Movingui	120	29	52	33	63	93	12	38	15
ent.ang	Tiama	78	28	71	38	61	78	6	56	58
ent.can	Kosipo	96	10	43	37	52	74	22	46	17
ent.cyl	Aboudikro	55	21	40	45	57	92	34	24	15
ent.uti	Sipo	134	40	67	54	103	153	32	26	16
ery.ivo	Tali	596	261	562	310	448	457	93	56	80
fun.afr	Pouo	12	15	12	4	10	56	1	4	3
gil.pre	Vaa, (Limbali)	22	239	45	40	1	7	0	177	261
gua.ced	Bosse	40	7	28	11	25	50	8	33	26
gui.ehi	Amazakoue	59	14	38	18	15	72	41	1	
her.uti	Niangon	113	104	216	156	75	74	8	63	44
hol.gra	Kekele	20	1	5	4	9	26	79	7	2
kha.ant	Acajou	81	36	81	38	77	140	19	43	27
lop.ala	Azobe	798	599	1232	293	497	181	5	13	11
lov.tri	Dibetou	44	48	81	96	50	59	10	50	31
man.alt	Bete	63	1	15	1	59	42	17	6	
mit.cil	Bahia	348	122	182	142	291	258	35	34	43
mor.mes	Difou	2	3	4	3	1	8	2	2	1
nau.did	Badi, (Bilinga)	111	116	254	340	109	156	49	84	143
nes.pap	Kotibe	95	14	41	18	65	123	44	49	10
per.ela	Asamela	92	2	0	0	0	1	0	2	0
pip.afr	Dabema	1546	1061	942	653	773	963	25	692	533
pte.mac	Koto	70	15	12	1	49	33	135	6	4
pyc.ang	Ilomba	693	377	614	479	416	892	63	247	143
rho.bre	Kondroti	140	55	122	106	223	212	39	57	32
ric.heu	Eho	266	103	154	60	113	380	55	61	61
sco.kla	Akossika	14	6	15	5	20	37	74	28	24
ste.obl	Bi	52	21	34	23	45	63	15	21	6
ste.rhi	Lotofa	1	1	1	0	3	80	71	45	15
ter.ivo	Framire	160	59	102	28	57	186	21	33	7
ter.sup	Frake	413	173	277	176	278	938	734	294	80
tie.hec	Makore	59	28	35	33	15	33	9	45	17
tri.scl	Samba, (Obeche)	3735	521	1214	140	1227	4053	1061	565	129
tur.afr	Avodire	2	1	1	1	0	1	1	80	66

Other species

		North-West region							Centre-South region	
species	vern. name	1NW	2NW	3NW	4NW	5NW	6NW	7NW	6CS	7CS
alb.adi	Bangbaye	82								
alb.zyg	Ouochi	152		68		51	171	19	106	47
amp.pte	Lati	121	68	74	79	60	127		76	47
ano.kla	Bodioa	191	40	138		128	98	27	82	70
ant.fra	Adomonteu	119	86	275	246	262	220		205	182
bei.man	Atiokouo								42	
bom.buo	Kapokier-Oba	220	73	157		107	189	36	83	
bos.pha	Daocou							7		
bus.occ	Nomotcho							17		
cal.aub	Guepizou	56	74	297	160	34			114	152
cel.zen	Asan							30		
chi.san	Bala	266	105	215	84	151	270	141		
chrys sp	Longui							20		129
cor.pac	Gaouo							6		
cor.pla	Bon					65	428	211	45	
det.sen	Bodo	86								
dia.aub	Kropio	68	87	134	51				150	157
did.ida	Broutou				315					
ery.man	Dabe					34	49	19		
gil.spl	Medjilagba a gros fruits									39
gym.zai	Zaizou		40	75	111					
irv.gab	Boborou		41	68	93	73	123	52		
kea.bri	Kohaingue							10		
kla.gab	Kroma	117	167	413	322	233	356	139	180	277
lan.wel	Loloti					32	61	13	85	52
man.obo	Fou	78								
mar.gla	Aramon		57	129	162	45	66		96	86
old.afr	Dantoue		48		193					
ong.gor	Kouero	93	61		62		57	11		
par.bic	Lo	415	244	246	250	205	274		639	430
par.exc	Sougue	169	196	249	444	98	114		331	228
pen.mac	Ovala	188	152	206	107	90	95			45
pet.mac	Abale	856	328	344	256	213	726	20	398	213
phy.afr	Abrahassa								85	56
pte.hyl	Koframire			64						
sac.gab	Akouapo	132	188	567	611				123	78
sap.aub	Cocoti					38	75			
sch.arb	Oualio							34		
scy.tie	Moussangoue				15				37	28
ste.acu	Fara							11		
tre.afr	Bleblendou								47	
uapac sp	Rikio	205	200	155	390	104	166		240	300
xyl.eva	Tchebuessain	142	83	118	115	137	332	136		
	primary species	13910	5303	8260	4258	6740	13018	4057	4255	2671
	other species	4644	2849	4837	4773	2761	4791	1150	4138	3349
	all species	18554	8152	13097	9031	9501	17809	5207	8393	6020
	area	215038	144737	171417	134658	139950	229601	90632	118208	94475
	% degraded forest	10%	23%	12%	5%	11%	10%	25%	N/A	N/A
	vol/ha 70+	86	56	76	67	68	78	57	71	64

SODEFOR Inventaire Perimetre XV (Clement 1973): timber volume above 70 cm d per inventory compartment
foret dense sur sol ferme (marecages et degrades exclus)

species	vernacular name	1XV	2XV	3XV	4XV	5XV
afz.bel	Azodau-Lingue	31	31	6	1	5
alb.fer	Iatandza	29	42	13	2	32
amp.pte	Lati	34	51	8	11	17
ani.rob	Aniegre blanc	14	25	24	7	37
ano.kla	Bodioa	25	108	12	4	60
ant.fra	Adomonteu	375	150	67	4	104
ant.tox	Ako	20	37	15	19	13
aub.ker	Kodabema	17	12	12	2	18
ber.con	Melegba	21	75	6	6	43
ber.occ	Pocouli	184	50	46	2	96
can.sch	Aiele	10	35	8	2	3
cei.pen	Fromager	92	196	98	11	30
cel.ado	Lohonfe	3	15	19	6	1
cel.mil	Ba	2	33	24	10	1
cel.zen	Asan				1	1
chlor sp	Iroko	9	30	11	12	9
cop.sal	Etimoe	21	5	1	0	13
dan.thu	Faro	43	42	17	2	32
det.sen	Bodo	11	6	0	6	5
dis.ben	Movingui	21	37	12	1	17
ent.ang	Tiama	9	25	12	1	7
ent.can	Kosipo	34	19	3	6	19
ent.cyl	Aboudikro	17	30	5	4	10
ent.uti	Sipo	28	29	16	10	20
ery.ivo	Tali	299	320	79	10	117
gil.pre	Vaa, (Limbali)	1	0	0	0	0
gua.ced	Bosse	5	33	9	3	3
gui.ehi	Amazakoue	12	1	1	1	33
gym.zai	Zaizou	74	138	53	12	12
her.uti	Niangon	178	88	17	2	12
kan.gue	Kantou	7	2	0	0	1
kha.ant	Acajou blanc	32	27	17	1	4
kla.gab	Kroma	201	338	105	18	140
lop.ala	Azobe	156	4	23	5	23
lov.tri	Dibetou	42	54	9	3	7
mam.afr	Djimbo	1	9	1	1	6
man.alt	Bete	2	4	5	1	1
mit.cil	Bahia	5	40	2	1	5
nau.did	Badi, (Bilinga)	117	212	22	2	42
nes.pap	Kotibe	13	21	6	1	19
par.exc	Sougue	108	144	20	8	50
pet.mac	Abale	54	28	32	18	85
pip.afr	Dabema	228	427	213	71	212
pte.mac	Koto	1	2	1	0	3
pyc.ang	Ilomba	148	272	116	11	126
rho.bre	Kondroti	81	130	22	5	46
ric.heu	Eho	14	63	28	7	19
sco.kla	Akossika	35	19	6	1	9
ste.rhi	Lotofa	7	8	21	1	24
ter.ivo	Framire	25	109	14	0	10
ter.sup	Frake	133	176	73	1	59
tie.hec	Makore	18	17	1	1	7
tri.scl	Samba, (Obeche)	93	438	143	58	106
tur.afr	Avodire		1	0	1	1
zan.gil	Bahe, (Olon-dur)	22	23	6	2	17
Commercial species:		3162	4231	1480	376	1792

surface tot: foret dense sol ferme	70963	87519	18511	5817	34138
surface echantillonne	569	755	147	27	278
% marec. foret dense du secteur	12	7	7	5	13
% degradee/cultivee du secteur	18	21	67	85	53

From the Liberian inventory (Sachtler 1968) I used timber volumes per 100 ha of trees exceeding 40 cm diameter.

