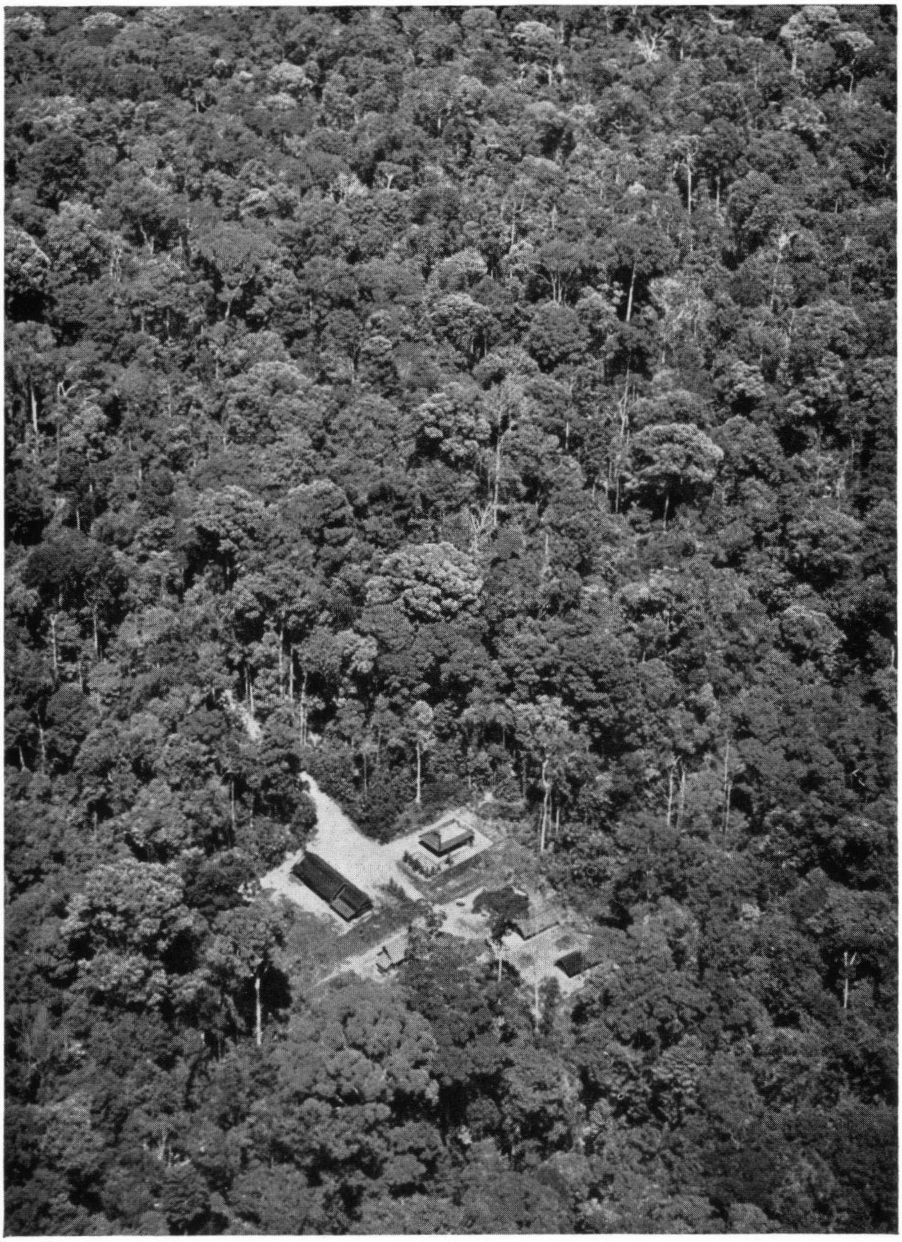
PLATE I



Aerial photograph of mesophytic forest of the Mapane region surrounding the large clearing of the main camp site.

ECOLOGICAL STUDIES ON RAIN FOREST IN NORTHERN SURINAME

BY

J. P. SCHULZ
(PARAMARIBO)

1960
N.V. NOORD-HOLLANDSCHE UITGEVERS MAATSCHAPPIJ
AMSTERDAM

CONTENTS

INTRODUCTION

PART I. CLIMATIC FACTORS OF HABITAT

PART II. EDAPHIC FACTORS

PART III. FLORISTIC COMPOSITION OF THE FOREST

PART IV. REGENERATION OF THE FOREST

ILLUSTRATIONS

INTRODUCTION

GENERAL REMARKS

This work is the outcome of a 3 years' stay (December 1954–November 1957) in the mesophytic lowland forests (rain forest) occurring in the northern half of central Suriname, i.e. the part South of the Savanna belt. The present investigations are concerned with the environmental factors prevailing in this forest type and with its natural regeneration. As the fast growing amount of literature on this subject seems to indicate, the latter has become a focus of interest for forest ecologists in several tropical countries in Africa and Asia where, after centuries of wasteful exploitation and devastation, the dawn of a real silviculture is breaking. Still, as has been stated in the latest general account of the tropical rain forest written by RICHARDS (1952, p. 40), information with regard to regeneration under undisturbed conditions is scanty, as much of what has been written on "natural regeneration" of rain forest refers to the reproduction of a few commercially valuable species under more or less unnatural conditions. Before regeneration under such artificial conditions can be understood and controlled, knowledge is needed of what is happening under undisturbed conditions. Next to nothing is known of natural regeneration in the largest continuous expanse of rain forest, the South American hylaea.

The first and second part of this paper will deal with observations made in a number of different habitats on various environmental factors. This study of habitat factors, viz. light, atmospheric humidity, evaporation, air- and soil-temperature, and soil factors, was thought to be both of importance in itself (as an addition to our knowledge on these factors obtained in other rain forest areas) and, indirectly, in connection with our regeneration studies. In view of the latter, particular attention was devoted to a comparison of the climate in closed forest with that in gaps of different size.

It was my good fortune that I was able to carry out the present investigations in a country largely covered with virtually undisturbed forest and for a period considerably longer than is usually allowed to expeditions to such remote areas. This relatively long period of observation, covering 2 whole years (1955 and 1956) and the dry season of 1957, was sufficient to obtain a fairly good idea of the seasonal range of variability shown by a number of micro-climatological factors in the forest type under consideration. Unfortunately, this does not apply to the light factor, which is of paramount interest especially in connection with regeneration. The technical difficulties of the light measurements and their time-consuming character allowed but a limited number of readings.

A systematic and detailed study of a number of selected soil factors has been made on a limited area in combination with an investigation of the horizontal pattern of distribution of some of the principal tree species. Special attention was paid to a comparison of the physical properties shown by different soil types. The results of these analyses are given in the second part. The principal object was to ascertain the variations in soil factors over short distances, and to what extent these variations may account for the discontinuities in the distribution of the tree species that were observed in the same area. Some results of the sample plot surveys and mappings of the distribution of a few selected tree species had revealed the patchy (i.e. non-random) distribution of a number of species.

In addition in various sites soil samples were taken in order to obtain a preliminary idea of the variations of soil types on which rain forest was found in this part of Suriname.

In the third part the results will be discussed of phytosociological observations. These analyses were carried out by means of sample-plot surveys made in forest stands found on the soil types described in the second part. This, however, does not imply that a causal relationship could be demonstrated between the various soil types and the floristic composition of the respective forest stands, and it is certainly not my intention to attempt a phytosociological classification of these communities on the results of the analyses obtained in a few widely scattered sample areas. The most I could hope to achieve was to give quantitative records of samples made in forest stands in different sites, whatever the phytosociological status of these phytocoenoses might be. These samples give an idea both of the variability in floristic composition over greater distances as well as of the attributes obtainable with the sampling method used. Moreover, the sample-area surveys provided data of direct interest for the regeneration studies, such as size-class representations and horizontal pattern of distribution of species, which will be discussed in the fourth part.

Right from the first, knowledge of the size-class distribution of the species—reflecting the history of the reproduction of the species concerned—was taken to be of principal importance. A superficial study of the data provided by the enumeration surveys conducted by the Forest Department, had already revealed that the vast majority of the emergent species in the Suriname rain forest are regenerating continuously; with a few exceptions the species from both middle and emergent storeys showed a logarithmic decrease in the number of individuals with increasing diameter. This was a strong indication that regeneration and silvicultural problems in Suriname forests differ fundamentally from those reported from the over-mature stands in West-African rain forests, where with many of the emergent species stems of medium size tend to be less abundant than the larger ones.

Because the routine enumerations as conducted by the Forest Department were limited to stems of 25 cm diam. and over, additional sample-plot surveys including the smaller sizes and the seedlings were necessary. Attention was paid also to the distribution of seedlings, the dispersal of seeds and their germination, and to the life-history of the seedlings of a few selected species, under different conditions.

Careful measurements were made of the growth rate in a large number of trees belonging to a few selected species, occurring in forest stands on different soils. Special attention was paid to the influence of different light intensities on increment.

Periodicity of flowering and fruiting too were studied.

The provisional results of growth measurements in the plots of a forest-conversion experiment where different grades of light had been let in by different degrees of opening of the upper storeys, will be discussed in the fourth part.

After my departure to Holland the growth measurements were continued by the Forest Department. The results of these measurements too have been incorporated in this publication.

A number of related questions raised during the course of this study will be discussed in separate publications.

ACKNOWLEDGEMENTS

The investigations were conducted under the auspices of the Foundation for Scientific Research in Suriname and the Netherlands Antilles and were made possible by the financial help of the Netherlands Foundation for the Advancement of Research in Suriname and the Netherlands Antilles (WOSUNA). The latter organisation bore the major part of the large costs of the field work as well as of the analyses of the soil samples conducted at the Soils Laboratory of the Royal Tropical Institute, Amsterdam.

I am greatly indebted to Ir. I. A. DE HULSTER, the Chief Conservator of forests in Suriname, who with the Suriname Forest Department rendered invaluable assistance.

For the identification of plant material I wish to acknowledge Dr. J. C. LINDEMAN and other members of the staff of the Institute for Systematic Botany, University of Utrecht (Director Professor Dr. J. Lanjouw).

My sincere thanks are due to Professor Dr. C. E. B. BREMEKAMP for his critical revision of the English text of the manuscript, and to Professor Dr. J. P. BAKKER (Institute for Physical Geography, University of Amsterdam) and Professor Dr. F. A. VAN BAREN (Soils Laboratory of the Royal Tropical Institute, Amsterdam) for valuable suggestions concerning pedological problems.

It is a pleasure to record my indebtedness to Dr. F. W. OSTENDORF (at the time Director of the Agricultural Experiment Station, Paramaribo) and to his staff of the soils laboratory for reporting on the soil moisture samples.

Part of the costs of the forest-refining experiment, described in part IV, were defrayed out of funds appropriated to the Forest Department by the Suriname Development Board.

GENERAL DESCRIPTION OF THE AREAS OF OPERATION

At the wish of the Forest Department the main work was carried out in the mesophytic lowland forest of the Mapane region, which is situated about 30 km SE from the old ruins of Jodensavanne and the Amerindian villages of Cassipora and Redidoti, (cf. the sketch maps, fig. 1 and 2). The major advantages of this choice were the accessibility, the existence of a permanent camp and the fact that the forests of this region already had been demarcated by the forest inventory department by cut base-lines into square compartments of 1600 ha each, of which accurate forest maps at 1 : 20.000 scale were available. The unit-compartments were subdivided by parallel sampling lines cut in EW direction at 500 m intervals, and data were available of a 2 % enumeration survey made in 10 m wide transects along these sampling lines, which provided a valuable basis for more detailed vegetational studies.

The luxuriant rain forest around the camp may be taken as being representative for the rain forests covering the greater part of the lowland region bordered by the Commewijne R. and the Suriname R. and lying between Zanderij-sands to the north and the hilly country in the south. The topography of this region is very gentle, without striking features of relief. The low rounded hills, generally below 40 m in elevation flatten out to the north in the Zanderij-sands and south of the Mapane Creek merge insensibly into more rugged country formed by higher schistose hills and hilly ridges which attain heights of over 100 m. South of the sands the underlying rocks are a crystalline complex of Pre-cambrian age. Drainage is free and the terrain is dissected by numerous creeks bordered by humid creek-margin forest (cf. the map shown fig. 46). The very deeply weathered soils which will be discussed in detail in part II, are red coarse sandy loams and clays with sandy "pockets" as found near the transition to the Zanderij-sands. The latter sands are covered with xeromorphic vegetation, varying from open savanna to "high savanna forest" (for an account of these terms see LINDEMAN *et al.* 1959).

Like elsewhere in the interior of Suriname, the population is extremely sparse. A few dozen families of Amerindians now live in 2 villages near Jodensavanne, about 25 km NW from the camp. There are, however, reasons to believe that the population of this region may once have been denser than it is at present and that long ago considerable areas of what is considered to be typical primary forest, have been disturbed by shifting cultivation. The findings of charcoal in nearly every soilpit, and of fragments of primitive Indian pots in a number of pits and during the construction of the road point unmistakably to a disturbance of the forest at some distant period, and are strong evidence for the fact that these primary forests are not primary in the sense that they never have been touched by man.

Commercial exploitation of the forests in this region has hitherto been

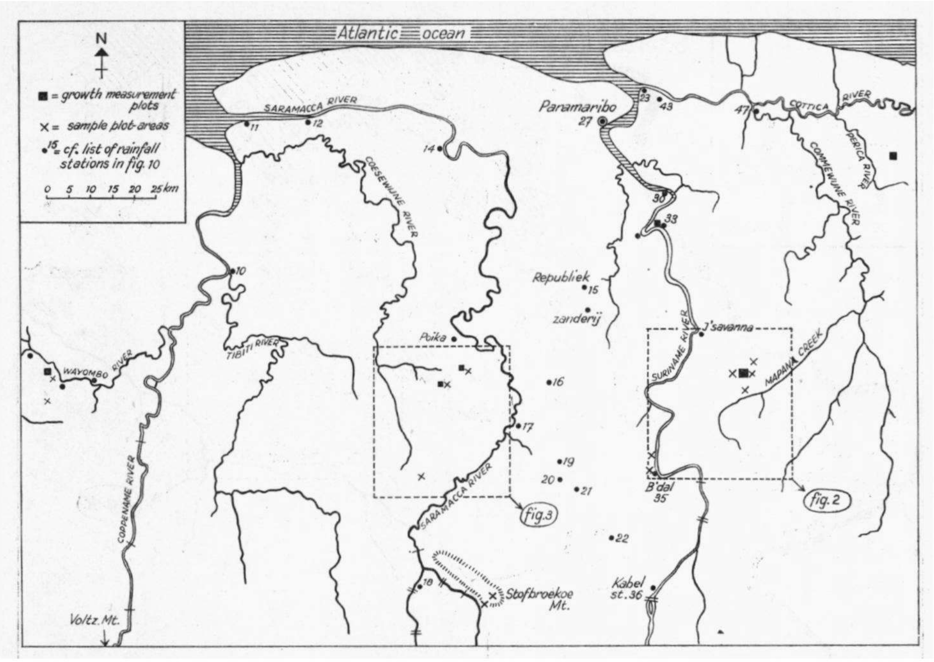


Fig. 1. Sketch map of the northern part of central Suriname.

confined to small belts along the rivers and along the Mapane Creek. The micro-climatological studies and most of the regeneration studies were carried out in the rain forest lying within a radius of about 4 km around the campsite (cf. figs. 2 and 46). A more detailed account of the physiognomy and of the floristic composition of this forest, which is typical for the Suriname firm-ground rain forest in its optimal development, will be given in part II. This forest is true mixed forest, without any clear dominant, although some species tend to a patchy distribution.

Although for reasons of convenience in the following chapters the terms "canopy" and "storey" will be used, neither a definite continuous flat-topped canopy, nor well defined tree-strata are recognizable. Where in the following mention is made of the "(main) canopy" or "dominant storey", the discontinuous surface of the uppermost foliage is meant, which in the Mapane forest on mesic sites has a height, varying between 25–38 m. This "canopy" presents the same picture as that described by RICHARDS (1933, p. 362 and 370) for the "mixed forest" of Moraballi Creek, and has excellently been pictured in the profile drawing reproduced in the publication of LINDEMAN (1959, right part of profile V, drawn in the Mapane forest). By main-canopy trees, or *canopy dominants* will be meant mature trees of those species which generally reach a total height of about 30–38 m. All commercially valuable timber trees belong to this class. There is no discontinuity separating these tall trees from the *"middle storey"*, i.e. from the trees belonging to species which – when mature – generally do not reach a total height of over 25 m, but which

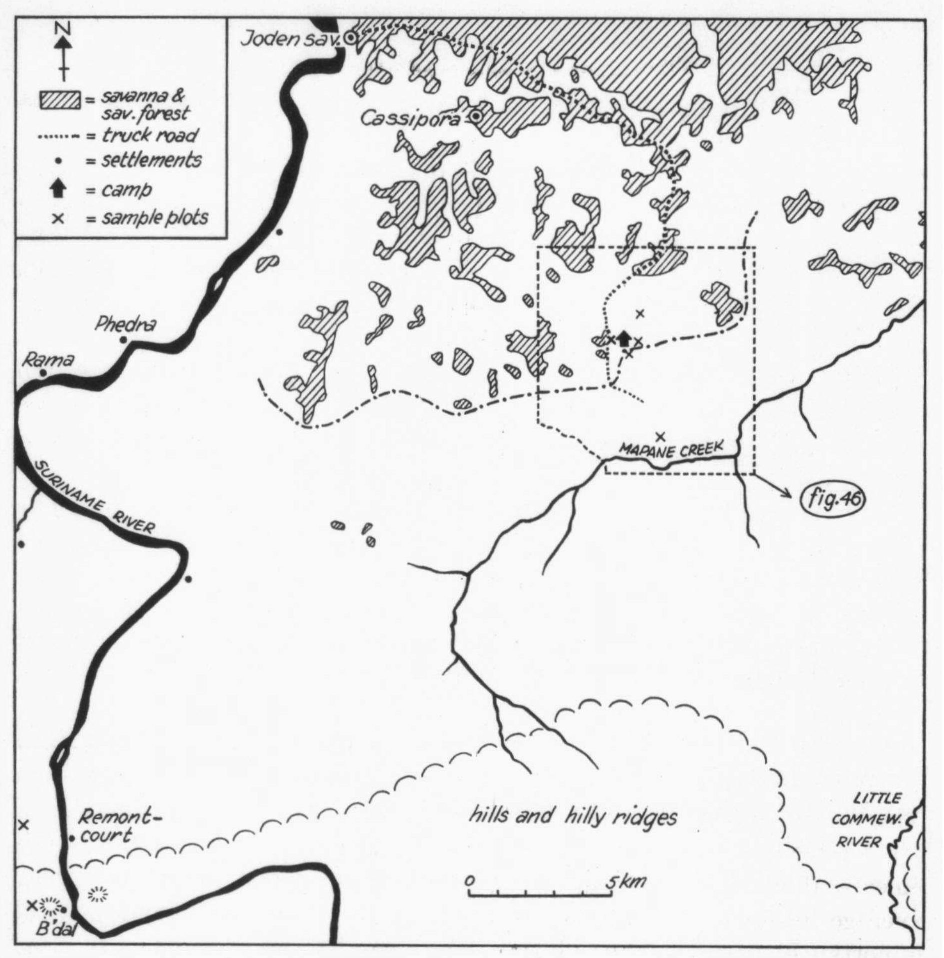


Fig. 2. Sketch map of the Mapane region. The unshaded areas represent mainly mesophytic mixed high forest (rain forest). The point-dash line marks the approximate boundary between the Zanderij formation and the Old Basement.

form the canopy in gaps between the taller trees. Neither is there a discontinuity with the crowns of the tallest species, called "emergents" (e.g. *Couratari* and a number of Mimosaceae), which may attain a height of 40–47 m. Although the crowns of these emergent species sometimes are lifted clear of their neighbours ("outstanding trees"), there is usually no discontinuity separating them from the neighbouring main canopy trees and their foliage commonly forms part of the strongly undulating and irregular main canopy. The frequent occurrence of individuals of the emergent species seems typical for the rain forest in its optimal development in this part of Suriname. The space under the foliage of the main canopy is more or less densely filled with young individuals of canopy species and with species of the under-storeys.

As mentioned above the *middle-storey* species, although generally not reaching a total height of over 25 m, may sometimes form the main canopy. To this class belong e.g. part of the *Eschweilera* species. For convenience a group of species attaining heights of 8–18 m (e.g. the very common *tajahoedoe, Paypayrola guianensis*) may be distinguished as "*lower storey*" species.

The "*undergrowth*" is made up of saplings of taller species and of true undergrowth species like stemless palms (*paramakka, Astrocaryum paramaca*, being very common in this region), dwarftree species (like *Bonafousia, mirkitikie*) and small shrubs and some tall herbs. The stemless palm stratum is the only well defined stratum, reaching a height of about 6 m.

In the micro-climatological studies recordings were made also in the "*herb and seedling layer*"; this is an ill-defined layer consisting of a few small ferns and other herbs, but largely consisting of seedlings of tree species.

Climbers are occasional to common. Stranglers belonging to the genus *Clusia* are not uncommon, and with their large leaves they are serious competitors with the trees for light.

Stem and crown epiphytes, although represented by many species and individuals, constitute no important factor in the composition of the mass of foliage.

Considerable time was spent also in the Goliath Creek – Upper Coesewijne R. – Saramacca R. watershed (cf. the sketchmap shown in fig. 3). The rain forest in the northern half of this region differs from that in the former one in its composition and in the relative rarity of trees that emerge above the average height of the main canopy, which attains an average height of 28–34 m. Still, it is luxuriant forest of great economic importance owing to the relative abundance of two valuable species: *basralokus* (*Dicorynia guianensis*) and *wana* (*Ocotea rubra*). This type of rain forest occurs in the very slightly undulating area extending from the Coesewijne savannas in the N, to the Goliath Cr. (and presumably beyond the latter) in the W, to the extensive Costerie Cr. savannas in the E; to the S it insensibly merges into savanna forests and less luxuriant hill forests. In the southern part of the area mapped in fig. 3, the hills and hilly ridges (which attain their maximum height in the Goliath hills), are covered with a forest which will be described in more detail in part III.4.

Regeneration (diameter-class distributions and growth measurements), soils and floristic composition were studied in the luxuriant forests between Upper Coesewijne R. and a line, say 10 km S of it, that is in the vicinity of the main truck road.

In this area, which geologically presumably belongs to the Zanderij-formation, rain forest is chiefly found on light soils of the yellow-red sandy type. In the creek valleys often white leached sands are encountered, covered with various types of forest ranging from humid to xeromorphic. Along the Goliath Cr. and particularly on schistose hills in the S, heavier

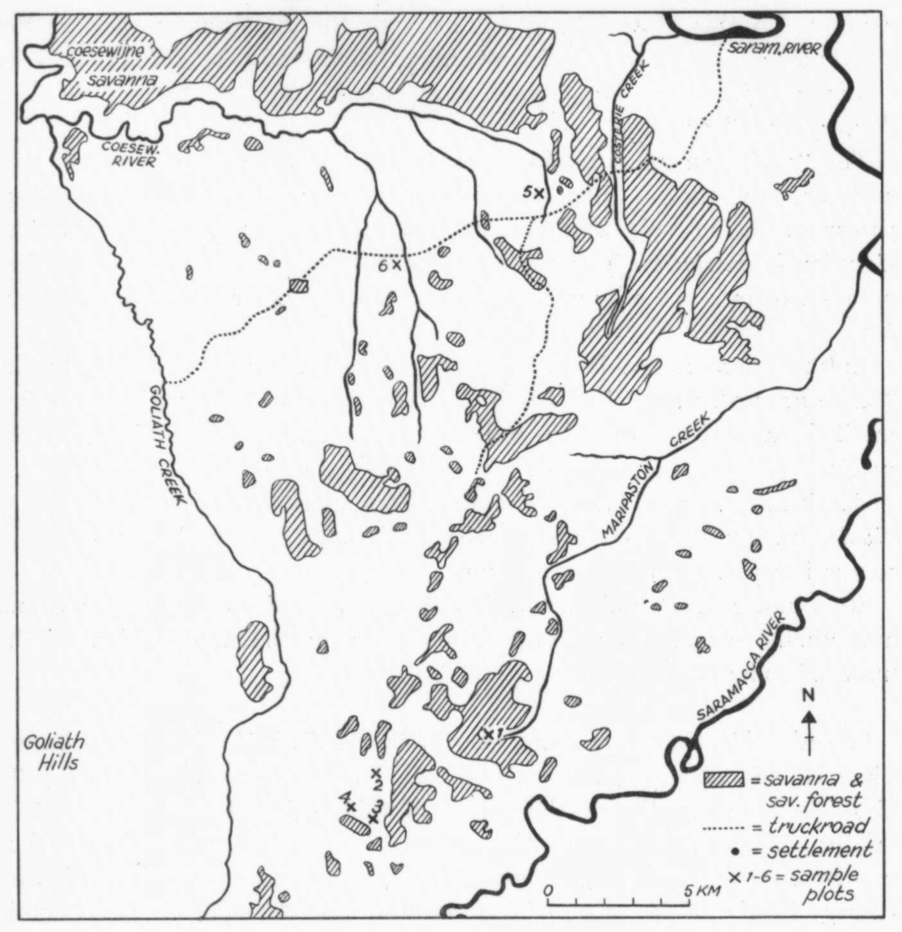


Fig. 3. Sketch map of the Upper-Coesewijne region. The unshaded areas represent mainly high mesophytic forest (rain forest).

soils are found, which often contain concretionary ironstone. The white sands on the watersheds in the W, centre and S are covered with various types of xeromorphic vegetation (open savanna to high savanna forest).

Although the population at this time is confined to a few dozen Amerindian families living in the village of Poika and visiting the country S of the Upper Coesewijne R. for fishing and hunting only, recent traces of farming (bush-fallow) are found everywhere in this area. Scattered patches of secondary forest (locally called "kapoewerie") in all stages of development are of very common occurrence, particularly along the Upper Coesewijne R. and affluent creeks. The regularity of their pattern and the sharpness of the boundaries with the surrounding high forest are proof of their way of origin. At this moment no Bushnegroes live in this region but traces of at least 2 villages were found (Maripaston and Jacksonkondre).

Up to 1957 the commercial exploitation of the forests for timber was confined to the more easily accessible sites in the vicinity of the rivers. Since the finishing of a truck road built in the years 1956–1957 by the Forest Department, felling of timber has begun in concessions along this road. The enumerations, however, had been conducted previously.

Some visits were paid to the mixed rain forest S of the Wayombo R. (cf. fig. 1) situated on silty alluvial clays of the Old Coastal Plain (Coropina formation). The composition of this forest differs markedly from that of the former sites and seemed of special interest in view of the greater tendency to local abundance of some species, viz. *moraboekea* (*Mora gonggrijpii*) and the valuable *basralokus* (*Dicorynia guianensis*). This tendency to single dominance is a feature which apparently increases from E to W. It is, in my opinion, not so much caused by the selective effect of less favourable climatic or soil factors, as by the occurrence, W of the Coppename R., of species which show a stronger tendency to gregariousness.

In addition a few trips were made to the *upland rain-forests* on the *ferrallitic* soils which cover the greater part of the hilly country farther inland, S of the coastal- and Zanderij-sediments. The soils and the forests of the hills near Remontcourt and Bergendal (Suriname R., cf. fig. 1), the Goliath Cr. region and the Stofbroekoe Mnt. (Little Saramacca R.) are described in II.4 and III.4. The soils and the forest in the vicinity of the Voltz Mnt., a granitic "inselberg" near the Upper Coppename R. (about 20 km S of the bottom line of the map shown in fig. 1), are discussed in II.5 and III.4.4.

PART I

CLIMATIC FACTORS OF HABITAT

I.1. REMARKS ON GENERAL CLIMATE

The most comprehensive compilation of meteorologic data obtained in name is that given by BRAAK (1935), which has been briefly summarized in the first two parts of the "Vegetation of Suriname" (LINDEMAN 1953, 1959). OSTENDORF (1953–1957) published a series of papers containing some general considerations on the climate and detailed analyses of the seasonal and annual distribution of rainfall, which were based on data covering periods that were considerably longer than those of which data were available at the time when Braak's compilation appeared.

The climate in the N half of Suriname is primarily determined by the distribution of the rainfall. The annual march of atmospheric humidity and of the amount of sunshine are strongly correlated with that of rainfall. The values of mean daily and monthly *air temperature* remain remarkably constant throughout the year and do not differ significantly from one station to another. Mean air temperature at Paramaribo (1899–1953) is 27.1° as based on readings at 8, 14 and 18 hr. (Jan.: 26.1°, Oct.: 28.3°). At this station maximum and minimum temperature over the same period averaged 30.9° and 22.7° respectively (absol. max. and min.: 37.4° and 16.6°). An idea of the annual variation of maximum and minimum temperature may be gained from the readings made in a large clearing at Mapane camp depicted in fig. 7.

The amount of *sunshine*, as measured with a Jordan sunshine recorder, has recently been discussed in detail by OSTENDORF (1956 b). In fig. 4 the monthly mean percentage of sunshine for Paramaribo, averaged over 24 years, is shown. The annual mean of the hours of sunshine between 7 and 17 hr. amounts to 5.7 hours (4.3 and 7.8 hours in May and Sept. respectively). This relatively low value is in accordance with the annual mean for British Guiana, viz. 5.5 hrs./day (DAVIS *et al.* 1933). Though the number of days with a sunshine percentage of 91 % or over averages 11 % per annum (OSTENDORF 1956 b), even during the dry season clouds are continually passing in front of the sun, and it was often difficult to find times when there was bright sunshine for long enough to make one continuous series of light measurements.

In section I.3.4 the frequency percentages are given for days with various numbers of sunshine hours.

In the coastal region NE trade *winds* blow almost steadily throughout the year. Going farther inland the wind direction becomes less constant

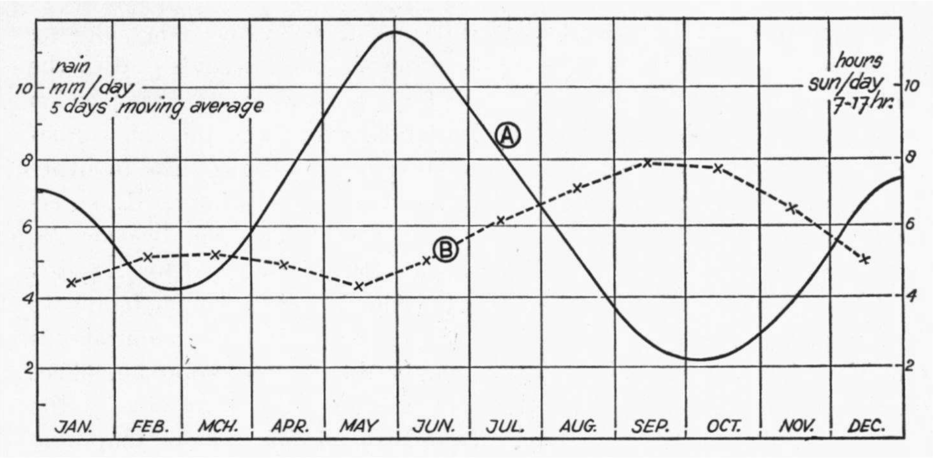


Fig. 4. A: smoothened graph of the annual march of rainfall at Paramaribo, based on 5-days' moving averages (after OSTENDORF 1957); B: monthly means of the number of hours of sunshine per day between 7 and 17 hr. for Paramaribo (after OSTENDORF 1956 *b*).

and during the mid-year rains the trade wind drops, and rain clouds approach from southern directions. In general wind-velocities in the lowlands are low to moderate and average about 5 km/hr. during the day (BRAAK 1935). The effect exercised on evaporation, particularly during the dry seasons, by dessiccating winds blowing from dry open savannas, as well as the mechanical effect of the wind, may locally be of significance. The superficial root system of the high forest trees, which frequently lack a taproot, does not offer much resistance to wind force. Violent winds of long duration are unknown, but, like elsewhere in the tropics, short violent squalls of wind (locally called "bush-broom") are not uncommon and particularly during the transition periods may precede thunder- and rain-storms. During such squalls everywhere in the forest trees — old or dead as well as vigorous ones — can be heard falling. This happens also during and after heavy rainfall, presumably on account of the top-heaviness caused by the extra weight added by water adhering to leaves and twigs. The winds are sometimes focussed on small areas and groups of trees and even stands several hectares in extent are felled by such squalls. For instance on aerial photographs of the Upper-Coesewijne region an area of several hundred hectares of windblown trees is easily recognizable. This action of the wind is of significance for the regeneration of the mature forest, as regeneration of most canopy species can take place in openings only. It is also of pedological significance; the root system of a windthrown tree lifts a disk of soil which subsequently falls in a heap at one side of the basin-like depression from which it was removed.

The *rainfall* in the N half of Suriname shows a marked seasonal distribution with 2 distinct maxima. This is shown in fig. 4 by the graph of the mean annual march of rainfall, represented by the 5-day moving averages. The rainfall records of the stations in the lowlands and in the coastal region are quite similar, except for a narrow coastal strip, which has a markedly drier climate. The lowlands, where the present studies were carried out, are well supplied with rainfall stations. The monthly averages for 3 selected stations in the Saramacca R.–Suriname R. watershed (Republiek, Kwakoegron and Kabelstation; for their location see fig. 1) are presented in fig. 5. The data for Paramaribo and for Kapoeri (a station in the extreme W, on the Corantijn R., about as far inland as Kwakoegron) have been added for comparison. In the mountainous hinterland greater variations occur, partly due to the approach effect on the N and NW slopes and the rain shadow at the lee side of the mountains. This is shown by recent records of rainfall stations that were set up in the basin of the Upper Suriname R. in connection with a barrage planned in this river.

As shown by the graphs reproduced in fig. 4 and 5, in the area under consideration the heavy rains usually fall from mid-April to mid-July. The periods February–March and mid-August to November are relatively

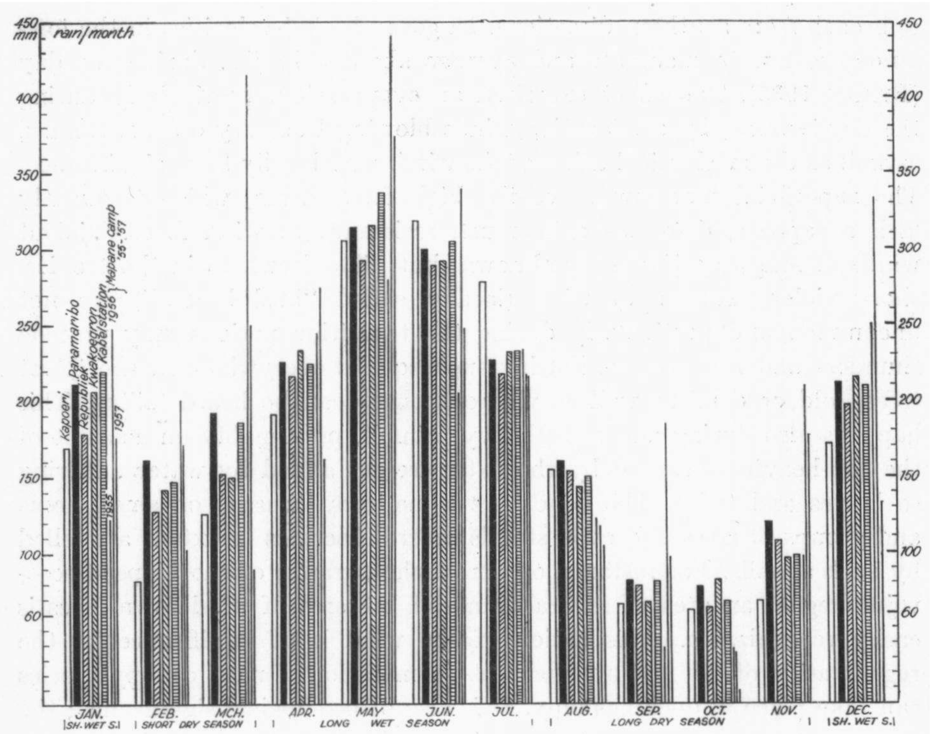


Fig. 5. Average monthly rainfall at 5 stations: Kapoeri (middle Corantijn R.) (1919–'55) — Paramaribo (1847–'54, 1864–'92, 1896–1956) — Republiek (1896–'97, 1906–'56) — Kwakoegron (1910–'45, 1950–'56 — Kabelstation (1910–'56). The rainfall data obtained at Mapane camp during the period of microclimatologic observations (1955–'57) have been added for sake of comparison.

Mesophytic forest in the Mapane region; the palms are *Astrocaryum paramaca.*

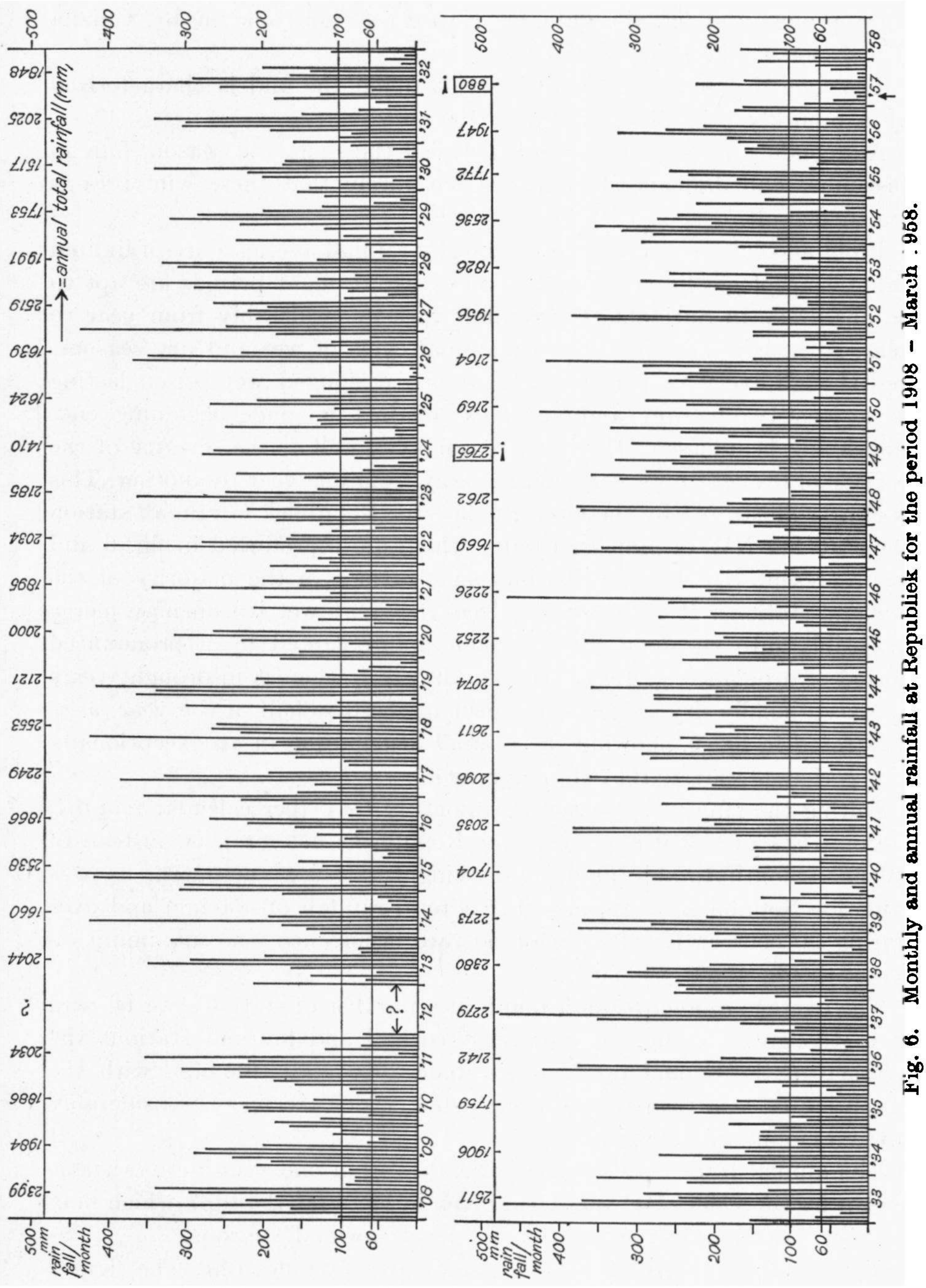


Fig. 6. Monthly and annual rainfall at Republiek for the period 1908 – March 1958.

dry, especially the latter one. In the spring there is sometimes only a suggestion of a short dry season, as happened during my first two years of observation (1955 and 1956). To the west the short dry season becomes more pronounced (cf. the data for Kapoeri station) and in Br. Guiana this season is the drier of the two.

The long dry season generally lasts 2–3 months and is characterized by a monthly rainfall of less than 100 mm.

A secondary maximum of rainfall, called the short wet season, falls in December and January. It happens but rarely that these winter rains are in default.

From an ecologic point of view monthly rainfall averages are of limited value, as ecologically significant features like drought periods are apt to be obscured. In Suriname the rainfall varies considerably from year to year. Although there is a distinct annual cycle of wet and dry seasons, and though every year shows at least one prolonged wet period lasting for at least two months, and one or two distinct dry ones, beginning, end, length and heaviness of the rainy season(s) as well as the severity of the periods of drought may vary considerably from one year to another. This is clearly illustrated by the monthly data for Republiek (a rainfall station some 40 km NW of Mapane camp), which are reproduced in fig. 6 and are representative for the distributional pattern in the majority of the lowland stations. It will be noted that the short wet season may merge insensibly into the long rainy season, uninterrupted by a pronounced period of drought (e.g. 1907, '08, '18, '39, etc.), whereas in drought years an exceptionally dry season may occur in the first half of the year, as is illustrated in fig. 9, showing the rainfall distribution in an exceptionally dry period (January 1957–January 1958).