Liberia National Forest Inventory (Sachtler 1968): timber volumes above 40 cm d in m3/100 ha

		Grebo			Krahn-Bassa										Sapo		
species	code	G51	G52	G53	K61	K62	K63	K64	K65	K66	K67	K68	K69	K167	S91	S92	S93
afz.bel	AFZ	13	47	15	7	9	10	0	4	21	2	25	0	0	13	29	12
als.boo	ALS	77	40	32	16	2	14	1	28	0	24	48	0	14	24	6	0
amp.pte	AMP	65	50	55	15	32	21	58	29	71	10	11	0	0	81	26	46
ano.kla	ANO	80	95	108	15	45	33	35	84	123	139	142	94	125	49	133	105
ant.fra	ANT	201	200	187	140	135	176	135	109	103	140	187	83	25	84	7	44
ant.tow	ANA	90	60	66	18	42	47	11	10	0	0	0	0	0	2	0	0
ara.soy	ARA	36	22	10	22	10	2	18	6	0	0	5	0	0	38	35	70
aub.pla	AUB	30	12	4	16	3	3	0	7	0	0	0	0	0	2	0	0
bei.man	BEI	53	31	22	52	29	23	45	17	14	139	7	4	52	142	41	24
berli sp	BER	74	62	16	24	93	42	97	28	9	27	5	14	34	50	42	8
bra.leo	BRA	0	0	0	0	241	N/A	560	235	40	130	116	0	0	680	156	75
calpo sp	CAL	192	126	135	759	418	688	456	765	829	724	874	635	1570	238	218	307
can.sch	CAN	111	122	143	99	89	123	67	94	62	181	0	5	286	185	94	77
cassi sp	CAS	0	1	1	0	0	10	95	34	0	0	0	0	0	305	157	222
cei.pen	CEI	86	98	195	54	121	27	249	82	70	148	17	0	0	24	0	9
celti sp	CEL				0	0	30	0	14	0	0	0	0	0			
chlor sp	CHL	9	9	16	13	11	10	35	26	0	32	0	0	0	40	23	11
chrys sp	CHR	29	26	63	36	40	30	11	2	9	5	31	0	0	121	50	16
cry.tet	CRY	1	10	7	6	1	5	8	0	0	0	0	0	0			
cyn.ana	CYN	107	200	12	28	0	290	353	284	402	654	259	366	58	184	171	48
danie sp	DAN	51	56	43	54	27	23	50	66	62	26	95	0	78	216	33	24
dia.aub	DIA	76	82	75	142	143	162	181	86	23	4	45	9	0	113	62	113
did.bre	TOU				0	0	0	6	159	268	0	516	230	0	444	748	143
did.ida	DID	331	37	3	4	0	1	9	10	66	118	7	60	8	76	0	0
dis.ben	DIS	17	26	27	4	21	4	1	14	0	10	0	0	0	5	0	5
entan sp	ENT	306	426	260	106	93	185	85	37	0	0	0	0	0	7	0	11
ery.ivo	ERY	144	277	174	154	111	201	153	186	55	148	108	84	157	92	188	76
fagar sp	FAG	20	13	22	12	8	6	103	6	45	8	0	10	0	36	28	9
funtu sp	FUN	17	19	100	0	10	0	126	4	20	8	0	0	0	94	55	33
gil.pre	GIL	288	429	178	857	773	964	869	207	342	206	137	75	0	276	163	181
gua.ced	GUA	10	12	7	17	6	3	0	0	0	0	0	0	0	0	0	0
gui.ehi	GUI				0	0	0	0	0	0	0	0	0	0			
hap.mon	HAP	3	1	3	0	0	0	0	0	0	0	0	0	0			
her.uti	TAR	285	423	325	911	665	1167	754	613	1272	451	991	1011	8	588	481	522
khaya sp	KHA	60	50	37	12	9	14	3	2	0	0	0	0	0	0	0	0
kla.gab	KLA	104	180	197	187	132	254	91	113	158	54	69	59	36	86	37	109
loe.kal	LOE				N/A	881	1281	797	1587	2104	1039	859	1488	1324	268	508	420
lop.ala	LOP	389	548	152	548	318	478	296	675	57	721	1194	185	1186	531	953	779
lov.tri	LOV	138	116	160	93	92	22	67	57	0	11	71	68	63	96	25	52
mam.afr	MAM	21	29	18	20	18	89	18	36	124	42	68	21	0	17	3	26
mit.cil	MIT	130	153	123	128	34	81	140	303	118	502	516	172	240	370	235	251
monop sp	MON	8	7	84	124	385	480	113	35	0	0	0	0	0	71	3	5
nau.did	NAU	265	254	175	154	68	36	37	37	364	345	214	55	132	60	49	61
nes.pap	NES	42	4	15	0	0	0	6	0	0	0	0	0	0	0	0	0
newto sp	NEW	7	35	18	31	24	65	68	75	95	82	119	38	108	40	28	20
old.afr	OLD	256	557	28	257	193	327	107	185	161	93	165	82	91	118	82	65
ong.gor	ONG	79	73	39	58	80	59	38	8	16	0	0	0	0	14	25	12
pac.sta	PAC	121	141	102	37	23	38	20	38	2	41	2	0	48	14	0	0
par.bic	PAK	190	112	268	161	254	221	242	194	122	134	141	71	135	228	162	196
parin sp	PAR	521	299	265	200	160	114	137	155	98	157	92	129	34	275	204	250
pet.mac	COM	332	155	271	56	53	7	138	41	23	0	0	0	0	63	71	41
pip.afr	PIP	451	377	529	222	322	191	512	163	194	351	51	50	185	284	254	197
pyc.ang	PYC	521	514	626	83	164	76	202	85	98	202	5	8	68	49	85	35
qua.und	HAN	2	10	42	44	43	57	151	35	0	0	11	0	0	147	120	220
rho.bre	BOM	104	91	113	23	18	24	16	13	7	0	0	0	0	6	0	0
ric.heu	RIC				0	14	4	27	4	13	0	0	0	0			
sac.gab	SAC	110	198	184	90	38	260	37	463	61	220	594	76	141	218	288	329
ter.ivo	TEI	7	11	16	2	9	18	162	49	138	0	9	0	0	53	60	0
ter.sup	TES	134	98	146	25	39	61	102	34	28	39	0	0	0	52	0	0
tet.tub	TET	0	3	13	446	328	1660	782	1739	4591	1615	1548	4688	406	1096	705	810
tie.hec	DUM	106	43	100	29	29	67	35	2	45	0	0	23	0	47	0	0
tri.scl	TRI	46	47	221	0	0	0	0	0	0	0	0	0	0	0	0	0
tur.afr	TUR	0	0	2	9	3	14	3	1	0	0	0	0	0	1	0	0
uapac sp	UAP	448	245	465	151	199	333	484	293	104	205	144	22	67	230	169	190
miscellaneous		1813	1659	1722	1926	1916	2221	1696	1956	1216	1263	1578	1398	1695	1443	548	1698
Total volume		9207	9021	8435	8697	9024	12852	11098	11624	13843	10450	11076	11313	8374	10086	7560	7957

Appendix III Detailed description of the physiographic units of the three study sites Zagné, Taï and Para by G.J. van Herwaarden (1991a), Rademacher (1992) and Nooren (1992)

The distribution of the different soil characteristics is shown in the physiographic soil maps together with the legends. A detailed description of the fieldwork and of the mapping units is given here.

Soil profile pits and soil augerings (van Herwaarden 1991a). Soil profiles were described along soil transects according to the FAO (1977) guidelines for soil profile description. Colours were defined with the use of the Munsell (1975) colour charts. A preliminary classification of the soils was made according to the revised FAO-UNESCO system (van Kekem 1984, FAO 1988). Altogether 10 soil profile pits were described in the Zagné survey area, 8 in the Taï survey area and 11 in the survey area near Para. In all, 186 augerings were described in the Zagné survey area, 261 in the Taï survey area and 115 in the Para survey area. The density of observation points is 1.4 per ha or 0.3 per cm^2 on the Zagné area map, 2.0 per ha or 0.5 per cm^2 on the Taï area map and 1.7 per ha or 0.4 per cm^2 on the Para area map. Line cutting, digging of the pits, augering and most of the slope measurements were done out by local personnel.

Soil analyses. In the survey area of Taï the studies of Fritsch (1980) and Fraters (1986) were used as the basis and source for soil descriptions and soil analytical data. For the other survey areas, eight additional soil profile pits were sampled and analysed by the soil laboratory of the *Direction et Contrôle des Grands Traveaux* in Bouaké, Côte d'Ivoire. Analyses concerned texture, acidity, organic matter content, total nitrogen content, cation exchange capacity and exchangeable bases per horizon (for more details see van Herwaarden 1991a).

1 The legends

To distinguish the mapping units four major differentiating characteristics are used: physiography, drainage, presence of hardened plinthite and depth of rotten rock (saprolite). By means of these easily recognizable characteristics the boundaries have been drawn. The description of the units is refined on the basis of diagnostic characteristics. These are texture, colour, slope form and degree, parent material and altitude.

In each mapping unit representative soils have been classified according to the FAO-UNESCO system (FAO, 1988), the Soil Taxonomy (Soil Survey Staff, 1987) and the french system of soil classification (CPCS, 1967). Classifications are partly based on analytical data of some soil profiles (see appendix 1 in van Herwaarden 1991a). These data are taken as representative for other soil types as well. Therefore it is assumed that base saturations in the soils are far less than 50% and that the cation exchange capacities of the non-alluvial soils are less than 24 cmol (+) per kg clay in at least some part of the B-horizon within 125 cm of the surface. This assumption is also based on results from prior investigations in the Taï region by de Rouw et al. (1990), Fritsch (1980), Fraters (1986) and Development and Resources Corporation (1967).

In Figures 38, 40 and 42 the legends of the four survey areas are shown with the mapping units and the differentiating and diagnostic characteristics in a hierarchical order (as far as possible). It should be noted that all these characteristics interact and cannot be seen in isolation. To distinguish the units of one survey area from those of another the prefixes of the codes are different: Z for the survey area Zagné 1, T for the Taï survey area and P for the Para survey area.

2 Description of the mapping units

For each of the four maps the units are described by means of the characteristics as mentioned above. The total extent of each unit is given in hectares and as a percentage of the total area of the corresponding survey (see Table 4). For Taï and Zagné this area is larger than the sample plot and its surroundings which are displayed in Figures 38 to 42. For most of the units a typical soil profile description can be found in van Herwaarden (1991a).

2.1 Mapping units of the survey area Zagné

ZC: Crest — Total extent: 8 ha (5%)

The highest part of the survey area Zagné does not reveal the features of a real crest and its physiography is not very pronounced. Boulders of ironstone are found at the surface, possibly remnants of an ancient ironstone crust. Cemented ironstone is absent in the soil profiles of this unit. The red, well drained soils are situated on gently sloping slopes They are gravelly (ironstone) throughout the profile. Clay ratios clearly increase with depth within the profile and an argic kandic B-horizon is present. The soils are classified as Ferric Acrisol (FAO/UNESCO), as Kanhaplic Haplustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié modal, sur migmatites (CPCS).

ZS1: Upper slope — Total extent: 36 ha (25%)

This unit covers the largest part of the survey area Zagné. It is found around the crest. The soils are strong brown and well drained. Their texture is gravelly (ironstone) clay loam. The soils are situated on very gently sloping convex slopes. They are classified as Haplic Ferralsol (FAO/UNESCO), as Kanhaplic Haplustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié, modal, sur migmatites (CPCS).

ZS2: Middle slope — Total extent: 29 ha (20%)

This unit concerns the southern middle slope of the survey area Zagné. The yellowish brown soils are moderately well drained and consist mainly of colluvium. Gravel and clay contents seem to increase with depth within the profile. In the lower part of the soil profile red mottles are present. They are associated with plinthite. The soils are classified as Plinthic Acrisol (FAO/UNESCO), as Plinthic Haplustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié, modal sur colluvions recouvrant les altérations de migmatite (CPCS).

ZS3: Lower slope — Total extent: 22 ha (15%)

This unit borders the valley bottoms in the North and in the South of the survey area Zagné. The white to light yellowish brown soils are imperfectly drained. The slopes are concave and gently sloping. Rotten rock (saprolite) is present below a depth of 100 cm. The soils are non-gravelly. They are classified as Haplic Acrisol (FAO/UNESCO), as Typic Kandiustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, rajeuni, hydromorphe, sur colluvions recouvrant les altérations de migmatite (CPCS).

ZV1: Ravine/gully Total extent: 4 ha (3%)

The upper parts of the ravines/gullies are gently sloping whereas the lower are almost flat. Locally a cascade is present on the border of these two. In the steep, 1 to 5 m high walls rotten rock below hardened plinthite is observed. The texture of the soils varies from very gravelly (ironstone) clay loam in the upper parts to non-gravelly coarse sand to sandy clay in the lower parts of this unit. The soils are classified as Ferralic Cambisol (FAO/UNESCO), as Typic Kandiustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, rajeuni, avec érosion, sur migmatites (CPCS).

ZV2: Valley bottom Total extent: 20 ha (14%)

In the survey area Zagné two valley bottoms have been mapped. They are almost flat and sedimentation occurs here. The thickness of the alluvium however is rarely more than 100 cm. Rotten rock is present below the alluvial deposits. The grey soils are poorly drained. They are classified as Dystric Fluvisols (FAO/UNESCO), as Tropaquent (Soil Taxonomy) and as Sol peu évolué d'origine non climatique d'apport hydromorphe sur alluvions (CPCS).

2.2 Mapping units of the Taï survey area

TC: Crest Total extent: 0.4 ha (0.3%)

This unit is confined to the highest topographic positions in the northern part of the Taï survey area. It concerns small, nearly flat tops, isolated from the surrounding landscape by relatively steep short slopes. The red soils are well drained and very gravelly. The gravel consists of reddish, hard, pea shaped, ferruginous nodules (ironstone). The texture of the fine earth fraction changes from sandy loam in the humus rich topsoil to clay in the subsoil. At a depth of about 70 cm a layer of continuously indurated ironstone is present, in which individual concretions can be recognised. The crust can only be broken with a hammer. Stones and boulders of ironstone are found on the surface. The soils are classified as Ferric Acrisol (FAO/UNESCO), as Orthoxic Palehumult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, induré remanié sur migmatites (CPCS).

TS1: Upper slope Total extent: 5 ha (4%)

This unit is located on relatively steep slopes adjacent to the highest crests. The red soils are well drained and very gravelly (ironstone). Gravel ratios decrease with depth within the profile. An argic/kandic B-horizon has been recognised and the texture of the fine earth fraction is sandy loam to sandy clay loam in the topsoil and clay in the subsoil. The soils are classified as Ferric Acrisol (FAO/UNESCO), as Orthoxic Palehumult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié modal sur migmatites (CPCS).

TS2: Middle slope Total extent: 23 ha (17%)

This mapping unit has some similarities with the previous (TS1) but is located on lower topographic positions (outside the survey area this unit locally changes into a sloping crest remnant). The soils are therefore more yellowish. They are well drained. The texture consists of very gravelly sandy clay loam to clay over non-gravelly clay. The soils are classified as Ferric Acrisol (FAO/UNESCO), as Orthoxic Palehumult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, faiblement appauvri sur migmatites (CPCS).

TS3: Lower slope Total extent: 56 ha (42%)

This is the most extensive mapping unit of the Taï survey area. The yellowish brown soils are moderately well drained. The soil material consist of colluvium, the topsoil being very gravelly sandy clay to clay and the subsoil non-gravelly sandy clay loam to clay. An argic/kandic B-horizon is present. In the subsoil red mottles and soft nodules (both associated with plinthite) are observed in the subsoil. The red mottling can be so abundant that it dominates the matrix colour. The soils are classified as Plinthic Acrisol (FAO/UNESCO), as Plinthustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé remanié modal sur colluvions recouvrant les altérations de migmatite (CPCS).

TS4: Lower slope Total extent: 16 ha (12%)

This unit concerns the lower slopes parts as well, but is confined to the areas adjacent to the valley bottom. The yellowish brown soils are moderately well drained. The soil material consists of colluvium. In the subsoil a very gravelly layer consisting of hardening plinthite (petroplinthite) is found. Clay ratios do not clearly increase with depth within the profile. An oxic/ferralic B-horizon is present. The soils are classified as Xanthic Ferralsol (FAO/UNESCO), as Tropeptic Haplortox (Soil Taxonomy) and as Sol ferralitique fortement désaturé, induré, appauvri, hydromorphe sur colluvions recouvrant les altérations de migmatite (CPCS).

TV: Valley bottom Total extent: 33 ha (25%)

This mapping unit covers the lowest parts of the Taï survey area. Because of this position the soils are poorly drained and white and greyish colours dominate. Mottling is frequently present. The texture of the soils is non-gravelly sandy loam to loamy sand. At a depth of approximately 80 cm a stone line of angular quartz fragments is present. The soils are classified as Dystric Gleysol (FAO/UNESCO), as Tropaquent (Soil Taxonomy) and as Sol hydromorphe peu humifère, à amphigley, à nappe phréatique profond sur alluvions (CPCS).

Gully/ravine
Gullies/ravines have not been separately mapped in the Taï survey area but are present from the middle slopes to the valley bottom. They are deeply incised with locally 2 to 5 m high vertical walls. In these walls hardened plinthite is present, often over rotten rock (saprolite).

2.3 Mapping units of the Para survey area

PC1: High crest Total extent: 2 ha (3%)

These crests form the highest parts of the Para survey area. They are convex and gently sloping (2-6%). The well drained soils found here are gravelly (to very gravelly) with a very clayey matrix. The gravel consists of pisolitic ironstone. At a depth of 125-150 cm a horizon consisting of cemented ironstone is present. This hardened horizon is more distinct on the western than on the eastern high crest. Rotten rock of schist (assumed to be the parent material) is not found within 150 cm depth. In comparison with other units organic matter contents are high (see appendix 1 in van Herwaarden 1991a). Tree growth is limited by the extremely hostile rooting conditions (caused by the high gravel content and the presence of the ironstone crust). Therefore small short trees are dominant. Larger trees topple over easily. Fallen trees create gravel holes and mounds resulting in a special micro topography. With respect to the FAO/UNESCO classification system, a ferralic B-horizon is present. With respect to the soil classification according to the Soil Taxonomy, the presence of a kandic B-horizon is noted. This horizon meets the weatherable mineral requirements of an oxic horizon. The soils are classified as Haplic Ferralsol (FAO\UNESCO), as Typic Kandiustox (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié faiblement induré sur schistes (CPCS).

PC2: Low crest Total extent: 3 ha (4%)

This unit consists of small and low summits. They are gently sloping (2-6%) and convex. Their strong brown, well drained soils contain large amounts of ironstone gravel. The gravel is absent at a certain depth (approximately 1 m) where rotten rock of schist is found within 150 cm depth. The presence of a ferralic or oxic horizon is not noted, but an argic/kandic B-horizon is present. The soils are classified as Ferric Acrisol (FAO\UNESCO), as Typic Kandiustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, rajeuni remanié sur schistes (CPCS).

PC3: Shoulder Total extent: 2 ha (3%)

This unit has suffered erosion to such an extent that ironstone gravel and/or colluvium have been removed and rotten rock (originating from schist) is present at shallow depth. Its physiography is not very clear and the units appear as gently sloping (2-6%) protuberant parts, appearing like shoulders. They are all located on barriers of two different watersheds. The soils are considered to be rejuvenated. Nevertheless analytical data of rotten rock in a profile on a low crest show very low values of the base saturation and CEC (see appendix 1). The colours of these well drained soils are dominated by the weathered schist and show a high variety (from red to yellow). They are non-gravelly. The soils are classified as Ferralic Cambisol, (FAO/UNESCO), as Typic Kandiustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, rajeuni avec érosion sur schistes (CPCS).

PS1: Upper slope Total extent: 7 ha (10%)

This unit is clearly associated with the high crests. The moderately steep (13-25%) upper slopes are located directly beneath the high crests. Ironstone gravel is abundantly present in the soil profile. In this unit as in PC1 relatively many fallen trees have been observed. This is probably caused by the difficult rooting conditions (because of the high contents of ironstone gravel) in combination with the relative steep slopes. Charcoal has been found in some profiles. The well drained soils are to some extent similar to the soils on the high crests but they are considered to be truncated here.
Furthermore they are not red but yellowish red. Rotten rock originating from schist has been found at a depth of 125 cm. The soils are classified as Haplic Ferralsol (FAO/UNESCO) as Typic Kandiustox (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié rajeuni sur schistes (CPCS).