During the long rainy season the monthly total (per calendar month!) seldom rises over 350 mm (max. for Republiek: 659 mm). If, instead of calendar-month totals, 30 days' moving totals are computed, as was done for Republiek, it appears that a total rainfall of 450 mm and over during 30 consecutive days is of no rare occurrence (the maximum on record being about 800 mm!).

The average *annual rainfall* found in a number of stations can be read from the graph in fig. 10. For most coastal and lowland stations the average of the annual total lies between 2000 and 2400 mm, with the exception of a narrow coastal drought-belt which receives a considerably lower amount of precipitation.

The annual total may vary considerably from one year to another as shown by the values for Republiek given in fig. 6 (at the top), which may be taken as being representative for most lowland stations.

The total *daily rainfall* seldom rises above 50 mm/24 hr. The figures which have been set out in fig. 7 may serve to illustrate the daily distribution of rainfall as recorded for most Suriname lowland stations. For the 49 years between 1919 and 1953, OSTENDORF (1956 a) computed a total number of 203 days (5 days per annum) having a rainfall of 50 mm or over. This yearly average of 5 days with 50 mm or over is in accordance with the estimate of BRAAK (1935). During the same period (1919–1953) only 8 days with 100 mm or over were recorded for Paramaribo. The rain gauges were read daily at 8 hr. and consequently the maxima during other periods of 24 consecutive hours may have been considerably higher (up to 300 mm, according to OSTENDORF 1956 a).

Data on intensity of rainfall are of special interest in connection with the study of soil moisture, and thus for estimating the ecologic effectivity of precipitation. In the next paragraph rainfall data will be used for an evaluation of ecological effectivity of rainfall, without paying attention to the intensity of individual showers, although the data should have been corrected for superficial run-off which takes place during showers of certain intensity, as was done, e.g. by HARDY (1946, 1947). For Suriname only few data are available on the intensity of the rains and no data at all on the relation between the latter and the percentage of infiltration in soils with different physical properties. For forest soils I observed that the superficial run-off is probably less than 5 % of the total annual rainfall. Only during exceptionally heavy showers (of, say, 30 mm per hour or over) did I observe, on sloping terrains in the Mapane region, a superficial run-off, filling the numerous gullies which are dry in other circumstances.

Pluviograph records are available only for Paramaribo, dating from 1951. During the relatively short period of recording (1951–1955) a maximum of 1½ mm/min. during 15 min. was recorded (OSTENDORF 1956 a). An amount of 4½ mm/min. (142 mm in ½ hour!) was reported during a cloudburst at Zanderij airport.

In fig. 7 the daily distribution of rainfall in Suriname lowland stations is illustrated by the records made at Mapane camp. In this figure also graphs of the *moving total* rainfall during 30 successive days are displayed. Each point of these graphs shows the total amount of rainfall during the previous 30 days. From these graphs also the number of *dry* and *wet* days (i.e. days with less than 60 mm and days with more than 100 mm precipitation during the previous period of 30 days) can be gathered.

The choice of the specific values of 60 and 100 mm and that of the period of 30 days are based on MOHR's (1938) findings which were confirmed by the experiments of HARDY (1946, 1947), and will be discussed below.

In fig. 8 the numbers of *wet, moist* and *dry* days have been set out for Republiek. These graphs clearly show the accidental character of the short dry season and the relative stability of the long wet and the long dry seasons. The short wet season differs from one year to another in length and in its beginning and end, but it never failed, although in one out of two years these winter rains (according to OSTENDORF 1957) are insufficient for certain agricultural requirements.

In fig. 9 the 30-days' moving totals for the days of an exceptionally dry

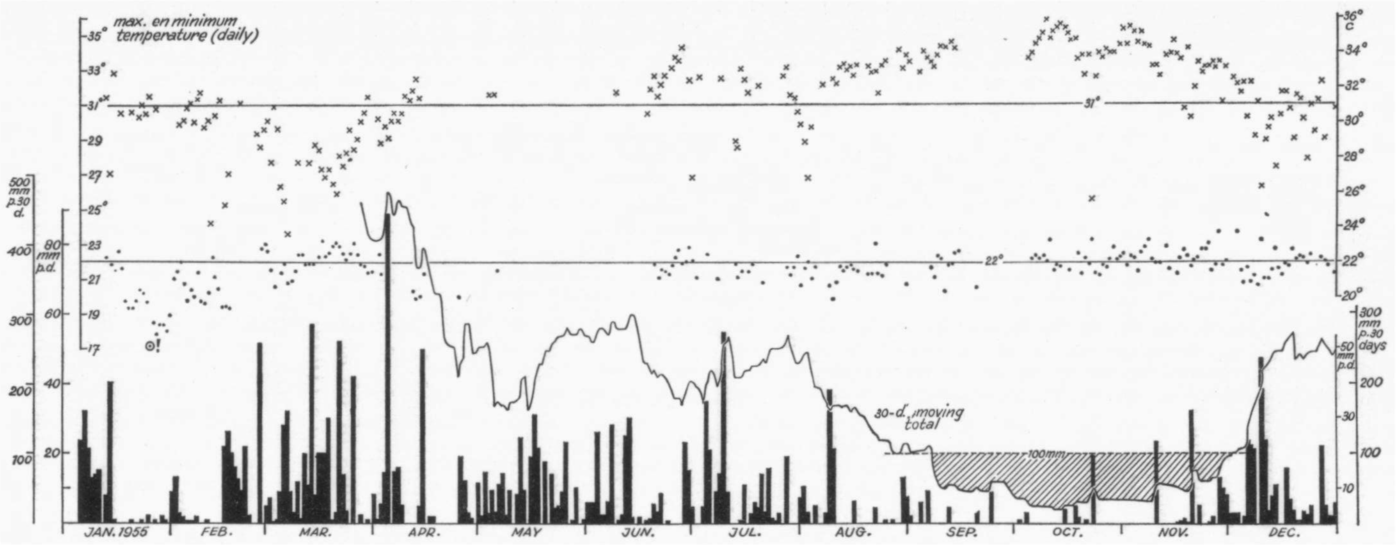
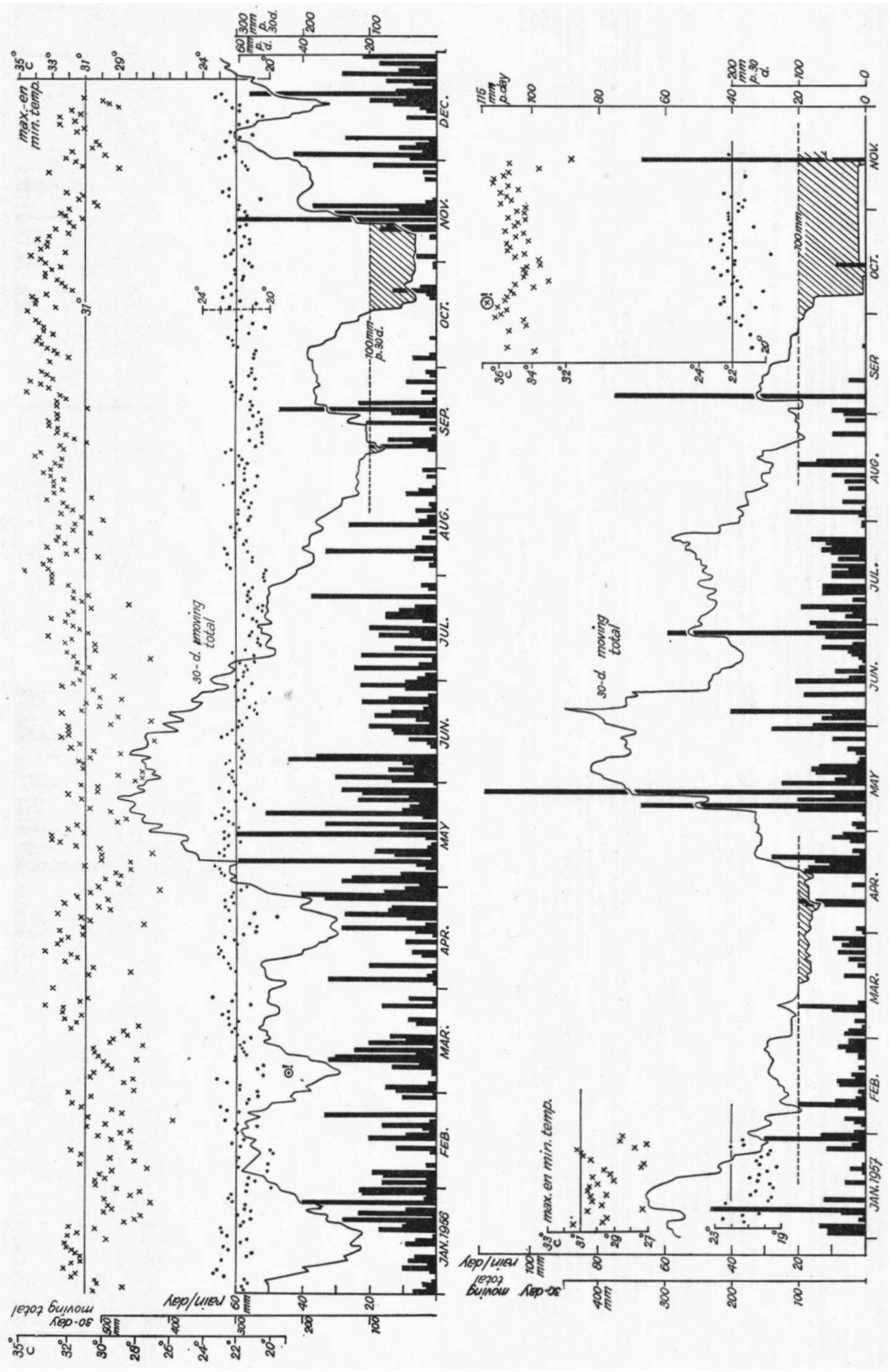


Fig. 7. Rainfall and maximum/minimum air temperature at Mapane camp (as measured in a large clearing). The black columns at the bottom of the figure represent daily rainfall in mm. The zigzag line above the rainfall columns gives the monthly rainfall, expressed as 30-*days' moving totals* (i.e. the total rainfall during the preceding 30 days). The shaded area represents the period during which rainfall during the preceding 30 days was less than 100 mm (= *not-wet* periods). The crosses and dots represent daily maximum and minimum air temperature respectively.


max.-en min. temp.
35° C
33°
31°
29°
24°
22°
20°
60 mm p. d.
300 mm p. 30d.
30-day moving total
rain/day
30-d. moving total
100mm p.30d.
JAN.1958
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.
115 mm p.day
200 mm p.30 d.
max. en min. temp.
400 mm
300
200
100
80
60
40
20
0
JAN.1957
SER
36° C
34°
32°

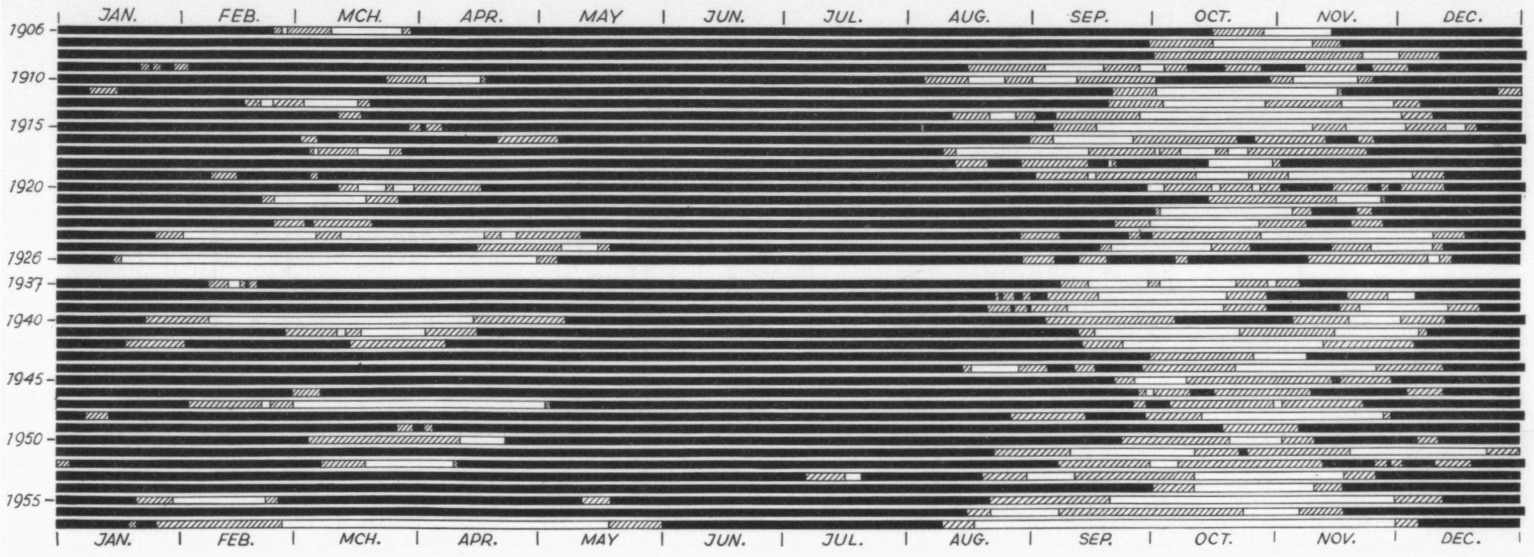


Fig. 8. Distribution of periods of *wet* (black), *moist* (cross-hatched) and *dry* days (unshaded), respectively with more than 100, 100–60 and less than 60 mm precipitation during the preceding 30 days, for Republiek (40 km NW of Mapane camp). For explanation see text. Diagrams constructed according to a method used by Ostendorf (1957).

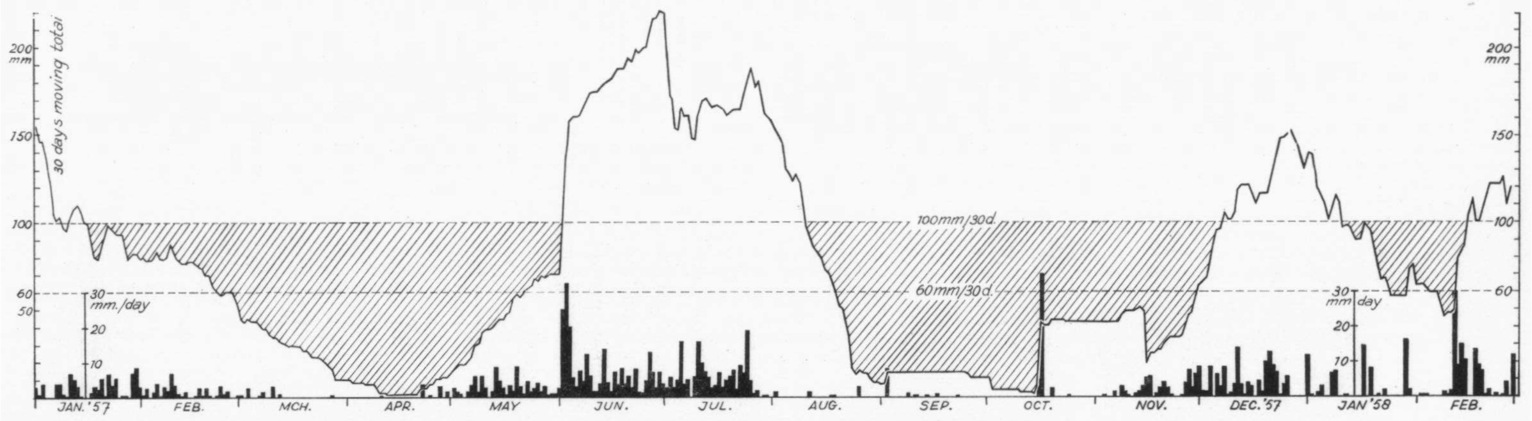


Fig. 9. Daily distribution of rainfall at Republiek during a very dry period (Jan. 1957–Jan. '58). Black columns: daily rainfall in mm. Zigzag line: 30-*days' moving total* rainfall (total amount of rainfall during the preceding 30 days). Note the long periods during which the 30-days' totals fell below the critical values of 100 mm (*not-wet* days) and 60 mm (*dry* days).

period have been given. During a similar extreme drought period in the spring of 1926 (cf. fig. 8) extensive areas of coastal swamp and savanna vegetation were destroyed by fire. The extensive areas of coeval forests of *mierenhout* (*Triplaris surinamensis*) found in the coastal plain represent in all probability a sub-climax caused by the fires of 1926, and may be taken as a striking illustration of the ecologic influence exercized by abnormal climatological extremes, even if occurring only once in a period of 15 or more years.

Many methods have been developed for estimating the *climatic effectivity of precipitation.* For this purpose the figures for the total rainfall per year are of secondary value only. The value of precipitation for the water supply of plants is best measured by direct studies of the degree of penetration and duration of moisture in the soil. However, this method is laborious, and detailed studies carried out in tropical countries are but few in number, those of HARDY and co-workers in Trinidad deserving special mention.

In the meantime efforts have been made to estimate this factor of the plant environment in an indirect way. This, however, is not the place to discuss the relative merits and disadvantages of the various empirical formulae which have been suggested by the various investigators. For equatorial lowlands the distributional pattern of the precipitation and the severity and length of annual periods of drought, if any, are of the greatest ecologic significance. For ecological purposes the best-known classification of climates is that of KÖPPEN, who sub-divides the class of "Tropical rain climates" according to the amount of rainfall during the driest month, which may be partly compensated by the annual total. According to this classification the greater part of the Suriname lowlands and of the coastal region falls in the *Af* (hot damp forest) climate, as shown by the scheme in fig. 10.

A number of stations falls in the group of *Am* climates (forest climates of monsoon type). To this second type, amongst others belong some stations on the Upper Suriname R. and between Kabelstation and Kwakoegron. It should be noted, however, that the periods of observation differed considerably for the various stations and hence the differences in their place in the *Köppen-diagram* partly may be due to accidental differences in precipitation during the periods of observation. For comparison the stations in the narrow dry coastal belt (distr. Coronie), encircled by a dotted line, and belonging to the *Aw* type (periodically dry savanna climates), have been given. For comparison also 3 stations from the lowland region in British Guiana have been added. Mara, less than 75 km NW of Kapoeri station has a markedly drier climate than the latter. The other two B.G. stations show considerably higher annual totals and a less severe drought period than the Suriname stations.

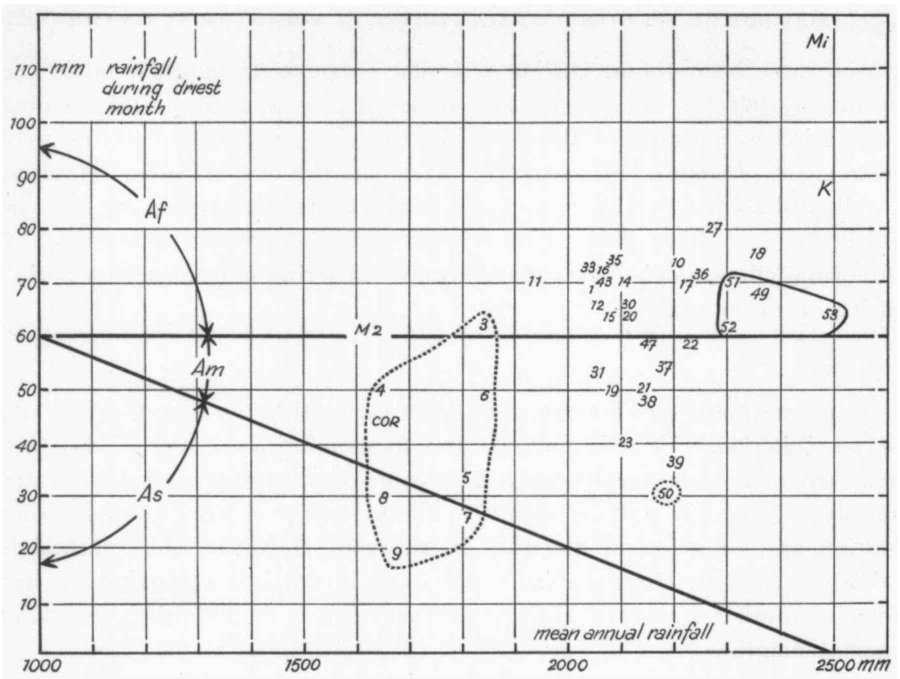


Fig. 10. Classification according to the system of Köppen of selected rainfall stations. *Af:* hot damp forest climates (with a mean rainfall for the driest month of not less than 60 mm); *Am:* forest climates, monsoon type (total annual rainfall sufficient to compensate for the seasonal drought); *As:* periodically dry savanna climate (dry season not compensated by mean annual rainfall).

The numbers of the stations correspond to those used in the list of rainfall stations given by Braak (1935) and indicated in the sketch-map reproduced in fig. 1. The rainfall figures are based on data taken from Braak, partly supplemented by data calculated from daily records provided by the Agric. Expt. Stat., Paramaribo. Data for Br. Guiana taken from Fanshawe (1952).

W. Suriname: 1. Kapoeri, Corant. R. (1919–'56); 2. Nw. Nickerie (mouth of Corant. R. (1896–1905; 1907–'33).

Dry coastal belt (stations encircled by a dotted line): 3–9. Distr. Coronie (various periods of observation between 1898 and 1933); COR: mean for Friendship/Totness, Leasowes and Hamilton (1919–'56); 50. Galibi, mouth of Marowijne R. (1928–'33; 1941–'55).

Centr. coastal region: 10. Tibiti (1911–'33); 11. Caledonia (1905–'23); 12. K. François (1924–'32); 14. Groningen (1896–'99; 1912–'33); 15. Republiek (1896–'97; 1905–'56); 23. Nw. A'dam (1900–'05; 1928–'33); 27. Paramaribo (1847–'54; 1864–'92; 1896–1956); 30. Domburg (1896–1905; 1910–'33); 31. Lelydorp (1911–'33); 33. Gr. Chatillon (1913–'33); 43. Mariënburg (1914–'33); 47. Slootwijk, Commew. R. (1911–'33).

Centr. lowland stations: 16. Sectie O (1910–'33); 17. Kwakoegron (1910–'56); 18. Jacobkondre (1915–'33); 19. Guyana Goudplacer (1915–'21); 20. Placer de Jong (1896–1902; 1920–'33); 21. Gros savanna (1910–'18); 22. Brownsweg (1910–'56); 35. Bergendal (1910–'31); 36. Kabelstation (1910–'56); 37. Sikakamp (1911–'33); 38. Dam (1912–'33); 39. Nw. Aurora (1921–'33).

E district (stations encircled by a continuous line): 49. Moengo (1919–'22; 1925–'33); 51. Albina (1896–1901; 1915–'26; 1928–'33); 52. Granman Staalkondre (1921–'33); 53. Lawa (1907–'29).

Br. Guiana: M. Mara (Berbice); K. Kurupakari; Mi. Mazaruni.

A great disadvantage of the Köppen system if applied to tropical countries, is the fact that no weight is given to the length of the dry season(s). This objection had already been made by MOHR (1933), who pointed out that this system does not give satisfactory results for the Malay archipelago. AUBRÉVILLE (1949) is of the same opinion for tropical Africa, although BERNARD (1945) found a fairly good agreement between the boundaries of KÖPPEN's climate types and the distribution of major plant communities in the central Congo basin.

At present it is fairly generally agreed that the climatic limits of equatorial vegetation types primarily depend upon the length of the dry season, i.e. on the number of dry months. No uniformity of opinion exists on the question as to how a *dry month* should be defined. Naturally no definition of general applicability can be expected, certainly not by using simple quantitative expressions based only on the distribution of rainfall.

The classification proposed by MOHR (1933, 1954) for Malaysia, takes into account both the severity of the dry season and the degree of wetness of the other months. MOHR empirically found that a monthly rainfall of 60–65 mm must be regarded as critical, and that the severity of the dry season can be measured by the number of *dry* months with less than 60–65 mm. This seasonal drought is compensated partly by the number of *wet* months with a precipitation exceeding 100 mm.

These specific monthly rainfall values agree closely with the critical values tentatively accepted by HARDY (1946, 1947) for the rainfall of the W. Indies. In the case of some sandy and clayey Trinidad sugar-cane soils the lower limit for rainy months indeed seemed to be roughly 100 mm, because these soils begin definitely to dry out when the previous 28-days' rainfall fell below this amount, whilst the upper limit for dry months appeared to lie near 60 mm, since, if the monthly rainfall after a dry spell exceeds this amount, the dry soil begins to accumulate some water.

The critical value of 60–65 mm found by MOHR also agrees with the critical amount of rainfall during the driest month which is taken by KÖPPEN as being the boundary line between *Af* and *Am* climates. By SCAETTA (1934) a dry month is characterized by a rainfall of less than 60 mm (if the mean air temp. is 26° C). DE MARTONNE (1926) calls a month dry when precipitation is less than $2 \times T$ (i.e. $\leqq 52$ mm for $T = 26°$ C). BERNARD (1945) takes 50 mm as the limit, whereas a number of other students take much lower values as critical for Africa and Asia; for a detailed account refererence is made to AUBRÉVILLE (1949) and BERNARD (1945).

From theoretical considerations, partly based on THORNTHWAITE's formulae, and from evaporation data and mean monthly discharge figures for the region of the Suriname R. between Kabelstation and Bergendal published by the Suriname Planning Board, for this part of the Upper Suriname R. basin a potential evapotranspiration of 100–140 mm/month was calculated (SCHULZ 1954), a value which is in agreement with experimental and theoretical findings under similar conditions in other equatorial countries. Hence the assumption that after a 30-day period with less than 100 mm rainfall, evaporation will exceed precipitation to such an extent that soil-moisture will fall appreciably below the requirements of at least part of the vegetation, is probably not far from the truth.

OSTENDORF (1957 b) gave an analysis of rainfall records of two coastal-plain stations from an agricultural point of view, and chose a 10-day period (decade) as a unit of time. This author classified a decade as *dry* when rainfall during this period was less than about 30 mm. The choice of a daily average of 3 mm as a criterium was based on the assumption that this amount of rain equalled average daily evapotranspiration. A daily mean of 5 mm (50 mm/10 days) was chosen as a lower limit for *wet* decades. In the above mentioned paper OSTENDORF has shown the succession of dry, moist and wet decades for Paramaribo (1905–1956) in a very convenient manner by means of graphs. This method of representation is borrowed here (though I used different specific values) to show the distribution of dry, moist and wet days for Republiek (fig. 8).

If we use the criteria applied by MOHR (1933, p. 106), the greater part of the Suriname lowland and coastal stations fall in his classes Ib (no dry month with rainfall less than 60 mm and 6–11 months with > 100mm) and II (climates with an ill-defined dry season: i.e., with 1–2 dry and 4–11 wet months). The narrow coastal drought-belt (distr. Coronie) belongs in class III (climates with a marked dry season, as for instance in the greater part of E. Java). Mazaruni and other lowland stations in British Guiana belong to type Ia: constant wet climate with no months with less than 100 mm rain.

This classification is based on monthly averages calculated over the whole period of observation. This has the serious disadvantage that the actual length of drought periods may be obscured. Since dry periods do not always occur in the same calendar-month (as is shown clearly in fig. 6 and 8), the actual number of dry months is considerably higher than the number of months which are dry on the average (as found on the basis of long-term monthly averages). This disadvantage was felt by SCHMIDT *et al.* (1951), who improved MOHR's method by determining the number of dry and wet months year by year. In table I for a number of Suriname lowland stations the same method of calculation has been applied. For comparison data have been added for an average coastal station (Paramaribo) and for a station in the drier coastal strip (Galibi). By the average numbers of dry and wet months is to be understood the averages of the actual number of such months in separate years.

Comparison with the figures given between brackets clearly shows the obscuring effect of averaging over long periods of observation.

Counting the wet and the dry months year for year yields an estimate

TABLE I

Actual average numbers per annum of *dry* (< 60 mm rainfall) and *wet* months (> 100 mm), based on calculations year by year of *wet* and *dry* months. Numbers based on long-term monthly averages are given between brackets.

Stations and period of observation	Dry months			Wet months total
	Short dry season	Long dry season	Total	
Paramaribo (1847–'54; 1864–'92; 1896–1957)	0.4(0)	0.9(0)	1.3(0)	8.5(10)
Republiek (1906–'57, excl. 1912) . .	0.5(0)	1.2(0)	1.7(0)	8.4(10)
Brownsweg (1910–'56)	0.3(0)	1.3(0)	1.6(0)	8.7(10)
Kabelstation (1916–'56)	0.4(0)	1.5(0)	1.9(0)	8.5(10)
Kapoeri (1919–'57)	0.4(0)	1.5(0)	1.9(0)	8.3(9)
Galibi (1927–'38; 1942–'56)	0.2(0)	2.6(2)	2.8(2)	7.8(9)

of the average number of wet and dry days per year which does not differ much from the real numbers, as computed day for day by adding the total amount of rainfall during the previous 30 days. For Republiek the latter method of computation of the *moving* 30-*days' totals*—shown graphically in fig. 8—for the period covering the years 1906–'56 showed an annual average of 47 dry and 268 wet days respectively, whereas the computation according to the method used by SCHMIDT *et al.* yielded averages of 1.7 and 8.4 months/year respectively.

The method described above gives an estimate of the average number of dry days per annum, but it unfortunately gives us no information with regard to the average length of the longest uninterrupted dry period. If, as is the case in Suriname, the dry periods are frequently interrupted by moist or even by wet periods (cf. fig. 8), the climate is probably less dry than it is in another locality where the same annual total of dry days is condensed into a few or only one uninterrupted dry period of greater length. The distribution of dry days for Republiek, which may be regarded as representative for the lowland stations, is shown in fig. 8 for the period covering the years 1906–1956. For this period the average length of the longest yearly period of successive dry and not-wet days (with < 100 mm in the previous 30 days), with only a few exceptions falling in the long dry season, amounted to 32 and 70 days respectively. The absolute maxima during the same period were 105 and 129 days. As stated previously, such an extreme drought, although occurring only once in several years, may have a far-reaching effect upon the vegetation.

In conclusion it may be stated that there are neither in the annual rainfall nor in the intensity of the dry seasons distinct differences between the rainfall stations in the northern half of Suriname, except for a small dry coastal belt, which falls outside the scope of the present study.

It looks therefore unlikely that differences in rainfall distribution — ecologically by far the most important climatologic factor in equatorial lowlands — could be responsible for the striking differences in composition of the high forest which will be discussed in some detail in the third part of this study. Selective action of other physiographic factors and also historical factors in all probability are responsible for the variation in composition and structure of these forests.

I.2. SURVEY OF THE MICRO-CLIMATOLOGICAL OBSERVATIONS

In the subsequent chapters the results of observations on the micro- (or local-) climate in various habitats in the Mapane forest will be discussed. The region in which these observations were made is that of the rich forest in the Mapane area described in the Introduction. As the present investigations were first of all meant to serve as a basis to more detailed autecological and regeneration studies, they were primarily conducted in habitats where seedlings and saplings of trees were met with. For comparison two extreme habitats were chosen: the undergrowth in a closed forest and a fully exposed habitat in an extensive clearing.

With a few interruptions during 2 full years and during the dry season of 1957 air temperature, atmospheric humidity and capillary evaporation were recorded in the forest and in the clearing at a height of 1½ m above groundlevel. A large number of measurements were made particularly during the periods in which more or less extreme conditions prevailed, i.e. during the long dry seasons. During selected periods a few simultaneous measurements were carried out at other levels in the forest: at 10 cm in the herb- and seedling-layer, and at about 5 m, just above the palm-stratum. A few records were made in a tree top, in the free air just above the main canopy. As will be shown in the following chapters, the close agreement between the latter and the readings made at the same time in the large opening seems to justify the assumption that the latter give a fair estimate of the climate to which the outer foliage of the canopy dominants and the outstanding trees are exposed.

Because of the occurrence of patches of *savanna forest* in the close vicinity there was good reason to take advantage of this situation by making simultaneous readings in this totally different type of forest, although this fell, properly speaking, outside the scope of this study.

By good fortune the long dry season of 1957 happened to be of abnormal intensity. Hence *the experimental records cover almost the whole range of variation* to be found in the ecological factors under consideration, the second year of recording (1956) being a super-normally wet year, with a prolonged wet season and subnormal drought in the long dry season. This will become clear if we compare the monthly rainfall data for Mapane camp during the period of observation with long-term averages for the nearby station Republiek (cf. fig. 5). Therefore the present recordings presumably give a more comprehensive picture of the micro-climate than most of the other ones obtained in tropical rain forest do.

Even if the latter were made during selected periods, there is some doubt with regard to the reliability of the average values and the range of seasonal variability, owing to the relatively short observation period.

It seems to me that the very extremes, even if occurring only once in a number of years, may very well be decisive from the standpoint of ecology.

Three permanent stations were equipped, viz. in the rain forest, in the clearing and in the savanna forest. The latter station was at a distance of 400 m from the first two, which were about 150 m apart. Thus the overall climate may be regarded as identical for the three stations.

The type of *rain forest* in which the measurements were made, was described on p. 8–9. The type of our *savanna forest* was intermediate between high and low savanna forest, with a closed canopy at a height of about 20 m and with a few emergent and outstanding trees. It closely resembles the forest type drawn in the same region and reproduced at the left-hand side of profile VI in the work of LINDEMAN (1959).

The *clearing* was a large rectangular space bulldozed around the camp, about ½ ha in extent. The bare ground was sparsely covered with grasses and weeds. Secondary regeneration was starting along the margins.

The sets of instruments, each consisting of a hygrograph, a thermograph, a minimum-thermometer and a standard thermometer and a Piche evaporimeter, were placed on a small shelf. This shelf stood at a height of 1½ m above the ground under a white-painted multiplex roof, arranged to keep off rain and direct sunlight, while allowing unhindred ventilation. This method of exposure, with the fullest possible ventilation, was preferred above a standard louvered shelter as used for macro-meteorological measurements. In the exposed station a double roof was used in order to avoid errors due to radiation. In addition the thermometers were placed in a small extra-insulating screen, as designed by the Netherlands Meteorologic Institute (cf. KRAMER *et al.* 1954) for recording air temperatures near the ground. Yet, in the clearing some radiation was still received from the insolated bare soil, but this caused an error of less than 0.4°, as checked with the ventilated psychrometer and an electrical resistance thermometer.

The utmost care was taken not to disturb the undergrowth at the forest stations more than was absolutely necessary for the observer to get at the instruments. For the readings near groundlevel thermometers were placed in the above mentioned special thermometer-screens and the hygro- and thermographs were placed on the ground with their sensitive elements screened from sun and rain by small aluminium plates. For the measurements at a height of 5 m a small shelf was constructed between two tree stems. A few readings just above the foliage of the main canopy were made in a small cage containing a thermo-hygrograph and a Piche evaporimeter, hoisted up to a height of 31 m by means of a pulley fixed at a branch of an outstanding, giant *ingipipa* tree (*Couratari*), whose base was 60 m from the undergrowth stations. The utmost care was taken that for the forest stations sites were chosen which were representative for the average conditions in the forest.

To gain an idea of the way in which the habitat factors in the forest vary at the same level, on selected days along a transect comparative readings were made. Evaporation and atmospheric humidity showed considerable variability caused by differences in the density of the vegetation. However, it appeared, that the records made at the sites that had been chosen, gave a fairly good picture of the average conditions.

I.3. LIGHT

I.3.1. *Introduction*

In this chapter the term *light* will be used for the part of the solar spectrum below 7500 Å, i.e. the range that can be measured with photoelectric barrier-layer cells (fig. 11), and which approximately corresponds to the visible part of the spectrum except that it includes wave lengths below 3600 Å. This part of the spectrum practically covers the entire range of wave lengths that are of importance in plant physiology.

Owing to the dominant role of the *micro-light-climate* (SHIRLEY) in determining composition and structure of the forest, knowledge of the horizontal and vertical variation of the light intensity in various storeys and in gaps of different size is fundamental for understanding the dynamics of the forest, and forms therefore the basis of silvicultural research.

In spite of the outstanding importance of this factor, the very great difficulties connected with the measurement of light intensities are responsible for the fact that during the present study only relatively few data could be collected.

The most serious difficulties are due to the enormous temporal and spatial variations in light intensity that are present under a vegetational cover of complex structure like the tropical rainforest. The light passing between the leaves may cause an increase in the light intensity to a value several hundred times as large as the *mean shade intensity.* Consequently a so-called average can be acceptable only, if it is calculated from a large number of readings made in all sorts of sites and at very different times.

Owing to their time-consuming character light measurements could be carried out only on a limited scale in this preliminary study. Consequently these provisional data do give no more than an indication of the order of magnitude of this factor in a few habitats and during selected periods.

The fact that the other factors vary concomittantly with light intensity makes a separate quantitative evaluation of the effect of differences in the latter practically impossible in field regeneration studies. It should be always borne in mind that a strong relationship exists between the micro-light-climate and the other factors of the micro-climate, such as, for instance, atmospheric humidity, temperature of air and soil and the air movement. An increase in the amount of incoming solar radiation, and consequently of luminous energy, runs parallel with a decrease in humidity and an increase in temperature due to the heating property of the long-wave reflection from surfaces (leaves and soil) and to the concurrent increase of air currents.

But in spite of the difficulty to separate the various environmental factors, the investigation of the light conditions remains an attractive subject to the experimental ecologist because the part played by this factor in the succession of the vegetation is more open to experimental studies than other environmental factors are. Moreover the direct practical importance of such studies for the silvi-culturist adds an incentive to the investigation of the relationship between light and plant growth in the forest.

Owing to the strong correlation between forest structure and the amount of light penetrating through the upper storeys, comparative light measurements might provide us with a useful and objective tool for distinguishing various forest types in Suriname. It is to be expected, however, that the great variability of the light intensity will necessitate a relatively large amount of measurements.

The greater part of the measurements were carried out at 1½ m height in the rain forest of the Mapane region. Some casual readings were made at other levels and in the neighbouring savanna forest and also at the Wayombo R. in *Dicorynia* forest. The observations made in artificial gaps will be discussed in part IV.

I.3.2. *Apparatus*

The technical difficulties of the measurements are even greater than the above mentioned complications due to the very nature of the light distribution in the forest. Since different wave lengths have different physiological effects, a type of a non-selective radiometer (integrating all wave lengths of radiant energy), used in combination with a suitable set of filters, undoubtedly would have been preferable. Such a radiometer will be used in future studies which are on program. For the present preliminary study, mainly on grounds of convenience, preference was given to photometers because the latter are easily portable and because their large current output permits the use of rugged, light-weight micro-ammeters.

Of all types available for general ecologic work no photometer yields absolute values of light intensity as quickly and conveniently as those employing photoelectric cells as sensitive units. But as was stated recently by EVANS (1956), one of the unfortunate features of the photocell as a field instrument is that very easily meaningless readings may be obtained! The most serious difficulties spring from the selective sensitivity of the cells to different wave lengths, which, moreover, differs materially from the sensitivity shown by plants. This difference is no very serious obstacle if our primary object is the comparison of light intensities in places where the light has approximately the same spectral composition. But when considerable differences in spectral composition are involved, the interpretation of the readings is difficult or impossible.

In this study selenium barrier-layer cells were used, type "Electrocell" with a sensitive area of 6.6 cm^2, manufactured by Frankenthal (Berlin). This latest type of cell fortunately does not show some of the technical disadvantages of the older ones. The fatigue factor and the solarization effect (damage by strong light) are reduced to a minimum, and this is essential when sampling light of strongly varying intensity (shade and sun flecks)!. The response of the cells appeared to be independent, within sufficiently wide limits, of the light intensity during the directly preceding measurement. When exposed to full sunlight the electric output decreased a few percent during the first minute, but after that it remained constant for at least 5 minutes. Although the cells have repeatedly been exposed to full sunlight, recalibration after 3 years of use revealed but a slight decrease (2 %) in sensitivity.

The spectral-sensitivity curve of the "Electrocell" cells based on data supplied by the makers and checked for five wave lengths at the Physical Laboratory of the Utrecht University, is shown in fig. 11.

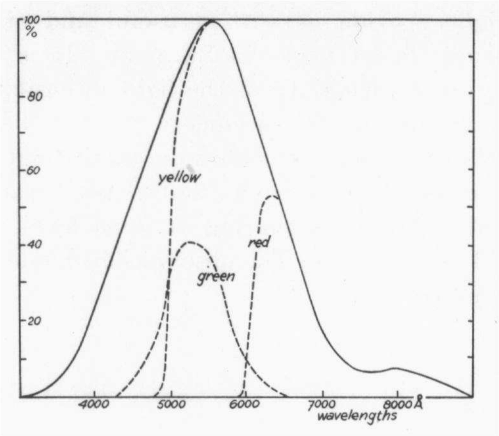


Fig. 11. Relative sensitivity of normal "Electrocell" photronic cell no. 735 in the various parts of the spectrum. Continuous line: cell alone; broken lines: cell in combination with different Schott 2 mm glass filters, viz. GG 14 (yellow), VG 9 (green) and RG 1 (red). The ordinates are expressed in percentages of the maximum sensitivity of the cell (at ca. 5750 Å). Taken from makers data.

There has been some difference of opinion among ecologists as to whether light should be measured by using a plane or a spherical absorbing surface, and if a plane surface is used, whether it should be oriented normal to the sun's rays or kept horizontally (Shirley 1935; Wassink *et al.* 1951, etc.). As will be mentioned later, the problem is analogous to that offered by the choice of a special form for the evaporating surface of an atmometer.

It should be pointed out that the aim of an integrating sphere should not be confounded with that of diffusers of various design which are necessary in connection with the correction of the plane absorbing surface for cosine sensitivity.

The great practical advantage of a spherical meter for routine field studies lies in the fact that it eliminates the errors resulting from differences in the angle of incidence of the sun's rays, and evens the variations due to random variations in the spatial distribution of light under a plant cover.