PS2: Middle slope Total extent: 35 ha (49%)

This unit is the largest of the Para survey area covering almost half of it. The topographical position is between low crests and upper slopes on the one side and lower slopes on the other. The middle slopes are straight to slightly convex and sloping (6-13%). The soils consist of colluvium (slightly gravelly clay loams) and are yellowish brown coloured. Rotten rock has not been found within 150 cm depth on middle slopes. Rooting conditions are good and in accordance with observations by Vooren (1985) only few fallen trees are present in this physiographic unit. In one of the profiles faint orange brown mottles have been observed, which possibly indicate the beginning of plinthite formation. In these well drained soils a ferralic B-horizon (FAO/UNESCO) is present. According to the Soil Taxonomy this horizon is a kandic horizon but it meets the weatherable mineral requirements of an oxic horizon. The soils are classified as Xanthic Ferralsol (FAO/UNESCO), as Xanthic Kandiustox (Soil Taxonomy) and as Sol ferralitique fortement désaturé, typique jaune recouvrement sur colluvions recouvrant les altérations de schiste (CPCS).

PS3: Lower slope Total extent: 18 ha (25%)

The lower slopes are situated between the middle slopes and the stream valleys. They are sloping (6-13%) and concave. Because of their position they are moderately well drained and the formation of plinthite appears within 125 cm depth. Plinthite is present in most but not all of the soil profiles of the lower slopes. It is assumed that this plinthite, which is easily recognisable by its red colour is related with a fluctuating water table. Probably it is formed by absolute accumulation of iron coming from the higher situated ironstone crust. The texture in the subsoil of the profiles is very clayey. Possibly some illuviation has taken place as well as the formation of kaolinite. In some augerings in lower slopes
in the western part of the Para survey area kaolinite has been clearly recognised by its distinct white colour. Parent material of the soils is colluvium. The soils are slightly gravelly and brownish yellow coloured. The gravel consists mainly of quartz and little ironstone (transported from higher parts of the landscape). Rooting is limited where plinthite is near the surface and hardened irreversibly. The phenomenon of hardened plinthite is more common in the western part of the Para survey area than in the central and eastern parts. The soils in this unit are classified as Plinthic Ferralsol (FAO /UNESCO), as Plinthic Kandiustox (Soil Taxonomy) and as Sol ferralitique fortement désaturé, remanié jaune recouvrement sur colluvions recouvrant les altérations de schistes (CPCS). In some profiles plinthite is absent and soils can be classified as Xanthic Ferralsol (FAO/UNESCO) and as Xanthic Kandiustox (Soil Taxonomy). According to CPCS the classification unit remains the same.

PV1: Gully/Ravine Total extent: 1 ha (1%)

This unit is the smallest in the Para survey area, covering approximately 1 ha. Its reflection on the map is slightly exaggerated. But the soil map would not be appropriate without indicating the location of the striking gullies/ravines. Not only their physiography with gently sloping (2-6%) bottoms and very steep (>55%) walls (being 1-3 m high) but also their soils are very different from other units. No distinction has been made between the smaller gullies and the larger and deeper ravines because the transition between the two is very gradual. Furthermore it would be impossible to map them separately because of their small size. Because erosion is dominant in this unit, rotten rock originating from schist is at or near the surface, sometimes covered by a very thin layer of deposits. The colours of the rotten rock are variegated ranging from yellowish red to olive yellow. The texture of the soils is slightly gravelly (quartz, schist, and ironstone gravel) clay loam. In the walls hardened plinthite can be found lying immediately on very slightly weathered schist. Drainage is imperfect, but the gullies/ravines only contain water after heavy rainfall. The soils are classified as Ferralic Cambisol (FAO/UNESCO), as Typic Kandiustult (Soil Taxonomy) and as Sol ferralitique fortement désaturé, rajeuni avec érosion sur schiste (CPCS).

PV2: Higher valley bottom Total extent: 2 ha (3%)

In the Para survey area one major valley bottom (also termed bas fond) is present, which is supposed to contain flowing water throughout the year. The valley bottom is almost flat (0-2%). This unit covers the upstream part of it. Sedimentation takes place here but the valley bottom is covered only by a rather thin layer of alluvium. Rotten rock as found in the gullies/ravines is present beneath it at a depth of 80 to 120 cm. The texture of the soils varies from clay to loamy sand, with the latter predominating. The domination of sand indicates a rather high stream velocity which allows only the coarser particles to sink. Fresh material is deposited regularly. Because of the poor drainage tree roots penetrate the soil only to shallow depths. Toppling of trees is therefore not uncommon. Certain tree species however are adapted to these circumstances. The alluvium has a grey colour. The soils are classified as Dystric Fluvisol (FAO/UNESCO), as Tropic Fluvaquent (Soil Taxonomy) and as Sol peu évolué d'origine non climatique d'apport hydromorphe sur alluvions recouvrant les altérations de schistes (CPCS).

PV3: Lower valley bottom Total extent: 1 ha (2%)

This unit is almost similar to the previous one, but because it covers the downstream part of the valley bottom (where the drainage basin is larger) conditions are wetter here. As a result of this, water is at or near the surface most of the time and drainage is very poor. The soils are reduced and iron is mobile. The dominant colour of the soil is therefore grey. In the upper part of the soil yellowish red mottles occur indicating where the air has penetrated in dry seasons thus oxidizing the iron compounds. The texture of these soils is non gravelly loamy sand. Although the morphological characteristics of the soils do not completely match the criteria of gleyic properties the soils are classified as Dystric Gleysol (FAO/UNESCO), as Typic Hydraquent (Soil Taxonomy) and as Sol hydromorphe peu humifère à gley ensemble sur alluvions (CPCS).

REFERENCES

For the Dutch reader: references are arranged in international alphabetical order. Names beginning with "de" or "van" should be searched for under D and V respectively.

Adam J.G. (1983). Flore descriptive des Monts Nimba (Cote d'Ivoire, Guinée, Liberia). Editions du Centre National de la Recherche Scientifique, 2181 pp.

Adejuwon J.O., Balogun E.E. & Adejuwon S.A. (1990). On the annual and seasonal patterns of rainfall fluctuations in Sub-Saharan West Africa. Int. J. of Climatology 10: 839-848.

Ahn P.M. (1970). West African soils. Oxford Univ. Press, 332 pp.

Aké Assi L. (1984). Flore de la Côte d'Ivoire: étude descriptive et biogéographique, avec quelques notes éthnobotaniques. Thèse Doct., Université d'Abidjan, Fac. des Sciences, Dépt. Phys. Végétale, 1206 pp.

Aké Assi L. & Pfeffer P. (1975). Etude d'aménagement touristique du Parc National de Taï. Tome 2: Inventaire de la flore et de la faune. BDPA, Paris, 58 pp.

Albers P. (1990). Contribution to a diagnostic key for the high forest trees of the Taï National Parc (Ivory Coast). Stageverslag, Dept. Plant Taxonomy, Univ. Wageningen.

Alder D. (1990). Ghafosim: a projection system for natural forest growth and yield in Ghana. Manas Systems Ltd., Oxford, 114 pp.

Alder D. & Synnott T.J. (1992). Permanent sample plot techniques for mixed tropical forest. Tropical forestry papers 25, Oxford Forestry Institute, Oxford, 124 pp.

Alexandre D.-Y. (1978). Le rôle disséminateur des éléphants en forêt de Taï, Côte d'Ivoire. Rev. Ecol., La Terre et la Vie 32: 47-71.

Alexandre D.-Y. (1980). Caractère saisonnier de la fructification dans une forêt hygrophile de Côte d'Ivoire. Rev. Ecol. (Terre et Vie) 34: 335-350.

ANAM (1987). Les normales pluviométriques 1951-1980. Agence Nationale des Aérodromes et de la Météorologie, Abidjan-Port Bouet, 37 pp.

ASECNA (1979). Le climat de la Côte d'Ivoire. ASECNA, Abidjan, 74 pp.

Ashton P.S. (1977). Variation of tropical moist forest with site: its relevance, and the methodological problems that its study presents in tropical forest systems. In: Brünig E.F. (ed.). Joint MAB-IUFRO Rainforest Ecosystem Workshop, Hamburg-Reinbek, May 1977, Chair of World Forestry, Hamburg-Reinbek.

Aubréville A. (1938). La forêt coloniale. Les forêts de l'Afrique occidentale française. Annales de l'Académie des sciences coloniales, tome IX, Soc. d'éditions géographiques, maritimes et coloniales, Paris, 243 pp.

Aubréville A. (1949). Contribution à la paléohistoire des forêts de l'Afrique tropicale. Soc. d'éditions géograph., mar. et colon., Paris, 99 pp.

Aubréville A. (1959). La flore forestière de la Côte d'Ivoire. Publ. CTFT no 15 (3 tomes), Nogent-sur-Marne, 1031 pp.

Aubréville A. (1962). Savanisation tropicale et glaciations quaternaires. Adansonia 2(1): 16-84.

Bagarré E. et Tagini B. (1965). Carte géologique de la Côte d'Ivoire au 1/1.000.000°. SODEMI, Abidjan.

Bech N.J. (1983). La durée du cycle sylvigénétique en forêt de Taï, Côte d'Ivoire. Thèse MSc, Univ. Wageningen, 79 pp.

Begon M., Harper J.L. & Townsend C.R. (1986). Ecology. Individuals, populations and communities. Blackwell Scientific Publ., Oxford, 876 pp.

Bertault J.-G. (1986). Etude de l'effet d'interventions sylvicoles sur la régénération naturelle au sein d'un périmètre expérimental d'aménagement en forêt dense humide de Côte d'Ivoire. Thèse de doctorat, Université de Nancy, Faculté des sciences, 254 pp.

Bertault J.-G. (1992). Comparaison d'écosystèmes forestiers naturels et modifiés après incendie en Côte d'Ivoire. Dans: Puig H. et Maître H.F. (éds.). Actes de l'Atelier sur l'aménagement et la conservation de l'écosystème forestier tropical humide, 12-16 mars 1990, Cayenne. MAB/Unesco, MAB/France, IUFRO, FAO, Paris, pp. 1-25.

Blokhuis W.A. (1993). Vertisols in the Central Clay Plain of the Sudan. Doctoral thesis, Agricultural University, Wageningen, 418 pp.

Boddez P. (1989). Comparaison des deux types de forêt: la structure, la composition et le sol dans le Parc National de Taï, Côte d'Ivoire. Rapport de stage I.A.H.L Velp.

Bolza E. and Keating W.G. (1972). African timbers. The properties, uses and characteristics fo 700 species. Division of building research, CSIRO, Melbourne, 760 pp.

Bongers F., Popma J., Meave del Castillo J. & Carabias J. (1988). Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. Vegetatio 74: 55-80.

Bonnéhin L. (1992). Importance des produits forestiers non ligneux pour la participation des populations locales à l'aménagement de la forêt dans la région de Taï, Côte d'Ivoire. Tropenbos, in prep.

Bonnis G. (1980). Etude des chablis en forêt dense humide sempervirente naturelle de Taï (Côte d'Ivoire). Rapport ORSTOM, Adiopodoumé, 28 pp.

Borcard D., Legendre P. & Drapeau P. (1992). Partialling out the spatial component of ecological variation. Ecology 73(3): 1045-1055.

Bormann F.H., Siccama T.G., Likens G.E. and Whittaker R.H. (1970). The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. Ecological monographs 40: 377-388.

Bos P. (1964). Rapport de fin de levé des coupures Taï 4a-4c au 1/50.000. Rapport no. 127, Société pour le Développement Minier de la Côte d'Ivoire, Abidjan, 58 pp.

Bosman P. and Hall-Martin A. (1986). Elephants of Africa. Struik, Cape town, RSA, 120 pp.

Bousquet B. (1978). Un parc de forêt dense en Afrique. Le Parc National de Taï (Côte d'Ivoire). Bois et Forêts des Tropiques 179: 27-46 & 180: 23-37.

Bouys Ph. (1933). Le bas Cavally (Afrique Occidentale Française) et son avenir. Etude sur les confins franco-libériens de l'ancienne Côte du Mauvais Peuple. Imprimerie Mari-Lavit, Montpellier, 183 pp.

Bray J.R. & Curtis J.T. (1957). An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27(4): 325-349.

Brock M.R. and Chidester A.H. (1977). Geologic map of the Harper quadrangle, Liberia. United States Geological Survey Misc. Inv. Ser. Map I-780-D, Reston, USA.

Bruijnzeel L.A. (1990). Hydrology of moist tropical forests and effects of conversion: a state of knowledge review. Unesco, Paris, 224 pp.

Brunet-Moret Y. (1976). Etablissement d'un fichier pluviométrique opérationnel et étude des averses exceptionnelles. Application à la Côte d'Ivoire. ORSTOM, CIEH, Montpellier, 14 pp.

Budowski G. (1965). Forest species in successional process. Turrialba 15(1): 40-42.

Burrough P.A. (1987). Spatial aspects of ecological data. In: Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. (eds). Data analysis in community and landscape ecology, pp. 213-252. Pudoc, Wageningen.

Busby J. (1986). BIOCLIM user's manual version 2.0. Bureau of Flora and Fauna, Canberra.

Cailliez F. and Alder D. (1980). Forest volume estimation and yield prediction. FAO Forestry Paper 22/1 and 22/2, FAO, Rome.

Casenave A., Flory J., Guiguin N., Ranc N., Simon J.M., Toilliez J. et Tourne M. (1980). Etude hydrologique des bassins de Taï. Campagnes 1978-1979. ORSTOM, Adiopodoumé, 47 pp.

Casenave A., Flory J., Mathieux A. et Simon J.M. (1984). Etude hydrologique des bassins de Taï. Campagne 1981. ORSTOM, Adiopodoumé, 85 pp.

Casenave A., Flory J., Ranc N. et Simon J.M. (1981). Etude hydrologique des bassins de Taï. Campagne 1980. ORSTOM, Adiopodoumé, 83 pp.

Chevalier A. (1909). Rapport sur une mission scientifique en Afrique occidentale. Recherches de 1906-1907 à la Côte d'Ivoire. Nouvelles Archives des Missions Scientifiques et Littéraires 18 (3): 73-82.

Chevalier A. (1948). Biogéographie et écologie de la forêt dense ombrophile de la Côte d'Ivoire. Rev. int. de Bot. appl. et d'Agr. trop. 28: 101-115.

Clément J. (1973). Inventaire forestier du Périmètre Industriel XV. CTFT, Nogent-sur-Marne, 68 pp.

Connell J.H. (1978). Diversity in tropical rain forest and coral reefs. High diversity of trees and corals is maintained only in a nonequilibrium state. Science 199: 1302-1310.

Curtis J.T. & McIntosh R.P. (1951). An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Davis T.W.A. & Richards P.W. (1933-34). The vegetation of Moraballi Creek, British Guyana: an ecological survey of a limited area of tropical rain forest. J.Ecol. 21: 350-384; 22: 106-155.

de Bie S. (1991). Wildlife resources of the West African savanna. PhD thesis, Agricultural University, Wageningen, 266 pp.

de Graaf N.R. (1986). A silvicultural system for natural regeneration of tropical rain forest in Suriname. Doctoral thesis, Wageningen Agricultural University, 250 pp. Also published in the series: Ecology and Management of Tropical Rain Forest in Suriname no. 1, Wageningen Agricultural University.

de Klerk M. (1991). Regeneration strategies of some emergent tree species in Côte d'Ivoire. MSc thesis AV 91/29, Department of Forestry, Agricultural University, Wageningen, 60 pp.

de Koning J. (1983). La forêt du Banco. PhD thesis, Section de Taxinomie et de Géographie botaniques, Univ. Agronomique de Wageningen, 921 pp.

de Namur Ch. et Guillaumet J.L. (1978). Grands traits de la reconstitution dans le Sud-Ouest ivoirien. Cahiers ORSTOM, sér. Biologie 13 (3): 197-201.

de Rouw A. (1991). Rice, weeds and shifting cultivation in a tropical rain forest. A study of vegetation dynamics. PhD thesis, Agricultural University, Wageningen, 263 pp.

de Rouw A., Vellema H.C. & Blokhuis W.A. (1990). Land unit survey of the Taï region, south-west Côte d'Ivoire. Tropenbos Technical series 7, Tropenbos, Ede, 222 pp.

Devineau J.-L. (1976). Principales caractéristiques physionomiques et floristiques des formations forestières de Lamto (moyenne Côte d'Ivoire). Ann. Univ. Abidjan, série E. (Ecologie), 9: 274-303.

Devineau J.-L., Lecordier C. & Vuattoux R. (1984). Evolution de la diversité spécifique du peuplement ligneux dans une succession préforestière de colonisation d'une savane protégée des feux (Lamto, Côte d'Ivoire). Candollea 39: 103-134.

DRC (1967a). Forestry resources of the Southwest region (Ivory Coast). Report to the government of the Republic of the Ivory Coast, Development and Resources Corporation, New-York, 60 pp.

DRC (1967b). Soil survey of the Southwest Region (Ivory Coast). Development and Resources Corporation, New York, 2 volumes.

Dudek S., Forster B., Klissenbauer K. (1981). Lesser known Liberian timber species. Desciption of physical and mechanical properties, natual durability, treatability, wordability and suggested uses. GTZ, Eschborn.

Durand Y. (1985). Nomenclature des essences ivoiriennes. Noms vernaculaires, noms commerciaux, noms scientifiques. (Mise a jour 1985). CTFT-CI, Abidjan.

Eldin M. (1971). Le climat. Dans: Avenard et al. Le milieu naturel de la Côte d'Ivoire, Mémoires ORSTOM no. 50, pp. 73-108.

Ellenberg H. (1979). Zeigerwerte des Gefäßpflanzen Mitteleuropas. Scripta Geobotanica 9, 2. Aufl., Göttingen, 122 pp.

Endler J.A. (1982). Pleistocene forest refuges: fact or fancy. In: Prance G.T. (ed.). Biological diversification in the tropics: 641-657. Columbia Univ. Press, New York.

Faber-Langendoen D. and Gentry A.H. (1991). The structure and diversity of rain forests at Bajo Calima, Chocó region, western Colombia. Biotropica 23(1): 2-11.

Fanta J. (1985). Groeiplaats: onderzoek, classificatie en betekenis voor de bosbouw. Nederlands Bosbouwtijdschrift 57 (10-11): 333-347.

FAO (1977). Guidelines for soil profile description. FAO, Rome, 66 pp.

FAO (1988). FAO/Unesco Soil map of the World, revised legend. World resources report 60, FAO, Rome, 138 pp.

FDA (1990). Annual Report 1989. Forestry Development Authority, Monrovia, 32 pp.

Force E.R. and Beikman H.M. (1977). Geologic map of the Zwedru quadrangle, Liberia. United States Geological Survey Misc. Inv. Ser. Map I-777-D, Reston, USA.

Fraters D. (1986). A study of a catena in the Taï forest, Ivory Coast. MSc thesis, Agricultural University, Wageningen, 64 pp.

Fritsch E. (1980). Etude pédologique et représentation cartographique à 1/15.000 ème d'une zone de 1.600 ha représentative de la région forestière du Sud-Ouest ivoirien. Rapport ORSTOM, Abidjan, 137 pp.

Fritsch J.M. (1992). Les effets du défrichement de la forêt amazonienne et de la mise en culture sur l'hydrologie de petits bassins versants. Opération ECEREX en Guyane française. Collection Etudes et Thèses, ORSTOM, Paris, 392 pp.

Gartlan J.S., Newbery D.McC., Thomas D.W. & Waterman P.G. (1986). The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroun. Vegetatio 65: 131-148.

Gaussen H. (1954). Théorie et classification des climats et microclimats. 8 ème Congrès International Botanique Paris, Sect. 7 et 3, pp. 125-130.

Gautier L. (1989). Le contact forêt-savane à Lamto. Bull. Soc. bot. Fr. 136, Actual. bot. 3/4: 85-95.

Gentry A.H. (1982). Patterns of neotropical plant species diversity. Evolutionary Biology 15: 1-84.

GFML (1967). Inventory of Grebo National Forest. German Forestry Mission to Liberia, Technical report no. 5, Monrovia, 54 pp.

Ghartey K.K.F. (1989). Results of the inventory. In: Wong J.L.G. (ed.). Ghana forest inventory project. Seminar proceedings 29-30 March 1989, Accra. pp. 32-46.