The use of a spherical integrator in sampling light in forest stands was recommended for instance by Atkins and co-workers and by Bacon (1939). Atkins (e.g. Atkins *et al.* 1937) is of opinion that the total quantity of light, regardless of angle (*total illumination*), is the most important for plant growth, and he constructed a globe of opal glass mounted above a photocell. Others preferred an indirect and highly arbitrary method, and measured the amount of light received by a plane sensitive surface from a standard reflector (e.g. Malaya: Smith 1936; Borneo and Malaya: Walton 1936; Nigeria: Evans 1956; Belg. Congo: Donis *et al.* 1951).

For the present investigations use was made of a *spherical lightmeter* as designed by Wassink and co-workers. This meter consists of 2 plane photocells, mounted back to back and each covered with an opaline glass of nearly hemispherical form (fig. 12). For a detailed description of this instrument and a discussion of its advantages and limitations reference is made to the original publication (WASSINK *et al.* 1951). With this instrument the influx of light in a sphere is measured, the response being nearly independent of the position in which the meter is held. A great advantage of this meter lies in the *reproducibility* of the measurements, and this was the main reason for its use in the present investigations.

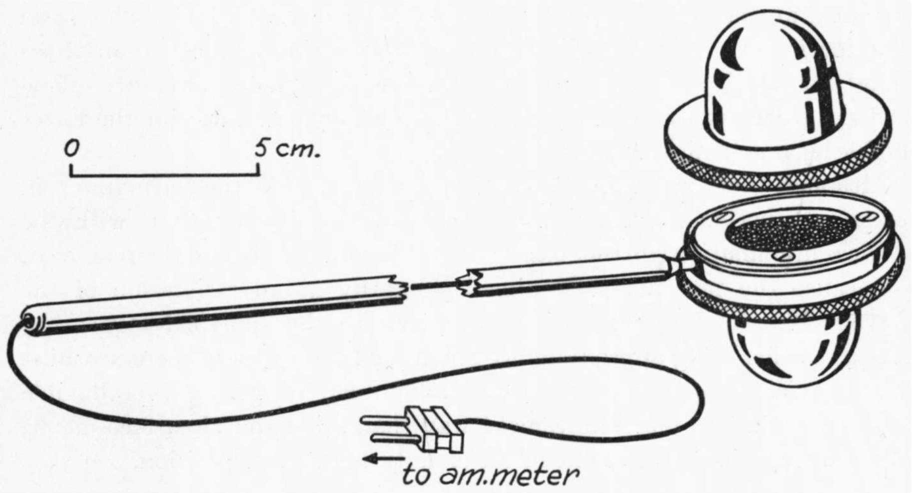


Fig. 12. The spherical lightmeter. One of the hemispheres of opaline glass has been removed to show the mounting of one of the two photo-electric cells.

As each of the 2 methods of recording provides information on different aspects of the micro-light-climate, an important question is which of the 2 types of meters, with a plane or with a spherical absorbing surface, gives the best approach to the light-climate to which the plant or plant community is exposed. In other words which of the 2 aspects of the light-climate, viz. *vertical* illumination or *total* illumination, is the better measure of the effect on plant growth?

With the spherical meter the influx of light into a space is measured, hence it seems to be preferable in investigations concerned with individual plants, i.e. in most autecological studies. If, on the contrary, the amount of light received by a closed vegetation of some extent (e.g. the forest as a whole or a mat of groundflora) is considered, a plane horizontal absorbing surface would better serve the purpose. Since comparative experimental data on this subject are lacking, further discussion seems fruitless.

A third aspect of light-climate, viz. *maximum illumination*, being the illumination on a surface set to catch the maximum amount of light (ATKINS, e.g. 1932, 1937), was found to be best in agreement with distribution of vegetation near the edges of a wood and also might prove to be very useful in photometer work in tropical woods, especially in clearings and their edges.

As will be reported in I.3.4, the *daylightfactor* (being the ratio between the intensity of illumination measured in the stand and the intensity in the open) when all the measurements made in the stand are averaged, appeared to be only slightly lower for *total illumination* than for *vertical illumination*. However, for individual readings or series of readings considerable differences between the two ratios sometimes occurred. For instance, at the border of a gap in the forest daylight factors for total illumination were found which were up to 10 times higher than those found for vertical illumination measured with a meter having a plane surface. In the centre of the gap, on the contrary, the ratio for the latter might be much higher.

Although there are indications that reproduction in the Suriname rain forest was better correlated with the total illumination than with the vertical illumination, further experimental investigations are the real need.

Because the present study aimed primarily at an estimation of the average illumination, preference was given to the spherical meter, the average ratios being approximately equal for both types of meters, whilst the spherical meter had the great advantage of giving reproducible measurements in a more convenient way than a horizontal-surface meter, which always has to be held in an exactly horizontal position.

In the present study for most measurements 3 spherical meters (fig. 12) were used, which were constructed at the Laboratory of Plant Physiological Research, Wageningen.[1] As galvanometers 2 portable AEG micro-ammeters with low inner resistance and with a scale graduated from 0–100 μA have proved remarkably sturdy and stable. With this combination light intensities of 0.1×10^4 erg/sec/cm^2 [2]) could be measured with an accuracy of about 15 % which sufficed between 8 and 17 hr. for the deepest shade in the forest. For higher currents the meters could be shunted 1/5, 1/20 and 1/100, which allowed measurement of bright sunshine. Because for light of higher intensities the cells do not show a rectilinear relation between current and illumination, for each combination of a set of photocells and ammeter a calibration curve had to be made.

Originally the cells were provided with neutral filters to ensure linearity for higher intensities, but this reduction of sensitivity made readings in heavy shade impossible or inaccurate, because the meter was then registering in larger units.

The meters were calibrated in c.g.s. units against a standardized thermopile. To this end we used as a lightsource a Philips 6070 C-250 W. projectionlamp provided with a Leitz infrared filter; this lamp emitted light with a spectral composition corresponding to that of the visible part of sunlight at the earth's

[1] For this valuable help and for the kind assistance in the calibration of the various lightmeters my thanks are due to the Director of this Institute, Professor E. C. Wassink and to Ir. P. Gaastra.

[2] Energy influx in a sphere with 1 cm^2 cross section.

surface. Recalibration after our return to Holland in 1958 revealed only slight alterations, which could be neglected in the computations.

A long handle of about 75 cm enabled measurements without disturbing the natural state of the vegetation, and reduced the error caused by light reflected from the clothes of the observer. Walking with the handle held in one hand and the ammeter in the other, light could be sampled conveniently, even in dense bush interwoven with lianas. The readings called out by the observer were noted by an assistant.

A few measurements were made with 4 *plane* photo-electric cells of the same type as used in the spherical meters ("Electrocell" cells with 6.6 cm^2 sensitive area); they were connected by long flexible wires via a switchboard with a sensitive tropical-proof Pye "Scalamp" light-spot galvanometer with battery feeding. The galvanometer was provided with a shunt designed to shunt 1/1, 1/5, 1/20 and 1/100, while the total effective resistance of shunt + ammeter was maintained. The cells were encased airtight in perspex cells, which did not alter significantly the spectral composition of the incident light, and which protected the photocells against moisture and sudden fluctuations of temperature. The plane cells were used in connection with a set of light filters to obtain a rough estimate of the spectral composition of the light in the shade of the forest as compared with that in the open. The set consisted of three 2 mm Jena glassfilters. With a yellow filter (GG 14) all wave lengths below about 5000 Å were cut out, whereas with a red one (RG 1) only wave lengths above 6000 Å were measured. A green filter (VG 9) transmitted light principally between 4750 and 5750 Å. In fig. 11 the transmission curves based on data supplied by the makers are reproduced. The various cell-galvanometer combinations were calibrated against a standard thermopile using a light source of known spectral composition.

As the photocells show a selective sensitivity for different wave lengths, their current output strongly depends on the spectral composition of the incident light. The photocells were calibrated for light having the spectral composition which sunlight has when the sun is at a particular distance from the zenith. The energy distribution of direct sunlight is a function of a number of variables (sun's zenith distance, water vapour, dust and ozone content of the air, etc.). In I.3.5 the results of the filter readings will be discussed. Although the spectral composition of total radiation in the open showed an appreciable reduction in the blue/violet part of the spectrum, as was reported by other students of light-climate in the tropics (ORTH 1939), the error that was caused by this difference from the spectral composition of the lightsource used for calibration, was, in the readings made in the open, less than 8 %.

Substantially larger errors were to be expected for observations made in the forest. The readings with the colour filters were primarily intended to obtain a rough estimate of the magnitude of the error that is inherent in photocell readings made in various habitats. As will be discussed in I.3.5 the sensitivity of the photocell for moderate shadelight under the forest canopy was reduced by about 30 % (as compared with the sensitivity for light having the spectral composition of total radiation in the open) owing to a relative increase in the green part of the spectrum, for which the cell shows maximum sensitivity. In other habitats and under other weather conditions the reduction of the sensitivity of the photocell used is in all probability much stronger. In certain habitats readings made by other students of forest light, have revealed an excess of long and/or short wave lengths, which might cause a reduction of the sensitivity of the photocell for the illumination concerned to less than one half of that for light with the spectral composition of sunlight in the open.

As will be discussed in I.3.5, no correction was necessary for the average light values in the forest as obtained during relatively clear days with the sampling method described in the next section; the error caused by the difference of the average spectral composition of the forest light (comprising sunlight falling through holes in the canopy) was negligible in comparison with other uncertainties which limit the absolute value of the sample means.

I.3.3. *Methods of sampling and calculation*

For the comparative routine measurements the spherical meters were standard, principally because of the above mentioned technical advantages from the standpoint of sampling technique and reproducibility.

In ecological and silvicultural studies the light-climate in a stand is expressed, as a rule, as a percentage of the illumination in the open. This is the "relativer Lichtgenusz" of WIESNER or the "daylightfactor" of ATKINS and co-workers. This comparative method has many advantages. Nevertheless, however convenient this practice may be, it should be borne in mind that the standard of comparison is not a fixed intensity, although, according to some authors (e.g. BACON 1939), the "daylight-factor" is nearly independent of the weather.

This method necessarily calls for a simultaneous series of measurements, one to record the variation in the open and the other to record the light values in the forest site. In extensive and very high forests this is usually impossible. In the Mapane forest only a few measurements were made simultaneously in the large clearing and in the adjacent forest, whereas most readings were made at greater distances from the clearing. In this case the ratio had to be computed from the averages of the samples taken in the forest and in the clearing. The great difficulties caused by the variability of the light in the forest have led some students to ignore *sunflecks*. This is done either by confining the observations to overcast conditions or to shade light or by other arbitrary limitations. WALTON (1936 a, b) working in the rainforest in Malaya and Brunei is of opinion that measurements should be made in cloudy weather, because this eliminates readings that "... cannot by any stretch of imagination be considered normal". But this criticism on the work done by SMITH (1936 a, b) in Malayan forests, is unfounded. Even when making comparative readings for silvicultural purposes, measurements should not be restricted to occasions when direct sunlight is lacking. Indeed, WALTON (1936 b) is right in stating that abnormally high light readings due to fortuitous patches of bright light, should not be permitted to carry undue weight. But this is a matter of sampling technique and of the choice of a suitable sample size. It will be clear that by wilfully neglecting an integral part of the light in the forest, a considerable underestimation of the available light is obtained.

Some workers rejected readings showing the influence of sunflecks, because they assumed that short bursts of strong light are of little or no significance for the CO_2-assimilation of the plant. Undoubtedly the *intermittent* character of the illumination in the forest caused by periodic and irregular changes in intensity renders doubtful any direct comparison of average data obtained for different sites. Taking for instance two sites, both receiving the same daily amount of illumination, station A receiving this amount of energy evenly distributed over the day, but station B receiving the same amount during one or more short passages of strong light, the rest of the day getting very weak light only, the results of laboratory experiments on induction phenomena do not justify the rejection of the *sunfleck readings* on account of their *intermittent* character, although the photosynthetic yield at station A would perhaps be somewhat higher than at B, as – according to the present state of our knowledge (e.g. RABINOWITCH 1956, chapt. 33) – in photosynthesis the most profitable utilisation of energy is achieved when it is spread uniformly over the whole available period.

A rejection of strong light readings cannot be justified either by referring to phenomena of injury and fatigue (decline of photosynthetic efficiency shown by plants adapted to weak light when they are brought into stronger light) to which plants adapted to shade are easily susceptible. I have observed vigorous growth of the seedlings of several tree species (including those of shade-bearers) in a patch in the forest which received direct sunlight through a small hole in the canopy during about 40 minutes per day. Growth in this spot was several times more rapid than that of plants in a neighbouring spot, although the light intensity was about the same for the rest of the day, as is shown in fig. 13.

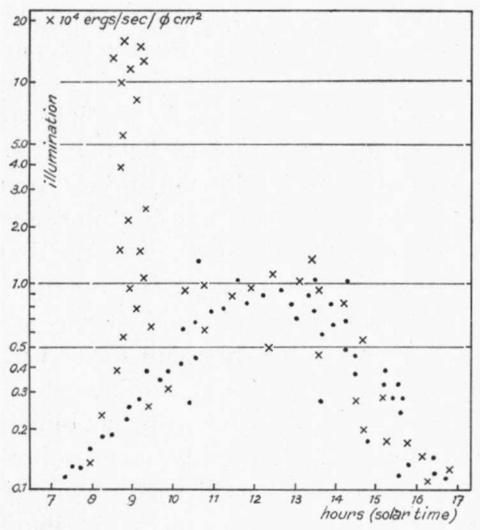


Fig. 13. Daily march of illumination at two neighbouring stations in the Mapane rain forest. Station A (×) receives strong light through a hole in the canopy during about $^3/_4$ hr. per day. For the rest of the day this station receives about the same illumination as station B (.). Each point represents the mean of 3 readings made with the spherical photometer at $1^1/_2$ m above groundlevel during two clear days, with the sun unobscured during approximately 85 % of the time.

Nor can the sunfleck readings be neglected because plants are assumed to be saturated with light of a relatively low intensity. As will be expounded below, this may be true for some typical shade-demanding herbs and for particular parts of the plant, but it does not apply to the plant as a whole. Moreover the term *sunflecks* is a rather vague and subjective one. Some observers classified under *sunflecks* all light intensities exceeding some arbitrary value of *mean shade intensity*, which itself is a very subjective value! We have measured light intensities less than 5 times the *average shade* value in *sunflecks*, the latter being camera lucida images of very small holes in the canopy. The typical complex structure of tropical rain forest causes a pattern of light intensities varying gradually from the deepest shade in the forest itself to bright sunlight in natural clearings. The artificiality of the distinction between shadelight and sunflecks also appears from the frequency curves (e.g. fig. 15) which clearly show a uniqodal (though skewed) distribution.

In the method used in the present study, readings in patches of bright sunlight have been included in the samples. Therefore rather large samples were necessary to obtain mean values capable of reproduction. From this investigation of limited extent no picture of the average light-climate could be expected, because automatic recording instruments were not at our disposal and because the available time did not permit adequate sampling throughout the various seasons by handreadings. Therefore, the extra complications arising when readings made under greatly varying light conditions are compared, were reduced as much as possible by limiting our observations to relatively clear days in the dry season when the sun remained unobscured during the greater part of the day. As uniformly clear days are extremely rare in this part of Suriname, even during these days considerable difference in the light conditions occurred.

The complicate problem of sampling light in the forest has been approached by various workers in different ways. CARTER (1934) working in Br. Guiana sampled in both shade and in "sunflecks of average size"; in order to arrive at an evaluation of the average illumination the area occupied by the sunflecks was measured and expressed as a percentage of the total area. It is clear that this method may lead to considerable errors. EVANS (1939) working in a Nigerian forest had the photocell set up in a fixed point to make a series of readings at short intervals thus elucidating the daily march of light intensity (passing sunflecks included) at a particular place. But, as stated by the same author in a recent article (1956), it would be necessary to repeat such observations a great many days before reproducible figures for sunfleck distribution would emerge. Moreover, in our opinion a serious disadvantage of this method lies in the difficulty to choose an "average" locality for the measurement.

In his latest article EVANS (1956) presents an elaborate description of an indirect method that is especially suited for the measurement of *sunflecks*, their size, distribution and intensity. A separate study of the light condition in the patches of bright light will probably be included in our investigation of the light-climate in the Suriname forest which will be undertaken in the near future. But this subject will not become topical until more is known with regard to the general features of the light-climate and of the autecology of the forest plants. In the present study a simple sampling technique was used, which shows some points of resemblance to the method used by NAEGELI (1939) in Swiss forests and by SMITH (1936 a) in the Malayan rain forest.

The data given in the next sections are the result of several series of readings that were systematically distributed along transects which themselves were distributed at random. In a given stand on selected days successive series of about 20–50 readings were made with intervals varying from ½ to 4 hours. Walking every time with the spherical meter along a straight line in a direction which was chosen at random, a reading was made after every 2 paces, thus avoiding personal bias as much as possible. In contrast to the method used by SMITH (1936 a) each series of readings was made along a different line.

Table II illustrates the results of the successive series of readings made during one day at different heights in a particular stand, every vertical column representing one series of readings made along a different transect.

The treatment of the data forms another problem. When the arithmetic averages of the readings are taken, the average daily march of the *mean* light intensity and the average daily amount of luminous energy may be computed. But may these averages and the total amount be regarded as the correct expression of the light-climate from the point of view of the plant ecologist? For most light-controlled plant functions the rule that the response is proportional to the light intensity, applies to low intensities only; at higher intensities the response tends to approach a constant value already far below the maximum intensity. This especially holds for photosynthesis. Optimum growth too is frequently achieved at an intensity which remains below 50 % of the available maximum. The low intensities at which some shade plants become light-saturated, is brought out for instance by the studies of LUNDEGÅRDH which afforded ground for NAEGELI'S (1939) proposal to use the *logarithmetic mean instead of the arithmetic* one for readings sampled at random in the forest. EVANS (1939) too considers integration of the high intensities prevailing in *sunflecks* in the whole set of readings of light intensities to be incorrect, because above a certain limit the photosynthetic effect of light falls off progressively with increasing intensity. As mentioned above, this consideration led EVANS to his indirect method of measuring the sunflecks separately. VETH (1940) assumes that in the tropics growth even shows a *decrease* with light intensities above 50 % of sunlight.

Although in laboratory studies for most plants rate-intensity curves were found which appeared to approach asymptotically to a limiting value which lies considerably below that of full sunlight, it should be borne in mind that these results which are based on studies with individual plant organs or cell- and chloroplast-suspensions should not be applied unreservedly to whole plants or to plant communities in the field. Individual leaves of any species may become light-saturated at intensities which are considerably lower than those needed to saturate the plant as a whole because the lower and inner leaves are shaded by outer leaves, and because the leaves are not all orientated perpendicular to the directions of the incident light. This explains why an increase of the light intensity above optimal values found for fully exposed leaves, often results in an increase in growth of the plant as a whole; the growth may even reach its maximum in full sunlight.

The experiments carried out with a number of tree species (described in IV.4) also indicated that the seedlings and saplings of most woody species (both of true understorey species and of emergents) reach their maximum growth when they are exposed to full sunlight. This possibly does not apply to some shade-demanding non-woody species belonging to the herbstratum and for some shrubs and dwarf-trees, which may become saturated at low light intensities, but it may be safely assumed that in by far the greater part of the tree species an approximately linear relation exists between growth rate and light intensity.

In studies of the light-climate in forests which are aimed particularly at the effect of light intensity on the growth of tree species (for these effects depend mainly upon the effect of light on photosynthesis), the *arithmetic mean* of the readings of the light intensity seems to be the most convenient expression for the light-climate.

I.3.4. *Light measurements in the forest*

Fig. 14 represents the results of 60 series of readings made with the spherical meter in the Mapane rain forest, mainly during the long dry season, each series consisting of about 50 readings. The method of sampling has been described in detail in I.3.3. The transects were chosen at random in an area of about 1000 ha in extent.

This rain forest showed a faint tendency, especially among the emergent trees of the upper canopy, to change its leaves mainly at one time of the year, viz. in the early half of the dry season. There was, however, at the site chosen for the observations no evidence that the readings were significantly higher than they would have been outside the long dry season when the canopy is somewhat more dense. Though a few emergent trees might be completely denuded, they generally stood bare for a few days only, the total percentage of completely denuded trees at any time being very low. The data that are given in this section may safely be regarded as representative for relatively clear days (with 85 % sunshine or over), no matter in what season the latter may fall.

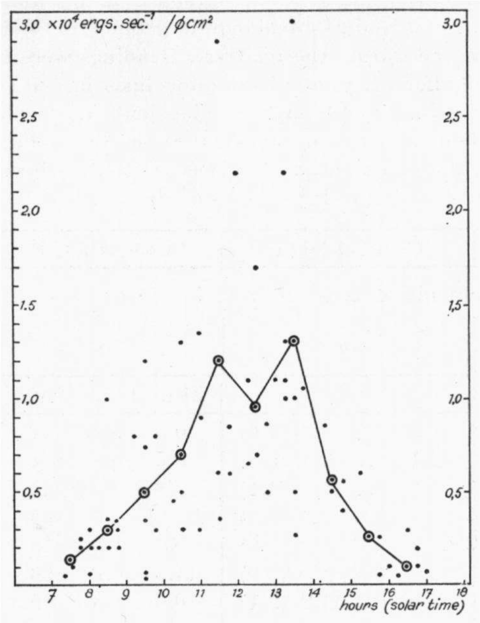


Fig. 14. Illumination in Mapane rain forest at 1½ m above ground level, expressed in ergs/sec, incident in a sphere of 8 sq. cm cross-section. Each point represents the mean of 50 random observations (for method, see text), made during days with partly clouded sky and with the sun unobscured during ca. 85 % of the time. The line connects hourly averages (⊙).

Measurements were made during relatively clear days such as are typical for the dry season and part of the transitional periods. Yet clouds and sunshine often alternated during one series of readings. On the average roughly 15 % of the readings were made with the sun obscured and 85 % with bright sunlight. Conditions of cloudiness varied greatly, but for most of the time at least one third of the sky was clouded.

The figures represented in fig. 14 apply to light conditions prevailing during 18 % of the 365 days of a year, as appears when we interpolate the data computed for Paramaribo by OSTENDORF (1956 a, table 2) from charts obtained with the Jordan sunshine recorder, in the years 1928–1955. The following yearly averages are taken from Ostendorf's data. The averages for the yearly periods with minimum (Apr. + May) and maximum (Sept. + Oct.) sunshine are added.

Frequency-percentages of number of sunshine hours per day	hours of sunshine per day between 7 a.m. and 5 p.m.					
	0–2	2–4	4–6	6–8	8–9	9–10
yearly means	13 %	15 %	21 %	26 %	14 %	11 %
averages for wet season (April + May)	26 %	20 %	20 %	19 %	8 %	7 %
averages for dry season (Sept. + Oct.)	1 %	4 %	12 %	32 %	25 %	25 %

TABLE II

Readings of light intensity made with the spherical photometer in the Mapane rain forest at 15 cm, 1½ m and 2½ m above the ground, between 8.30 and 16.30 hr., with the sun unobscured during the readings. Readings were taken at intervals of two paces along 12 different, random sampling lines in the same stand.
Light intensity expressed in 10^4 ergs/sec, incident in a sphere with 1 sq. cm cross-section. The figures between brackets in the 6th column are simultaneous readings made with the plane photocell, placed so that it faced vertically upwards (in 10^4 ergs/sec/cm^2)

8.30–9.00 hr.			11.00–11.30 hr.				13.45–14.30 hr.			16.15–16.45 hr.		
sunlight in large clearing in 10^4 ergs/sec/cm^2 ø												
56			78				75			24		
2½ m	1½ m	15 cm	2½m	1½m	15 cm		2½ m	1½ m	15 cm	2½ m	1½ m	15 cm
0.3	0.2	0.2	1.5	0.9	1.8	(1.0)	0.8	0.8	0.4	0.2	0.4	0.4
0.4	0.2	0.2	2.4	0.7	1.1	(0.8)	0.9	0.8	0.4	0.3	0.3	6.4
0.4	0.3	0.3	1.5	0.8	1.8	(1.7)	0.8		0.5	0.2	0.3	0.1
3.5	0.2	0.2	1.3	1.8	0.7	(0.5)	0.6	0.6	0.3	0.2	0.3	0.5
0.2	0.2	0.2	1.9	0.8	0.7	(0.6)	0.7	1.6	0.5	0.2	0.4	0.2
50.5	0.2	0.2	2.0	0.4	1.0	(0.9)	11.5	0.9	0.6	0.2	0.4	0.2
0.3	0.3	20.5	3.0	0.5	**11.2**	**(2.1)**	10.0	5.8	1.6	0.3	0.5	0.2
0.3	1.0	0.3	20.5	0.5	1.2		9.4	1.1		0.4	0.3	0.2
0.3	0.4	0.2	3.4	0.4	0.6		60.0	1.5	4.1	0.3	0.3	0.2
0.4	0.2	0.2	1.7	0.5	0.8		1.3	7.2	0.7	0.4	0.3	0.6
0.4	0.3	0.2	1.5	0.8	1.1	(0.7)	0.8	1.2	1.0	1.2	0.2	0.3
0.4	0.3	0.2	1.9	0.4	1.3	(0.9)	0.7	0.8	1.3	0.4	0.3	0.2
0.4	0.2	0.2	2.2	0.5	1.1	(1.0)	0.7	0.8	0.9	0.2	0.3	0.3
0.5	0.2	0.2	4.7	0.4	0.9	(0.4)	1.0	0.6	0.5	0.1	0.3	0.2
0.6	0.3	0.2	2.4	0.7	0.7	(0.2)	1.0	0.8	0.6	0.3	0.3	0.2
4.7	0.3	0.5	1.8	0.5	0.7	(0.5)	1.0	0.9	0.4	0.3	0.3	0.2
7.2	0.9	0.5	1.7	0.4	0.8	(0.6)	1.3	0.9	0.4	0.3	0.2	0.2
50.5	4.8	0.3	1.8	0.5	0.7		1.8	1.3	0.6	1.0	0.2	0.2
0.6	45.0	1.4	1.7	0.5	1.0		0.8	1.2	0.7	0.4	0.2	0.1
4.7	0.5	0.3	1.8	0.7	0.7		0.7	0.8	0.4	0.5	0.2	0.1
0.9	55.0	0.3	1.7	0.4	1.1		0.7	0.8	0.9	3.1	0.2	0.2
0.7	4.0	1.2	2.4	0.6	0.9	(0.7)	0.6	0.5	4.9	0.3	0.2	0.2
0.3	0.3	0.3	0.7	0.4	2.4	(1.9)	0.7	0.6	10.2	1.2	0.1	0.2
0.4	0.9	0.3	0.4	0.4	1.2	(0.7)	0.8	0.7	8.3	0.3	0.3	0.1
0.9	0.3	1.0	0.6	0.6	1.0	(0.7)	0.9	0.7	2.5	0.3	0.3	0.1
0.3	0.4	0.4	0.6	0.7	1.0		0.8	0.6	1.0	0.8	0.4	0.1
0.4	0.4	45.0	0.6		0.8			0.7	1.5		0.4	0.1
0.5	0.3	0.7	0.7		0.2			0.9	0.5		0.5	0.1
0.6	0.3	1.2	1.0		0.3				0.5		0.5	0.1
0.5	0.2	0.2	1.0		0.1				0.4			0.1
4.8	0.3	0.2	0.8		0.1				0.7			0.1
0.4	0.2	0.2	0.6		0.1	(0.1)			0.4			0.1
0.3	0.4	0.2	1.0		0.1	(0.1)			0.4			0.1
0.6	0.3	0.2	0.8		0.6	(0.5)			0.3			0.2
0.4	0.4	0.3	0.5		0.4	(0.2)			0.3			0.2
	0.6		0.6						0.8			0.2
												0.3
average												
4.0	3.4	2.2	2.1	0.7	1.1		4.7	1.3	1.3	0.5	0.3	0.3

The great variation in the arithmetic averages of the individual series set out in fig. 14 is caused both by the above mentioned variations in overall illumination and by variations in the density of the foliage.

The arithmetic averages of the sample means for one-hour intervals have been set out and are connected by a line indicating the broad general trend of the daily march of illumination. Owing to the wide scatter of the values of the series-averages, not too much value can be set on this trend line. Yet it shows some similarity with the shape of the curves published by EVANS (1939) and by ASHTON (1958) for the march of intensity of illumination near the ground, respectively in Nigerian rain forest and in Amazonian evergreen rain forest; these curves also reached a maximum 1–1½ hr. after noon.

From the readings represented in fig. 14 it appears that during days with 85 % sunshine (i.e. during 18 % of the days of a year) illumination at 1½ m height in the Mapane rain forest *averaged* 1.2×10^4 *ergs/sec/cm*^{2} Ø around noon (11–14 hr.).

In table II the complete records of 4 series of readings made at various times of the day during periods with unobscured sun have been set out to illustrate the enormous width of variation shown by the individual readings. These data also may serve to show the arbitrariness of a distinction between "sunfleck"- and "shade"-readings, which has already been discussed in I.3.3.

This is even more clearly shown by the frequency distribution of the measurements made at two different times of the day that are set out in fig. 15. The readings show a unimodal, though negatively skewed distribution.

Table II and fig. 15 also show that the occurrence of patches of strong light in the undergrowth is not restricted to a period of 4–5 hours in the middle of the day as was reported by some other students of the light distribution in tropical forest.

It should be noted that the readings presented in table II and in fig. 15 are confined to periods with bright sunlight. From the measurements made during suchlike periods it appears that around noon with the *sun unobscured,* light intensity in the undergrowth at 1½ m height averaged 1.6×10^4 *ergs/sec/cm*^{2} Ø (arithmetic mean). The *modal value* (i.e. the value at which the frequency density is at a maximum, cf. fig. 15) amounted to 1.2×10^4 *ergs/sec/cm*^{2} Ø. The latter value probably comes nearest to that which is called *mean shade intensity* by other authors.

To give an impression of the gradient of light intensity in the undergrowth, a few series of readings were made at 3 different heights (15 cm, 1½ m and 2½ m) in the Mapane rain forest, during a day in which the sun was unobscured during about 15 % of the time.

The readings made with the sun shining are given in detail in fig. 15 and in table II. In fig. 16 the arithmetic averages of all series of readings, *including those made with the sun clouded,* are presented.

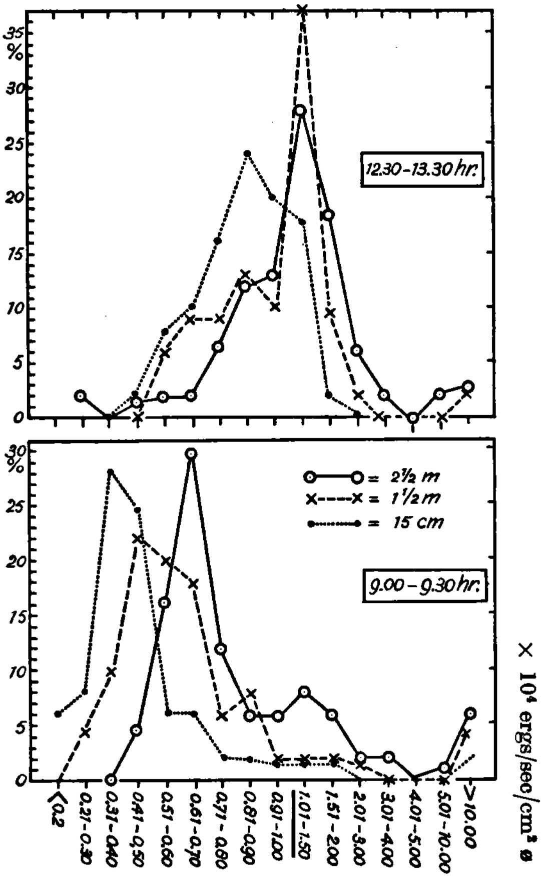


Fig. 15. Frequency polygon of the light intensity in Mapane rain forest at 15 cm, 1½ m and 2½ m height, at 9 hr. and at 13 hr. The readings were made with the spherical photometer during a day in the dry season (12 Sept. 1955), with the sun unobscured during the periods of observation. Light intensity expressed in 10^4 ergs/sec. Readings were made along a random sampling line (cf. p. 39), each series of readings consisting of about 50 readings. Note the differences in class-boundaries beyond 1.00 × 10^4 ergs/sec/cm^2 ø.

In view of the wide scatter of these sample-means not too much value should be attached to the lines that have been drawn through the averages of the sample-means, computed for one-hour intervals. These lines only give a rough indication of the daily march of illumination at the 3 levels, the samples being too few in number to give reliable hourly means.

The daily march of illumination at a fixed station is represented by the data given in fig. 13, showing the readings made at two neighbouring stations, each consisting of a sample area, 5 × 5 m in size. These squares were sampled systematically during 2 successive days. Both areas received about the same amount of illumination during the course of the day, except that in one of the two stations during three quarters of an hour a short burst of light fell slant-wise through a gap in the canopy. The influence exercized by this extra amount of illumination on the growth of the seedlings, will be discussed in part IV. This graph further shows that the daily maximum was reached about one hour after midday.

The average *daily amount of energy* received at 1½ m above ground-level as computed from the sample means shown in fig. 14 was 22 x 10^7 *ergs*, incident in a sphere with 1 cm^2 cross section. This figure applies to days with about 85 % sunshine.

The readings made with the spherical meter are not comparable with those made with a meter having a plane surface, because with the two devices two fundamentally different aspects of light climate are measured. As shown by the data given by WASSINK *et al.* (1951, table I, fig. 2–3) the ratio between the measurements made with the two types of photometer varies considerably with the character of the illumination, the measurements with the spherical meter being 1.2–6 times higher than those made with the plane meter. Under cover of the vegetation the ratio varied only between 1.3 and 1.6. For the Mapane forest a conversion factor was found varying between 1.2 and 1.7 for the sample means between 9 and 15 hr. For individual readings the variation in the ratio was much greater. For instance in the vicinity of leaves reflecting a shaft of direct sunlight falling through the canopy, the readings obtained with the spherical meter were up to 10 times higher than the vertical illumination measured

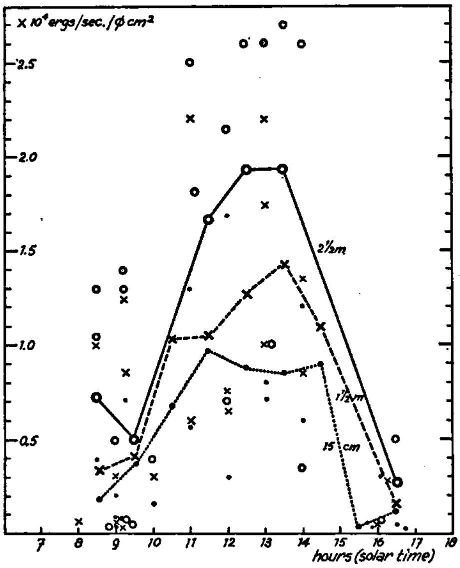


Fig. 16. Illumination in Mapane rain forest at 15 cm (●), 1½ m (×) and 2½ m (°) above ground level. Each point represents the mean of about 50 readings made along a transect (cf. p. 39). Samples were taken at random during days with the sun unobscured during c. 85 % of the time. The lines connect the arithmetic averages of the sample means for one-hour intervals. Illumination expressed in ergs/sec, incident in a sphere with 1 sq. cm cross-section.

with the plane-surface meter. This is for instance shown in the sixth column in table II, where the two figures obtained in such a situation are given in bold type.

For the Mapane forest only a few incidental readings were made with the plane-surface meter, but from the average daily total of 22 × 10^7 ergs found for a sphere with 1 cm^2 cross section, and allowing for a conversion factor of 1.5, *the daily total of the luminous energy received at a horizontal surface of* 1 *cm^2 averages* 15 × 10^7 *ergs/day*. This value applies to days with 85 % sunshine.

With the spherical meter a few measurements were made *in the large clearing* around the camp. In fig. 17 the readings made during a clear day are given for hours that the sun reached the place of observation in the centre of the clearing. The averages of the series of readings made with the spherical meter during the same day respectively in rain forest and in savanna forest, have been added.

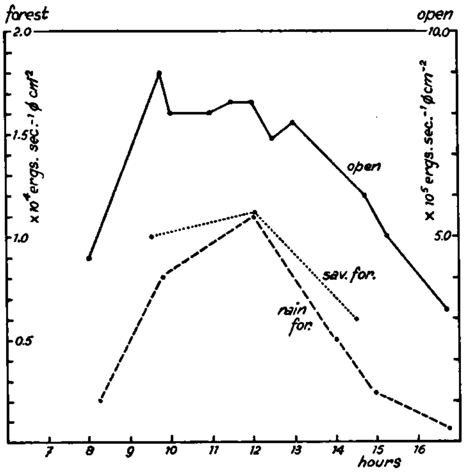


Fig. 17. Daily march of the intensity of illumination in a large clearing (scale at right hand), in the Mapane rain forest (broken line) and in savanna forest (dotted line), during a day with the sun unobscured during ca. 85 % of the time. In the curves for the forests each point represents an average of 50 readings made along random sampling lines (cf. p. 39). Readings made with the spherical meter at about 1½ m above ground level.

The *maxima* obtained with the spherical meter in the open in Suriname (7.6 × 10^5 ergs/sec/cm^2 Ø) are considerably lower than those obtained in Holland during the summer (8–10 × 10^5 ergs).

This also refers to the luminous energy measured with the plane-surface meter. With this meter in June in Holland values of 3.7 × 10^5 ergs/sec/cm^2 were measured against maximum records of 3.0 × 10^5 in Suriname. Such lower light intensities, notwithstanding a higher altitude of the sun, were reported by several students of the light climate in the tropics. ORTH

(1939) measuring light in the spectral region 3500–7400 Å for Kampala (Uganda) and for Lake Kivu found intensities of 0.52 cal/min/cm^2 (3.6 × 10^5 ergs/sec/cm^2) for sun's zenith distances of 23–30°. In Tanganyika (Albertville) and in the Upper Congo R. Basin (Lualaba) even values as low as 3.0 and 2.5 × 10^5 ergs were found. That these values, which are of the same order of magnitude as the present readings, are markedly lower than total radiation measured during the summer in higher latitudes with a lower altitude of the sun, is attributed to the high content of water vapour and dust particles of the air in most tropical lowlands.

BÜNNING (1947) using a photocell, measured light intensities of 3.5–4.3 × 10^5 ergs/sec/cm^2 in the lowlands of Indonesia. EVANS (1956) for S Nigeria computed from meteorological tables for the total solar radiation between 4000 and 7000 Å which reaches the ground, a value of 65 cal/dm^2/min (4.6 × 10^5 ergs/sec/cm^2), allowing for 20 mm of water vapour and 300 particles of dust per cubic cm near the ground. This value is markedly higher than the present values found in Suriname. The figures published by CARTER (1934) for openings in the British Guiana forest (up to 880 × 10^5 ergs/sec/cm^2) must be due to some miscalculation as this value is about 6 times the solar constant!

From the readings made in the open with the sun unobscured (7.6 × 10^5 ergs/sec/cm^2 Ø) and from the averages of those series of readings made in the forest under the same conditions during mid-day (0.16 × 10^5 ergs/sec/cm^2 Ø) the percentage relation under these conditions existing between the light in the forest and in the open can be computed. Thus for illumination at 1½ m a *daylight factor* (ATKINS) of 2.1 % was computed for light falling into a sphere with 1 cm^2 cross-section for times near mid-day, with the sun shining. A few simultaneous readings taken in the open and in the forest with the sun clouded rendered it probable, that the ratio under other weather conditions remained about the same (BACON 1939 also concluded that weather conditions have no appreciable effect upon the percentage transmission values in forest).

The daylight factor of 2.1 % applies to the arithmetic average of the readings made in the forest undergrowth around noon with the sun shining. For the *modal value* of the frequency distribution of the readings under these conditions (cf. fig. 15) – which value naturally is lower than the mean and probably comes nearest to the "mean shade light" of other authors – the daylight factor amounted to 1.5 %.

The daylight factor for the average illumination on a horizontal surface (*vertical illumination*) under the same conditions, though it only could be estimated very roughly from some occasional measurements, is higher than the ratio for *total illumination* and amounts to ca 3% (arithmetic mean).

During a relatively clear day (with over 85 % sunshine) measurements were taken with the spherical meter in the *savanna forest*, in the vicinity of the station where the other micro-climatological studies were made.

The average values of these series of readings are shown in fig. 17, together with those made in the rain forest and in the open during the same day. Light intensity in this type of savanna forest is not much higher than in rain forest at the same height, which is in accordance with the results of other microclimatological measurements that will be presented in the next chapters. Readings made with the spherical meter in openings in the savanna forest and in open savanna were about 1.3 times higher than in clearings in the rain forest owing to the reflection from the bare white sand that is present in the first-named stations.

As will be discussed in more detail in III.5, near the Wayombo R. a type of rain forest is found, which shows a pronounced dominance of *basralokus* (*Dicorynia guianensis*). This forest type looked markedly lighter than real mixed rain forest, and this was confirmed by the results of a series of 50 readings taken at $1\frac{1}{2}$ m height along a transect crossing such a *Dicorynia* stand. The frequency-% distributions of the readings made between 12.30 and 13.30 hr. (with the sun unobscured) are given in fig. 18. During the readings in a large clearing an overall radiation of 8.1×10^5 ergs/sec/cm² Ø was measured, which is identical to the total radiation in the open found during the readings made in the Mapane forest reproduced in fig. 15 (12.30–13.30 hr.); these readings have been set out once more in fig. 18 for comparison.

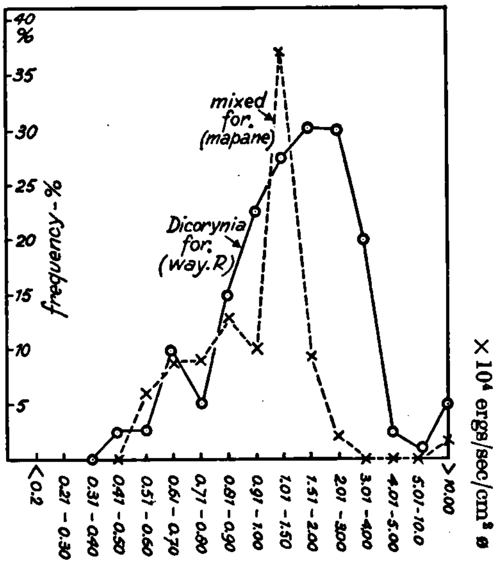


Fig. 18. Frequency polygon of 50 readings made along a random sampling line in Wayombo rain forest, crossing a stand with much *Dicorynia guianensis*. Readings were made with the spherical meter between 12.30 and 13.30 hr., with the sun unobscured. The frequency distribution of readings made with similar overall-illumination in Mapane rain forest (cf. fig. 15) have been added for comparison (broken line).