Gillison A.N. & Brewer K.R.W. (1985). The use of gradient directed transects or gradsects in natural resource surveys. Journal of Env. Manag. 20: 103-127.

Gillman L. & McDowell R.H. (1973). Calculus. Norton & Cie, New York, 674 pp.

Gleick J. (1991). Chaos : de derde wetenschappelijke revolutie. Contact, Amsterdam, 314 pp.

Glück P. (1987). Das Wertsystem der Forstleute. Cbl. ges. Forstwesen 104 (1): 44-51.

Goodall D.W. (1954). Vegetational classification and vegetational continua. Angew. Pflanzensoziologie, Wien. Festschrift Aichinger 1: 168-182.

Gornitz V. & NASA (1985). A survey of anthropogenic vegetation changes in West Africa during the last century - Climatic implications. Climatic Change 7: 285-325.

Grace J. (1989). Pattern analysis for forest ecology. In: Schmidt P., Oldeman R.A.A. & Teller A. (eds.). Unification of European forest pattern research. Proceedings of a ESF-FERN Workshop, Strasbourgh, France, 24-26 April 1989. Pudoc, Wageningen.

Gregory S. (1965). Rainfall over Sierra Leone. Dept. Geography, Univ. Liverpool, Res. Papers pp. 2-58.

Griffiths J.F. (ed.) (1972). Climates of Africa. World Survey of Climatology, vol. 10, Elsevier, Amsterdam, 604 pp.

Guillaumet J.L. (1967). Recherches sur la végétation et la flore de la région du Bas-Cavally (Côte d'Ivoire). Mémoires ORSTOM no. 20, ORSTOM, Paris, 247 pp.

Guillaumet J.L. & Adjanohoun E. (1971). La végétation de la Côte d'Ivoire. Dans: Le milieu naturel de la Côte d'Ivoire, Mémoires ORSTOM no. 50, pp. 156-263.

Guillaumet J.L., Couturier G. et Dosso H. (1984). Recherche et aménagement en milieu forestier tropical humide: le Projet Taï de Côte d'Ivoire. Notes techniques du MAB no. 15, UNESCO, Paris.

Hall B.P. & Moreau R.E. (1970). An atlas of speciation in African passerine birds. Trustees of the British Museum, London, 423 pp.

Hall J.B. & Swaine M.D. (1976). Classification and ecology of closed-canopy forest in Ghana. J. of Ecol. 64: 913-951.

Hall J.B. & Swaine M.D. (1981). Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana. Geobotany 1, Dr W. Junk Publishers, The Hague, 383 pp.

Hamilton A.C. (1976). The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. In: van Zinderen Bakker E.M. (ed.). Palaeoecology of Africa 9: 63-97.

Hamilton A.C. (1982). Environmental history of East Africa: a study of the quaternary. Academic Press, London, 311 pp.

Hamilton A.C. (1992). History of forests and climate. In: Sayer J.A., Harcourt C.S. & Collins N.M. (eds.). The conservation atlas of tropical forests: Africa. MacMillan, Basingstoke, pp. 17-25.

Hamilton A.C. & Taylor D. (1991). History of climate and forests in tropical Africa during the last 8 million years. Climatic Change 19: 65-78.

Hammermaster E.T. (1985). Forest resource mapping in Liberia. FAO Tropical Forest Project, Rome, 29 pp.

Hart T.B. (1990). Monospecific dominance in tropical rain forests. Tree 5(1): 6-11.

Hawthorne W. (1993). Fire damage and forest regeneration in Ghana. NRI-ODA, Chatham.

Hawthorne W. & Juam Musah A. (1993). Forest protection in Ghana. Forestry Dept., Kumasi, Ghana, 186 pp.

Hayward D.F. and Oguntoyinbo J.S. (1987). The climatology of West Africa. Hutchinson, London, 271 pp.

Hendrison J. (1990). Damage-controlled logging in managed tropical rain forest in Suriname. Doctoral thesis, Wageningen Agricultural University, 204 pp.

Hill M.O. (1973). Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology 61: 237-249.

Hill M.O. (1979a). Decorana. A Fortran programme for detrended correspondence analysis and reciprocal averaging. Ecology and systematics, Cornell University, Ithaca, New York, 52 pp.

Hill M.O. (1979b). Twinspan. A Fortran programme for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Ecology and systematics, Cornell University, Ithaca, New York.

Hill M.O. & Gauch H.G. (1980). Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47-58.

Hoekman D.H. (1985). Radar backscattering of forest stands. Intern. Journal of Remote Sensing 6(2): 325-343.

Hommel P.W.F.M. (1990). A phyto-sociological study of a forest area in the humid tropics (Ujung Kulon, West Java, Indonesia). Vegetatio 89: 39-54.

Hoppe-Dominik B. (1989). Habitatpräferenz und Nahrungsanprüche des Waldbüffels, Syncerus caffer nanus im Regenwald der Elfenbeinküste. Ph.D. thesis, Univ. Braunschweig, 187 pp.

Hornby A.S., Cowie A.P. and Gimson A.C. (eds.) (1974). Oxford advanced learner's dictionary of current English. Oxford University Press, Oxford, 1037 pp.

Hubbell S.P. and Foster R.B. (1983). Diversity of canopy trees in a neotropical forest and implications for the conservation of tropical trees. In: Sutton et al. (eds.). Tropical rain forest: ecology and management. 41 Brit. Ecol. Soc. Spec. Publ. 2, Blackwell, Oxford, pp. 25-41.

Hubbell S.P. and Foster R.B. (1986). Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soulé M. (ed.). Conservation biology: science of scarcity and diversity. Sinauer Ass., Sunderland, Massachusetts, pp. 205-231.

Hutchinson J. & Dalziel J.M. (1954-72). Flora of West Tropical Africa. 3 volumes, (Second edition by Keay R.W.J. & Hepper F.N.) Crown Agents, London.

Huttel Ch. (1977). Etude de quelques caractéristiques structurales de la végétation du bassin versant de l'Audrénisrou. Rapport ORSTOM, Adiopodoumé, 33 pp.

IFAN (1968). International atlas of West Africa = Atlas international de l'ouest africain. Organisation of African Unity, Scientific, Technical and Research Commission, Dakar, 44 plates + text.

IGN (1965). Cartes topographiques au 1:50.000 ème. Feuilles Taï 4c, Guiglo 2b et Taï 2d. Institut Géographique National, Paris.

Jacobs M. (1988). The tropical rain forest, a first encounter. Springer, Heidelberg, 295 pp.

Jager J.C. & Looman C.W.N. (1987). Data collection. In: Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. (eds). Data analysis in community and landscape ecology, pp. 10-28. Pudoc, Wageningen.

James N.D.G. (1982). The forester's companion. Basil Blackwell, Oxford, 381 pp.

Jans L., Poorter L., van Rompaey R.S.A.R. and Bongers F. (1993). Gaps and forest zones in tropical moist forest in Ivory Coast. Biotropica 25(2), accepted.

Jeambrun M. (1965). Rapport de fin de levé de la coupure Taï 1b-2a-2c au 1/50.000. Rapport no 115, Société pour le Développement Minier de la Côte d'Ivoire, Abidjan, 53 pp.

Jeambrun M. (1966). Rapport de fin de levé des coupures Taï 2d-4b-4d et Guiglo 2b au 1/50.000. Rapport no. 153, Société pour le Développement Minier de la Côte d'Ivoire, Abidjan, 89 pp.

Johansson D. (1974). Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica 59, 136 pp.

Jonkers W.B.J. (1987). Vegetation structure, logging damage and silviculture in a tropical rain forest in Suriname. PhD thesis, Agricultural University, Wageningen, 172 pp.

Koop H. (1989). Forest dynamics. SILVI-STAR: a comprehensive monitoring system. Springer-Verlag, Heidelberg, 229 pp.

Köppen W. (1936). Das geographische System der Klimate. In: Köppen W. & Geiger R. (eds.). Handbuch der Klimatologie. Band I, Teil C, 44 pp., Verlag von Gebrüder Borntraeger, Berlin.

Koptur S. (1985). Alternative defenses against herbivores in Inga (Fabaceae: Mimosoideae) over an elevational gradient. Ecology 66(5): 1639-1650.

Krajewski W.F. (1987). Cokriging radar-rainfall and rain gauge data. Journal of Geophysical Research 92: 9571-9580.

Krebs C.J. (1985). Ecology. The experimental analysis of distribution and abundance. Harper & Row, New York, 678 pp.

Krige D.G. (1951). A statistical approach to some basic mine evalution problems on the Witwatersrand. Journal of the Chemical, Metallurgical and Mining Society of South Africa 52: 119-138.

Lawson G.W., Hall J.B. and Armstrong-Mensah K.O. (1970). A catena in tropical moist semi-deciduous forest near Kade, Ghana. Journal of Ecology 58: 371-398.

Leersnijder R.P & Boeijink D.E. (1990). Modal transect construction for silvicultural design. In: Oldeman R.A.A., Schmidt P. & Arnolds E.J.M. (eds.). Forest components. Wageningen Agric. Univ. Papers 90-6, pp. 13-26.

Leneuf N. (1959). L'altération des granites calco-alcalines et des grano-diorites en Côte d'Ivoire forestière et les sols qui en sont dérivés. Mémoires ORSTOM, 191 pp.

Lescure J.P. & Boulet R. (1985). Relationships between soil and vegetation in a tropical rain forest in French Guiana. Biotropica 17(2): 155-164.

Letalenet J. (1965a). Rapport de fin de levé de la coupure Guiglo 2a au 1/50.000. Rapport no. 101, Société pour le Développement Minier de la Côte d'Ivoire, Abidjan, 40 pp.

Letalenet J. (1965b). Rapport de fin de levé des coupures Taï 2b- Soubré 1a Tabou 4d,4b- Sassandra 3c, 3a. Rapport no 149, Société pour le Développement Minier de la Côte d'Ivoire, Abidjan, 99 pp.

Letouzey R. (1968). Etude phytogéographique du Cameroun. Lechevalier, Paris.

Lhomme J.P. (1981). L'évolution de la pluviosité annuelle en Côte d'Ivoire au cours des soixante dernières années. La Météorologie VIe Série 25: 135-140.

Lieberman M., D. Lieberman, G.S. Hartshorn & R. Peralta (1985). Small scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73: 505-516.

Lincoln R.J., Boxshall G.A. & Clark P.F. (1982). A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, 298 pp.

Lindeman J.C. and Moolenaar S.P. (1959). Preliminary survey of the vegetation types of Northern Suriname. The vegetation of Suriname, Vol. I part 2, Van Eedenfonds, Amsterdam.

Loetsch F., Zöhrer F. and Haller K.E. (1973). Forest inventory. Volume 2, B.L.V., München, 417 pp.

Longman K.A. & Jeník J. (1987). Tropical forest and its environment. Longman Sc. and Techn., Essex.

Maître H.F. (1991). Silvicultural interventions and their effects on forest dynamics and production in some rain forests of in Côte d'Ivoire. In: Gómez-Pompa A., Whitmore T.C. and Hadley M. (eds.). Rain forest regeneration and management. Man and the Biosphere Series 6, pp. 383-392, Unesco, Paris.

Maley J. (1987). Fragmentation de la forêt dense humide africaine et extension des biotopes montagnards au quaternaire récent: nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. Palaeoecology of Africa 18: 307-334, Balkema, Rotterdam.

Maley J. (1991). The African rain forest vegetation and palaeoenvironments during late Quaternary. Climatic Change 19: 79-98.

Mandelbrot B.B. (1983). The fractal geometry of nature. Freeman, New York.

Mangenot G. (1955). Etude sur les forêts des plaines et plateaux de la Côte d'Ivoire. Etudes Eburnéennes IV, pp. 5-61, Inst. Fr. d'Afr. Noire, Centre de Côte d'Ivoire.

Marchesi P., Marchesi N. et Boesch Ch. (1990). Estimation des surfaces forestières de Côte d'Ivoire d'après des images satellites. Unpublished manuscript, 9 pp.

Martin C. (1989). Die Regenwälder Westafrikas: Ökologie-Bedrohung-Schutz. Birkhäuser Verlag, Basel, 235 pp.

Martin L. (1972). Variations du niveau de la mer et du climat en Côte d'Ivoire depuis 25 000 ans. Cah. ORSTOM, sér. Géologie 4 (2): 93-103.

Mayer H. (1980). Waldbau auf soziologisch-ökologischer Grundlage. Gustav Fischer Verlag, Stuttgart, 483 pp.

Mayers J. (1992). Liberia. In: Sayer J.A., Harcourt C.S. & Collins N.M. (eds.). The conservation atlas of tropical forests: Africa. MacMillan, Basingstoke, pp. 214-220.

Mayr E. & O'Hara R.J. (1986). The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. Evolution 40: 55-67.

Meijers G.J. and Saye J. (1983). Rainfall data book of Liberia 1981. Liberian Hydrological Service, Monrovia, 37 pp.

Mengin-Lecreulx P. (1990). Simulation de la croissance d'un peuplement de forêt dense. Le cas de la forêt de Yapo. SODEFOR-CTFT, Abidjan, Nogent-sur-Marne.

Ministère des Eaux et Forêts (1988). Plan directeur forestier 1988-2015. Min. des Eaux et Forets, Abidjan.

Monteny B.A. & Casenave A. (1989). The forest contribution to the hydrological budget in Tropical West Africa. Annales Geophysicae 7(4): 427-436.

MPEA (1983). Republic of Liberia planning and development atlas. Ministry of Planning and Economic Affairs, Monrovia, Liberia, 67 pp.

Munsell (1975). Soil color charts. Kollmorgen corporation, Baltimore, Maryland, USA.

Nakashizuka T., Zulkifli Yusop & Abdul Rahim Nik (1992). Altitudinal zonation of forest communities in Selangor, Peninsular Malaysia. Journal of Tropical Forest Science 4(3): 233-244.

Newbery D.M., Alexander I.J., Thomas D.W. & Gartlan J.S. (1988). Ectomycorrhizal rain-forest legumes and soil phosphorus in Korup Forest Reserve, Cameroon. New Phytol. 109: 433-450.

Noirfalise A. (1984). Forêt et stations forestières en Belgique. Les Presses Agronomiques de Gembloux, 234 pp.

Nooren C.A.M. (1992). Detailed soil survey of a watershed & Study on the role of earthworms in the formation of sandy surface soils in Taï National Park (Côte d'Ivoire). Practical period & MSc. thesis, Department of Soil Science and Geology, Agricultural University, Wageningen, 68 pp.

Nye P.H. (1954). Some soil-forming processes in the humid tropics. I. A field study of a catena in the West African forest. Journal of Soil Science 5: 7-21.

Ohsawa M., Nainggolan P.H.J., Tanaka N. & Anwar C. (1985). Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. J. Trop. Ecology 1: 193-216.

Oldeman R.A.A. (1964). Revision of Didelotia Baill. (Caesalpiniaceae). Primitiaea Africanae IV, Blumea 12: 209-239.

Oldeman R.A.A. (1974). L'architecture de la forêt guyanaise. Mémoires ORSTOM no. 73, ORSTOM, Paris, 204 pp.

Oldeman R.A.A. (1983). Dood hout in tropische regenbossen. Nederlands Bosbouw Tijdschrift 55 (1983): 112-118.

Oldeman R.A.A. (1990a). Forest ecosystems and their components: an introduction. In: Oldeman R.A.A., Schmidt P. & Arnolds E.J.M. (eds). Forest components. Wageningen Agricultural University Papers 90-6, pp. 3-12.

Oldeman R.A.A. (1990b). Forests, elements of silvology. Springer Verlag, Heidelberg, 624 pp.

Oldeman R.A.A. (1991). The paradox of forest management. Proceedings Xth World Forestry Congress, 1991, Paris, 4: 153-182.

Oldeman R.A.A. (1992). Forest resource utilization. In: Hummel J.A. & Parren M.P.E. (eds.) Forests, a growing concern. Proceedings XIXth International Forestry Students Symposium, September 1991, Wageningen. IUCN, Gland, pp. 27-32.

ORSTOM-CIEH (1973). Précipitations journalières de l'origine des stations à 1965. Comité Interafricain d'Etudes Hydrauliques CIEH, ORSTOM, Paris.

Papon A. (1973). Géologie et minéralisations du sud-ouest de la Côte d'Ivoire. Synthèse des travaux de l'opération Sacsa 1962-1968. SODEMI, Abidjan.

Parren M.P.E. (1991). Silviculture with natural regeneration: a comparison between Ghana, Côte d'Ivoire and Liberia. MSc thesis AV. 90/50, Department of Forestry, Agricultural University, Wageningen, 82 pp.

Parren M.P.E. and de Graaf N.R. (1993 in prep.). Forestry in West Africa : the quest for natural forest management : lessons to be learned and examples to be followed. Tropenbos series, The Tropenbos Foundation, Wageningen, 202 pp.

Perraud A. (1971). Les sols. Dans: Avenard et al. Le milieu naturel de la Côte d'Ivoire, Mémoire ORSTOM 50, pp. 265-391.

Poker J. (1989). Struktur und Wachstum in selektiv genutzten Beständen im Grebo National Forest von Liberia. Abschlußbericht zum GTZ-Projekt Nr. 87.2050.0-01.100, Institut für Weltforstwirtschaft und Ökologie, Hamburg, 274 pp.

Poker J. (1992). Struktur und Dynamik des Bestandesmosaiks tropischer Regenwälder - Entwicklung eines Modellansatzes zur Simulation natürlicher Mischbestände. Dissertation, Universität Hamburg, 221 pp.

Poorter L., Jans L., van Rompaey R.S.A.R. and Bongers F. (1993 in prep.). Spatial distribution of gaps along a catena gradient in Taï, Ivory Coast. Journal of Tropical Ecology, submitted.

Rademacher F.E.P. (1992). A detailed soil survey in the northern part of the Taï National Park, southwest Côte d'Ivoire. MSc. thesis, Department of Soil Science and Geology, Agricultural University, Wageningen, 58 pp.

Ramensky L.G. (1910). On the comparative method for ecological study of plant communities (in Russian). Dnevnik S'ezda russk. Estestvoisp Vrach. 2(9): 389-390.

Ramensky L.G. (1930). Zur Methodik des vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und andere Objekten, die durch mehrere, verschiedartigen wirkende Faktoren bestimmt werden. Beitr. Biol. Pfl. 18: 269-304.

Richard J.F. (1989). Le paysage, un nouveau langage pour l'étude des milieux tropicaux. Initiations - Documentations techniques no 72, ORSTOM, Paris, 210 pp.

Rollet B. (1974). L'architecture des forets denses sempervirentes de plaine. CTFT, Nogent sur Marne.

Rougerie G. (1960). Le façonnement actuel des modelés en Côte d'Ivoire forestière. Mémoires de l'Institut Français d'Afrique Noire (IFAN) 58, Dakar, 493 pp.

Russell-Smith J. (1991). Classification, species richness, and environmental relations of monsoon rain forest in northern Australia. Journal of Vegetation Science 2: 259-278.

Sachtler M. (1968). General report on National Forest Inventory in Liberia. Technical report no. 1, German Forestry Mission to Liberia, Monrovia, 149 pp.

Sachtler M. and Hamer K. (1967). Inventory of Krahn-Bassa and Sapo National Forest. Technical report no. 7, German Forestry Mission to Liberia, Monrovia, 92 pp.

Sayer J.A., Harcourt C.S. & Collins N.M. (1992). The conservation atlas of tropical forests: Africa. MacMillan, Basingstoke, 288 pp.

Schmidt E. (1990). Inventarisation of the bufferzone of the Park Taï by remote sensing. MSc thesis, Depart. of Silviculture and Forest Ecology, Wageningen Agr. Univ.

Schnell R. (1950). La forêt dense. Introduction à l'étude botanique de la région forestière d'Afrique occidentale. Manuels Ouest-africains 1, P. Lechevalier, Paris, 330 pp.