I.3.5. *Spectral composition of illumination in the forest*

It was desired to measure the light intensity separately in different parts of the spectrum, first of all to obtain a rough estimate of the error that is made when readings are taken at different stations (e.g. in direct sunlight and in deep shade in the forest) by the aid of a selenium cell, which has a markedly selective sensitivity to different wave lengths.

The characteristics of the filters were described in I.3.1 and have been shown in fig. 11. The spectral composition could be differentiated broadly in three parts by means of the yellow and the red filter: A. below 5000 Å (reading with the cell uncovered minus reading with the cell + yellow filter); B. over 6100 Å (red filter); C. 5000–6100 Å (first minus second reading). A third filter (green) with maximum transmission 4800–5900 Å was used as a check on the third reading.

In table III are set out ratios between the readings taken with the plane cell uncovered, and the readings with the cell covered by a filter. Owing to the changes in light intensity for the forest station, the first values had to be obtained by taking a mean of about 10 readings made during 10 seconds before and after the reading with a filter. The variation in light intensity was reduced as much as possible by making all readings with the cell fixed in the same horizontal position and by confining the readings to periods when no direct sunlight fell on the surface of the cell. The ratios given in table III apply to conditions with the sun unobscured, and are confined to the middle of the day, with the sun's zenith distance not exceeding 45°. During the readings the intensity of the illumination in the openings varied between 2.8 and 3.1 × 10^5 ergs/sec/cm^2. The intensity at the forest station averaged 0.7 × 10^4 ergs/sec/cm^2. The readings made with the sun clouded and at lower altitudes of the sun will be discussed below (cf. fig. 19).

TABLE III

Spectral composition of the illumination in the open and in the undergrowth (1½ m height) of the Mapane rain forest around noon with the sun shining. Mean ratios as percentages of total illumination (3500–8500 Å).

Spectral region	Sensitivity	Open		Forest	
	(1)	(2)	(3)	(4)	(5)
(a) violet + blue (3500–5000 Å) = 100%–(4)	—	24 %	20 %	28 %	25 %
(b) green + yellow (4600–6100 Å)	53 %	20 %	38 %	17 %	32 %
(c) green + yellow (5000–6100 Å) = (4)–(5)	—	50 %	33 %	45 %	26 %
(d) 5000–8500 Å	95 %	76 %	80 %	72 %	75 %
(e) orange + red + infra red (6100–8500 Å)	55 %	26 %	47 %	27 %	40 %

Notes. Column (1): relative sensitivity of the cell + filter combination in the spectral region concerned, as a % of the average sensitivity of the cell alone in the region 3500–8500 Å, computed from the spectral sensitivity curve of the cell and from the transmission curves of the filters shown in fig. 11.

Columns (2) and (4): readings with the filters as a % of the output of the cell uncovered.

Columns (3) and (5): readings in columns (2) and (4) corrected by means of the relative sensitivity of the cell + filter combination (column 1), thus giving the real distribution of energy in the spectrum as a % of total energy in the region 3500–8500 Å.

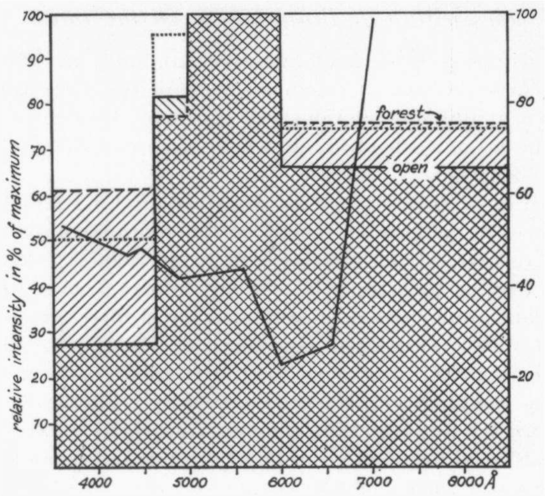


Fig. 19. Diagram of spectral composition of direct sunlight in an extensive clearing (continuous line) and of shade light (broken line) in Mapane rain forest. Based on ratios set out in columns (2) and (5) in table III. The dotted line represents spectral composition of solar radiation at the earth's surface, as computed from meteorological tables, allowing for an airmass of 1 and a water vapour pressure of 20 mm. The zigzag line shows the spectral composition in an African montane rain forest (taken from ORTH 1939, fig. 15).

In fig. 19 diagrams of the spectral composition of direct sunlight in the opening as well as of shade light in the forest have been plotted, based on the values given in columns (3) and (5) in table III. With the 3 filters used, the ratios could be determined only for wide ranges in wave length, and consequently in fig. 19 only averages over rather wide spectral ranges could be given.

The diagrams show in the region 6100–8500 Å an average increase in the transmission of the forest canopy of about 10 % (of the maximum intensity), but it is still unknown in what part of the red and/or infrared this relative increase occurs. Yet the results of the measurements given in table III clearly show *a relative reduction in the green and yellow* (5000–6000 Å) and *an excess in the blue and violet, and in the red and/or infrared.* The relative excess of the short wave lengths in the forest shade also appears from the necessity of using a pink filter when making colour photographs in the forest with blue-sensitive films.

The maximum excess in the red part of the spectrum is likely to fall beyond the red end of the visible spectrum as was shown by the comprehensive studies made by ORTH (1939) in a number of African forests. In fig. 19 one of the series of readings made by ORTH in an African rain forest (Mt. Virunga, Ruanda Urundi) has been given as an example. ORTH's graphs show a strong reduction in the orange. Owing to the wide range of wave lengths covered by the ratios determined in the present study, it is impossible to say whether this was also the case in the Mapane forest, for the orange part of the spectrum is just covered by the red filter, and a reduction, if any, in the orange is masked by an excess in the red/infrared. Evidence of an increase in the transmission of the forest canopy just beyond the red end of the visible spectrum was provided also by studies made in European beech woods (SEYBOLD, 1936 and COOMBE, 1957) and in Nigerian rain forest (EVANS 1939).

The reduction in the red light reported by CARTER (1934) is not necessarily in contradiction with the results of other investigations. As has already been pointed out by EVANS (1939), the low proportion of red rays was probably due to the type of cell used by CARTER, which had very little sensitivity beyond 7000 Å. In fact, with his Bernheim cell + red filter CARTER only measured in the 5800–6700 Å range of wave lengths, and this is the very region in which ORTH reported maximum reduction under the forest canopy.

The relative increase in the transmission of the canopy in the violet/blue part of the spectrum shown by the ratios in table III, also appears from the readings made by ORTH and by SEYBOLD in the lighter parts of African and of European deciduous forests, where illumination suffices for a fairly good development of the ground flora, just as in the station chosen in the present study for the colour readings. The excess in blue of the light in suchlike stations – which ORTH rightly called a *red-blue shade* – is caused by the relatively greater part of direct skylight penetrating through holes in the canopy. The *decrease in blue* (below ca. 5000 Å) reported by EVANS, obviously resulted from the fact that this author compared shade light in the forest with sky light in the open, as the cell during the readings in full sunlight in the open was screened from the sun by a small disk placed 2 m away. The greater part of CARTER's readings showed a relative *increase in blue.*

The ratios given in table III are restricted to readings made near midday during periods when the sun was unobscured. As was to be expected, the degree of clouding had a considerable effect on the composition of the light in the undergrowth. As is shown by the data given in fig. 20 any decrease in total illumination (either caused by clouding of the sun or by lowering of the sun's altitude) results in an increase of the short wave lengths and a proportionate decrease in the red part of the forest light. This shift of the spectral composition in the undergrowth to shorter wave lengths obviously is due to an increase of the part played by the sky light in the total overall radiation.

As a check on the *readings made in direct sunlight,* in fig. 19 the theoretical intensities in the spectral regions have been added (dotted line). For this purpose the proportion of the different wave lengths was worked out at 500 Å intervals for ground-level sunlight, using the transmission coëfficients given in the Tabulae Biologicae, allowing for an optical airmass of 1.0 (sun in zenith), a partial water vapour pressure at ground

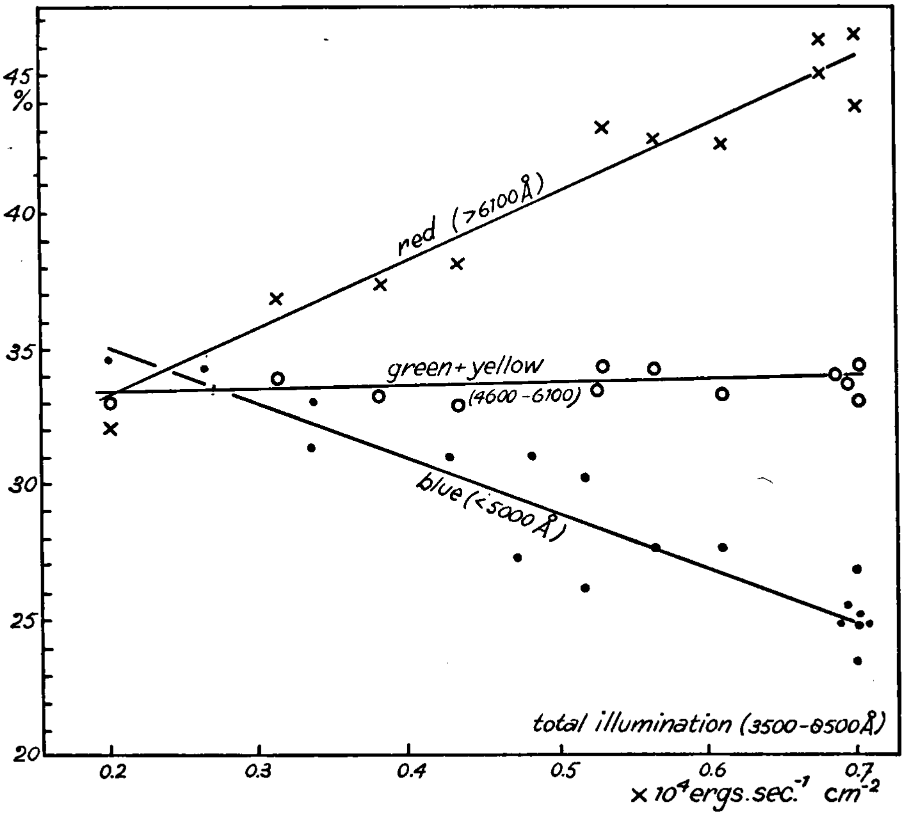


Fig. 20. Spectral composition of illumination in dependence of intensity of illumination in the Mapane rain forest. Readings were made with a plane photo-cell in a fixed horizontal position at 1½ m height, between 11 and 15 hr., except the readings with 0.2–0.3 × 10^4 ergs/sec/cm^2 total illumination, which were made at 16.30 hr. Variation in total intensity of illumination was caused by variation in cloudiness. Ratios are given as percentages of total illumination, corrected for sensitivity of cell + filter (cf. column (1) in table III).

level of 20 mm, a height of 40 m above sea level, and an atmospheric pressure of 760 mm. The present data show a marked reduction in the violet/blue part of the spectrum as compared with the theoretical values. This is partly due to the fact that for the computation of the theoretical values no allowance was made for the strong scattering effect exercised by dust particles, particularly on the short wave lengths. ORTH (1939) too reported for tropical lowlands a striking poverty of the solar radiation in short wave lengths, which he imputed, not merely to the high water content, but also to the great number of dust particles in the air.

As mentioned before, the spectral composition of the light in the forest was studied primarily in order to obtain a rough estimate of the order of magnitude of the error that is made when photocell readings from different habitats are compared. From the data given above and from the selective sensitivity of the cells it can be calculated that the sensitivity of the cells for the moderately weak shade light (about 0.1×10^5 ergs/sec/cm^2) that prevails in the forest during the middle of the day (10–15 hr.), is only 70 % of that for direct sunlight in the open. Accordingly a daylight-factor for such stations in the forest has to be multiplied by a factor 1.6. For the daylight-factor given in I.3.4 (2.1 % for the spherical meter) which has been computed for the average light intensity in the forest (including direct sunlight readings in *sunflecks*), the correction factor is lower, because the quality of the light in the *sunflecks*, which made such a considerable contribution to the arithmetic average of the light intensity, will resemble that of sunlight in the open. The sunlight penetrating through little openings between the leaves is likely to be relatively poor in blue, as was shown by measurements made by ORTH (1939, fig. 16); this is partly due to the scattering of short wave lenghts by edges of leaves and twigs, but particularly to the fact that sky light is cut out.

On the other hand the proportion of blue light will be much higher, and consequently the correction factor will greatly exceed 1.6, in light places in the forest, where mainly diffuse sky light has access through gaps in the canopy. As mentioned above, the frequent occurrence of such *blue-red shade* light has been established in various types of forests. Such a reduction in the green part of the spectrum, for which the photocell shows maximum sensitivity, may cause a reduction in the sensitivity of the cell to less than one half the sensitivity for direct sunlight.

SUMMARY

Owing to the wide range of wave lengths covered by the ratios given in table III, these ratios do not give us a complete picture of the composition of the shade light in the forest, and of the ecologic significance which the pecularities of the spectral composition have for the undergrowth. The readings only indicate that the light in the undergrowth under overstoreys of moderate density shows an excess in both short (< 5000 Å) and long (> 6100 Å) wave lengths, and consequently is poorer in green and yellow. As mentioned before, the increase in red probably is largest in the range above 6500 Å, and in that case it might be considerably greater than appears from the ratios found with the red filter, which can provide only an average for the range of wave lengths beyond 6100 Å. In addition the increase in the far red and/or near infra-red in all probability is masked by the considerable decrease in the orange (6000–6500 Å), shown by ORTH's graph given in fig. 19. A similar strong decrease in the region of maximum absorption by chlorophyll has been established by ORTH and by SEYBOLD for shade light in a great number of forest types.

During the present studies no measurements of spectral composition were made in the darkest parts of the forest, but on account of the results of the studies made by ORTH and SEYBOLD, it seems likely that in the Suriname forests too the ratio of the short wave lengths to the rest of the spectrum will decrease with increasing density of the overstoreys (whereas, as shown in fig. 20, in a given station the blue increases when the light intensity decreases owing to clouding of the sun, etc.). A similar relation between the proportion of short wave lengths and density of vegetation may also be extracted from the data given by EVANS (1939, table IX). For instance, in the darkest station (no. 3) with the blue filter only 11 % was found of the output which the meter registered with the same filter in the lightest station (no. 2), whereas for the red filter this ratio was 26 %.

I.3.6. *Comparison with data from other tropical forests*

The most comprehensive observations on illumination in tropical forests, and particularly on the spectral composition of the light, are those of ORTH (1939), which have already repeatedly been mentioned in the foregoing sections. The light intensities found by ORTH in African forests of different types are of the same order of magnitude as those found in European forests, and he strongly denies that plants living in the undergrowth in tropical forests should be adapted to lower intensities than those found in deciduous forests in temperate regions. The lowest light intensity in which a ground flora occurred in African forests of various types, was of the same order as the critical value found for temperate forests.

Integration of ORTH's curves of spectral composition in rain forests gives values for total illumination (ca. 3500–7000 Å) which are not very different from those obtained in the Mapane rain forest.

EVANS' (1939) observations on the daily march of illumination in the undergrowth in the Nigerian rain forest reveal that its general trend is similar to that of the corresponding curves found in the present study. Although direct comparison with EVANS' readings is impossible, because his readings are expressed in arbitrary units, the conditions of illumination in his primary and 14-year-old secondary forest are not very dissimilar to those found in the Mapane forest when considering the *daylight-factor*. Although EVANS did not compare total intensities inside and outside the forest when the sun was shining, he had good reasons for assuming that the ratio found for the sun clouded (½–1 %) remained probably the same when the sun was unobscured. This factor only applies to readings made in *shade light*, excluding sunflecks.

In a later publication EVANS (1956) evaluated the contribution of sunflecks to the light reaching a plant in the undergrowth around noon with the sun shining, at about 80 %. Accordingly the daylight-factor for the average illumination in the undergrowth (including sunflecks) would be 2½–5 %, which value is of the same order of magnitude as that found for a plane-surface meter (3 %) in the Suriname forest. He estimated the average daily total of *sunfleck light* reaching a plant in the undergrowth of the Nigerian rain forest at 500 cal/dm^2 (21 × 10^7 ergs/cm^2). The daily average for *shade light* is shown not to exceed 200 cal/dm^2 (8 × 10^7 ergs/cm^2). Thus total daily illumination on a horizontal surface averaged about 29 × 10^7 ergs/cm^2 during a period (January–March) having a daily average of 78 % sunshine. This value is based on a calibration of the measuring apparatus against total solar radiation in the open, which was taken to be 4.55 × 10^5 ergs/sec/cm^2 around noon. As has been mentioned on p. 47 this value, which was computed from meteorological tables, is considerably higher than the figures obtained in other tropical lowlands.

Possibly this might explain the discrepancy with the daily total found in the present study (22×10^7 ergs/cm^2 ø and roughly 15×10^7 ergs/cm^2).

The data given by CARTER (1934) for various types of forest in British Guiana, are expressed in absolute units, but—as stated above—the values given for illumination both in the forest and in the open are at least 150 times too high (up to 880×10^5 ergs/sec/cm^2 in the open!).

The ratios of intensity inside to total intensity outside the forest given by CARTER, presumably are correct and are summarized in table IV, since they are of interest for Suriname, where the same types of forest are met with.

TABLE IV

Illumination on the floor in various forest types in the Essequibo region, Br. Guiana, expressed as a percentage of the total amount of light in the open. Made with a Bernheim photoelectric cell between 11 and 15 hr. with the sun unclouded. The average illumination evaluated from the measurements in *shade* and in *sunflecks* in combination with an estimate of the percentage of the area of sunflecks. Selected from CARTER's data (1934) after rounding off of the figures. For the sampling method used see I.3.3.

	Low second. forest	*Wallaba* forest	*Manicole* swamp	Mixed forest	High *Mora* forest
Shade	0.9 %	0.8 %	0.8 %	0.3– 0.4 %	0.2– 0.4 %
Sunfleck . . .	73 %	39 %	13 %	54 –72 %	24 –49 %
Average illumination . . .	4.6 %	1.8 %	1.2 %	0.8– 1.9 %	0.4– 0.9 %

In a recent paper GERMAIN *et al.* (1956) reported an average daylight-factor of 0.8 % at 1 m height in mixed evergreen *Scordophloeus*-forest in the central Congo basin. MAUDOUX (1953) in the same forest found a value of 0.4–1.3 %. In both cases readings were made at random, including sunflecks. In a darker community dominated by *Brachystegia*, the ratio averaged 0.65 %.

The data presented by GERMAIN *et al.* show the interesting fact that in both types of forest the ratio decreased with increasing altitude of the sun.

From the older investigations passing reference is made to those of WIESNER (1895), who, using an actinometer, found that in Javanese rain forest the "phanerogam limit" was in general about 0.8 % of the outside daylight.

BÜNNING (1947) found that in Indonesian rain forests at light intensities of 0.2–0.7 % still an undergrowth was present, consisting a.o. of Begoniaceae, Rubiaceae, Zingiberaceae, etc.. MCLEAN (1919) working in a rain forest in S Brazil with an actinometer covered by a filter cutting out all wavelengths beyond 5000 Å, obtained a daylight-factor of 0.7 % in "deep shade".

There is little information as to the form of the *vertical gradient* of the light intensity. From ALLEE's (1926) data obtained in a rain forest, it might be concluded that this type of forest shows a rather abrupt rise in intensity between the lower tree tops (12–18 m) and the upper canopy (23–25 m). The same is probably true in evergreen rain forest in the state of Pará (Brazil), where readings were taken by ASHTON (1958) at different heights, all up one tree; these readings too showed that light intensity and the time during which sun flecks were present were mainly controlled by the density of the second storey. Possibly this can partly be explained by the fact that the observations were made in the beginning of the dry season, when there were fewer leaves on the emergent trees than at any other time. It is unknown if the same situation exists in true mixed rain forest in Suriname, where relatively few trees of the canopy show a tendency to change their leaves principally at one time of the year, and where there is no well-defined second storey forming a dense cover under an upper storey of emergent trees, as was the case in the forest type described by ASHTON. Yet the light measurements made in the experiment plot described in IV.7 might indicate that the shading effect of the emergent canopy (trees over 40 cm d.b.h.) is relatively small as compared with that of lower storeys. This appears from the relatively slight rise in the intensity of illumination in the undergrowth after the trees of over 40 cm d.b.h. had been poisoned. But because death and leaf fall were very slow, the readings in this experimental plot are not decisive. Since the degree to which the different levels of foliage contribute to the interception of light, is of great importance to silviculture, studies with regard to this subject are on program. Measurements of illumination will be made at ground level in experimental plots where foliage at different levels is eliminated by killing trees with quick working arboricides like arsenites.

Studies of spectral composition made by ORTH (1939), EVANS (1939) and CARTER (1934) already have been discussed in I.3.5. From these studies it may be concluded that the spectral composition in tropical rain forests does not differ essentially from that in deciduous forests in temperate regions, where similar light conditions (like "red-green shade" and "blue-red shade") were found. The luxuriant growth found under the tropical rainforest canopy need not be caused by an extraordinary high proportion in longer wave lengths due to reflection by the shining surface of leaves from the upper storeys, as suggested by KARSTEN (1924–'26).

I.4. ATMOSPHERIC HUMIDITY

I.4.1. *Methods and instruments*

During 25 months on (Jan. 1955–Jan. 1957) and also during the dry season of 1957 (Sept.–Nov.) either daily or weekly hygrograph records were made at the rain-forest station at 1½ m height. For the large clearing and the savanna forest records are available for 1956 and 1955 respectively.

Occasionally, especially in selected periods during the dry seasons, simultaneous hygrograph records were made in the rain forest at 10 cm, 5 m and approximately 30 m height above ground level.

For recording the relative humidity 4 hygrographs, manufactured by Fuess in Berlin, were used. The hygrographs tended to be inaccurate above 95 %, to such an extent that individual readings above 96 % could not be considered significantly different from saturation. Every day, at 7 and at 18 hr., and in periods of high humidity also sometimes during the day, readings were taken either with a ventilated Assman psychrometer or with a whirling psychrometer in order to ascertain the exact humidity at the beginning and the end of the period of high humidity. The correction of the graphs for the nocturnal periods was based on the assumption that the deviation from the correct setting had been progressive and regular during this period. Another control reading with a psychrometer was made around midday, during the period of lowest humidity. Even in exposed positions, with daily variations of over 60 %, the deviation of the hygrograph records from the values measured with the psychrometer, were small (1–5 %), and very seldom exceeded 8 %. During a number of dry days at the beginning and at the end of the period of observation the daily march of relative humidity as computed from psychrometer readings taken every 5 minutes was compared with the curves on the hygrograph charts; for the hourly means the difference did not exceed 5 % in exposed places and 3 % in the forest, and daily means agreed with each other within 2 %.

The mean daily value of the relative humidity was obtained from the charts by averaging the corrected half-hour values.

Because, as a rule, simultaneously temperature records were made, it was possible to calculate also the *saturation deficit*; to this end a barometric pressure of 760 mm (BRAAK 1933) was assumed. The saturation deficit has been evaluated from the half-hour readings of the thermograph and hygrograph records. The mean saturation deficit over a given period can obviously not be calculated from the corresponding means of relative humidity and temperature, as is sometimes done in ecological studies. When simultaneous temperature records were not available, hourly and daily averages of the saturation deficit were computed from the relative humidity data with the help of the relation shown in fig. 21, which will be discussed below.

This laborious task was undertaken because, from the standpoint of physiological ecology, the most useful gauge of the atmospheric humidity is the saturation deficit of the air; it is a far better measure of the evaporating power of the air than relative or absolute humidity are. Relative humidity being a percentage of the max. vapour tension at the prevailing air temperature, may be a very misleading measure of the influence exercised by air mosture on evaporation and hence on transpiration, especially if considerable differences in temperature occur. Vapour pressure deficit (saturation deficit) on the other hand is the difference between the saturation pressure at the prevailing air temperature and the actual partial water-vapour pressure. Because the evaporating, or drying, power of the air is determined by the rate of movement and the saturation deficit, the latter should replace relative humidity data in all studies concerned with the drying influence of the environment, as already has been emphasized by many ecologists.

A still better index of the evaporating power of the air would be the difference between vapour pressure at the temperature of the evaporating surface and at the dew point temperature, but the first value is seldom known. Moreover, measurements carried out with an electric resistance thermometer showed that leaf temperature of undergrowth plants under forest cover did not differ significantly from the air temperature.

In the following sections relative humidity data have been given too, because some readers may be more familiar with this measure of humidity. This is done also to facilitate comparison, since this factor has been used in many studies on the microclimate of the tropical rain forest, and since data on the saturation deficit are seldom available for tropical stations. Although the disadvantage of the use of the relative humidity lies in its unsuitability for comparing values obtained at different temperatures, this disadvantage is of less weight when stations are compared where the variation in temperature is so small that it is permissible to regard the relative humidity as a more or less approximate measure of the evaporating of the air.

As could be expected from the causal relation between rate of insolation, air temperature and air humidity, a strong correlation was found between relative humidity and saturation deficit. As shown by the graph reproduced in fig. 21, the correlation between the data found for relative humidity and saturation deficit, both for the rain forest and the large clearing, are fitted by the same curved regression line (correlation coëfficient between 35 and 100 % relative humidity: 0.991 for 30 weekly means and 0.901 for 20 daily means). This relation appeared to be nearly independent of the season. The same regression line also fits the data obtained in savanna forest and at other levels in the rain forest. For the part of the curve between 0 and 26 mm (35 %) the deviation of the individual data (about 1200 daily means in different habitats) did not exceed 1½ mm or 5 %. Owing to the close relation between relative humidity and saturation deficit, it has been possible to represent the variability of these two factors by the same graph, by using separate scales for them (e.g. figs. 22, 23, 32, etc.).

For averages calculated for shorter periods (e.g. hourly means) the deviations were occasionally much larger, viz. up to 2½ mm or 12 %. Hence the curves for the *daily* march of saturation deficit and of relative humidity (e.g. fig. 27) had to be presented separately.

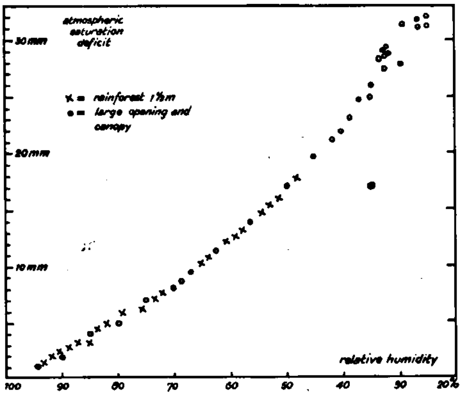


Fig. 21. Relationship between relative humidity and saturation deficit; the points represent daily or weekly means computed from hourly readings of simultaneous hygrograph and thermograph records, obtained in the rain forest and in a large clearing.

I.4.2. *Humidity in closed rain forest*

The most complete series of observations relating to the rain forest are those made at 1½ m above groundlevel, which cover the full seasonal range of conditions during 2 years and also the dry season of 1957.

The *average daily march* of relative humidity and saturation deficit at 1½ m during the years 1955 and 1956, based on the yearly averages of the hourly readings of the charts, is represented in figs. 22 and 23.

The slightly lower values that are found in the curve for 1956 during the day hours are to be accounted for by the higher humidity which prevailed in that year during the dry season. One of the striking features of these graphs is the long duration of the nightly period of high humidity (over 95 % rel. hum. = under 1 mm sat. deficit), which has an average

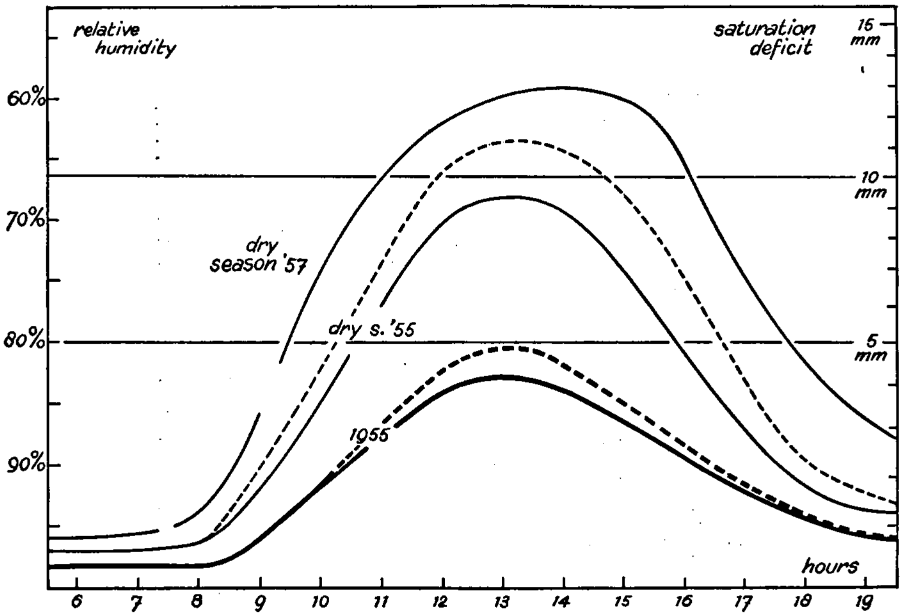


Fig. 22. Average daily march of atmospheric saturation deficit during selected periods in rain forest (continuous lines) and in savanna forest (broken lines) at 1½ m height. Based on averages computed from hourly readings. Approximate values for the relative humidity (error ± 3 %) can be read from the scale at the left (based on the relationship shown in fig. 21).

duration of 14 hours. The minimum humidity (83 % rel. hum. = 4.2 mm sat. def. in 1955 and 85 % = 3.6 mm in 1956) was found around 13 hr. It should be borne in mind that the tops of these curves should not be confused with the mean daily minimum of atmospheric humidity, which of course is lower, and which is of little physiological importance. These 2 year curves show the general trend in the daily march, but from the viewpoint of ecology they are of limited interest. Therefore, the curves for 2 dry seasons and for the wettest period in 1956 have been shown separately. The average daily march of humidity in the dry season of 1955 (mid-Sept. to mid-Nov.) shows a minimum of 70 % (max. of 10.6 mm) at 13 hr., whereas during the drought of 1957 the humidity at 14 hr. averaged 58 % (mean max. deficit 13 mm). In this period of drought the rarity of rain showers and the relatively low degree of cloudiness in the afternoon as compared with the dry seasons of 1955 and 1956, is responsible for the fact that the average daily march of humidity reached its minimum one hour later than in the dry seasons of the other two years.

The curve for the dry season of 1955 may be taken as representing the average daily march during the long dry season of a *normal* year. It may be mentioned that during the less marked dry season of 1956 the average humidity was higher.

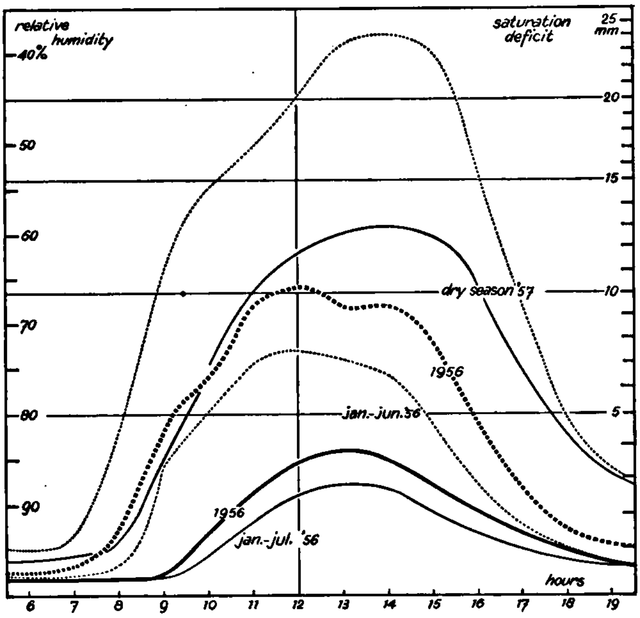


Fig. 23. Comparison of the average daily march of atmospheric saturation deficit in rain forest (continuous lines) and in an extensive clearing (dotted lines) during selected periods. Based on averages computed from hourly readings.

For a better evaluation of the humidity factor a consideration of the fluctuations appearing during the individual days is essential, as the daily records show considerable deviations from the above mentioned long-term averages.

The march of humidity in the day hours is, just like that of the temperature, largely controlled by the rate of sunshine and by the quantity of water that is directly available for evaporation. Puffs of wind in the undergrowth are actually responsible for sudden changes in humidity, resulting in the numerous drops and rises of short duration appearing in the daily records, but the average rate of the daily air movement did not seem to vary much during the year, and these differences could, in our opinion, but seldom be held responsible for significant changes in the daily humidity.

Though the variations in the march of humidity were considerable from one day to another, the daily records invariably showed a long nocturnal period during which the humidity did not differ much from saturation.

Outside of the long dry season this *night period of maximum humidity* (90 % or over) lasted, with a few exceptions, at least from 18 hr. till 9 hr., with an average duration of 17 hours. For much the greater part of this nocturnal period a humidity prevailed approaching or reaching saturation. During the wettest months nearly every day from 17 hr. till 10 hr. a relative humidity of 98–100 % (satur. deficit 0.4–0 mm) was recorded, as shown in the upper half of fig. 24, which represents the march of the relative humidity during a random week in the wettest period.

The drier periods differ from the wet ones, amongst other things, in the shorter duration of the daily period of high humidity, but *even during the long dry season a deficit of less than* 1 *mm* (*rel. hum. over* 95 %) *was generally maintained for at least* 10 *hours a day.* This is shown in the uppermost curve in fig. 27 representing the daily records obtained during the driest period at the end of the dry season in 1955. Even in this period a satur. deficit of 1 mm was reached before 22 hr. (and often much earlier, the curve for 5 Nov. being an exception) and lasted till 7–8 hr. This was observed also during the exceptionally dry period in 1957, when not until the end of the drought the deficit dropped under 1 mm for less than 5 hours on end. But this comparatively short duration of the daily period of high humidity was confined to a few days, two of which are shown in fig. 28.

Unlike the nightly periods, which did not show great daily and seasonal variations, the *humidity during the diurnal hours was subject to considerable fluctuations* from one day to another. Outside the long dry season very wet days with relative humidity constantly above 90 %, alternated with days or longer periods with a considerably lower humidity. Particularly in January, February and March spells of dry sunny weather lasting from 3–10 days, causing a prompt decrease in the humidity, were common. During years with a pronounced short dry season (cf. fig. 9), the humidity may drop in that period too to low values, similar to those recorded in the present study for the main dry season. During the period of observation (1955 and 1956) a short dry season was hardly noticeable.

The highly variable course of the daily humidity, which in addition shows great variations from one year to another, only allows a few general remarks on the humidity during the day. During the *wettest* months of the year (in the period of recording: Jan.–July and Dec.) for several days on end relative humidity did not fall below 90 % (sat. def. 2 mm) for longer than 1 hour a day, but during dry days it might drop below this value for 6 hours. Often a value of 80 % (5 mm) was approached or passed for $\frac{1}{4}-5$ hours. During half of the days the relative humidity at 1½ m in the rain forest did not drop below 80 % (sat. def. over 5 mm). Sometimes 75 % (7 mm) was approached, but a drop below 70 % (a rise over 8½ mm) for periods longer than one hour was of very rare occurrence. Fig. 24 records the march of humidity during a period considered typical of the wettest months.

During the humid, *transitional* months (Aug. and first half of Sept.) relative humidity during the diurnal hours fell under 75 % (sat. def. exceeded 7 mm) frequently for periods of 1–4 hours and values of about 60 % (12.5 mm) were approached for a moment during spells of dry weather, which are not uncommon in these months. In the upper half

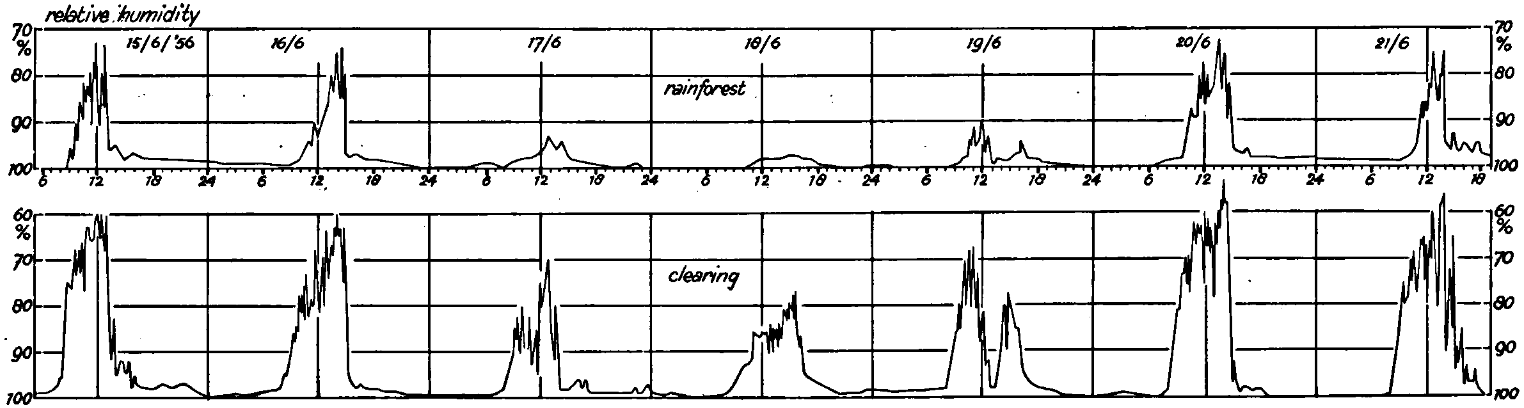


Fig. 24. Example of the march of the relative humidity in closed rain forest and in a large clearing at 1½ m height during the wettest months. Smoothened curves, each point representing the moving average of 3 successive readings made at intervals of 10 min.

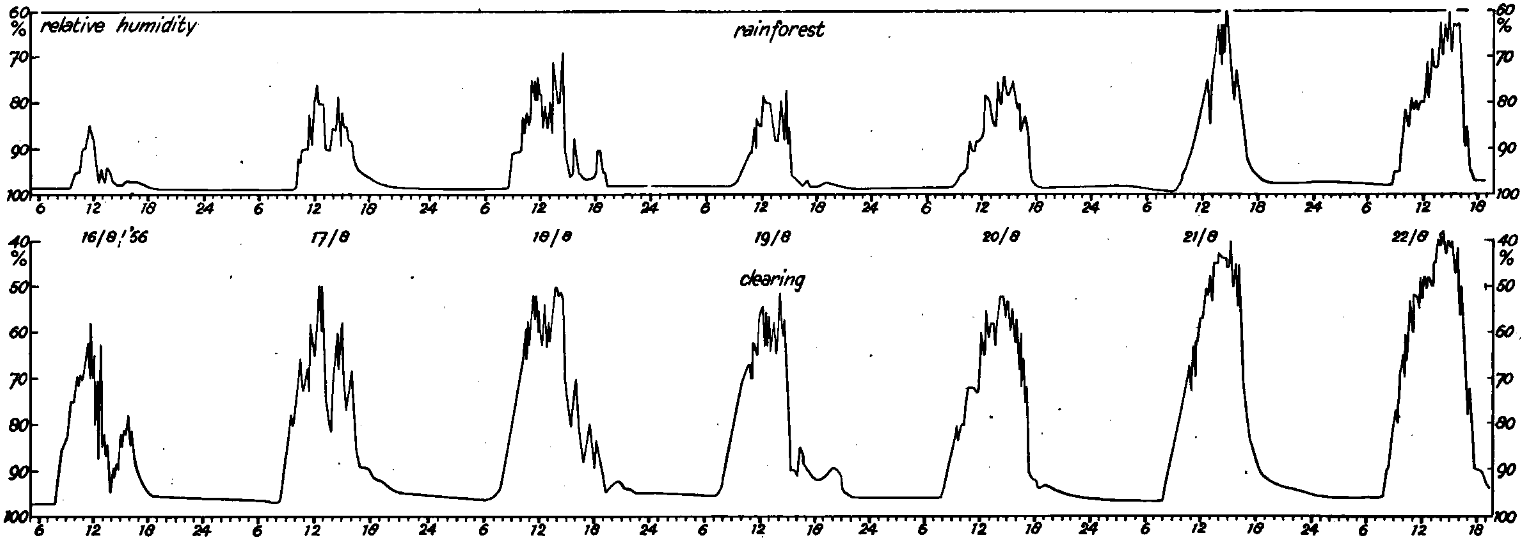


Fig. 25. As fig. 24 during a week typical of the transitional period between the wet and the dry season (16–22 Aug. 1956).

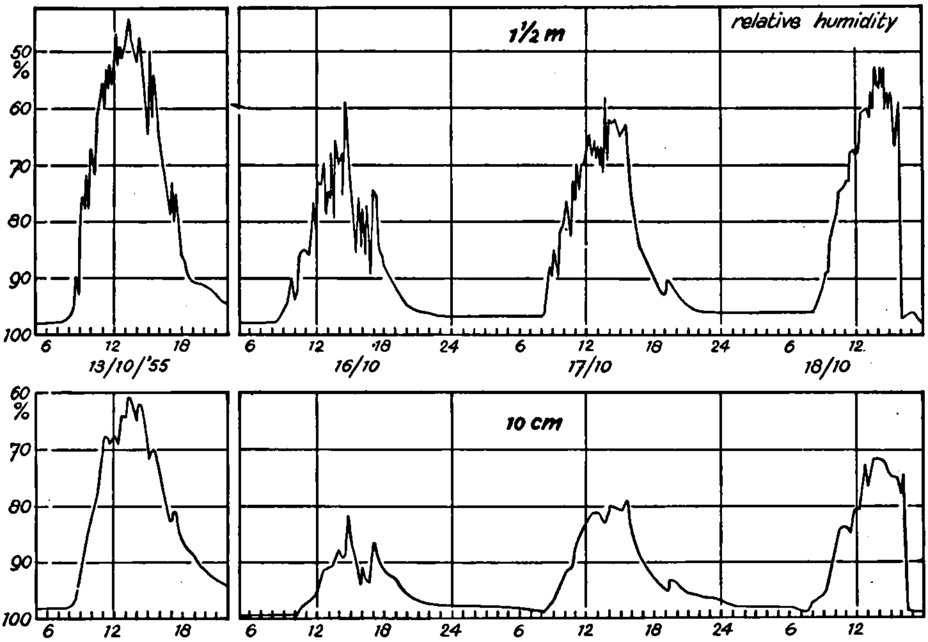


Fig. 26. Recordings of relative humidity in rain forest at 1½ m and at 10 cm above ground level during days that may be regarded as typical for the dry season. For the construction of the curves cf. fig. 24.

of fig. 25 the hygrograph records of a week in Aug. 1956 have been reproduced; they were selected to show the march of humidity considered typical of the transitional period between the wet and the dry season.

The period of recording covered 3 *long dry seasons*, two of which happened to differ more or less from the mean (as is shown by the graphs in fig. 5): in 1956 it was relatively humid, and in 1957 relatively severe. The latter, in addition, was preceded by a wet season with a subnormal amount of precipitation. Thus in our opinion the available records may be regarded as a fair representation of the range of humidity conditions the driest months.

In the dry season of 1955 which lasted from the beginning of September to mid-November, the saturation deficit rose practically every day above 8 mm (the rel. hum. fell under 72 %) during 1–5 hours a day, as may be seen from the average daily march for this dry season shown in fig. 22. On several days values over 10 mm (rel. hum. under 65 %) were reached for 1–5 hours. Sometimes the deficit rose above 12 mm (the rel. hum. fell under 60 %) longer than one hour. Exceptionally (8 times) a value of 17 mm (50 %) was approached during ¼–2 hours. The values found for the saturation deficit during the driest week on record in the dry season of 1955 are given in fig. 27, which shows a maximum of 17 mm (rel. hum. 50 %) reached during one hour (with an absolute maximum of 18 mm). In the first half of this dry season similar values were approached (fig. 26).

In the smoothened graphs shown in figs. 26, 27 and 28, low humidities of short duration (less than 5 min.) have not been considered. When during the day a steep vertical humidity gradient is set up, the actual course of the curves shows numerous fluctuations, and for periods of a few minutes the humidity may rise or fall as much as 10 % (3-5 mm) above or below the quarter-hourly average. These brief and sudden fluctuations are caused chiefly by puffs of wind, passing clouds or a spell

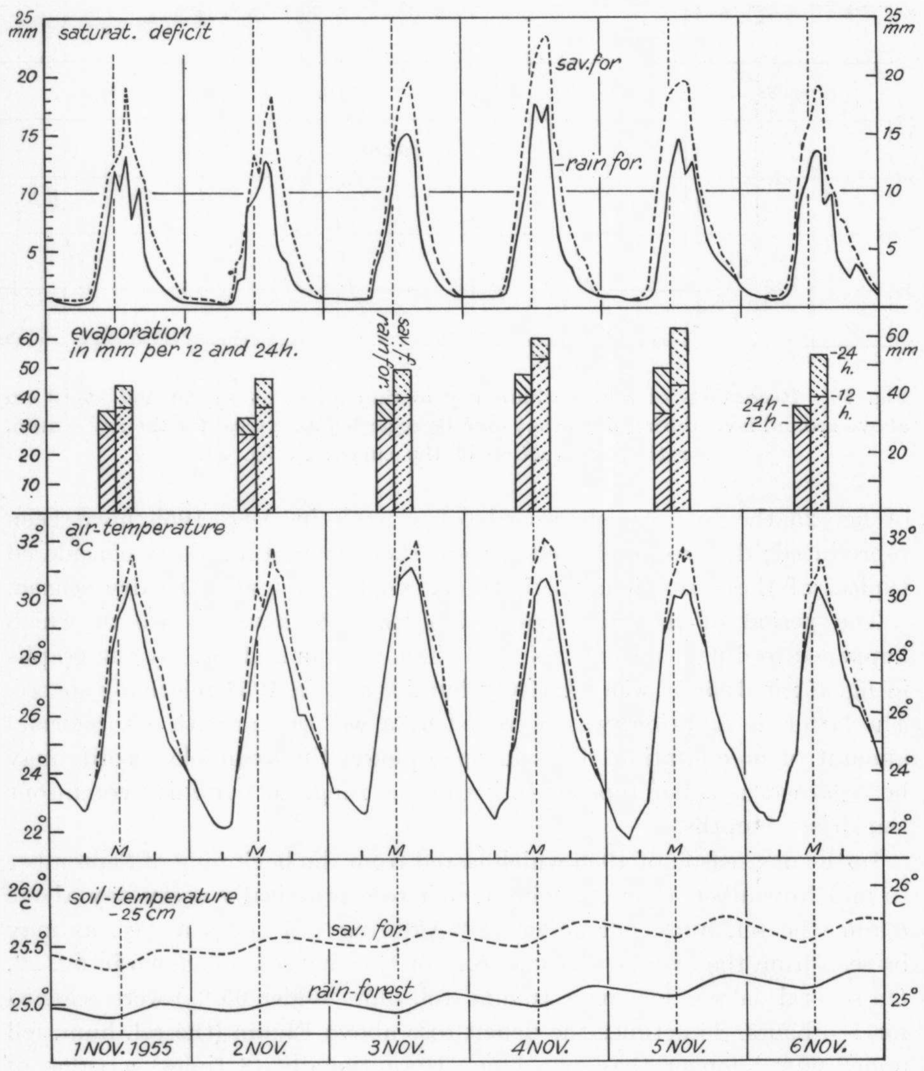


Fig. 27. Daily march of saturation deficit, air temperature and soil temperature at 25 cm depth, and daily Piche evaporation for the periods between 6–6 hr. and 6–18 hr., in rain and savanna forest during the driest week of the dry season of 1955. Smoothened curves of saturation deficit and air temperature are based on moving averages of 3 successive readings taken at 10 min. intervals. Piche evaporation is expressed in arbitrary units.

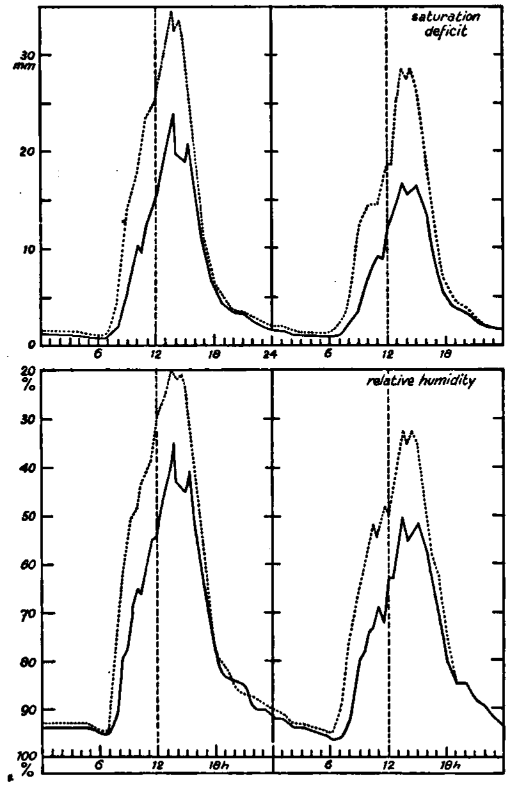


Fig. 28. March of relative humidity and saturation deficit in the rain forest at 1½ m height and in the open air just above the main canopy, during two very dry days in the dry season of 1957 (11 and 12 Nov.). For the construction of the curves cf. fig. 24.

of sunlight. I agree with **Evans** (1939) that their physiological effect probably is negligible. For that reason the figures of the absolute minimum humidity have been left out of discussion, these minima generally being reached in one of these brief fluctuations.

In figs. 27 and 28 the values found for the humidity during the *driest* days of the dry season are shown, but the long dry season generally is interrupted by rainy days and even by rainy periods with high humidity, as appears from the graphs given in the foregoing chapter (fig. 7) and from the daily means of humidity shown in fig. 30.

In fig. 29 is given the daily march of humidity based on the hourly averages calculated for the 15 driest days of the dry season of 1955 (A), as compared with that based on the averages calculated from the records of humid days (B).

During the less pronounced dry season of 1956 the periods during which the humidity dropped to the above mentioned values were markedly shorter. A saturation deficit of 17.5 mm (rel hum. 49 %) was reached only once, and even a value of 12 mm (60 %) was exceptional. A rise

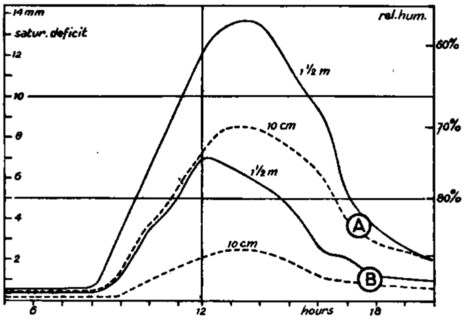


Fig. 29. Daily march of saturation deficit in rain forest at 1½ m and at 10 cm height, averaged over dry (A) and *h*umid (B) days in the dry season of 1955. Relative humidity can be estimated (error ± 3 %) from the scale at the right (cf. fig. 21).

above 10 mm (fall of rel. hum. below 65 %) during one hour or over, was recorded only during 12 days. Frequently the daily record did not even approach 8½ mm (70 %).

In 1957, which was characterized by a wet season with subnormal precipitation followed by a rainless period of abnormal length, the humidity in the forest reached correspondingly low values; this appears when the graph of the mean hourly values for this dry season is compared with that for the dry season of 1955 (fig. 22 and 23). The humidity fell lower than would perhaps have been expected from the smoothened curve for the precipitation given in fig. 7. The period in which this curve dropped under the 100 mm threshold, did not differ much in length from the *not-wet* period in the corresponding curve for 1955. But in that year the extension of the *wet* period (i.e. the period consisting of days with 100 mm rain or over during the previous 30 days) was caused by a single heavy shower of 75 mm on the 6th Sept. Such a single heavy shower may actually have a prolonged influence on the water content of the soil, as shown by the soil moisture data for this period, but the consequences for the atmospheric humidity apparently are of much shorter duration. Moreover, the dry season of 1957 was characterized by a relatively long duration of daily sunshine; this is also reflected in the higher daily maxima of the air temperature during this period.

For at least 2 months in this dry season the records, with a few exceptions, showed a daily rise of the saturation deficit above 10 mm (a drop of the rel. hum. below ca. 65 %) during 2–7 hours, with an average of 5 hours, as shown in fig. 23. Values approximating 13 mm (58 %) were approached frequently for 2 hours or longer. A saturation deficit of 18 mm (rel. hum. 48 %) – being the absolute maximum for 1955 – was maintained during a few days for one hour. The record for the driest day (absol. max. of 24 mm = 35 %) is shown in fig. 28.

The *daily mean* of the atmospheric humidity may have some physiologic significance. It is obtained from the daily records by calculating the

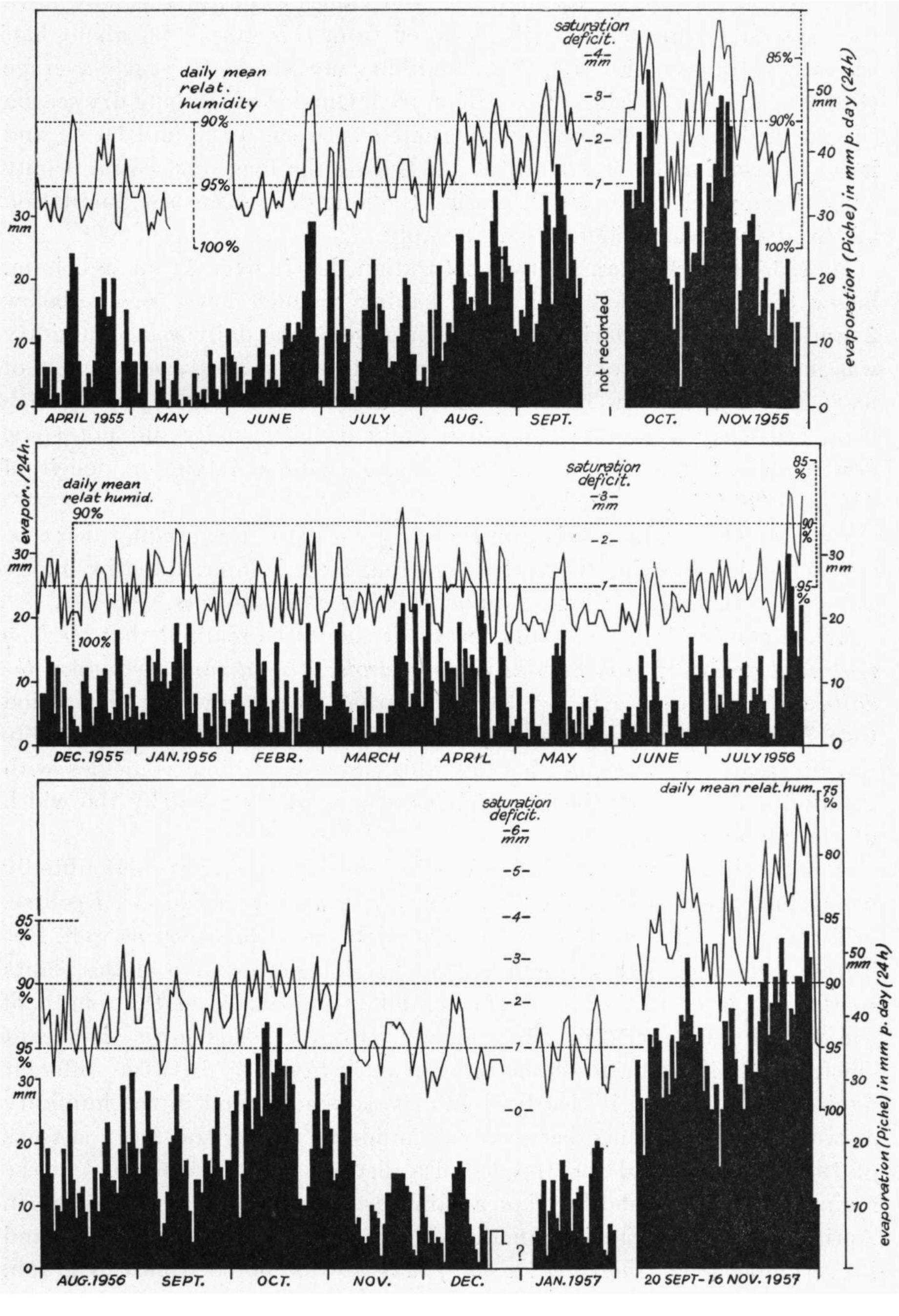


Fig. 30. Daily averages of relative humidity (0–24 hr.) and total daily Piche evaporation (0–24 hr.) in rain forest at $1\frac{1}{2}$ m height during April–January 1957 and in the dry season of 1957. The approximate value of the mean daily saturation deficit (based on the relationship shown in fig. 21) is also indicated. Evaporation expressed in arbitrary units.

mean of the 24 hourly readings, and the values found in this way have been set out in fig. 30. As will be noted from this graph, for about half the number of days the mean daily humidity was above the yearly average (1 mm saturation deficit = 94 % rel. hum.). Outside of the long dry season the mean daily value generally fluctuated between 98 % and 90 %, and it only exceptionally fell below 90 %. During the long dry season it only exceptionally fell below 90 %. During the long dry season the fluctuation of the daily mean widened considerably.

In 1955 days with an average saturation deficit over 3 mm (rel. hum. below 88 %) alternated with days having a much lower mean (below 2 mm = over 91 %). During 1956 the average of the daily mean humidity was markedly higher and with a few exceptions did not reach a value of 88 % (3 mm). The low humidity in the dry season of 1957 also appears from the daily averages: the mean daily deficit usually did not come down under 3 mm (rel. hum. 88 %), and twice a maximum deficit of 6½ mm (76 %) was reached.

Another thing which this graph clearly shows, is the gradual decrease of the humidity during the periods of drought; it is interrupted by higher values for the days following upon the few rain showers.

When considering these daily means, it should be realized that *the long nocturnal period of high humidity has a strongly equalizing effect upon the daily mean.* Therefore in fig. 31 the diurnal means covering the period 6–18 hr. also have been given. The means over the diurnal period probably are of greater significance, because this interval of time coincides with the period of photosynthesis, which process is partly ruled by the width of the stomata.

A smoothened curve of the *moving* weekly averages undoubtedly would have been preferable. The choice of a weekly period is, of course, arbitrary; a period of say 5 or 10 days might have done just as well. But in the absence of detailed data on the physiologic response of the plants to the course of the atmospheric humidity, the choice of the length of the period must perforce be arbitrary. However, this graph is meant chiefly as an illustration of the differences in humidity between different habitats. In addition it clearly shows the seasonal trend in the humidity as well as the difference between the humidity during the 2 dry seasons of 1955 and 1956 and the absence of a distinct "*short dry season*" in the spring, although in both years a faint drop in humidity was noted in April. The marked rise in humidity in the second half of November and in December (the "*short wet reason*") may also be noted from this graph.

The humidity in the *other strata* of the rain forest, at 10 cm, 5 m and about 30 m above groundlevel, has been recorded only occasionally, viz. during selected periods in 1955 and 1957. The graphs for the mean hourly values during the very dry season of 1957 shown in fig. 32 refer to the only period during which simultaneous records were made at all the four

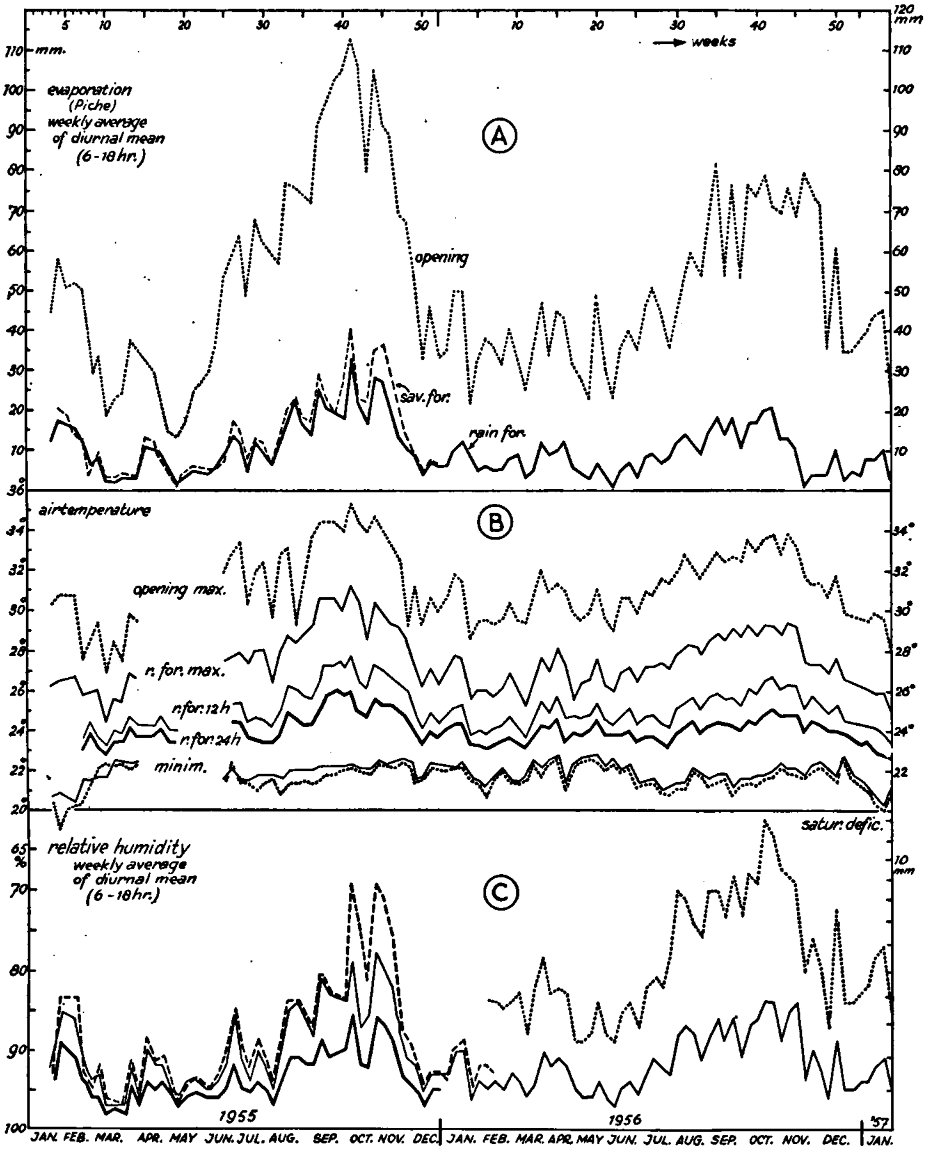


Fig. 31. Yearly march (Jan. 1955 – Jan. '57) of the weekly means of Piche evaporation, air temperature and atmospheric saturation deficit in rain forest (continuous lines), savanna forest (broken lines) and a large clearing (dotted lines) at 1½ m height above groundlevel.

A: total daily Piche evaporation for the period 6–18 hr., expressed in arbitrary units.

B: daily average (both for the period 6–18 and 0–24 hr.) and daily maximum and minimum air temperature.

C: saturation deficit; thick continuous line: in rain forest for the period 0–24 hr; thin line: idem for the period 6–18 hr.

Relative humidity can be estimated (error ± 3 %) from the scale at the left (cf. fig. 21).

levels. In the right half of this figure are given the average *humidity gradients* at 4 different times of the day; to this end the hourly readings over this dry period were averaged. The following are the general features shown by the humidity at different levels during a dry season:

(a) During the long nocturnal periods of maximum humidity, which proved to be of approximately equal length, practically the same high degree of humidity was recorded at all 4 levels. From about 20 hr.–7 hr. the humidity gradient in the forest was only faintly or not at all distinguishable, the humidity at all levels approaching saturation.

(b) The differences in humidity between the various levels increased with decreasing humidity.

(c) During the day hours the relative difference in humidity is greatest in the undergrowth; the difference between humidity at 10 cm and at 1½ m was much greater than between the 1½ m and 5 m levels.

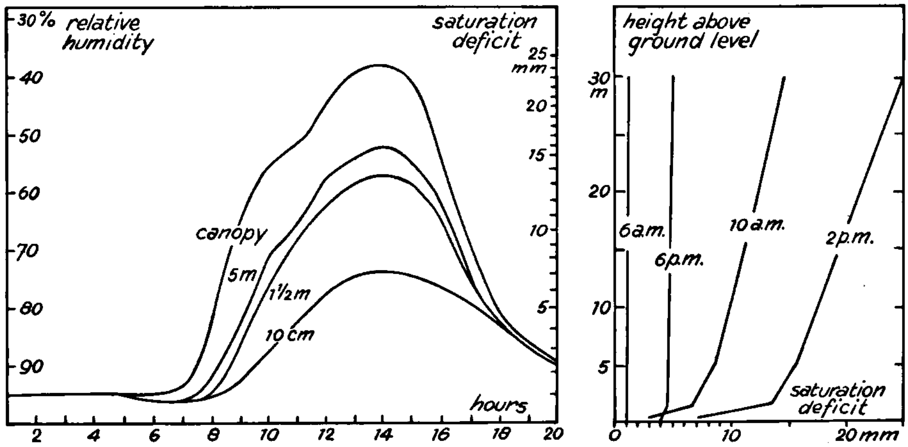


Fig. 32. Average daily march of atmospheric humidity and the average humidity gradient in rain forest during the dry season of 1957 (mid-September to mid-November). *Canopy* means the recording at ca. 30 m height, just above the foliage of the main canopy.

The most likely interpretation of the steepness of the humidity gradient in the undergrowth (10 cm–about 1.5 m), as compared with the gradient between 1.5 m and 30 m, seems to be the assumption of a corresponding steep gradient of the air movement in the undergrowth. This assumption is in agreement with the steadiness of the hygrograph records in the herb and seedling layer, which did not show the sudden and brief changes that have been mentioned previously as occurring at a greater height. It is noteworthy that these observations are consistent with those made with the Piche evaporimeter which will be discussed in the next chapter.

Direct measurements of the gradient of wind velocity and turbulency are not available for the interior of this forest nor for any other tropical forest. The observations made in temperate forests are presumably not applicable to the very complex structure of the tropical rain forest.

The humidity data of the *canopy* essentially resemble those of the clearing as may be seen by comparison of the curves for the mean hourly humidity in the dry season of 1957, given in figs 22 and 32. From the average daily curve of the humidity just above the tree crowns the very low humidity which prevailed at this station during the dry season of 1957, may be noted. An average saturation deficit of 24 mm (38 % rel. hum.) was reached at 14 hr. A maximum saturation deficit of 35 mm (rel. hum. 20 %) was recorded in November 1957. The march of humidity during this day is shown in fig. 28 which, amongst other things, reveals that even on very dry days both the duration of the nocturnal period of high humidity (ca. 18–6 hr.) and the values reached in this period are approximately the same at the various levels in the forest. Although this very high saturation deficit of 35 mm has to be regarded as a great exception, during the 2 driest months of 1957 a value of 22 mm (rel. hum. 42 %) was repeatedly exceeded for periods of 3 hours or over in the tree crown. Although humidity at this level has been recorded only during one dry season and during a few days in other periods, on the strength of the very close agreement of these records with records obtained simultaneously in the large clearing, it may be safely assumed that the atmospheric humidity in the latter station is the same as that of the open air just above the crowns of the main canopy. The perfect resemblance between the simultaneous evaporation records obtained in the two stations is a further argument in favour of this assumption.

Hence for a more detailed account of the humidity just above the canopy reference is made to the next section which deals with the atmospheric humidity in an extensive clearing in the rain forest.

At 5 m height, i.e. just above the *palm-stratum*, in the dry season of 1957 a maximum saturation deficit was recorded which on the average lay about 2½ mm above that at the 1½ m station; this corresponds with a difference in relative humidity of about 6 %. Accordingly almost every day a deficit of 14 mm (55 % rel. hum.) was exceeded for at least 2 hours, and repeatedly values of 16 mm (57 %) were approached for about 1 hour. For the wet season no data for this station are available, but during the wettest months the humidity at this level presumably will not differ much from that at 1½ m. The resemblance of the humidity in the savanna forest at 1½ m with that in the rain forest at 5 m will be discussed in the next chapter.

The steepness of the humidity gradient between 10 cm and 1½ m has already been mentioned. Generally speaking during the diurnal hours the difference in humidity between 10 cm and 1½ m was about as large as that between the latter level and the open air just above the canopy. The steepest humidity gradient was found during the diurnal hours in the dry seaon of 1957. In this period the difference of the deficit between 1½ m and 10 cm averaged 6 mm (diff. in rel. hum. 15 %) between noon and 16 hr., as against an average difference of 2½ mm (7 %) between

1½ m and 5 m. But during this dry season even in the herb- and seedling-layer humidity fell to very low values; a deficit of 10 mm (rel. hum. about 65 %) was approached frequently and a maximum of 13 mm (58 %) was recorded. In fig. 26 hygrograph records made in the dry season of 1955 at 10 cm have been reproduced. October the 13th was a very dry day, whereas 16 and 17 Oct. were relatively humid. As will be noticed by comparison with the corresponding records made at 1½ m, the difference in humidity between the 2 stations amounted between 10 and 16 hr. to a 10–15 %. In fig. 29 the average daily march at both levels is represented by the hourly means for a number of selected dry days and for some humid days (following rain showers) respectively. The relatively greater difference in humidity between both levels during humid days in the dry season is obvious. This is presumably due to evaporation from the moist leaf litter and from the soil surface during such days.

I.4.3. *Humidity in openings*

The humidity in the clearing in the rain forest has been recorded throughout 1956 and in the dry season of 1957, and will be discussed in some detail principally on account of the above mentioned resemblance which was observed between the climate in this station and that just above the main canopy in the forest. As a characterization of the humidity in a clearing these data are of limited value. Humidity under an opening in the canopy depends on various factors, but is determined chiefly by the amount of radiation which is permitted access through the gap in the upper strata. Openings in the forest vary in size from a little gap which owes its origin to the death or overthrowing of a large tree, to the extensive gaps caused by wind or created by man. The clearing under consideration provided data which may be taken as typical of the humidity in a relatively newly-made clearing of about 50 are in extent with only a few shrubs and herbs left and with some regeneration starting along the margins. The data obtained in this station may thus be taken as representing extreme environmental conditions, and contrasted with the microclimate recorded in the interior of the forest. They illustrate the extreme conditions to which the plants of the seedling- and the herb-layer are suddenly exposed when the other strata are removed over an area of considerable extent. These humidity data also show the extreme fluctuations and especially the very low humidity which the seedlings of secondary forest species found in such large clearings, apparently can stand during the first stages of the succession. Moreover, the humidity in this extensive clearing may be regarded as practically identical with the general or standard (macro-) climate measured by meteorologists.

The weekly averages of the diurnal means for the 12-hour period (6–18 hr.) are represented by the graph in the upper part of fig. 31 which shows the much greater seasonal range of humidity in the clearing as compared with that in the forest.

In fig. 23 are given for both the opening and the forest undergrowth the yearly average of the daily march of humidity as well as the daily march as averaged over the wettest period (Jan.–July 1956) and over the dry season of 1957.

It will be noted from these curves and from the daily records shown in figs. 24 and 25 that (a) the difference between both stations was greatest before noon and (b) that the humidity in the nocturnal period of maximum humidity between 18 and 7 hr. did not differ significantly in the forest and in the open.

The unsymmetrical form of the average daily curve for the opening is partly caused by the relatively higher degree of cloudiness which sets in shortly after noon, as appears also from the curve for the daily march of light intensity. The relative decrease in the rise of humidity between 9 and 10 hr. (fig. 23) also may be accounted for by the increase of cloudiness after a clear period in the early morning. During the dry season of 1957 humidity on the average reached its minimum in the open as well as in the forest around 14 hr.; this was due to the marked clearness and to the rarity of rain showers in the afternoon during this period. The daily records of humidity showed considerable variations from one day to another.

In the 8 wettest months humidity in the opening very seldom dropped below a saturation deficit of 12 mm (60 % rel. hum.) for longer than ¼ hr./day, but frequently values around 8 mm (70 %) were approached for longer than 2 hours. Nearly every day the deficit rose above 5 mm (the rel. hum. fell under 80 %), on the average during 5 hours (fig. 22). Days with a deficit of over 14 mm (rel. hum. under 55 %) were of very rare occurrence during the wettest months of 1956. In fig. 24 the course of humidity in the opening is shown during a week which was selected as typical for the wettest months in 1956.

In the transitional period and the dry season of 1956 the saturation deficit every day rose above 8 mm (the rel. hum. fell below 70 %) for 2–8 hours and above 12 mm (rel. hum. below 60 %) for 1–6 hours. A value of 17 mm (rel. hum. 50 %) was reached nearly every day for at least ¼ hr. (in Oct. during 1–5 hours). In Oct. during 10 days humidity fell even below 45 % (20 mm) during ¼–2 hours, but a value of 35 % (sat. def. 26 mm) was approached by way of exception only.

In 1957 during Sept.–Nov. much lower humidities were recorded. In the two driest months of this season a deficit of 22 mm (rel. hum. 42 %) was reached nearly every day for at least 2½ hours and frequently values above 25 mm (below 36 %) were recorded during ½–3 hours a day. The daily march of humidity during two very dry days in this dry season are given in fig. 28. Because the curve for the upper canopy and that for the clearing resembled each other in every detail, only the former has been reproduced. The curve for 11 Nov. represents the humidity during the driest day on record. The course during the next day may be taken as typical for most days of these very dry months.

I.4.4. *Humidity in the savanna forest*

During the wettest months of 1955 the records of the humidity in the savanna forest at 1½ m height did not differ significantly from those in the rain forest at the same height; this will be seen from the graphs reproduced in fig. 31 C. It will be noted from these graphs that the smaller equalizing effect of the overstoreys on humidity in the undergrowth of the savanna forest did not manifest itself markedly until the driest weeks of the long dry season. The difference between savanna forest and rain forest also appears from a comparison of the average daily graphs shown in fig. 22. From these curves it will be noted that the difference in humidity between the two habitats reached its highest values in the afternoon. The differences are shown in greater detail by the graphs reproduced in fig. 27, which represent the march of humidity during the driest week of 1955. In this dry season the saturation deficit in savanna forest often rose above 18 mm (rel. hum. fell below 48 %) and was at 13 hr. on the average 1 mm higher than in the rain forest station. As may be seen by comparing the graphs shown in figs. 27 and 28 the humidity which prevailed in the savanna forest during a normal dry season (1955), was of the same order of magnitude as that recorded in the rain forest during an exceptionally dry season (1957).

For the dry season of 1957 no humidity records of the savanna forest are available, but judging from the evaporation data humidity must have sunk during this period to a very low degree. From an extrapolation of the relation between saturation deficit and evaporation shown in fig. 34 it may be assumed that during a very dry season in savanna forest at 1½ m the diurnal mean (6–18 hr.) of the saturation deficit may rise to about 17 mm (the relative humidity may fall to 50 %).

A few hygrograph records were made in a clearing of medium size in the savanna forest, which indicate that humidity in this opening with bare white sandy soil was of approximately the same order of magnitude as that in the clearing in the rain forest.

I.4.5. *Comparison with data from other tropical rain forests*

When the humidity data presented in the foregoing chapters are compared with the observations made by EVANS (1939) in a Nigerian rain forest (which also have been discussed in detail by RICHARDS, 1952), one is struck by the markedly *lower humidity* prevailing during the dry season *in the Suriname type of forest,* notably in the upper storeys. This is shown in the upper half of fig. 33, which represents the average march of the saturation deficit in the undergrowth throughout the two driest months of 1955 and that of the saturation deficit just above the main canopy during October 1956 in comparison with the records obtained during a selected day of the dry season in the Nigerian forest. It should be borne in mind that the curves for the dry season in the Suriname forest represent the humidity averaged over a period which included humid interruptions. The average humidity during the driest days of the dry season (fig. 29 A) shows a still greater difference with the Nigerian figures. This difference may be partly due to the fact that the records in the Nigerian forest were made at a height of 0.7 m as against a height of 1.5 m in the Suriname forest. But the figures given by EVANS for a selected day in the dry season are even lower than those recorded in the Suriname forest at 10 cm height during many days in the dry season as appears from the graph in fig. 28. However, EVANS' data refer to observations made during two short periods which did not fall either in the wettest or in the driest months and, accordingly, they do not show the full seasonal range of conditions. Hence it is not certain whether the differences noted between the two types of forest may be regarded as general. This also refers to the humidity during the wet season. In the lower half of fig. 33 the march of humidity during a selected wet day in the Nigerian forest is compared with the average hourly values throughout the wettest half of the year in the Suriname forest. The last graph represents the average daily march, but days with much lower humidity were not uncommon as can be seen in figs. 24 and 25.

The very low humidity in the Suriname forest in the dry season of 1957 becomes apparent when the daily march in the undergrowth in the Suriname forest as averaged over this period (figs. 22 and 23) is compared with the Nigerian curves reproduced in fig. 33; the average humidity in the undergrowth in the Suriname forest during this dry season is comparable with the humidity in a treetop in the Nigerian forest during a selected day in the dry season. The lower humidity in the Suriname forest as compared with the records of EVANS is quite unexpected when the rainfall data of both countries are taken into consideration. Both regions have approximately the same annual rainfall, but for the region of the Shasha forest reserve a relatively severe dry season (5 successive months with less than 100 mm rainfall!) is recorded against an average of 2 such months in the greater part of Suriname. Moreover, the Nigerian forest under consideration was described by RICHARDS (1939, 1952) as belonging to the wet evergreen type with upper-storeys more open than in true rain forest.

The present observations closely agree with those made by EVANS in respect of the long duration of the nocturnal period of very high humidity during both seasons and at various levels. This fact also appears from most of the humidity charts given by MCLEAN (1919) for a low rain forest near Rio de Janeiro (23° S lat.). MCLEAN's records made at 1.5 m height are consistent with the march of humidity during the wettest months in the Suriname forest, but the reproduction of a record made during two other days at groundlevel show a minimum rel. humidity of 60 % (sat. def. about 10 mm), which at this level in the Suriname forest has been recorded only during very dry days (fig. 26). Since, as stated

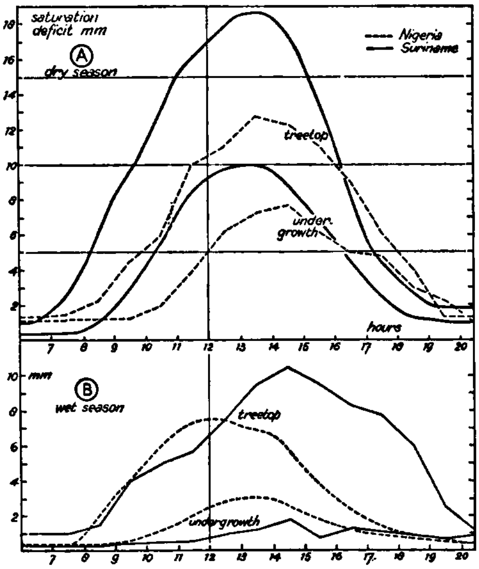


Fig. 33. Daily march of saturation deficit in the undergrowth (at 1½ m) and just above the main canopy (ca. 30 m) in the Mapane rain forest (broken lines), as compared with the daily march in Nigerian rain forest (continuous lines), after EVANS (1939, fig. 8).

Upper half (A): average daily graph for the dry season in the Suriname forest (graph for 30 m based on hourly averages for Oct. 1956, graph for 1½ m based on readings from 15 Sept.–15 Nov. 1955), and graph of a typical dry day in the Nigerian forest.

Lower half (B): average daily graph for the wet season in the Suriname forest based on hourly readings made in Jan.–July 1956, and graph of a typical wet day in the Nigerian forest.

by the author, the instruments were not screened against sunrays, these recordings are not decisive. But this fact can not be held responsible for the relatively low humidity observed throughout the night, nor for the very irregular course of the humidity during some nights as compared with the very steady curves of high humidity reported from other tropical rain forests.

According to the measurements of CARTER (1934) made in mixed rain forest in the Essequibo region (Br. Guiana) during 2 weeks in the wet season at 1.5–2 m height, humidity at 14 hr. amounted on the average to 85 % and 90 % respectively. These figures are in very close agreement with the average value recorded at 14 hr. during the wet season in the Mapane forest (88 %). CARTER's data reveal the interesting fact that the humidity in the *Mora* forest is markedly higher, viz. 91 % at 14 hr. against 85 % in the mixed forest.

The humidity data reported by HADDOW *et al.* (1947) from a rain forest in Uganda during warm dry weather following the wet season catches, are considerably lower than those recorded in the Mapane forest during the dry season.

Long-term observations extending over 12 months were made by BAKER *et al.* (1936) in the undergrowth of rain forest at Hog Harbor (New Hybrides, 15° S lat.). In this considerably unseasonal climate at 14 hr. an almost uniform mean monthly saturation deficit was recorded varying from 2–4 g/m^3, which value is consistent with the present data, viz. about 4 mm satur. deficit at 14 hr. averaged over 1955 and 1956.

I.5. EVAPORATION

I.5.1. *Introduction*

If a direct measurement of transpiration under natural conditions proves practically impossible, the use of a mechanical device that measures the integrated effect of the various factors by which transpiration over unit periods of time is promoted, may provide data of great ecologic value, notably for comparative purposes. The important advantage offered by the measurement of evaporation lies in the fact that the data obtained in this way can be used for this purpose without any attempt to analyse them into their components.

During the present study extensive use was made of a set of Piche evaporimeters. Yet I was fully aware of the limited value of data which are obtained with an instrument that by its nature can never fully integrate the effect of various stimuli to water loss in exactly the same manner in which this is done by plants, which dispose of means by which the transpiration can be influenced in various ways. Notwithstanding these limitations evaporation stands in such an intimate relation to transpiration that measurements of the first can throw much light on the water economy of plant communities.

An additional merit of the evaporation data is that they can be used as a fairly accurate measure of the mean atmospheric humidity that prevails in various habitats and over periods of various lengths.

A serious disadvantage of most evaporimeters lies in the difficulty or impossibility to compare observations made with evaporimeters of different pattern. The loss of capillary water that is measured with an evaporimeter, is the result of an evaporation process whose intensity is proportional to the evaporativity of the air, but it depends also on the properties of the evaporating surface. This is the reason why the results obtained with different types of evaporimeters are but rarely directly comparable with each other.

I.5.2. *Methods*

Of the various types of combined response instruments which are available for the measurement of capillary evaporation, preference was given to the disk evaporimeter designed by PICHE. This is one of the best instruments for obtaining almost instantaneous readings, and has been in general use with European ecologists since the rediscovery of the instrument.

This simple instrument is not favourably regarded by physicists, but in this respect it does not differ from other atmometers. The Piche evaporimeter consists of a graduated glass tube to the lower end of which a disk of green filter paper is affixed. The disk is kept constantly wet by the water in the tube, and the loss by evaporation may be read from the graduated tube at intervals of any desired length.