Schnell R. (1952). Végétation et flore de la région montagneuse du Nimba (A.O.F.). Mém. IFAN 22, 604 pp.

Schulz J.P. (1960). Ecological studies on rain forest in Northern Suriname. The vegetation of Suriname Vol. II, Van Eedenfonds, Amsterdam, 267 pp.

Schumann W. (1979). Elsevier gids voor stenen & mineralen. Elsevier, Amsterdam, 232 pp.

Snoeck J. (1975). Variations de la pluviosité en zone forestière ivoirienne. Cafe-Cacao-Thé 19(3): 165-176.

Sobolev L.N. & Utekhin V.D. (1973). Russian (Ramensky) approaches to community systematization. In: Whittaker R.H. (ed.). Ordination and classification of communities. Handbook of vegetation science 5: 77-103. Junk Publishers, The Hague.

SODEFOR (1976a). Inventaire forestier national. Résultats de la région centre-sud. SODEFOR, Abidjan.

SODEFOR (1976b). Inventaire forestier national. Résultats de la région nord-ouest. SODEFOR, Abidjan.

Sokal R.R. & Rohlf F.J. (1969). Biometry. The principles and practice of statistics in biological research. Freeman, San Francisco, 776 pp.

Sosef M.S.M. (1993 in press). Glacial rain forest refuges in relation to speciation in Begonia sect. Loasibegonia and sect. Scutobegonia. Proceedings of the 13th AETFAT congress, Zomba, Malawi 1991.

Spichiger R. & Lasailly V. (1981). Recherche sur le contact forêt-savanne en Côte-d'Ivoire: note sur l'évolution de la végétation dans la région de Beoumi (Côte d'Ivoire centrale). Candollea 36: 145-153.

Stein A. and Corsten L.C.A. (1991). Universal kriging and cokriging as a regression procedure. Biometrics 47: 575-587.

Stoffers, A. (1989). Groeimetingen in het Parc National de Taï. Stageverslag, Larenstein Internat. Hogeschool, Velp.

Swaine M.D. & Hall J.B (1976). An application of ordination to the identification of forest types. Vegetatio 32: 83-86.

Swaine M.D. & Hall J.B. (1988). The mosaic theory of forest regeneration and the determination of forest composition in Ghana. Journal of Tropical Ecology 4(3): 253-269.

Swaine M.D., Hall J.B. & Alexander I.J. (1987). Tree population dynamics at Kade, Ghana (1968-1982). Journal of Tropical Ecology 3(4): 331-345.

Swaine M.D., Hall J.B & Lock J.M. (1976). The forest-savanna boundary in west-central Ghana. Ghana J. Sci. 16(1): 35-52.

Swaine M.D. & Whitmore T.C. (1988). On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81-86.

Tagini B. (1972). Notice explicative à la carte géologique de Côte d'Ivoire à 1/2.000.000. Rapport SODEMI No. 279, Abidjan, 19 pp.

Taylor C.J. (1952). The vegetation zones of the Gold Coast. Bull. Gold Coast For. Dep. 4: 1-12.

Taylor C.J. (1960). Synecology and silviculture in Ghana. Nelson, Edinburgh, 418 pp.

ter Braak C.J.F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67(5): 1167-1179.

ter Braak C.J.F. (1987a). Ordination. In: Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. (eds). Data analysis in community and landscape ecology, pp. 91-173. Pudoc, Wageningen.

ter Braak C.J.F. (1987b). The analysis of vegetation-environmental relationships by canonical correspondence analysis. Vegetatio 69(1/3): 69-77.

ter Braak C.J.F. & Looman C.W.N. (1987). Regression. In: Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. (eds). Data analysis in community and landscape ecology, pp. 29-77. Pudoc, Wageningen.

ter Braak C.J.F. & Prentice I.C. (1988). A theory of gradient analysis. Advances in Ecological Research 18: 271-317.

Touber L., Smaling E.M.A., Andriesse W. & Hakkeling R.T.A. (1989). Inventory and evaluation of tropical forest land. Guidelines for a common methodology. Tropenbos Technical Series 4, Ede, 170 pp.

Tysdal R.G. (1977). Geologic map of the Juazohn quadrangle, Liberia. United States Geological Survey Misc. Inv. Ser. Map I-779-D, Reston, USA.

van der Werf S. (1991). Bosgemeenschappen. Pudoc, Wageningen, 375 pp.

van Donselaar J. (1965). An ecological and phytogeographic study of northern Surinam savannas. North-Holland Publ. Co., Amsterdam.

van Herwaarden G.J. (1991a). Compound report on three soil surveys in the Taï forest (Côte d'Ivoire). UNESCO/ Dept. of Soil science and geology, Agricultural University, Wageningen, 59 pp.

van Herwaarden G.J. (1991b). Some physical soil properties on a catena in the Taï region (south-west Côte d'Ivoire). Unesco, Dept. of Soil Science & Geology, Agricultural University, Wageningen, 58 pp.

van Kekem A.J. (1984). Légende pour la carte des sols du sud-ouest de la Côte d'Ivoire. Application de la méthode utilisée dans le programme pédologique du M.A.B. Projet Taï, UNESCO.

Van Miegroet M. (1976). Van bomen en bossen. Story-Scientia, Gent, 2 vol., 1166 pp.

van Tongeren O.F.R. (1987). Cluster analysis. In: Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. (eds). Data analysis in community and landscape ecology, pp. 174-212. Pudoc, Wageningen.

Vanclay J.K. (1989). A growth model for North Queensland rainforests. Forest Ecology and Management 27: 245-271.

Vivien J. et Faure J.J. (1985). Arbres des forêts denses d'Afrique centrale. Min. de Coopération, Paris, 565 pp.

Vooren A.P. (1979). La voûte forestière et sa régénération. Analyse structurelle et numérique d'une toposéquence en forêt de Taï, Côte d'Ivoire. MSc thesis, Agricultural University, Wageningen, 89 pp.

Vooren A.P. (1985). Patterns in tree and branch-fall in a West African rain forest. Report D85-05, Dept. of Silviculture, Agricultural University, Wageningen, 33 pp.

Vooren A.P. (1986). Nature and origin of tree and branch fall in the Taï Forest (Ivory Coast). Neth. J. Agricult. Sci. 34: 112-115.

Vooren A.P. (1987). Development versus conservation: avoiding a conflict in the Taï region (Ivory Coast). In: Beusekom, C.F. van; Goor, C.P. van; Schmidt, P. (eds.) Wise utilization of tropical rain forest lands, Tropenbos Scientific Series 1: 130-137, Tropenbos/ MAB Unesco, Ede.

Vooren A.P. (1992a). Appropriate buffer zone management strategies for Taï National Park. In: Puig H. et Maitre H.F. (eds.). Actes de l'Atelier sur l'aménagement et la conservation de l'écosystème forestier tropical humide, mars 1990, Cayenne, pp. 26-39.

Vooren A.P. (1992b). Côte d'Ivoire. In: Sayer J.A., Harcourt C.S. & Collins N.M. (eds.). The conservation atlas of tropical forests, Africa. MacMillan, Basingstoke, pp. 133-142.

Vooren A.P. (1992c). Harvest criteria for tropical forest trees. In: Cleaver K. et al. (eds.). Conservation of West and Central African rainforests. World Bank environment paper 1: 134-140, The World Bank, Washington, D.C.

Voorhoeve A.G. (1964). Some notes on the tropical rainforest of the Yoma-Gola National Forest near Bomi Hills, Liberia. Commonwealth Forestry Revue 43(1): 17-24.

Voorhoeve A.G. (1965). Liberian high forest trees. A systematic botanical study of the 75 most important or frequent high forest trees, with reference to numerous related species. PhD thesis, Agricultural University, Wageningen, 416 pp.

Walter H. (1979). Vegetation of the earth and ecological systems of the geo-biosphere. Springer Verlag, Heidelberg.

Walter H. & Box E. (1976). Global classification of natural terrestrial ecosystems. Vegetatio 32: 75-81.

Walter J.-M.N. (1974). Arbres et forets alluviales du Rhin. Bull. Soc. Hist. Nat. Colmar 55: 37-88.

WAU (1991). Annual report 1990. Centre Néerlandais d'Adiopodoumé, Côte d'Ivoire & Research programme: "Analysis and design of land-use systems in the Taï region". Wageningen Agricultural University, Wageningen, 28 pp.

Webster's (1976). Webster's seventh new Collegiate dictionary. Merriam Co., Springfield, Mass., 1224 pp.

White F. (1983). The vegetation of Africa, a descriptive memoir to accompany the UNESCO/ AETFAT/ UNSO vegetation map of Africa. Natural resources research XX, UNESCO, Paris, 384 pp.

Whitmore T.C. (1984). Tropical rain forests of the Far East. Oxford Science Publ., Oxford, 352 pp.

Whitmore T.C. (1990). An introduction to tropical rain forests. Clarendon Press, Oxford, 226 pp.

Whitmore T.C. and Silva J.N.M. (1990). Brazil rain forest timbers are mostly very dense. Commonwealth Forestry Review 69(1): 87-90.

Whittaker R.H. (1956). Vegetation of the Smoky Mountains. Ecological Monographs 26: 1-80.

Whittaker R.H. (1967). Gradient analysis of vegetation. Biological Reviews 42: 207-264.

Williams W.T., Lance G.N., Webb L.J., Tracey J.G. & Connell J.H. (1969). Studies in the numerical analysis of complex rain forest communities IV. A method for the evaluation of small-scale forest pattern. J.Ecol. 57: 635-654.

Wöll H.J. (1981). Silvicultural evaluation. Diagnostic sampling 1978-1980. Internal report, German Forestry Mission to Liberia, Monrovia, 65 pp.

WRR (1992). Grond voor keuzen. WRR rapport 42, WRR, Den Haag, 149 pp.

Zonneveld I.S. (1988). Establishing a floristic classification. In: Küchler A.W. & Zonneveld I.S. (eds). Vegetation mapping, pp. 81-88. Handbook of Vegetation Science 10, Kluwer, Dordrecht.