In the present studies a set of 10 evaporimeters of a slightly modified type was used; they had kindly been supplied by the Royal Netherlands Meteorological

Institute, de Bilt, Netherlands. The essential modification was the substitution of the paper filter by a ceramic disk of standardized colour, composition and dimensions. The ceramic disk, which has a diameter of 3.4 cm, is affixed to the lower end of the glass tube by means of a tightning nut with a capillary bore through it, which functions as an air-valve. This air-valve can be a source of difficulties when the apparatus is used in the field. The minute canal is choked by the slightest amount of dirt, and this results in a considerable suction pressure and subsequently in the absorption of water after rain showers and formation of dew. Cleaning is difficult in the field, and for this reason a set of tightning nuts should always be kept in reserve.

The above mentioned difficulty is connected with the absence of a rain-proofing valve, like that with which the Livingston atmometer is equipped. Therefore readings had to be taken before and directly after every rain shower and the amount of water that had been absorbed in the meantime, had to be substracted. It is true that the meters were sheltered from direct rainfall, but this did not protect them against splashes. The sets of meters which were fully exposed, occasionally absorbed considerable amounts of dew, especially during clear evenings and nights, and the readings of these instruments for the night period had to be discarded.

Before describing the data collected by means of the Piche instrument, it may be profitable to discuss shortly the physical principles on which it is based. For a more detailed description of the behaviour of the Piche evaporimeter reference is made to the publication of DE VRIES *et al.* (1954). These authors showed that the following equation which is the mathematical outcome of a theoretical consideration of the behaviour of this instrument, based on the theory of evaporation from an irradiated wet surface, appeared to agree satisfactorily with the experimental data:

$$E = \frac{H_w \cdot s + h_w(e_a - e_d)}{(s+\gamma)\,L}.$$

E:	evaporation from a wet surface (in mm/cm^2/sec).
H_w:	amount of heat supplied to the evaporating surface apart from the heat exchange with the air (in cal/cm^2/sec);
$H_w =$	(amount of effective radiation) + (heat conducted from the graduated tube to the outer edge of the disk) — (outgoing long wave radiation).
s:	average value of the slope of the saturation vapour pressure curve between temperatures t_a-t_d (in mm Hg/°C); it increases rapidly with increasing air temperature.
h_w:	coëfficient of heat transfer, proportional to air movement; an empirical relation between h_w and wind velocity is derived by DE VRIES *et al.* (1954) for the Piche instrument.
$(e_a - e_d)$:	(satur. vapour pressure at air temp.) — (id. at dewpoint temp.), in mm Hg.
γ:	psychrometric constant; almost independent of temperature: 0.49 mm Hg/°C.
L:	vaporization heat of water (in cal/g).

The equation shows that evaporation becomes directly proportional to the saturation deficit $(e_a - e_d)$, if the other parameters remain constant or if, as was the case in the habitats under consideration, atmospheric humidity is strongly correlated with H_w and with air temperature (and accordingly with the term s). In that case E may provide a precise measure of the mean atmospheric humidity during the period under consideration. This is demonstrated by the graphs reproduced in fig. 34, which show the relation between the readings of the evaporimeter and the humidity

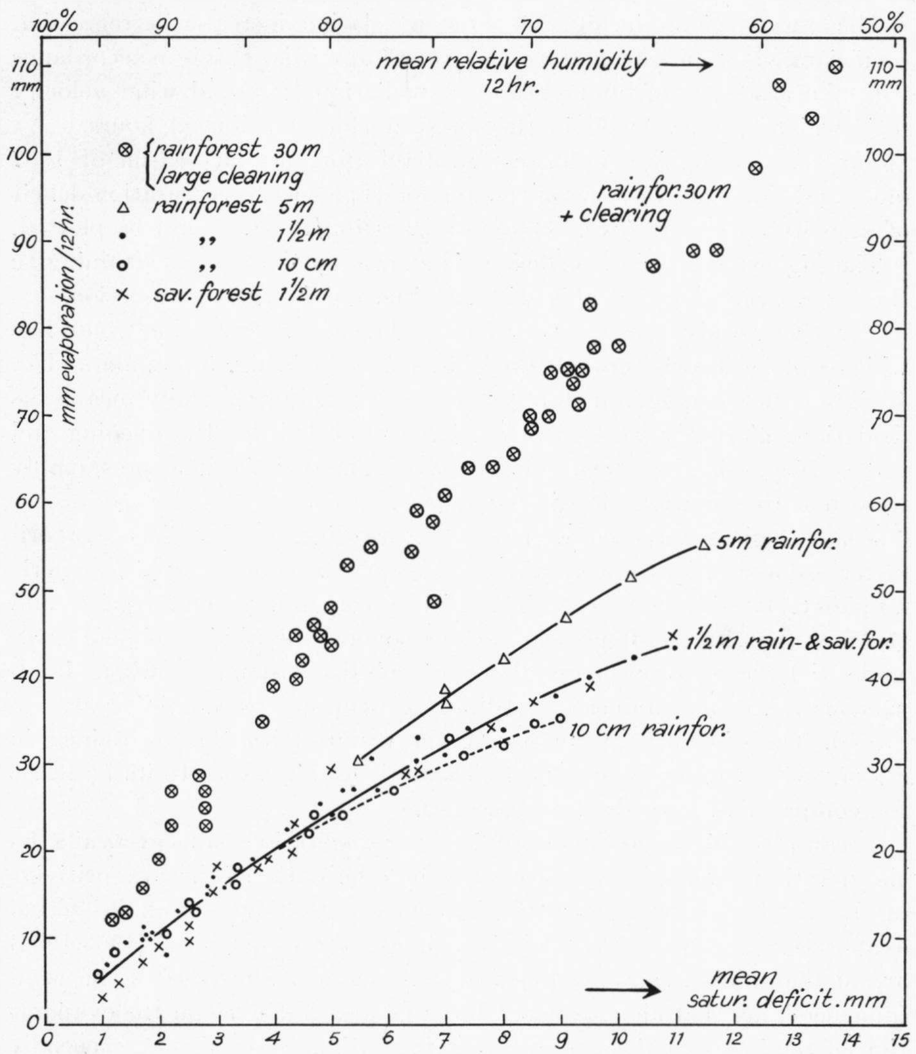


Fig. 34. Relation between Piche evaporation and mean atmospheric humidity for different habitats in the Mapane region. The points represent weekly means of the records made for the diurnal period 6–18 hr. Evaporation expressed in arbitrary units. The evaporimeters were screened from direct sunlight.

for various stations; the figures are weekly means of total diurnal (6–18 hr.) evaporation and diurnal mean humidity (expressed in the same graph as saturation deficit and as relative humidity on account of the relation between these two expressions shown in fig. 21).

As will be noted from these graphs, the data for rain and savanna forest are fitted by the same curved regression line. This is in agreement with the conclusion based on the results of light measurements, viz. that the amount of radiation does not differ significantly for the two forest types, while the values of the term h_w (proportional to wind velocity) also may be taken as nearly equal.

The curves given in fig. 34 show a relative increase in regression coëfficient when going from the undergrowth upwards. This is in accordance with the gradients of temperature (s), radiation (H_w) and wind velocity (h_w), which are developed in the forest during the diurnal hours.

For the 5 m station data were available for the dry season of 1957 only, and thus only the part of the line for values with a saturation deficit of more than 5.5 mm (over 30 mm evaporation/12 hr.) could be plotted.

The highest regression coëfficient is shown by the curve pertaining to the large open clearing; this will be discussed in the next section.

For the weekly means the greatest deviations from the trend line which can be drawn through the points plotted in fig. 34, amounted to 10 % for the opening and to 5 % for the forest. For the daily means the deviations naturally were greater, viz. up to 20 % for the opening and up to 10 % for the forest undergrowth. These deviations presumably were due to variations in air movement.

For ecological purposes even the daily readings of the Piche evaporimeter are a sufficiently accurate measure of the mean daily atmospheric humidity. Its simplicity combined with a very low purchase price, and the fact that its handling does not go beyond the ability of field staff, make the Piche evaporimeter the most suitable instrument when simultaneously a great number of readings of atmospheric humidity are required. The difficulty of comparing the results with those obtained in regions with a different standard climate, is no hindrance to its local use for comparative and absolute readings.

Because at this stage of our studies no transpiration data are available, the question cannot be answered whether the data on the evaporitivity of the air do not exaggerate the influence of that power on the actual evaporation at the surface of living plants. De Vries *et al.* (1953,1954) are of the opinion that the Piche evaporimeter "overestimates the wind influence", i.e. that air movement has a greater influence on the evaporation of the instrument than on the transpiration of the plants, especially during periods when the stomata are closed.

The data on Piche evaporation appearing in the following sections are given in arbitrary units, viz. in mm of water evaporated from the calibrated tube. A conversion of the values into mm/cm^2 would have been useless, because these values would be no more comparable with those obtained in other countries, where Piche evaporimeters with different surface and colour of the evaporating disk are used.

I.5.3. *Comparison of evaporation data*

The data of total daily evaporation for the rain-forest station at 1½ m height were presented in fig. 30. In fig. 35 the daily evaporation at different levels is shown. The graph marked *canopy* was not based entirely on observations which were made in the tree crown; additional figures have

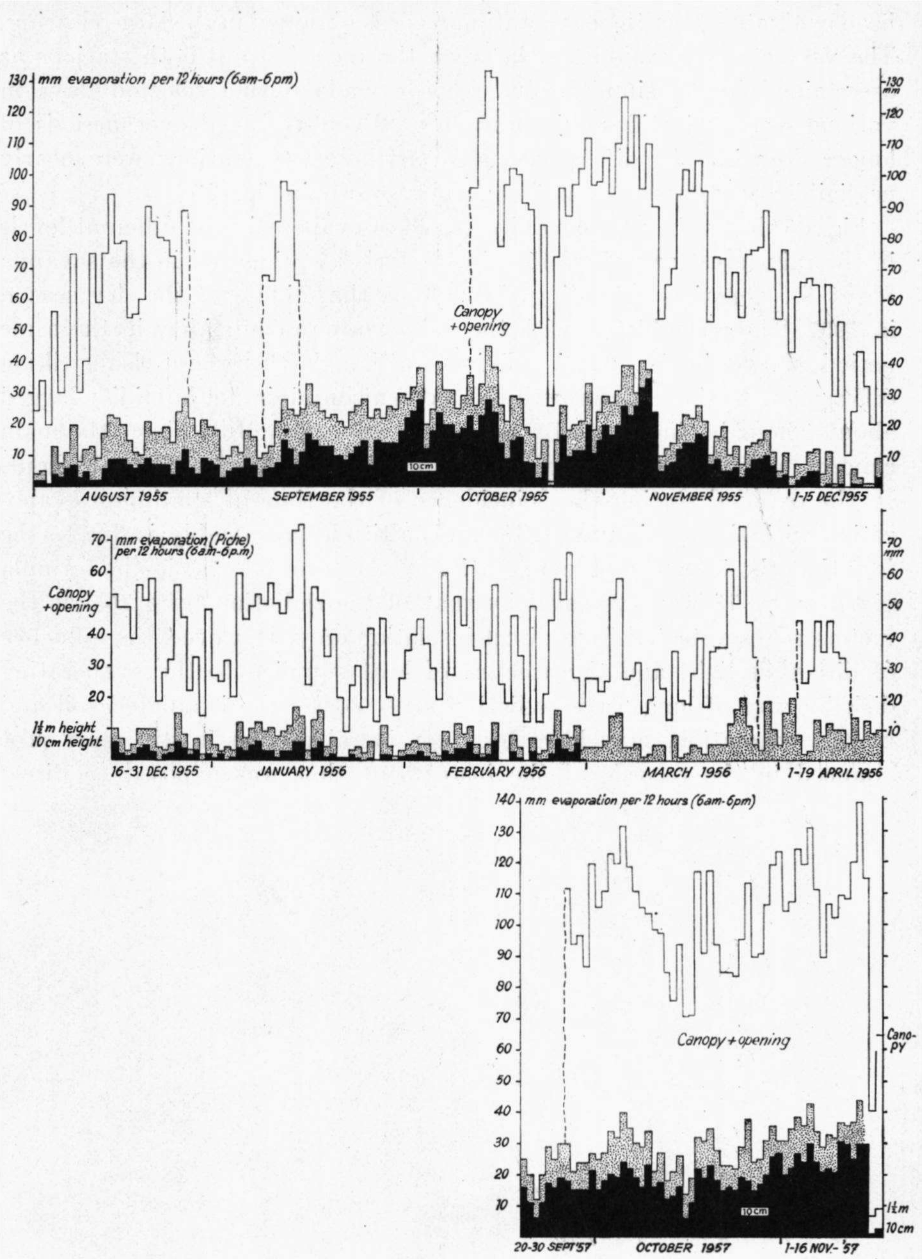


Fig. 35. Daily evaporation (6–18 hr.) at different levels in rain forest. The data marked *canopy* partly represent observations made at 30 m above groundlevel, and are supplemented with records made in a large clearing, where evaporation was nearly identical with that just above the main canopy. Evaporation measured with Piche evaporimeter screened from direct sunlight, and expressed in arbitrary units. Evaporation at 10 cm was not recorded during March–April 1956.

been evaluated from the evaporation records obtained in the large clearing. The very strong resemblance between the records from both stations as ascertained by 60 simultaneous records made during selected days in various seasons justifies this procedure. When averaged over periods of longer duration the differences between these two stations were nearly negligible, as appears from the graphs shown in fig. 36.

Fig. 36 shows the average daily march of evaporation at different levels in the rain forest as well as that in the large clearing and in the savanna forest for a period extending throughout the middle of the dry season in 1957. The resemblance with the daily march of humidity in the same period shown in fig. 32, is obvious, although there are also striking differences. In the undergrowth the moment of minimum humidity lagged about 1 hour behind that of maximum evaporation. Just above the main canopy, and in the opening too, the lag in time amounted to 1½ hour. In the exposed station the coincidence of the time of maximum evaporation with the maximum of the sun's altitude presumably is due to the fact that the influence on evaporation of the term $(e_a - e_d)$ in the formula given on p. 78 was overruled by that of the radiation term H_w, as the meters were protected from direct insolation only. However, the influence of direct skylight and the amount of heat supplied to the evaporating disk by way of long wave radiation reflected by the irradiated soil and by the vegetation, may have been considerable. This is still more prot nounced in the records of the instrument that was exposed to direc-

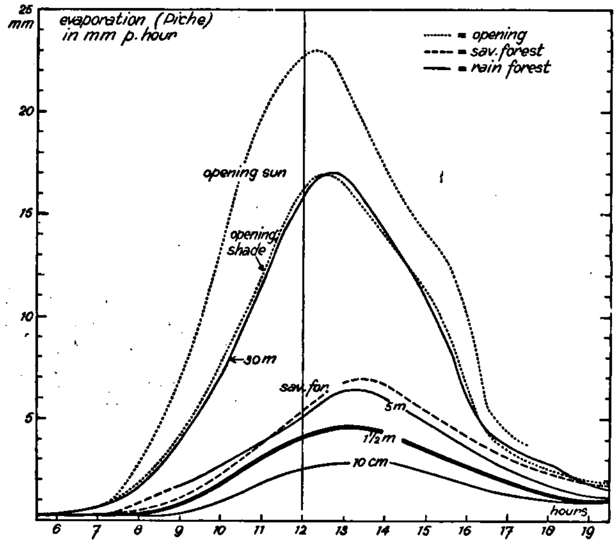


Fig. 36. Daily march of Piche evaporation (in arbitrary units) during part of the dry season of 1957 (28 Sept.–23 Oct.) at 10 cm, 1½ m, 5 m and ca. 30 m height in rain forest, and at 1½ m height in savanna forest and in an extensive clearing. Meters sheltered from direct sunlight, except one meter in the opening which was exposed to direct sunlight (cf. graph marked *opening sun*).

radiation (*opening sun*); the latter reached their daily maximum on the average around noon.

As mentioned earlier, during the dry season the evaporation in *savanna forest* at 1½ m was comparable to that in rain forest just above the palm layer (at about 5 m). As appears from the graphs shown in figs. 36 and 37 the difference in evaporation between the two types of forest was greatest during the afternoon, which is in agreement with the course of humidity shown in figs. 22 and 27.

In fig. 45 the values for the evaporation in 9 stations along a transect crossing different types of forest, have been set out. The measurements were made during a clear day at the height of the dry season, i.e. when the differences in microclimatological factors between habitats of various kinds were at their maximum. The records of soil temperature made simultaneously, clearly show the correlation between the latter and the evaporation, a point that will be discussed on p. 95.

In fig. 31 the seasonal variation of evaporation in different habitats is represented by the weekly averages of the total daily evaporation during the diurnal period (6–18 hr.). The course of these graphs resemble that for humidity in detail.

As appears from these graphs, as well as from the foregoing curves, the Piche evaporation data over any period of desired length, characterize the atmospheric humidity quite as well as the data obtained from hygrographs. The spatial and temporal differences in evaporativity of the air found in various habitats and in different periods, appear to run closely parallel to the corresponding figures for the atmospheric humidity. When the relation between Piche evaporation and atmospheric humidity once has been established for a given habitat, the evaporation data may be used as a quantitative measure of sufficient accuracy for the humidity in ecological studies.

I.5.4. *Evaporation data from other tropical forests*

The most comprehensive measurements of capillary evaporation in tropical forest were made by Brown (1919). Because the readings were made by means of a Livingston atmometer I shall not attempt to compare Brown's data with the present recordings. It is nevertheless interesting to note that the *ratio* between the rate of evaporation in the top of a dominant tree and that on the forest floor found by Brown during 4 weeks of maximum evaporation, was about the same as that found in the Mapane forest.

The data published by Louis (1939) for Piche evaporation in rain forest in central Conto (Yangambi) show at different levels in mixed forest approximately the same ratios as were found in the Suriname rain forest. The absolute values given by Louis, however, seem improbably low (e.g. 3.7 mm/cm^2/24 hr. during a clear day, at 1.5 m height in a clearing).

Very comprehensive measurements of Piche evaporation at different levels in two types of forest in the central Congo basin were made by Germain *et al.* (1956). At 1.5 m height evaporation in the forest during 3 dry weeks in the dry season averaged about 15 mm/cm^2/24 hr. In the open the evaporation averaged

48 mm/cm²/24 hr. during the same period. Hence *the ratio between evaporation inside and outside the forest averaged* 1:3 (for meters screened from direct insolation), which is *exactly the same ratio as that found for the Suriname forest during dry weather* (cf. figs. 31 and 35). Unfortunately exact comparison of the absolute evaporation values published for the Congolese forest with those obtained in the Suriname stations is impossible, owing to the differences in the evaporating disks. Yet a rough comparison may be made when the Suriname data are multiplied with a factor 0.5. A few simultaneous readings made in the Suriname forest with the meters with a green ceramic disk and a standard Piche meter provided with white blotting paper (with an effective evaporating surface of 11.3 cm²), indicated that evaporation of the latter (expressed in mm/cm²/24 hr.) was about 2 times as large as that of the meters used during the present study (expressed in arbitrary units/24 hr.).

Allowing for this factor, Piche evaporation (for white blotting paper with 11.3 cm² elective surface) in the Suriname forest averaged over 20 mm/cm²/24 hr. during dry periods. This is higher than the value found in the Congolese forest by GERMAIN *et al.* Allowing for this conversion factor, evaporation in the open also was considerable higher in the Suriname station. Atmospheric humidity in both forest types was about the same during very dry weather. The difference in Piche evaporation perhaps might be accounted for by the higher rate of air movement in the Suriname stations, the Piche meter being very sensitive for this factor.

I.6. AIR TEMPERATURE

Air temperature was recorded primarily for the purpose of computing the saturation deficit of the air as dealt with in a previous chapter.

I.6.1. *Methods*

The recording instruments used included two bimetallic strip thermographs, a Fuess thermograph with ordinary temperature scale, and an instrument specially constructed by Thiess (Göttingen) with a scale graduated from + 10° to + 40°C. Because of the greater width of that part of the scale which is essential in the tropical lowland climate, the last-named instrument recorded the temperature more accurately than the other ones. In addition a number of meteorological standard as well as maximum and minimum thermometers were used. The readings of the latter were checked daily by comparison with the readings of the standard thermometers. The daily thermograph records were corrected with the help of 6 daily thermometer readings.

Under the shelters erected in the exposed places, the thermometers were placed with their bulbs in a miniature shelter of the model designed by the Royal Netherlands Meteorological Institute for microclimatological measurements of temperature near the ground (for a description of these miniature huts cf. KRAMER *et al.* 1954, fig. D). The thermometer readings obtained in this nearly radiation-free arrangement, which at the same time ensured a most favourable ventilation, were in perfect agreement with the dry-bulb readings of the ventilated psychrometer.

I.6.2. *Comparison of records*

Air temperature in the rain forest has been recorded at 1½ m height over a period extending from 1955 through 1956, and in the dry season of 1957. Occasional readings were made in the open air just above the main canopy and at 10 cm height above the forest floor.

The *daily march* of the air temperature *at 1½ m in the rain forest* as

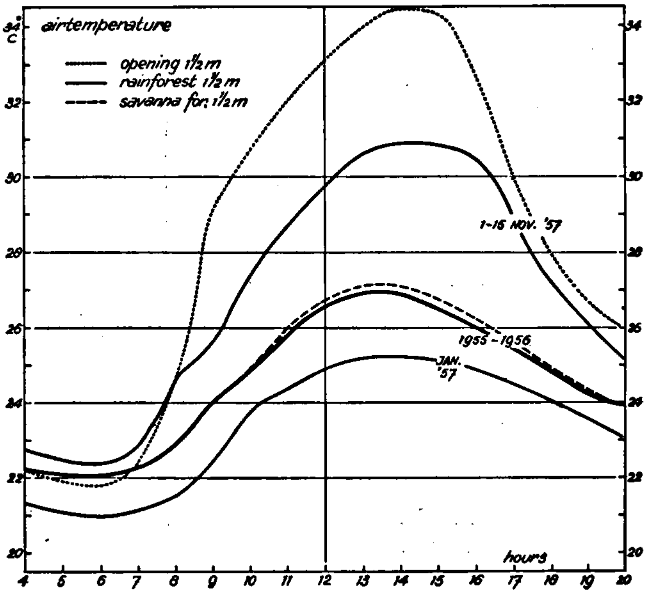


Fig. 37. Diurnal march of air temperature during various periods at 1½ m in rain forest, in savanna forest and in an extensive clearing. 1–15 Nov. 1957 and Jan. 1957: hottest and coolest period on record. Based on hourly readings of thermograph charts.

averaged over 2 years is given in fig. 37, which also shows the daily march during the coolest (Jan. '57) and the hottest period (Nov. '57) on record.

The *weekly* averages both for the period 0–24 hr. and 6–18 hr. (computed from the ½-hourly readings of the charts) were already presented in fig. 31. In the same figure the curves for the weekly averages of maximum and minimum temperature in the rain forest were given. As this graph shows, the seasonal variation of the air temperature closely follows that of the total daily insolation and of the precipitation (cf. fig. 4). Accordingly the temperature is highest during the long dry season (generally mid-Oct. to mid-Nov.). Temperature also rises during minor droughts outside the long dry season. The lowest temperatures were obtained during January after the December solstice (cf. averages of the daily march during Jan. and Nov. '57 in fig. 37).

The daily means and daily maxima and minima during a cool-humid and a dry-hot period respectively, are shown in figs. 38 and 39. In fig. 40 the smoothened curves of the daily march of temperature in the forest are given for the hottest period on record (A) and for a cool period in the wet season (B). The graph in fig. 40 A may be taken as characteristic for the course of temperature at the end of a very dry season. During this period (Nov. '57) in the forest exceptionally high temperatures (over 31° C) were recorded.

The above mentioned graphs show the greater range of the daily temperature fluctuation during dry periods as compared with the more

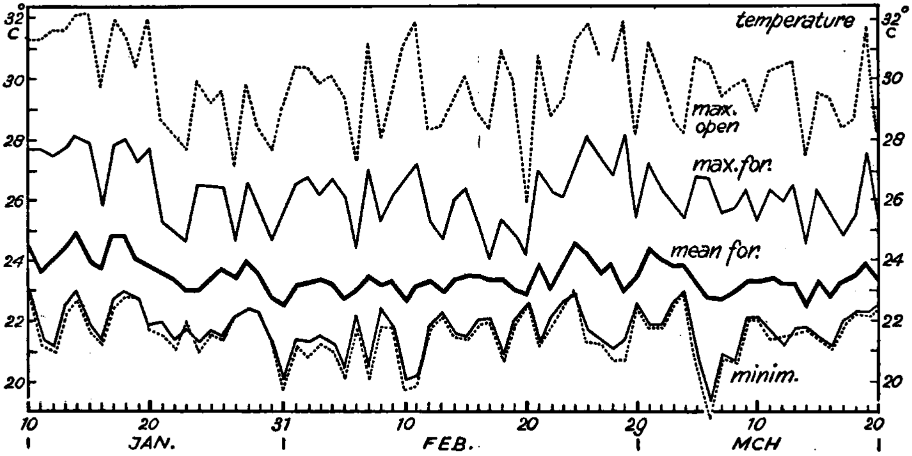


Fig. 38. Daily mean and daily maximum and minimum air temperature at 1½ m height in rain forest (continuous lines) and in a large clearing (dotted lines) during a period characteristic for the 8 months of the year outside the long dry season.

moderate daily amplitude during humid periods. The greater daily range as well as the higher daily mean that are observed during the dry periods, are due to the higher daily maxima; the minima, as is clearly shown by the graphs presented in figs. 7 and 37–40, remain nearly constant.

Therefore, the already rather slight seasonal variation of air temperature recorded in the open (cf. Braak 1933), is still further damped under forest cover. As may be noted from the graphs shown in figs. 38 and 39, the fluctuations of the *daily mean* in the rain forest (at 1½ m) remained throughout the year on the whole between 22° and 26½° C (an exceptionally high value of 27½° C was reached only in the very hot dry season of 1957). The deviation from the yearly average for this station (24.1° C) therefore did not exceed 3°. During the dry season the daily average for the daylight period (6–18 hr.) approached a value of 28° C.

In the other strata in the forest only a few records were made during selected periods when the differences were greatest, i.e. during the dry season.

Just like other factors, temperature fluctuated less widely *in the herb- and seedling-layer* (at 10 cm) than it did at higher levels. This is shown by the graphs for max. and min. temperature for the 10 cm and 1½ m station in the rain forest presented in fig. 39. As would have been expected, the seedling-layer showed a smaller temperature range due to lower maxima, the minima being equal to or only slightly higher than those at 1½ m. Owing to the lower maxima, the mean daily temperature at 10 cm was slightly lower (½–1°) than it was at 1½ m.

For the *open air* just above the main canopy only a few records were available, but they sufficed to show the close resemblance with the temperature recorded at 1½ m height in an extensive clearing. Hence, for the

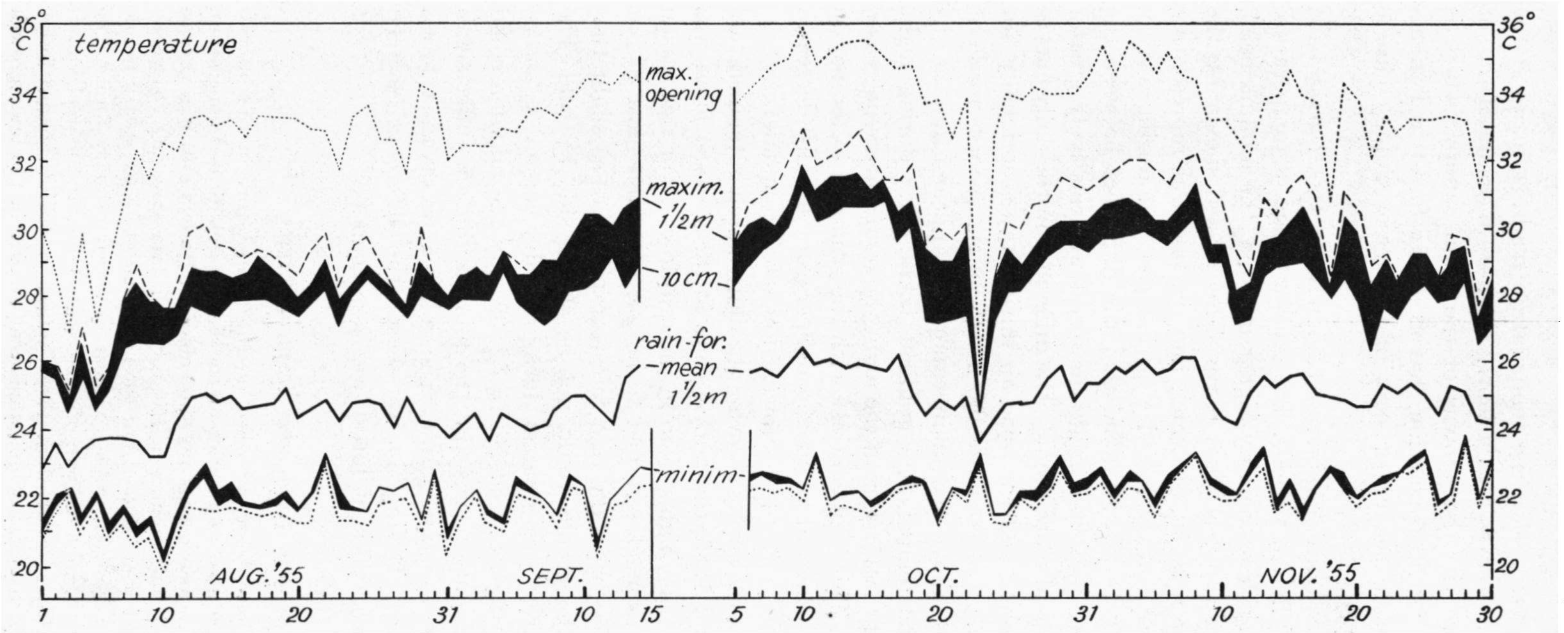


Fig. 39. Air temperature in different habitats during the period 1 Aug. – 30 Nov. 1955, covering the end of the long wet season, the long dry season and the beginning of the short wet season.

Dotted lines: daily max. and min. in a large clearing at 1½ m; continuous lines: daily mean at 1½ m and daily max. and min. at 1½ m and 10 cm height in rain forest (for the maxima the upper boundary of the blackened area represents the max. at 1½ m and the lower boundary those at 10 cm, whereas for the minima the positions are reversed). Broken line: daily max. in savanna forest at 1½ m; the minima had to be left out for sake of clearness.

rest of the period of observation the temperature readings made at the latter station were accepted as a sufficiently accurate measure of the air temperature just above the tree crowns of the main canopy, which is supported by ALLEE's (1926) conclusion that in a rain forest in Panama temperature conditions in the upper part of the forest canopy closely resembled those in open places.

In figs. 38 and 39 the daily maxima and minima for the *clearing* have been set out for two different periods. The greater range of temperature in the open is due to the considerably higher maxima, the minima being only slightly lower than under forest cover. This is also shown by the smoothened graphs given in fig. 40 which may be taken as representing the daily march during a very hot dry period (A) and during a very humid, cool period (B). It will be noted that the difference between the temperature in the open and that inside the forest was relatively greater if the days were cooler and more humid. The difference in the daily curves for the forest undergrowth and the open air during an exceptionally hot period (1–15 Nov. 1957) was shown in fig. 37. From the records made at 10 cm, 1½ m and just above the main canopy it appears that in the forest a reversal of the temperature gradient takes place during night hours, so that during the latter part of the night the temperature decreases with increasing height. This is in contrast with the situation in temperate single-layered forests, where at night the temperature usually decreases with the height, i.e. from the tree crowns down to ground level.

As will be noted from the curves showing the daily march of temperature averaged over 1955 and 1956, the temperature in the *savanna forest* was on the average only a trifle higher than in the rain forest. For this reason the graphs for the savanna forest had to be left out from most of our figures as the differences with the rain forest graphs were so slight that with the scale used the graphs could not be shown side by side. The difference with rain forest was greatest during the dry season, as shown by the graphs given in figs. 27 and 39. In fig. 39 only the maxima could be shown, because the daily means and the minima did not differ significantly from those in the rain forest. The minima in savanna forest averaged only 0.1° lower. During the wet season the difference between the maxima in the two types of forest was less than 0.2°.

I.6.3. *Comparison with data from other tropical forests*

Among the data that have been published on the temperature in the interior of tropical forests only a few give information on the daily march of the temperature. By far the most complete measurements are those made by BROWN (1919) in various altitudinal zones of a Philippine mountain. His very full data, covering 2½ years, also comprise figures for a lowland forest, but the latter refer to a secondary jungle where conditions need not be comparable to those in closed primary forest. The daily averages recorded in the undergrowth of *Dipterocarp* forest at 300 m elevation (20–25.5° C) are only slightly lower than those found in the Suriname forest (22.4–27.5° C). The weekly averages of minimum temperature in the undergrowth

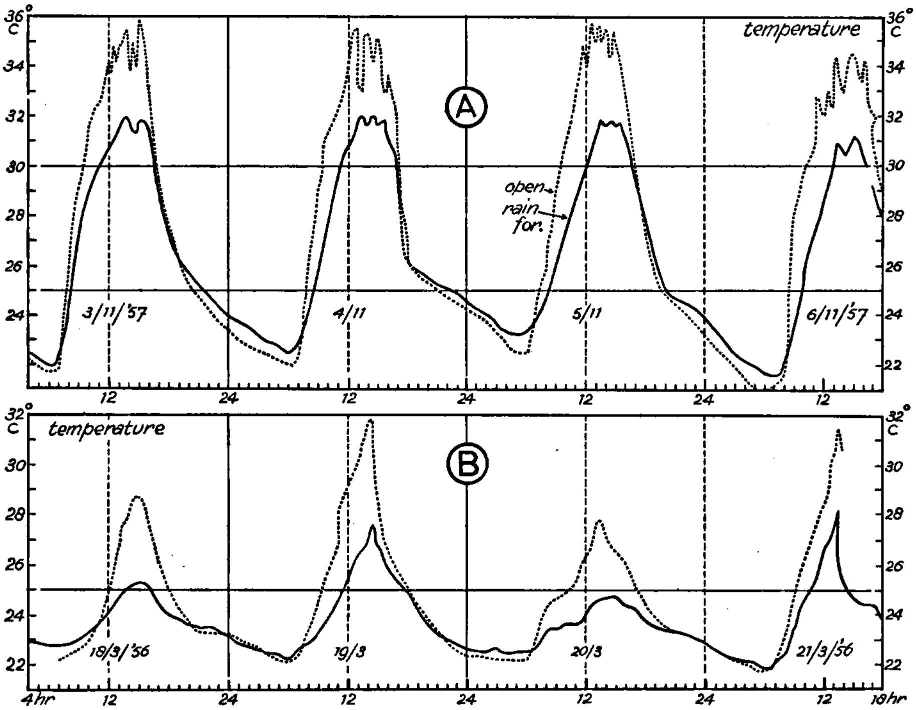


Fig. 40. Daily march of air temperature in rain forest (continuous lines) and in a large clearing (dotted lines) at 1½ m during two selected periods. A: hot, dry season (3–6 Nov. 1957); B: wet season (18–21 March 1956). The smoothened curves represent the moving averages of three 5-min. readings of the charts.

and in a tree top in the *Dipterocarp* forest varied between 18° and 23° C (Mapane forest: 19°–23° C, cf. fig. 31), whereas the maxima fluctuated between 24° and 29° C in the undergrowth and between 30° and 36° C in a second-storey tree.

The extreme constancy of the temperature near the forest floor (mean daily range 1.1°–2.9°) measured by ALLEE (1926) in a rain forest in the Panama-Canal zone during the height of the dry season, differs markedly from the recordings in the Mapane forest, where repeatedly a daily range of 8° at 10 cm height was recorded (cf. fig. 39). The values measured in the Suriname forest at 1½ m approach the mean daily range of 9.5° reported by ALLEE for the second storey (17 m). The greater daily amplitude found in the Suriname forest is due to the markedly lower night temperatures, which generally sank down to 21–22° C (cf. figs. 37–40), as against a minimum of 24–25° C in the recordings of ALLEE. His temperature measurements in a tree top are not reliable, as the thermometerbulbs were not protected from direct insolation.

For a S-Nigerian forest EVANS (1939) reported a mean daily range of 3.5° and 5.8° in the undergrowth (at 0.7 m) in a wet and a dry period respectively, which values are lower than the daily amplitude in the Suriname forest. Both the minima and the maxima recorded by EVANS are somewhat higher than our figures. His records for the tree tops resemble those for the clearing in the Suriname forest, except for a somewhat greater daily range in the latter (up to 15° in the dry season).

The daily observations of BAKER *et al.* (1936) in a rain forest in the markedly unseasonal climate of Hog Harbour (New Hybrides) covered a full year. The mean monthly maxima in the undergrowth (24.3–27.6° C) are lower than in the Suriname forest (26–30° C), the minima in the two regions being approximately equal.

CARTER's (1934) data for mixed forest in the Essequibo region (Br. Guiana) during the rainy season are in close agreement with our data. As might have been expected, in *Mora* forest the temperature appeared to be lower than in mixed forest.

The temperature observations made by HADDOW *et al.* (1947) in the Uganda rain forest, which have already been mentioned on p. 76 are markedly lower than the Surinam data.

LOUIS (1939) published some recordings made in mixed evergreen forest (rain forest in the broad sense) in the Central Basin of the Congo (Yangambi); in this forest the daily range amounted to 6° (19.5–25.5° C) at 1.5 m height. At 10 cm and at 28 m (on a branch of an emergent tree) values were measured of 19.5°–28° C and 19°–32.5° C respectively. In the same region, in mixed forest and in a community dominated by *Brachystegia*, the temperature was studied by GERMAIN *et al.* (1956) during 3 dry weeks in the dry season. The mean daily amplitude (6.6° and 6.0°) for the two types of forest is lower than that found in the Mapane forest during similar periods of drought (cf. fig. 37: mean amplitude of 9° at 1½ m during the end of the season of 1957). This difference is due to the markedly lower maxima in the Congolese forests, corresponding to the lower maxima of overall air temperature during the dry season. An interesting difference between the microclimatic conditions in the Suriname forest and the *Brachystegia* forest is the fact that in the latter the records show that the undergrowth (at 1.7 m) is cooler at night than the overstoreys are (e.g. mean minimum at 1.7 m: 19.8° C and at 9.5 m: 21.4° C). A decrease of the nightly minima with decreasing height is seen also in the records made by LOUIS and in the measurements of BROWN, mentioned above.

I.7. SOIL TEMPERATURE

I.7.1. *General*

Strictly speaking the temperature of the soil belongs to the group of edaphic factors, but in view of the strong connection with climatic factors like air temperature and radiation, it seems appropriate to consider it along with the atmospheric factors.

The most interesting conclusion to be drawn from the observations presented in the following sections, is the fact that even single soil-temperature readings may provide us with a significant indication of the integrated effect of microclimatic factors varying with the type of cover, and thus may provide us with an extremely convenient and useful integrating index of environmental differences in various forest types, a fact which already has been emphasized by SHANKS (1956) in his study of microclimatological variation in various altitudinal zones in the US.

I.7.2. *Methods*

Some 10.000 readings were taken during 25 consecutive months (Jan. 1955–Jan. 1957) at various depths—generally at 2, 5, 25, 50 and 75 cm—under rain forest and in the almost bare soil of the large clearing. During 1955 readings were taken also under savanna forest. Some occasional observations of maximum temperature were made in natural and artificial gaps in the rain forest and also in the rain forest on sandy soils in the Upper-Coesewijne R. region. Readings were taken within a few feet of the reference air-temperature stations.

In view of the higher price and the inaccuracy of soil thermographs, preference was given to special soil thermometers with different lengths of stem.

Moreover, a continuous record was not required, because throughout the year, the diurnal variation appeared to follow sinusoidal curves of constant form. Hence, only during the first weeks readings were taken at intervals of 2 hours. These observations, which were checked by readings in the dry season, enabled the determination of the daily trend, the times at which maxima and minima occur, and the length of the time-lag of soil temperature at various depths after air temperature. Afterwards daily and monthly means and daily maxima and minima were computed by means of interpolation from the readings made at a few selected hours (7, 11, 14, 18 and 22 hr.). Because in the exposed places just around midday the course of the temperature in the surface layers sometimes showed considerable irregularities, and because the maximum temperature often was reached in the interval between two readings, in these places maximum thermometers were used. This in addition allowed the recording of at least the maximum temperature reached during periods when and at places where reading of the standard thermometers was impossible. The soil thermometers were inserted vertically after a narrow hole had been punched in the soil of about the same diameter as the thermometer stems. Thus the natural soil arrangement was hardly disturbed, and after a few spells of rain complete contact between thermometer and soil was secured.

The mercury reservoirs in the bulbs were taken very large in proportion to the diameter of the tubes, thus avoiding too large errors when measuring at great depth in a soil with a steep temperature gradient. It could be computed that with the steepest gradient on record (32° C difference between the soil's surface and a depth of 75 cm) the error caused by the fact that the stem passed through soil layers with temperatures different from that in the layer of which the temperature was measured, was less than 0.2° (less than 1 %).

The soils in which the temperature was recorded, will be described in greater detail in a following chapter. A few remarks may suffice.

The soil in the rain forest consisted of a red sandy loam with humus shading into a heavy loam, and containing some ironstone and quartz gravel; it was covered with a thin layer of leaf litter. Drainage was rather good. Main root zone 5–40 cm. The soil of the clearing was a yellow-red heavy loam with occasional gravel particles and with moderate drainage. The top soil which contained the humus (about 40 cm) had been removed by erosion, and the surface was sparsely covered with grasses. The soil under savanna forest was of the coarse white-sand type mixed with humus and covered with a thin layer of leaf litter.

I.7.3. *Soil temperature under forest cover*

The marked equability of the air temperature *in the closed forest* is reflected in the *very small diurnal and seasonal range*, even in the surface layers, of the soil temperature. In fig. 41 the monthly averages of the soil temperature at 2 cm and at 75 cm depth are shown. For comparison the graph for the air temperature has been added. The means for the other depths (5, 25 and 50 cm) are intermediate between the values shown in these graphs.

In fig. 42 the mean daily march of temperature at 3 different depths is given, averaged from the daily readings over the period from 15 Jan. 1955 – 31 Jan. 1957; added are the mean hourly temperatures for the coolest and for the hottest month on record. Despite the fact that Oct. 1957 was an exceptionally hot month, the seasonal variation appeared

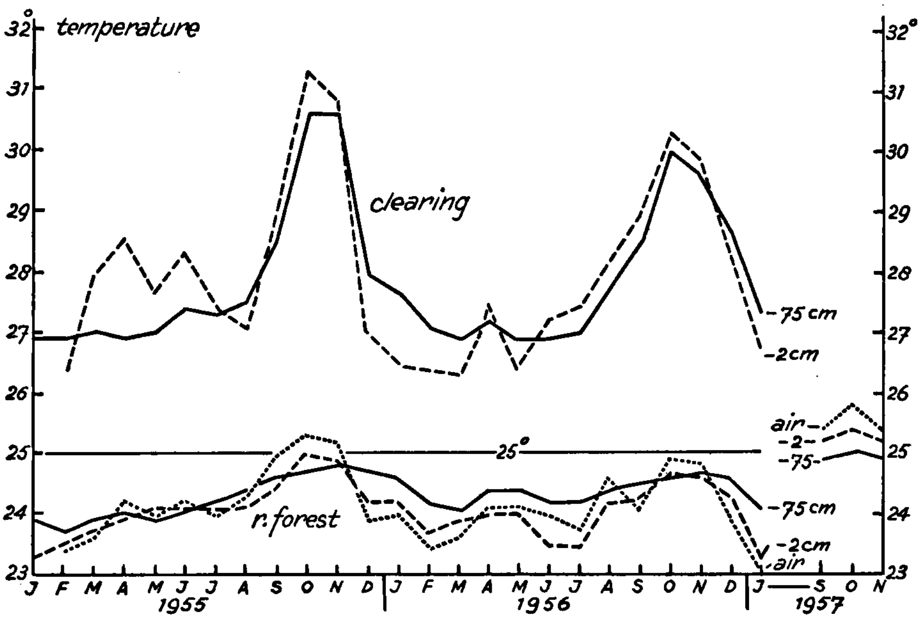


Fig. 41. Monthly means of soil temperature at different depths in rain forest and in the bare soil of an extensive clearing. Air temperature at 1½ m height in the rain forest has been added for sake of comparison.

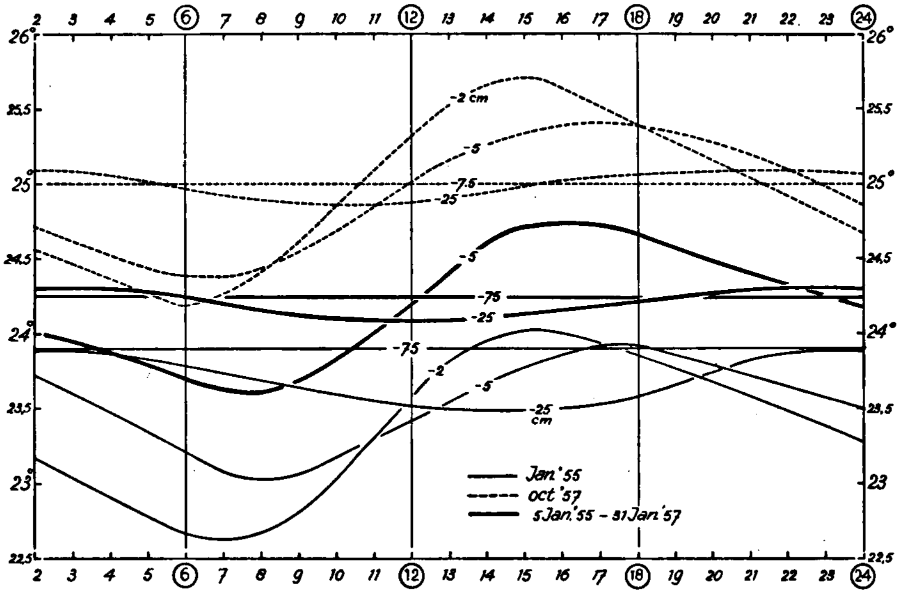


Fig. 42. Average daily march of soil temperature measured at different levels under the rain forest during various periods: Jan. '55 (representing the coolest period on record), Oct. '57 (hottest idem) and the long-term average over the whole period of observation (Jan. '55 – Jan. '57).

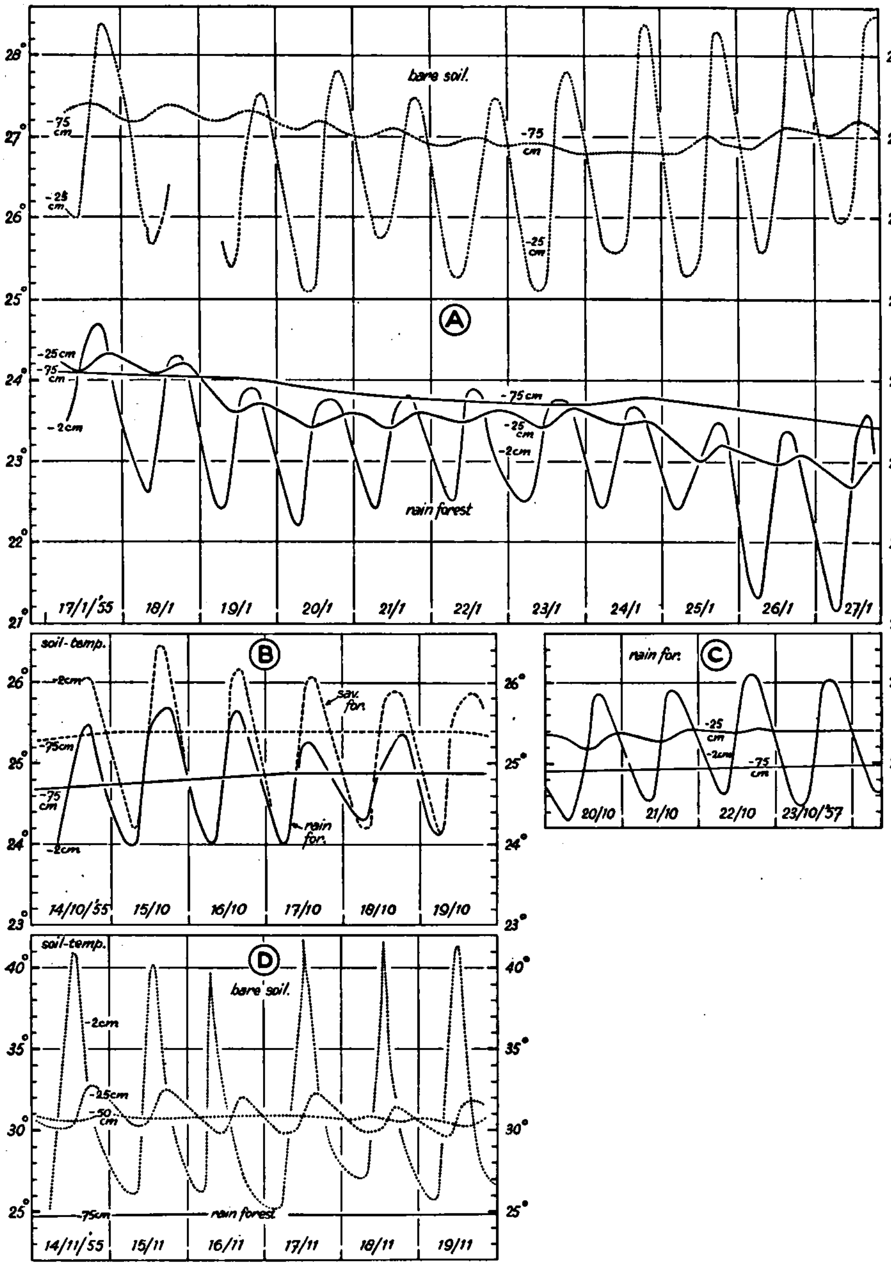


Fig. 43. March of soil temperature. A: under rain forest and in bare soil in a clearing during a cool period in Jan. 1955. B: under rain forest and savanna forest during the height of the dry season 1955. C: in rain forest during the very hot dry season of 1957. D: in bare soil in a clearing during the height of the dry season of 1955 (graph for temperature at 75 cm depth in rain forest is added for comparison). Continuous lines: rain forest; broken lines: savanna forest; dotted lines: bare soil in a large clearing.

to be very small. At a depth of only 2 cm the fluctuation of the monthly mean did not exceed 2°.

Fig. 43 shows the march of soil temperature under forest cover during the yearly period with the lowest night temperatures (graphs A: Jan. '55) and during the dry season when the daily maxima are highest (graphs B and C: dry seasons of 1955 and '57). At the end of the dry season of 1957 soil temperatures reached somewhat higher figures than are given in fig. 43 A, as may be noted from the figures for the absolute maxima given in table V, which were recorded during Nov. '57.

The graphs given in figs. 42–44 also may serve to show the *time-lag* of the soil temperature at different depths behind the air temperature at 1½ m. The lag of the daily maximum averaged approximately 2, 4 and 10 hours at a depth of 2, 5 and 25 cm respectively. The daily variation at 50 and 75 cm was less than 0.1°. For the daily minimum the lag after the minimum at 1½ m amounted to ¼–1 hr. (2 cm), 1–2 hr. (5 cm) and 5–7 hr. (25 cm). For the maxima no significant seasonal variation in the length of the lag was observable, whereas for the minima the lag increased with decreasing overall-temperature (cf. fig. 42).

From the foregoing the extremely small range of the seasonal and daily variation of soil temperature under forest cover will be noted. This also appears from the absolute maxima and minima given in table V: at a depth of 2 cm the temperature one time reached a maximum value of 26.2° C and only during one hour dropped to 21° C. Because the period of observation covered both the night with the lowest minimum ever recorded in Suriname and an exceptionally hot dry season, the absolute minimum and maximum given in table V may be regarded as a satisfactory indication of the extremes in soil temperatures occurring in the region under consideration.

Comparative readings were made simultaneously in other sites in the Mapane rain forest, but as they show only insignificant deviations from the above mentioned data, the latter may be regarded as representative for the whole region. Quite similar values were obtained in the loamy sands and in red sand soils under forest in the Upper–Coesewijne R. region.

Making allowance for local rises which the temperature in the surface layers of the soil may undergo on account of an extra amount of radiation due to discontinuities in the density of the canopy, it may thus safely be assumed that the soil temperature under closed forest in the area under consideration fluctuates between 23° and 26° C. In the surface layers (1–5 cm) the temperature will seldom rise over 27° C and probably never exceeds 28° C, whereas it seldom falls under 22° C. In the main root zone (5–40 cm) temperatures over 26° or below 23° C are very exceptional.

At all depths the yearly means are practically equal to the mean air temperature in the undergrowth (cf. table V). The monthly means differed but slightly. At 25 cm depth the extreme range in temperature (absol. max. minus absol. min.) during the period of observation was less than

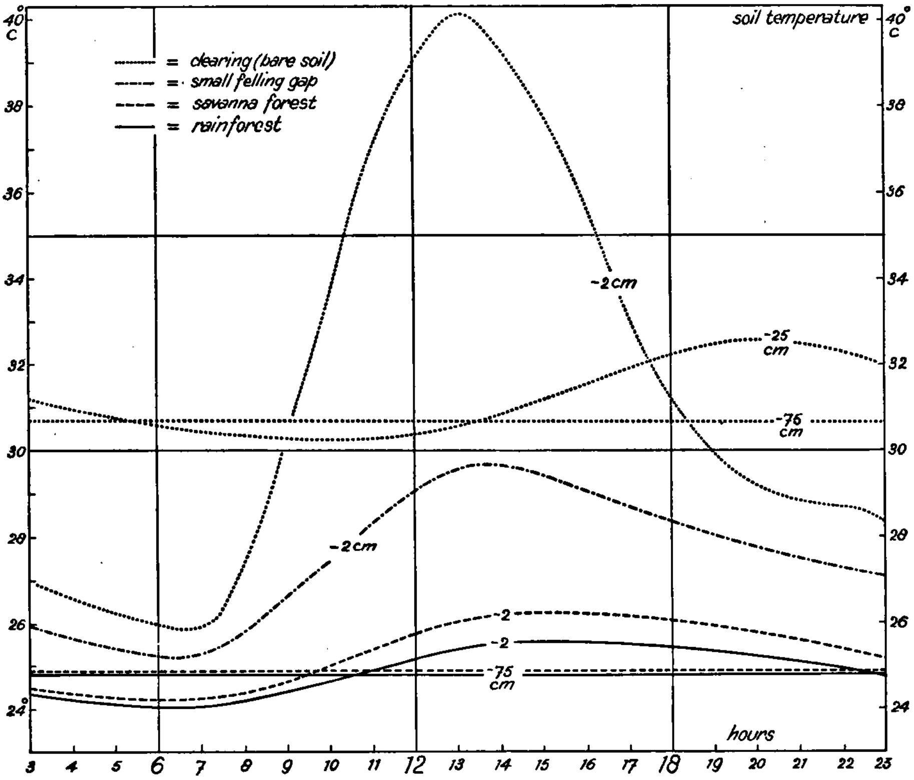


Fig. 44. Daily march of soil temperature in rain forest, in a large clearing and in a small felling gap, averaged over the dry season of 1955 (Oct.–Nov.).

3½° and at 75 cm it only amounted to about 1½°. Thus *a single temperature reading made at 75 cm depth at any time of the year, agrees with the average temperature at this depth, and also with the mean air temperature in the undergrowth!, to within* 1°. Even a single reading at 25 cm provides us with a sufficiently accurate indication of the air temperature in the undergrowth.

Soil temperature under forest cover appeared to be largely controlled by air temperature, and consequently to be closely correlated with the type of forest. Moreover it appeared to be practically unaffected even by considerable differences in soil texture and in the amount of soil moisture, as is clearly shown by a series of simultaneous readings made at 25 cm depth along a transect passing through rain forest and old secondary forest growing on different types of soil and through two types of savanna forest on white coarse sand. The readings were made at the height of the long dry season when the differences in the microclimatological factors between the forest types reached their highest values.

The readings embodied in fig. 45 show amongst other things: (a) the higher soil temperature under old secondary forest (with somewhat lower upper storeys and a less perfectly closed canopy than is found in real rain forest); (b) the independance of the soil temperature of soil texture and soil moisture (in a dry white sand "pocket" in the rain forest soil temperature did not differ significantly from that in heavy textured, moist soils in the same rain forest); (c) the strong correlation between soil temperature and the super-terranean climate (this is shown by the agreement between the soil temperature and the total Piche evaporation measured during the same day). These observations may serve to illustrate the fact that a single series of comparative readings of soil temperature taken at, say, 25 cm provides us with a sensitive index of the environmental differences that must be present between contrasting habitats in the same area (assuming a uniform standard climate, a condition which is fulfilled over large areas in the lowland in Suriname). The correlation between the soil temperature and the other environmental factors is due to the fact that the soil temperature is largely controlled by the air temperature near the forest floor; and between this latter factor and the

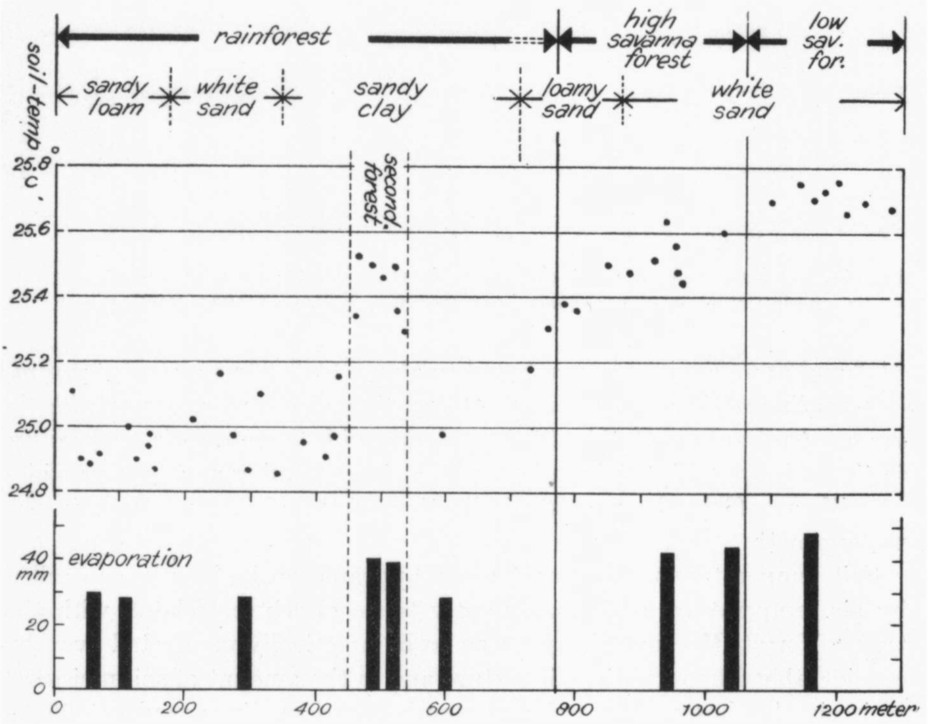


Fig. 45. Upper half: soil temperature at 25 cm depth along a transect, crossing rain-, savanna- and secondary forest on various soils; this graph demonstrates the relative independence of soil temperature from the type of soil and the strong correlation between the type of vegetation and soil temperature. Readings were made at the height of the dry season (3 Nov. 1955) between 11 and 12.30 hr. Lower graph: total (6–18 hr.) Piche evaporation in arbitrary units on the same day at 9 stations along the same transect, showing the strong relation between type of vegetation and evaporation, and, accordingly, between the latter and soil temperature.

TABLE V

Soil- and air-temperature in different habitats in the Mapane region, based on hourly means as computed from the thermograph charts.

	mean temperature[1]	mean daily maximum[1]	mean daily minimum[1]	mean daily amplitude[1]	absolute maximum[2]	absolute minimum[3]
rain forest						
air (+1.5 m)	24.1	27.4	21.9	5.5	32.1	17.9
2 cm depth	24.1	25.1	23.2	1.7	26.2	21.1
5 cm ,,	24.2	24.8	23.5	1.3	25.7	21.9
25 cm ,,	24.2	24.4	23.9	0.5	25.4	22.6
75 cm ,,	24.3	24.3	24.3	<0.1	25.2	23.3
savanna forest						
air (+1.5 m)	24.2	27.6	21.7	5.9	33.0	17.7
2 cm depth	24.2	25.6	23.2	2.4	27.8	21.1
5 cm ,,	24.2	24.9	23.5	1.4	26.7	21.9
25 cm ,,	24.3	24.5	24.0	0.5	-	22.6
75 cm ,,	24.4	24.4	24.4	0.1	26.1	23.5
clearing (bare soil)						
air (+1.5 m)	-	30.8	21.6	9.2	36.1	17.1
2 cm depth	28.6	35.4	23.0	12.4	52.0	23.0
5 cm ,,	28.5	31.0	24.5	6.5	46.5	24.2
25 cm ,,	28.4	30.0	26.9	3.1	35.6	25.0
75 cm ,,	28.4	28.4	28.4	<0.1	32.5	26.6

¹) 15 Jan. 1955 – 1 Febr. 1957 for rain forest and clearing, and 15 Jan. 1955–1 Febr. 1956 for savanna forest.

²) Oct. 1957.

³) Jan. 1955.

vertical and horizontal gradient of air movement, the atmospheric humidity and the air temperature at other levels there are strong mutual relations.

From the data given in table V it will be noticed that the soil temperature under the type of *savanna forest* that was studied by us, did not differ much from that under the rain forest. The daily and yearly means as well as the daily and seasonal variation throughout the year were slightly higher under the savanna forest; this must be due to the somewhat higher air temperatures prevailing in the latter. But even during the hottest days on record the temperature at 2 cm depth was less than 1.5° higher than it was in the rain forest at the same depth. As mentioned before, these slight differences are a good indication for the differences in microclimate between rain forest and savanna forest.

The march of soil temperature at 2 cm and 75 cm depth under savanna forest, as compared with that under rain forest, is shown in fig. 43 B. The average daily course during the dry season of 1955 is given in fig. 44. The march at 25 cm during this period is given in the lower part of fig. 27. During the wet season the soil temperature under the savanna forest differed less than 0.1° from that under the rain forest.

The graphs illustrate the rather unexpected fact that the lag of the soil temperature behind the air temperature in the savanna forest (in dry coarse sand) during the dry season did not differ from that found in the rain forest (wet sandy clay!) in the wet season.

I.7.4. *Soil temperature in openings*

The data from the extensive clearing, which cover a period of about 2 years, give a picture of the temperature prevailing in a patch of almost bare soil of yellow-red colour, 10 m in diameter, and surrounded by an area, about 30 acres in extent, which was sparsely covered with herbs and low shrubs. This area formed a gap in the forest extending for about 100 m in the E-W direction. This meant that the bare patch was insolated during about 6–8 hrs. a day. Similar conditions are found in some eroded places formed in heavily exploited forests as a result of tractor logging, in abandoned cultures, etc.

Under closed forest cover the heat exchange with the air is the principal factor controlling soil temperature and the latter therefore closely agrees with the mean air temperature in the undergrowth. The soil temperature gradient under a natural forest canopy is quite different from that found in an exposed place. In an opening the transfer of heat past the soil-atmosphere boundary is a complex geophysical phenomenon, which largely depends on the amount of radiation received by the surface, and to a lesser extent on other factors like the reflecting power of the surface, thermal conductivity and heat capacity of the soil (as determined by porosity, water content, etc.), wind conditions, amount of heat lost by evaporation, etc. As the soil temperature is determined by so many interacting factors, it differs considerably from one clearing to another. Accordingly the following figures are to be taken only as a rather extreme example of soil temperature in bare soil.

In table V and in figs. 43 A, 43 D and 44 data on the temperature in the extensive clearing are given, showing the soil temperature to be considerably higher than under forest cover. During clear days in the dry season at a depth of 2 cm temperatures of 45° C have repeatedly been recorded, while at 5 cm temperatures of 40° C were not uncommon. At a depth of 75 cm the monthly average exceeded that of the air temperature with 0.2–3.5°.

As shown by the figures given in table V, the daily amplitude decreased with increasing depth, and shrank to less than 0.1° at 75 cm depth (the amplitude of 0.2° shown by the curve in fig. 43 A is an exception).

In bare soil the time-lag of the daily maxima appeared to be nearly independent of the season; it amounted to ½, ¾, 6 and 20 hrs. at 2, 5, 25 and 50 cm depth respectively. The minima lagged about ½, ¾, 4 and 11 hrs. behind the daily minimum of the air temperature at 1½ m. Of an effect which differences in soil moisture in different seasons might exercise on the time-lag and on the difference between air- and soil-temperature, hardly a trace was to be seen.

The seasonal variation at 2 cm and at 75 cm depth as compared with that under forest cover, is illustrated by the course of the monthly means given in fig. 41. This graph shows that the difference between the mean monthly values under forest and in bare soil varied between about 3° and 6°. Apart from the direct physiological significance which the much higher soil temperature in a clearing has for the plants, the high soil temperature has a considerable effect on the *level of organic matter in the soil.* As may be noted from the curves shown in fig. 41 as well as from the long-term averages given in table V, the temperature in the bare soil was on the average throughout the year above 25° C. Under forest cover the temperature rises only exceptionally (and then only in the upper 2 cm) above this critical value, which is assumed to be the temperature at which humus formation and decay proceed at the same rate, and at which the organic matter content of the soil therefore remains constant (e.g. SENSTIUS 1923, JENNY 1930, CORBET 1935 and MOHR *et al.* 1954, fig. 56).

Because, according to JENNY's law, an exponential ratio exists between the nitrogen content of the soil and the temperature, the very high temperatures recorded in the extensive clearing will result in a rapid decrease of the amount of organic matter (and consequently of nitrogen) until a level is reached which is much lower than that which is maintained in the forest where the soil temperature is on the average about 24° C.

The disappearance of nitrogen after the forest has been cleared, may according to CORBET (1935) also be promoted by some (rather vague) photo-chemical process.

In gaps in the forest caused by normal exploitation the soil temperature shows a prompt rise. In the top layers (2–5 cm) of such gaps frequently temperatures of 30° C and over were recorded. Fig. 44 shows the daily march of the soil temperature during the dry season in a felling gap where the soil was reached by the sun's rays during approximately 2 hours per day. This graph shows that the temperature at 2 cm depth was at least during the dry season on the average above 25° C.

I.7.5. *Comparison with data from other tropical countries*

Data concerning soil temperature under tropical forest are scanty. The monthly mean at 14 hr., varying between about 24° and 26° C, recorded by BAKER *et al.* (1936) for a depth of 30 cm under the rain forest in Hog Harbor, agrees within 1° with our own data from the Suriname rain forest.

These data are consistent also with the value (25–27° C at 1 m depth) assumed by MOHR (1933) for the lowland forests in Indonesia and with the assumption made by RICHARDS (1952) that the temperature below the soil surface rises in the rain forest but rarely far above 25° C. For the lowland forest soils of Malaya CORBET (1935) mentions that the temperature near the surface is slightly below 25° C, and that the daily variation is less than 1°.

Interesting comparative data showing the enormous difference between the soil temperatures occurring under various types of vegetation as well as in denuded soils, have been published by a number of students working in the Belgian Congo. The figures given by LOUIS (1939 and unpublished data quoted by BERNARD 1945) are in general 1½°–3° lower than those recorded in the Suriname forest. LOUIS' records made at 4, 10 and 30 cm depth show values varying between 19½° and 24½° C, whereas the soil temperature under the Suriname forest never fell below 23° C (cf. fig. b). His data also reveal the considerable decrease of temperature caused even by a light vegetational cover. BEIRNAERT (1941) reports average temperatures of 24°, 24° and 23½° C at 1, 5 and 9 cm depth respectively under primeval forest in Yangambi. Under secondary forest soil temperatures were on the average only ½° higher.

From the abundant literature on soil temperature in various types of *bare soil* and under grass cover in the tropics, only a few general facts can be quoted. LEATHER (1915) in an exhaustive study on the temperature in bare fallow soil in India showed among other things the interesting fact that even a very large increase in soil moisture during the monsoon had hardly any effect on the maximum and minimum temperatures in the soil. Hence the relation between soil temperature and air temperature remained practically the same during hot weather as well as in periods of rain (excluding the case of odd showers), as was also observed in the present study.

In bare soil the temperatures at greater depths reported by BERNARD (1945) in Bambesa, which has a climate comparable to that of the Suriname lowland region, are of the same order of magnitude as those recorded in this study; the mean at 50–75 cm was about 27½° C (28½° in the Mapane clearing). Near the surface the temperatures in Bambesa were considerably lower than those reported here; the mean monthly max. at 10 cm was 35½° C in the dry season and 30½° C in July (compare the considerably higher values in table V). The temperatures recorded by BEIRNAERT (1941) in bare soil at Yangambi (41½° and 39° C at 5 and 9 cm depth respectively) are comparable to our own data.

At 60 cm depth under bare red soil in Djakarta the temperature was on the average about 30° C, a value similar to that found in the very exhaustive and precise temperature recordings made under a lawn (BRAAK 1928–1929). At depths from 3–110 cm the temperature under the lawn showed an average of about 29½° C (mean air temperature 26°). The absolute maxima reported by BRAAK are considerably lower than those recorded in bare soil in Suriname.

PART II

EDAPHIC FACTORS

II.1. INTRODUCTION

The primary aim of the investigation of the soil conditions was to obtain a detailed description of soil profiles, as a supplement to the corresponding phytosociologic descriptions given in part III.

Accordingly the soil studies were largely carried out on typical lowland-forest soils in the Mapane and in the Upper Coesewijne region. In addition various sites of lateritic (ferrosiallitic) soils in the upland region were sampled.

Naturally this is no attempt to arrive at a classification of the Suriname high-forest soils. The only result that may be expected from a few scattered investigations is that they give us an impression of the edaphic factors operating in the lowlands of central Suriname, behind the coastal belt, under selected stands of high upland forest.

It follows from the aims of the present study, that the soil properties to be investigated, were chiefly those that were most likely to be effective ecologically. Owing to the paucity of fundamental data with regard to the relation between the forest trees and their environment, and to our imperfect knowledge of the differential edaphic factors in particular, the first problem was that of the factors which should be analysed in the laboratory.

It has been emphasized by various students of tropical forest soils (e.g. HARDY 1936, BEARD 1946) that soil depth and other physical edaphic factors, especially those affecting the water and oxygen supply of the roots, play a far larger part than chemical factors like soil acidity, base content and the organic-matter content, except in so far as the latter affect the behaviour of soil water.

Therefore in the present study the analysis of soil texture was made a part of the standard laboratory analyses of the samples, and much time was spent on a direct study of pore space and water content in a few selected profiles in situ, the results of which will be presented in II.6.

As could be expected, the results of the laboratory analyses of chemical factors showed that the majority of the soils in the sites studied, though varying in many of their characteristics (structure, texture, topography, parent materials, etc.), share many characteristics which may be regarded as typical for the majority of the soils in the rain forest belt, and which have been summarized by RICHARDS (1952, p. 205). *In texture* they are generally *loamy or clayey*, but *invariably sandy*, especially in the upper horizons. They are *highly deficient in exchangeable bases, particularly in calcium, the kaolinitic clay-colloid being strongly degraded,* and they are *invariably acid to very acid.* Their *organic-matter content is rather low,* and the *narrow carbon/nitrogen ratio* (which is noted even in the upper horizons) indicates that *humification is nearly complete* and must have taken place very rapidly.

Apart from the purely descriptional aspect of the investigations of the soil conditions, it was also hoped that some relation would be detected between differences in the composition of the rain forest and certain edaphic factors. Although the effect of edaphic differences on the composition of tropical plant communities in general and of the tropical rain forest in particular can no longer be questioned, there are different opinions as to the relative importance of the physical and the chemical characteristics of the soil. HARDY (1936) is of opinion that the distribution of the species is mainly controlled by the physical features on which the moisture relationships in the soil depend. The chemical properties and attributes are supposed to ... "exert little or no influence, except in so far as they affect the behaviour of soil water". The view that chemical factors in themselves are of quite secondary importance in deciding the floristic composition of the tropical forest, is more or less shared by other students of tropical forest ecology in S America. However, recent studies, especially those made in India (e.g. PURI 1950), have made it clear that the different demands made by tropical-forest trees on soil minerals, are responsible for the preference which species with similar requirements as to soil minerals show for the same type of substrate.

Although, as will be discussed below, the soils of the Mapane region differ in some characteristics from those in the Coesewijne region, there is no proof that these differences in soil actually are responsible for the striking differences in the composition of the rain forest found in these two regions.

In the Mapane area the soil was sampled in a small compartment of mesophytic (rain) forest, 50 ha in extent, which contained various soil types. The samples were taken in the first place to ascertain the order of magnitude of the variations shown by the soil factors over short distance. In addition, in the same compartment, the distribution of twenty tree species was mapped, and it was intended to find out whether there was any correlation between the distribution of these species and the soil qualities. The fact, that for the majority of these species such correlations could not be established, is no proof that they do not exist. For a final conclusion more soil factors have to be included in the investigation, and the latter, moreover, would have to be conducted on a larger scale than was possible in this preliminary study. However, for the occurrence of two species, *wanapisie* (*Ocotea* sp.) and *birgiegronfoeloe* (*Qualea rosea*), a significant correlation was found with some soil characteristics.

II.2. SOILS OF THE MAPANE REGION

II.2.1. *Geology and topography*

The area of the Mapane region where the ecological studies were carried out, belongs geologically to the *transitional zone between the Old Basement and the Zanderij formation*. The boundary between the two is shown very schematically in fig. 2. Actually in this zone southern protrusions and isolated remnants of Zanderij sediments form a complex pattern with weathered outcrops of the cristalline Basement. Towards its southern boundary the coarse sands, which form the weathering products of the unconsolidated sediments of the Zanderij formation, form a shallow cover only (often less than 3 m thick, cf. figs. 48 and 49) over the deeply weathered cristalline bedrock.

The *Zanderij formation* which occurs as a nearly continuous belt running approximately parallel to the coast between the cristalline Basement in the S and the younger Coastal sediments (Coropina and Demerara formations) in the N, presumably is identical with the White Sand Series in British Guiana, which were formerly believed to result from the weathering of granitic rocks in situ. The same opinion was held by HARRISON (in a report quoted by DAVIS *et al.*, 1934) concerning the white sands in Suriname. Recent evidence, however, has shown that they are alluvial deposits, probably of Miocene to Pliocene age. IJZERMAN (1931) considered them to be continental alluvia. BAKKER (e.g. 1957) is of opinion that the Zanderij formation consists of a complex sediment, deposited along a marine coast ("beachhead sands"), the deposits extending up the estuaries of the rivers which emptied in the sea. ZONNEVELD (1950) and VAN DER EYK (1957) pointed to the striking similarity in form between the mechanical-composition curves of the Zanderij sands and those of fluviatile sediments. The names used in neighbouring countries for this formation (*White Sand Series, Sables Blancs*) might give the false impression that this formation mainly consists of bleached sands. In Suriname less than 17 % of the soils of the Zanderij formation is formed by bleached sands, whereas by far the greater part is made up by red sandy clay (-loam) and even clays.

The vegetation map shown in fig. 46, is also a soil map, in the sense that in this region, the boundaries of the open savannas and savanna forests coincide exactly with those of the excessively drained bleached sands, whereas rain forest (high upland forest) is found on red coloured soils containing at least 5 % clay. As is shown by the drainage pattern of the creeks, the white-sand plateaus in this area are found on the watersheds, capping the low, rounded hills and ridges. N of the area shown in fig. 46, the extensive open white-sand savannas of Jodensavanna and Cassipora are found (cf. fig. 2).

The heavy-mineral content of the sedimentary sands in the Mapane

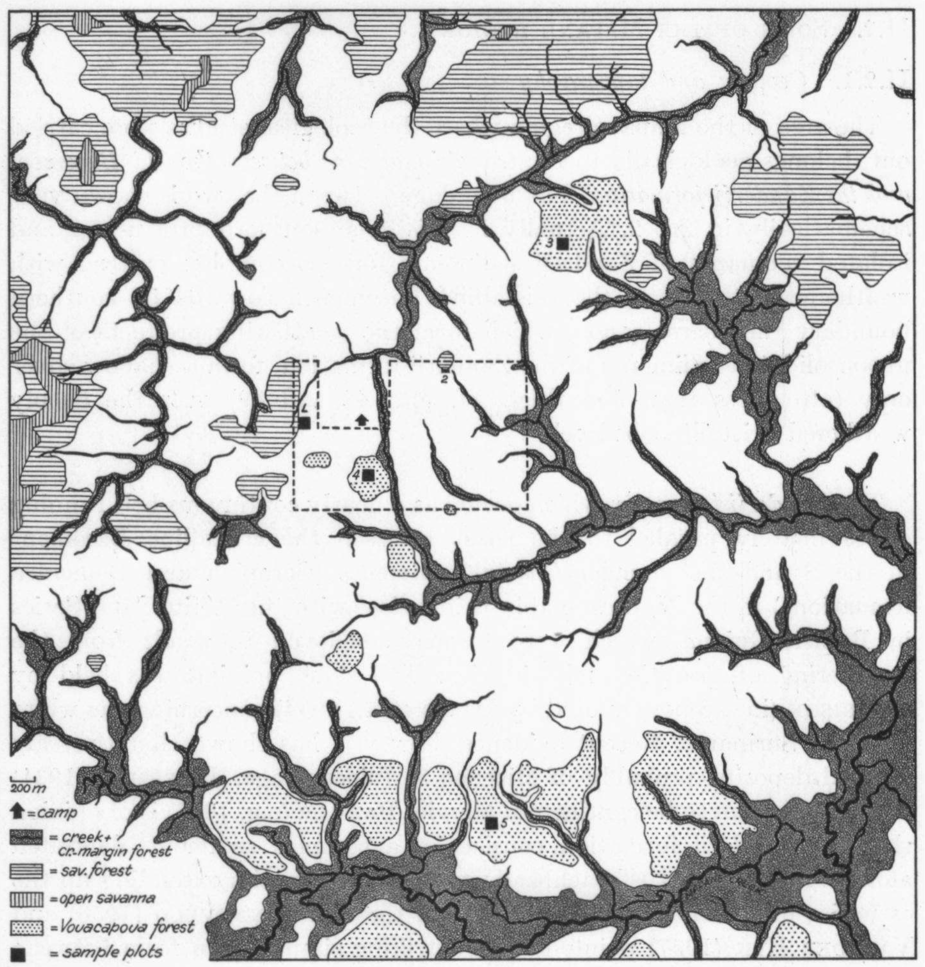


Fig. 46. Detailed map of a part of the Mapane region. For location, cf. fig. 2. The unshaded parts represent mesophytic (rain-)forest. Based chiefly on forest map no. 836 of the Forest Department. The area marked by a broken line is given on a larger scale in figs. 47, 52 and 69.

region (cf. table VI), which contain chiefly zircon and staurolite with subordinated rutile, kyanite and tourmaline, closely resembles that of Jodensavanna sands (cf. e.g. Bakker 1957, append. II). The constant occurrence of rather high percentages of kyanite in the heavy-mineral associations in the sand deposits of this region (in contrast to those in other watersheds) probably is related to the occurrence of kyanite-containing metamorphous rocks in the basement complex S of the Mapane Cr., and hence might be another argument for a transport of the Zanderij sands over rather short distances in a S–N direction.

The rocks of the *Old cristalline Basement* found between and S of the Zanderij sediments, being of Pre-cambrian age, are of very complex composition and structure, and consist in the area under consideration mainly of acidic, highly metamorphous rocks plus igneous intrusions: gneissose granites and grano-diorites, pegmatites, muscovite-gneisses, quartzose sericite schists, etc. Outcrops of younger igneous intrusions are found in the bedding of the Mapane Creek. For the rest outcrops of unweathered rocks are extremely rare, and the very deep weathering makes it practically impossible to decide with certainty in the field from what kind of parent rock the soil has been derived.

N of Mapane Creek the *topography is very gentle,* and large areas have no noticeable slope. The flat plateaus and ridges between the shallow and broad creek valleys attain heights of 50 m above sea level. The ground rises gradually, becoming more and more hilly to the S, particularly S of the Mapane, where the schistose hills of the Taffra- and Bonidoro-series (Orapu formation) are found; on the aerial photographs the latter are easily distinguishable because of the conspicuous dendritic pattern of the drainage system.

The slopes to the creeks are gentle, as may be seen from the relief map (fig. 47) which depicts a small area that may be regarded as representative for the S half of the area shown in fig. 46. Yet there must have been a rather recent erosion-rejuvenation, recognisable by the deeply indented creek-heads, which presumably was caused by a relative lowering of the local erosion basis.

The numerous small forest streams (mapped in fig. 46), which are a typical feature of the lowland region, carry water throughout the year. The course of these creeks is easily distinguishable on aerial photographs owing to the occurrence of the photo-typical *pina* palm (*Euterpe oleracea*), which is characteristic for the creek-margin forest; the latter may widen locally to swamps and marshes (cf. LINDEMAN 1953 and 1959), a few hundred meters or more (e.g. alongside the Mapane Cr.) in width.

The Mapane Cr. is a typical *white water* creek, because most of the small streams by which it is fed, are *white-water* streams (which means that they have clear or turbid, but always colourless water), draining red earths covered by rain forest. To the N – in the region of the bleached sands of the Zanderij formation – the creeks rising in the savanna forests are typical *black-water* streams (having clear water, dark brown by reflected light and red by transmitted light), which are a well-known feature in podzolised areas in the tropics.

Apart from the forest streams which even at the end of the dry season carry some seepage water, the area is dissected by numerous dry *gullies* which contain water only during and shortly after exceptionally heavy showers.

Summarizing the contents of this section, we may say that *soils were studied in a geologically complex region, consisting of an intricate pattern formed by acid quartzose metamorphous and igneous rocks and younger intrusives, partly overlain by unconsolidated coarse sandy deposits of varying depth.*

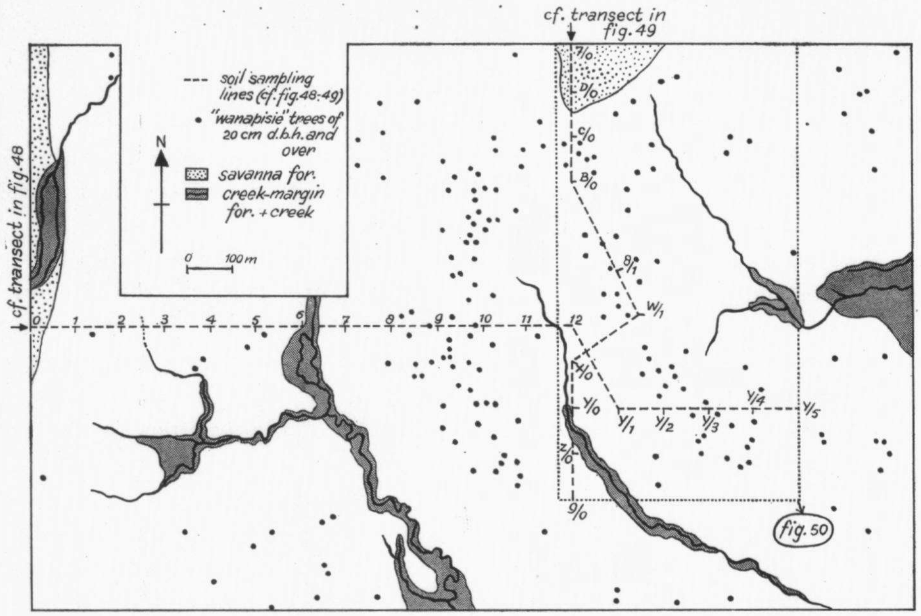


Fig. 47. Part of the map in fig. 46 enlarged to show the location of soil-sampling lines and the distribution of *wanapisie* trees (*Ocotea* sp.)

II.2.2. *Detailed study of the soils in the Mapane region*

The soils of the area selected for detailed study, were investigated in sixty 1–2 m deep pits, situated on the crossings of the cut lines dividing the 50-ha experimental area (pictured in fig. 50) in 50 square compartments of 1 ha each.

The principal object was to ascertain how much the soil varied over a small area, and to what extent variations in the soil factors might account for the striking irregularities of the distributional pattern of the trees established by the enumerations carried out in the above mentioned compartments. In addition some 15 pits were dug and borings with a soil auger (1–6 m) were made in the neighbouring areas, especially along transects crossing different types of vegetation (cf. fig. 48).

Three of the sites in the rain forest showing a conspicuous abundance of *bruinhart* (*Vouacapoua americana*) were also sampled. Laboratory analyses of selected samples were made at the Soils Laboratory of the Royal Tropical Institute, Amsterdam.

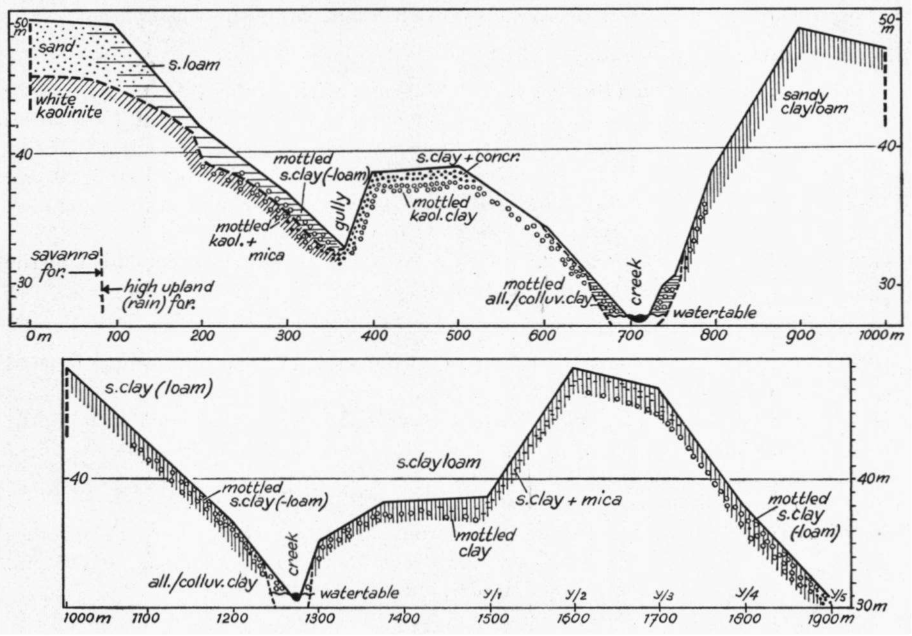


Fig. 48. Schematic cross-section along a transect in the Mapane region (cf. fig. 47). 0–90 m: high savanna forest; 90–1900 m: rain forest, with creek-margin forest bordering the creeks. Heights in m above sea level.

0–350 m: sandy horizons, varying from pure sand on top of the terrace (dotted area) to sandy clay (-loam) lower down the slope (horizontally shaded area), probably belonging to the Zanderij formation and overlying impermeable kaolinite, being the weathering product of sedentary decomposed rock belonging to the basement complex. Drainage is excessive in the sands on top of the terrace, but becomes less free on the slope down to the gully, as the heaviness of texture increases and as the depth, at which the impervious kaolinite begins, decreases. The slope drains the terrace, and lateral movement of ground water is considerably facilitated by the presence of a porous layer consisting of coarse sand and quartz gravel just above the impervious kaolinite (in the figure indicated by a broken line). That the drainage lower down the slope is more and more impeded, is indicated by the increase of *mottling;* the latter is shown in the figure by open circles. At the base of the slope the red flecks are indurated to iron-oxide concretions. The gully only conveys water during and shortly after heavy showers.

350–700 m: red sandy clay (-loam), with much pisolithic iron-oxide concretions (perdigón) in the upper layers (0–100 cm), merging into impervious mottled pipe-clay. Parent rock weathered in situ. The layer with concretions possibly marks a fossil B-horizon, truncated by erosion after the uplift and subrecent dissection of the terrain (see p. 118–119). Drainage is free in the rooting zone (0–80 cm), but impeded at lower depths, where the heavy textured, compact soil is relatively impervious.

700–1900 m: red sandy clay-loam to sandy clay. Mottling—indicating more or less impeded drainage—is found at a rather slight depth at the foot of the slopes. 700–1450 m: probably parent rock weathered in situ (except colluvial and alluvial clay/sands alongside the creeks). 1450–1900 m: parent rock weathered in situ; mica (muscovite) (indicated in the fig. by short horizontal lines) often found already near the surface.

Description of a few selected profiles (Munsell colour values between parentheses);

Profile at 0 m: (high savanna forest)

0–440 cm: grey-brown (40 cm: 10 YR 3/2) *sand* with humus (bleached in upper 5 cm), merging at a depth of 200 cm into white coarse sand (coarseness increasing with depth). Roots and other signs of biological activity seen to a depth of at least 200 cm. Conspicuous rootmat 5–20 cm.

440–460 cm: very coarse white sand with *much gravel* (angular quartzose fragments). Very moist, even at the end of the dry season.

below 460 cm: pure, white *kaolinite* with a few quartz fragments imbedded in the top layer. Very dry and compact. No mica.

Profile at 150 m: (rain forest)

0–175 cm: grey-brown *sand* with humus, bleached at the top. Coarseness of sand increasing with depth.

175–340 cm: reddish sand, containing 5 % clay; colour tends to deepen with depth;

340–400 cm: sharply delimited layer of white coarse sand, coarser than above;

400–420 cm: idem, but yellowish;

420–430 cm: white idem;

430–450 cm: red idem, very moist. This profile is almost identical to the profiles *B*/0 and 7/0 (cf. fig. 49). Maximum biological activity at 10–125 cm. No distinct rootmat. Rootlets seen below 200 cm.

450–460 cm: very coarse white sand + *quartz gravel* and stones. Very moist.

below 460 cm: pure, white *kaolinite* with quartz fragments at the top.

Profile at 250 m:

0–160 cm: reddish-brown *sandy clay-loam* with humus (80 cm: 10 YR 6/6), merging at 120 cm into greyish sandy clay mixed with pipe-clay from underlying layer and with faint orange mottling.

160–180 cm: idem with much coarse sand and *quartz gravel.*

below 180 cm: greyish-white *pipe-clay* with some mica and many dark-red flecks. Very dry, even in wet season. Probably rotten *sericite schist* (Rosebel-facies of Orapu formation?), presumably identical with material found in prof. 8/1 and *D*/1 (cf. fig. 49).

Profile at 500 m (typical for soils between 400 and 650 m):

0– 25 cm: red-brown *sandy* (*clay-*)*loam* with much humus at the top with bleached quartz grains (15 cm: 10 YR 4/2). Merging into:

25– 60 cm: main zone of occurrence of angular iron-oxide *concretions* (perdigón), ½—2 cm in diameter, imbedded in sandy clay (10 YR 7/6–6/4). Angular quartz gravel frequent. Main rooting zone 0–150 cm. Humus visible to a depth of 60 cm, but organic matter demonstrable to 150 cm. Drainage excessive: even after heavy showers no standing rainwater in soilpits. Merging into:

60–400 cm and lower: compact, friable *kaolinitic clay,* reddish (10 YR 7/6–5/6) with yellowish (5 YR 6/6) and red (10 R 4/4) flecks in the upper layers. Colour of matrix gradually becoming lighter with depth: at 300 cm creamy-white pipe-clay, with violet/red (5 R 5/4) mottling. Concretions becoming gradually softer below 60 cm, but even at 400 cm dark red flecks are still somewhat harder than the matrix. Below 150 cm, even during wet season, very dry. Quartz fragments frequent to occasional throughout the profile, partly rotten and easily crushable to coarse sand. No roots seen below 120 cm.

Profile at 900 m: typical for deeply homogenized red sandy clay-loam, merging at greater depth into sandy clay. Humus visible to 80 cm. Comparable to prof. 8/1 (cf. fig. 49). No mottling above 200 cm. Signs of biological activity at least to 100 cm. Drainage good to considerable depth. It is uncertain if this soil is of residual origin, or—like for instance in profile 8/1—is sandy sediment of Zanderij-age, overlying weathered bedrock.

Profile at 1150 m:

0– 30 cm: red-brown sandy clay-loam with humus, merging into:

below 30 cm: compact *sandy clay*, yellow-red (5 YR 6/6) with red *mottling* (10 R 4/6), somewhat harder than matrix (mottlings lower down the slope, e.g. at 650 m, indurated to real concretions). Zone of biological activity markedly thinner (45 cm) than higher up the slope.

Presumably Old Basement rock, weathered in situ, though colluvial movement of soil above 90 cm is apparent. Between 1125 m and 1250 m frequently a *stone line* of angular quartz gravel was found at 90–100 cm depth, presumably of colluvial origin. Drainage below 30 cm not altogether free.

Profile at 1300 m:

Identical to prof. *X/0* (cf. fig. 49): 0–125 cm red sandy clay (-loam), yellow red clay with dark red spots below 125 cm, tending to separate out as semi-hard concretions in upper part of layer.

Profile at 1500 m (Y/1):

0– 50 cm: brown-red sandy clay-loam with humus (15 cm: 9 YR 5/4, 30 cm: 5 YR 6/6). Zone of biological activity rather shallow. Only occasional rootlets seen below 40 cm. Merging into

below 50 cm: compact bright red sandy clay with partly worn quartz fragments and with plentiful muscovite (colour intermediate between 10 R 4/8 and 5 YR 5/6). Polygonal, nutty structure, part of the polygons being slightly harder and darker in colour. Drainage fairly good.

Profile at 1700 m (Y/3):

0– 45 cm: red-brown sandy clay-loam (10 cm: 10 YR 5/4, 40 cm: 7½ YR 5/4). Main root zone 0–30 cm. Gradually merging into

45–130 cm: red sandy clay, still with humus in top, with small yellowish spots and with some muscovite. 110 cm: 5 YR 5/8. Merging into:

130–200 cm: red (5 YR 5/8) micaceous sandy clay and worn quartz gravel, merging gradually into:

200–300 cm: white speckled, pinkish (5 YR 7½/6) kaolinite with much gravel and less muscovite. Merging into:

below 300 cm: pinkish kaolinite with red/purple (10 RP 4/2–3/2) mottling. This soil has been developed from *residual* parent material, as indicated by the heavy-minerals profile given in table VI.

Profile at 1900 m (Y/5):

0– 90 cm: red-brown/yellow red sandy clay-loam/clay (10 cm: 10 YR 4/4, 40 cm: 10 YR 5/8, 90 cm: 10 YR 6/7). Main rooting zone 0–40 cm. Rather shallow zone of biological activity (0–50 cm). Much quartz gravel below 35 cm. To the base colour becoming yellowish with faint reddish mottling. Merging gradually into:

below 90 cm: mottled yellow-red sandy clay (10 YR 6/7) merging gradually into yellowish white kaolinite (10 YR 9/4 at 250 cm) with friable, slightly cemented red spots (between 10 R 5/8 and 5 YR 5/8), giving rise to semi-hard concretions in the upper part of the layer. Number of quartz fragments increasing with depth. No muscovite visible. Drainage partly impeded below 90 cm.

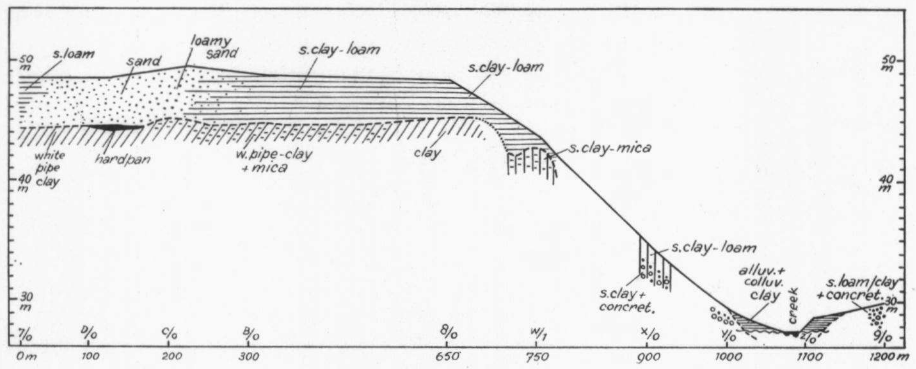


Fig. 49. Cross-section along a transect in the Mapane region (cf. fig. 47). Heights in m above sea level.

0– 150 m: transitional forest between high savanna forest and rain forest.

150–1200 m: rain forest with creek-margin forest between 1000 and 1150 m.

0– 700 m: free draining coarse sandy deposits (presumably belonging to the Zanderij formation) overlying white or mottled kaolinized sedentary parent material developed from basement rock weathered in situ.

700–1200 m: soils developed from rocks of basement complex weathered in situ (except more or less colluvial transport in upper layers); ca. 700–ca. 850 m: free-draining red soils; ca. 850–1000 m: mottled soils; 1200 m: lateritic soil.

For mechanical and heavy-mineral composition of horizons cf. table VI.

Profile 7/0:

0– 10 cm: light greyish-brown humic coarse *sand* with plentiful bleached quartz grains (10 YR 3/2).

10–100 cm: greyish-brown humic coarse loamy sand/sandy clay-loam; humus content diminishing very gradually with depth (25 cm: 5–10 YR 3/2, 75 cm: 5 YR 5/8). Main rooting zone: 5–40 cm, but roots frequent to a depth of 75 cm. Merging very gradually into:

100–250 cm: reddish, coarse sandy clay-loam (5 YR 5/8), merging into:

250–360 cm: loamy coarse sand, yellowish red (10 YR 6/6) with red flecks (2½ YR 5/10), merging into:

360–450 cm: base of transported material yellowish/white coarse sand, becoming coarser with depth (between 10 YR 8/6 and 5 Y 8/4, becoming lighter below).

below 450 cm: pure, white *pipe-clay.*

Profile D/0:

0– 25 cm: light-greyish, humic coarse *sand* with many bleached grains.

25–150 cm: greyish-brown coarse sand with humus. 60–70 and 110–125 cm: slightly darker and somewhat compacter horizon (B?). A few charcoal flecks and a fragment of an Indian pot at 60 cm. Concentration of roots just below surface, but roots frequent downwards to 100 cm (average colour: 10 YR 3/2).

150–250 cm: coarse sand of a greyish colour due to the presence of organic matter, decreasing with depth (150 cm: 10 YR 5/6, 250 cm: 10 YR 5/7). Occasional fibrous roots to a depth of 250 cm and probably lower.

250–290 cm: bright orange-red coarse sand (5 YR 6/10).

290–380 cm: yellowish coarse sand, becoming lighter in colour and coarser with depth (350 cm: 10 YR 7/6). Merging gradually into:

380–400 cm: brownish, very coarse sand, becoming more cemented with depth (390 cm: 10 YR 5/4).

400–435 cm: *hardpan*. Dark brown/blackish very coarse sand and angular *quartz gravel*, cemented with humous material (darker than 10 YR 2/2).

435–450 cm: greyish, bleached, very coarse sand and quartz gravel.

below 450 cm: pure, white *pipe-clay*.

Profile C/0:

0– 10 cm: light-greyish coarse *sand* containing humus and with much bleached grains.

10–100 cm: greyish-brown, humic coarse sand (30 cm: 5 YR 3/2, 60 cm: 5 YR 4/2, 80 cm: 5 YR 4/4). Organic matter very gradually decreasing with depth. Main rooting zone: 10–40 cm, but roots and rootlets still frequent at 100 cm. Merging gradually into:

100–150 cm: bright yellowish-red coarse sand (5 YR 5/7–5/10). Rootlets occasional.

150–300 cm: pinkish coarse sand (5–10 YR 8/4), with reddish marbling (5 YR 5/10). Merging into:

300–320 cm: base of transported deposit, marked by zone of white very coarse sand and angular *quartz gravel.*

320–380 cm: white *pipe-clay* with red flecks and bands (10 R 6/6) and with plentiful muscovite flakes. Many rootlets and fibrous roots.

below 380 cm: white pipe-clay without mica. Fibrous roots frequent at least to 450 cm.

Profile B/0:

0– 5 cm: coarse, bleached sand with many roots.

5–100 cm: reddish-brown, humic coarse *sandy clay-loam.* Organic matter diminishing very gradually with depth (20 cm: between 5 and 10 YR 4/4, 100 cm: 5 YR 5/6). Rootlets frequent down to 100 cm, but with a marked concentration in the upper 25 cm.

100–330 cm: red sandy clay-loam/sandy loam (5 YR 5/6), clay content decreasing with depth. 100–150 cm: still containing some rootlets and organic matter.

330–400 cm: coarse *sand,* becoming coarser and lighter in colour with depth.

400–430 cm: very coarse white *sand and quartz gravel,* with red and yellow bands. *Marking the base of the sandy deposits of the Zanderij formation.*

430 cm and below: white-speckled red *pipe-clay,* with plentiful mica and mixed with coarse sand at the top, merging into white pipe-clay without visible mica (440 cm: 10 YR 6/6, with white spots; 460 cm: 5 YR 7/6, idem).

Profile 8/1: (typical for *deeply uniform and homogenized profiles* of the well-drained, heavier sedimentary sands with very good root penetration).

0– 5 cm: brownish-red coarse sandy loam with much bleached grains.

5–100 cm: brownish-red coarse sandy clay-loam with humus, merging below into sandy clay fairly hard and coherent when dry. Organic matter content decreasing very gradually with depth and colour consequently becoming brighter (40 cm: 5 YR 5/7, 60 cm: 5 YR 5/6, 100 cm: between 5 YR 5/6 and 10 YR 5/8). Concentration of roots at 2½–40 cm, but rootlets well distributed down to 60 cm. At 40 cm plentiful pieces of charcoal. Merging very gradually into:

100–190 cm: red sandy clay, becoming somewhat stiffer with depth. Still containing some organic matter and fibrous roots to a depth of at least 150 cm (150 cm: ca. 10 R 5/8).

190–250 cm: red sandy clay, becoming sandier with depth.

250–290 cm: zone with more clay, presumably transition to sedentary decomposed rock. Merging very gradually into:

below 290 cm: stiff, red *pipe-clay* (10 R 4/5) with minute white and pink spots (5 R 5/4). No mica visible to the unaided eye. Presumably bed rock (granitic gneiss?), *weathered in situ.*

Profile W/1:

0– 5 cm: dark brown humic sandy clay-loam with many roots and bleached quartz grains.

5– 40 cm: reddish-brown coarse sandy clay with humus and with rather few roots (average colour 5 YR 6/7). At 20 cm zone of angular quartz fragments, pieces of charcoal and minute grains of concretionary ironstone. At the base of the layer continuous zone of angular quartz stones, presumably marking the base of colluvially transported deposits (Zanderij-material originating from top of the plateau).

below 40 cm: kalolinized muscovite-gneiss, still showing the structure or the parent rock. Alternating layers of purplish (colour presumably caused by manganese), red and white kaolinite (e.g. 10 R 3/2, 5 R 5/4, etc.), becoming lighter in colour with depth. Plentiful, large flakes of muscovite. Many quartz veins, composed of partly worn, angular quartz stones and gravel. Strongly impervious. Very dry, even during wet season. No roots seen below 50 cm.

Profile X/0:

0– 60 cm: light-brown, humic sandy clay. Main rooting zone 0–40 cm.

60–125 cm: yellow-red sandy clay with some quartz gravel. In top still containing some organic matter and a few rootlets.

125 cm and below: sandy clay, becoming more yellowish with depth (indicating a less satisfactory drainage), with friable slightly cemented red spots, passing into semi-hard (and a few hard) concretions in the upper part (150 cm: 5 YR 6/6 with 10 R 4/4 spots). At various depth quartz veins, consisting of (partly worn) angular quartz fragments.

Profiles Y/0 and Z/0 (colluvial and alluvial clay, bearing creek-margin forest):

0– 30 cm: brownish-red fine-sandy clay/clay with many roots (10 YR 4/2). Plentiful worm-casts on the surface.

30– 40 cm: faint *B horizon* (slightly darker and more compact, 10 YR 3/2).

40– 70 cm: greyish (10 YR 6/2) clay with humus and with light-brown spots (10 YR 4/2–5 YR 5/10). Rootlets frequent. Plentiful traces of earth worms.

below 70 cm: grey clay with slight blue (*gley*) tinge (between 10 YR 3/2 and 10 PB 4/2). Breaking into prismatic crumbs with shining surface. Some rust-flecks around rootlets and fibrous roots, which are found at least 40 cm below lowest level of free water (at 90 cm at the height of the dry season).

Profile 9/0: (similar to prof. at 500 m, fig. 48).

0– 45 cm: reddish-brown, sandy clay-loam with humus and with plentiful angular *iron concretions* and *quartz* fragments with iron-coating. Bleached sandy loam in top. Roots plentiful, mainly between 0 and

45 cm (2 cm: 10 YR 3/2, 15 cm: 10 YR 4/2). Iron concretions ½–3 cm in diam., containing quartz grains, red/dark red on cross-section (10 R 2/2).

45–120 cm: Idem. Some rootlets in top (matrix: 10 YR 6/5). Concretions becoming less hard with increasing depth. Plentiful quartz fragments (iron-coated).

below 120 cm: greyish kaolinite with friable, slightly indurated spots (5 YR 5/6–10 R 5/8), partly indurated to hard concretions.

TABLE VI

Texture and mineralogical composition of a number of selected profiles in the Mapane region. For detailed description of profiles, cf. figs. 48 and 49.

Depth in cm	MECHANICAL COMPOSITION												MINERALOGICAL COMPOSITION											
	2-1mm	1-0.6mm	0.6-0.3mm	0.3-0.21mm	210-150µ	150-105µ	105-75µ	75-50µ	50-20µ	20-2µ	2-1µ	<1µ	opaque	tourmaline	zircon	garnet	rutile	staurolite	kyanite	sillimanite	fibrolite	"alterites"[2]		
15 - 25	5	9	45	16	7	tr	tr	tr	16	2	tr	tr	13	14	29	-	7	35	7	-	-	6	bleached sand	PROFILE D/0
60 - 70	12	13	44	16	2	tr	tr	tr	12	tr	1	tr	44	6	36	-	15	14	1	3	-	25	id., faint B-hor.	
100 - 125	11	10	39	8	4	tr	tr	tr	24	1	2	tr	18	4	48	-	16	21	8	1	-	2	id., 2nd B.-hor.	
260 - 280	1	3	30	18	6	tr	tr	tr	37	tr	1	4	6	5	40	1	8	34	6	2	-	2	or.-red sandy loam	
350 - 375	12	19	32	6	2	tr	tr	tr	26	1	2	tr	3	5	42	-	14	22	12	-	-	5	yellowish loamy s.	
400 - 430	48	19	14	5	1	tr	tr	tr	10	1	1	1	6	2	60	-	13	14	6	-	-	5	hardpan	
500 - 525	2	3	3	5	5	tr	tr	tr	15	20	25	20	8	4	75[1]	-	4	8	5	-	-	4	micaceous pipe-clay	
25 - 30	18	10	21	9	3	tr	tr	tr	28	4	1	5	3	7	55	1	11	20	4	-	-	2	loamy sand	PROFILE D/1
140 - 165	36	10	12	8	1	tr	tr	tr	20	6	4	3	7	1	62	-	10	9	12	-	-	6		
190 - 205	1	1	9	10	2	tr	tr	tr	18	tr	45	14	1	-	82[1]	-	3	10	3	-	-	2	mottled, micaceous pipe-clay	
400 - 460	1	1	10	8	1	tr	tr	tr	18	17	27	17	-	1	94[1]	-	-	1	-	-	-	4		
25 - 30	17	11	22	12	3	tr	tr	tr	26	3	1	5	15	19	24	-	9	36	8	-	-	4	bleached sand	PROFILE C/0
100 - 110	11	10	25	17	3	1	tr	tr	21	1	1	10	8	5	42	1	8	27	5	-	-	12	or.-red loamy sand	
180 195	48	15	12	8	1	tr	tr	tr	14	1	1	tr	19	7	42	-	10	26	7	-	-	7	pinkish sand	
450 - 470	3	3	13	7	1	tr	tr	tr	23	27	8	15	43	5	49	-	4	10	1	-	-		white pipe-clay	
15 - 25	15	9	21	11	2	tr	tr	tr	19	1	1	21	28	4	40	1	9	38	5	-	-	2	sandy loam	PROFILE B/0
100 - 110	15	9	19	9	1	tr	tr	tr	22	2	1	22	21	10	35	-	13	24	6	2	-	10		
365 - 390	39	16	19	7	1	tr	tr	tr	13	4	tr	1	10	14	30	-	13	29	4	2	-	8	white sand+gravel	
430 - 460	1	1	10	9	2	tr	tr	tr	12	1	51	12	10	-	1	-	91	1	-	-	-	7	pinkish pipe-clay	
40 - 45	16	6	14	6	1	tr	tr	tr	17	3	1	36	30	5	34	-	4	35	9	-	-	13	sandy clay loam	PROFILE 8/1
110 - 120	7	6	17	8	4	tr	tr	tr	13	2	1	42	34	7	35	-	4	36	7	1	-	10	sandy clay	
200 - 250	19	11	19	5	1	tr	tr	tr	9	8	2	26	45	1	45	-	4	29	3	-	-	17	sandy loam	
475 - 490	1	2	8	3	1	tr	tr	tr	10	37	12	26	5	1	93[1]	-	2	1	1	-	-	2	red, mottled pipe-clay	
15 - 25	8	4	9	4	2	tr	tr	tr	30	10	8	25	15	8	37	1	9	32	4	1	1	6	colluvial	PROF. W/1
50 - 60	5	3	6	3	1	tr	tr	tr	6	42	6	28	23	1	46	-	8	9	3	-	-	32	rotten muscovite gneiss	
325 - 360	1	13	8	14	tr	4	tr	tr	20	32	3	5	8	-	71	2	-	3	-	-	-	24		
10 - 15	6	3	8	4	1	tr	tr	tr	32	4	5	34	6	31	25	-	13	13	4	1	1	9	clay loam	PROFILE Y/3
40 - 45	8	9	10	4	2	tr	tr	tr	24	11	8	24	11	25	29	-	5	20	2	-	-	19		
150 - 180	8	5	10	4	1	tr	tr	tr	19	16	6	31	5	23	33	-	4	9	3	-	-	22	micaceous clay loam	
370 - 400	2	2	6	3	1	tr	tr	tr	16	26	10	34	6	38	12	-	1	6	19	1	3	20	mottled pipe-clay	
10 - 20	4	2	7	5	3	tr	tr	tr	42	8	1	27	40	47	23	-	3	10	3	3	3	7	lateritic soil + much ironstone gravel	PROF. 9/0
175 - 225	17	7	11	4	1	tr	tr	tr	19	10	3	28	42	26	34	-	2	9	1	2	1	25		
90 - 110													25	1	35	-	3	28	18	-	-	15	"bruinhart" plot 3	
40 - 60													9	31	26	-	9	22	2	-	4	6	idem no. 4	
40 - 60													15	40	9	-	1	14	3	28	-	4	idem no. 5	

Note: Mechanical analysis: humus removed by digestion with 30 % hydrogen peroxide; followed by dispersion by boiling during 15 min. with 2 N-hydrochloric acid; coarser fractions were separated by *dry-sieving*. Heavy-mineral composition determined in the sand + silt fraction (2 μ–2 mm), using the method of EDELMAN–DOEGLAS (as described e.g. by MOHR *et al.* 1954, p. 220). Very rare minerals, such as brookite, epidote, etc. have been left out in the table.

[1] strongly deviating, more turbid variety of zircon.

[2] group name for minerals, weathered beyond recognition.

Already on first view the profiles in the relatively small area under survey proved to be remarkably variable. They are probably most conveniently classified according to their natural drainage:

(a) *hydromorphic soils*

The many small forest streams and larger creeks are bordered by colluvial and alluvial deposits, the profile development of which is dominated by the effect of impeded drainage caused by a perennially high water table resulting from depressed topography. The distribution of these hydromorphic soils in a part of the Mapane region may be made out by looking at the distribution of the swampy and marshy creek-margin forest, shown in fig. 46, as the latter is confined to these soils.

Texture varies with that of the soil on the adjacent slopes from which the material was derived. In the bleached-sand areas, where drainage impedance is superimposed on podzol development, *peaty podzol* profiles are noted. Sometimes, in clayey material, horizons are found which strongly resemble the *gley* soils occurring in temperate regions. Because their vegetation falls outside the scope of the present study, the hydromorphic soils will not be discussed in detail.

(b) *mottled soils with partially impeded drainage*

In these soil types drainage is not altogether free throughout the year, as indicated by a mottling beginning at relatively small depths. For the classification of these soils a distance of 60 cm below the surface has been taken arbitrarily as the critical depth. If mottling was found at less than 60 cm below the ground level, the soil was assumed to have a more or less deficient aeration during the wet season. These soil types are rather heavily textured (clays to sandy clay-loams), although containing a considerable proportion of coarse sand (cf. table VII). The occurrence of mottling is primarily related to topography (i.e. to the *relative* height of the site), and mottled layers have developed in profiles from various origin as the lower-lying members of drainage catenas. The catena may consist of well-drained, deeply homogeneous red soils or excessively drained, bleached sands on the top of the plateaux or ridges, passing into mottled soils lower down the slope towards the creek (the depth at which mottling begins decreases, descending the slope), and ending in hydromorphic intrazonal soils in the valleys. Naturally, the zone where mottling begins, is found lower down the slopes when the latter consist of light-textured soils developed from Zanderij sands than when they consist of the more heavily textured colluvial flanks of e.g. the schistose hills. Such catenas are shown in fig. 48, which depicts mottled layers both in soils derived from Zanderij sediments and in what are considered to be residual soils derived from basement rock. The relative excess of water by which the mottling is caused, is primarily due to lateral seepage down the slope. Moreover the soils on the slopes generally show a more or less restricted permeability due to a heavier texture (probably in connection with colluvial transport).

Below fig. 48 (in which mottling has been indicated by open circles) descriptions of such profiles are given (prof. at 1150 m and 1900 m). Both yellowish-red mottling in a red matrix and reddish mottling in a yellowish matrix are met with. The mottling itself presumably is due to variations in the degree of hydration of ferric oxides. According to HARDY (1940) in Trinidad soils red mottling and speckling is developed especially in soils with a low base content (particularly with a low content of exchangeable calcium), which indeed is also a feature of the Suriname soils under consideration. Sometimes a distinct relation between the pattern of the mottling and that shown by the plant roots is distinguishable. The mottling perhaps might result from differential leaching along the root traces or along the surfaces of other structural elements (as supposed e.g. by HARDY 1940), or else from local micro-variations in redox-potential and/or in moisture conditions caused either by the physiological activity of living roots or by the decomposition products of decaying roots.

Where the drainage becomes more strongly impeded (i.e. at the foot of the slopes), the hardness of the flecks is seen to increase, and in the lower profiles true iron-oxide concretions are found together with all stages between flecks and concretions in statu nascendi.

That in the mottled soils aeration is more or less deficient, at least during part of the wet season, is indicated by the determinations of free pore space discussed in II.6. In the mottled soils the zone in which roots are found and in which other biological activities take place is thinner than in the soils which are sufficiently and uniformly aerated down to greater depths. However, this difference might partly be due to a greater compactness. Judging from the colour, humic substances also seemed to penetrate to a smaller depth in these soils, but this is disproved by the results of the laboratory analyses, which show (cf. table VII) that the organic-matter content of these soils, even at greater depths, does not differ from that in the better aerated soils. In the latter the more strongly pronounced darkening caused by organic matter is due to a lighter texture in the lower horizons.

The laboratory analyses (table VII) show that the *provision with nutrients is in the upper horizons of the mottled soils significantly better* than in the more permeable soils on top of the terraces. This especially holds for potassium and nitrogen (both as NH_4 and as NO_3), and may be caused by the erosion-rejuvenation and/or by lateral seepage of nutrients washed out from soils lying at a greater height. As appears from table VII, the NH_4/NO_3 ratio does not increase significantly with depth, nor is it higher than in soils that are well aerated to greater depths. This is rather unexpected, as this ratio generally tends to widen in less aerated soils, but it should be borne in mind that laboratory analyses do not necessarily show the actual NH_4/NO_3 ratio in the soil, because in soil samples that

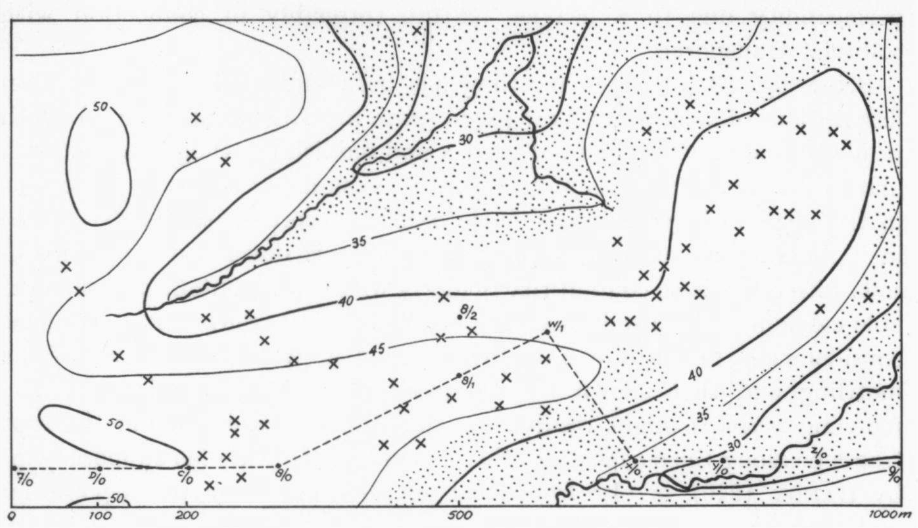


Fig. 50. Relief map of the experimental plot in the Mapane rain forest (cf. fig. 47), showing the distribution of *wana pisie* trees (*Ocotea* sp.) in relation to topography. Heights are in meters above sea level. The broken line denotes the cross-section shown in fig. 49. 7/0, D/0, etc. are the indices of soil pits (cf. table VI and fig. 49). The crosses denote the *wana pisie* trees of 20 cm d.b.h. or more. Dotted area: mottled soils and hydromorphic soils. Unshaded area: free-draining and excessively drained soils.

are dried and stored under tropical conditions, conversion of ammonium salts into nitrates is to be expected.

The greater amount of mineral nutrients as found in some samples of the mottled soils might be the cause of the *greater luxuriance of the forests on the slopes*. It might be thought that this luxuriance would partly be due to better moisture conditions prevailing during the dry season, but a determination of the moisture content of the well-drained soils on the terraces and ridges (cf. II.6) indicated that this factor is presumably of slight significance only.

Although the forest on the mottled soils of the slopes often had a more luxuriant appearance, the sample plots failed to show significant floristic differences with forest on soils at a higher level. Only for one tree species (viz. *wanapisie* = *Ocotea* sp.) a well-marked correlation could be established between distributional pattern and mottling. This appears from the relief map in fig. 50 which shows the distribution of *wanapisie* trees; they appear to avoid the soils where mottling begins at less than 60 cm from the surface.

(c) *free-draining red soils*

The greater part of the soils in the region under consideration is made up of open, porous earths containing a fair amount of coarse sand, and the profiles of these soils are remarkably uniform down to great depths. The latter feature is due to good internal drainage, implying perennially good aeration, which allows both plantroots and animals to penetrate to a fairly great depth. The assumption that aeration is adequate down to the full depth of the profile, is supported by the results of analyses of free pore space given in II.6.

The mechanical composition of these soils varies with the nature of the parent material, but in this region the soils nearly always contain a considerable proportion of coarse sand (which is one of the reasons of the good drainage). This is shown by the analyses of mechanical composition presented in table VI (profiles B/0, 8/1, W/1 and Y/3). The proportion of coarse sand and clay, as averaged over various horizons in selected profiles, is given in table VII, showing that the amount of sand diminishes with depth. Especially the large percentage of coarse sand in the top layers (0–10 cm) is a conspicuous feature of nearly every profile. The figures for 0–5 cm are even higher. In the uppermost layer (0–5 cm) the coarse sand grains are strongly bleached, forming the A-horizon of a *micro-podzol.*

In the N half of the Mapane region under consideration free-draining red soils have developed both from Zanderij sediments (e.g. in fig. 48: 0–375 m; fig. 49: prof. 7/0–8/1) and from residual parent material (basement rock weathered in situ, e.g. in fig. 48: 800–1100 m and 1400–1775 m). It should be noted, however, that a distinction between soils derived from sedimentary and residual parent material would necessarily be artificial, because – at least the upper layers – of residual soils often have undergone colluvial transport over some distance.

In many profiles (cf. the explanation accompanying figs. 48 and 49) at varying depth a *stone line* is encountered, being a more or less continuous layer of angular quartz stones and gravel, partly weathered to such an extent that the stones are easily crushable between the fingers. The stone line sometimes is running parallel to the present surface relief and probably marks an old erosion surface, overlain by later colluvial deposits. Sometimes the stone lines have the appearance of unweathered quartz veins, and are running in an oblique direction down to the rotting rock. The free-draining red soils developed from Zanderij sediments belong to the *non-bleached "dek" soils* mentioned in the classification of VAN DER EYK (1957) ("dek" being Dutch for cover). In the field this distinction between the more heavily textured "dek" soils and light residual soils derived from quartziferous basement rock weathered in situ, sometimes is difficult, and – as will be discussed below – laboratory analyses were necessary to ascertain the origin of the various horizons. The soils derived from the transported deposits are generally characterized by the presence of a sharply delimited layer of very coarse sand and quartz gravel forming the boundary with the underlying pipe-clay which presumably is the weathering product of the basement rock (cf. the descriptions appended to fig. 48: prof. at 250 m, and fig. 49: prof. 7/0, B/0 and 8/1). The zone of biological activity in the well-drained soils is rather deep. Although the greater part of the plant roots is confined to the upper horizon (5–25 cm), the roots and rootlets may penetrate to a rather great depth, and often rootlets were seen at depths of 80 cm and over. Abandoned worm and insect channels were abundant.

The chemical composition, as averaged over a number of profiles, does not differ significantly from that of the less well aerated soils (cf. table VII).

(d) *lateritic (ferrallitic) soils*

As a matter of fact this soil type belongs to a different category than the other soil types that are distinguished in this work, as the latter are based only on drainage characteristics. As far as drainage and aeration are concerned, the lateritic clays generally belong to the free-draining soils, although the yellowish colours of the lateritic soils found at a lower level indicate that at greater depths drainage may not be free throughout the year. At higher levels the lateritic clays are well-drained owing to the porous character of the concretion layer. In the pits that had been dug in these soils even after heavy showers no standing water was found.

The lateritic clays comprise red brown to deep red clays and sandy clays changing by degrees downward to reddish-yellow clays, and they are characterized by the presence of a *concretion layer* of varying thickness, found at varying depth. If developed from parent material containing a fair amount of quartz, as they generally are in the Mapane region, the soils contain much sand, and this, together with the concretions, causes the pervious character of the soil.

At depths varying from zero to about one meter, there occurs a horizon consisting of angular lateritic gravel, red in colour, and generally varying in size between a few mm and 2 cm. Below this concretion horizon, which has a thickness varying between 1 m, or even more, and 10 cm, and mixed up with it, a layer of red (sandy) clay is found which becomes mottled with white and yellow as a greater depth is reached, and ultimately, as the rotting rock is approached, the white colour becomes predominant. As depth increases the concretions often become softer, and may merge gradually into the red or purple flecks of the underlying kaolinitic weathering product of the rock. In the explanation belonging to fig. 48 a description of a typical profile (at 250 m) is given. In fig. 49 prof. 9/0 is a lateritic clay.

This is not the place to speculate on the possible mode of origin of the concretion layer, it may suffice to state that considerable differences of opinion still exist as to the mechanism of laterite formation in general. From an ecological standpoint the most interesting question is whether the vegetational, topographical and weather conditions, under which the concretion layer was formed, were similar to the present conditions or not. HARRISON (e.g. 1934) is of opinion that the *formation of "secondary" laterite* in the Guianas *primarily depends on the composition of the parent rock,* and that to this end no regular alternation of dry and wet seasons is required. This author concludes that in the Guianas the only factor governing the production of lateritic deposits (as opposed to that of pipe-clays), is the original composition of the rocks. The decomposition in situ of *basic* rocks, like hornblende, schists, dolerite, diorite, etc., in which plagioclase felspars with their usual concomitants of ferromagnesian minerals are abundant, has resulted in the formation of red earths consisting chiefly of kaolinite, deeply stained with hydrous iron oxides or haematite, and containing concretions of iron oxide and pieces of aluminous laterite. *Acidic* rocks, in which alkali-felspars are predominating, decompose as a rule to pipe-clay and quartz-sand. This opinion is shared by HARDY *et al.* (1931) working in Br. Guiana, and also by VAN DER EYK (1957), who found in N. Suriname very seldom ironstone gravel in soils derived from granitic rocks (the granite-laterite soils being an exception).

The opinion that the occurrence of concretionary ironstone is determined primarily by the composition of the parent rock, is not necessarily in contradiction with the widely held belief that a horizon with iron-oxide accumulation develops only in the presence and under the influence of a high ground-water level, and that it marks the zone of intermittent saturation.

The concretion layers in the soils of the region under consideration may likewise have originated under peneplanic conditions as *pseudo-illuvial deposits in the zone of fluctuating ground-water table.* But in that case, because the soils now generally are well above the groundwater level, a later uplift followed by dissection (and in many sites by a subsequent truncation of the upper layers) has to be assumed. This has also been assumed for profiles of this kind which are present throughout large areas in central Brazil (MARBUT 1932) and elsewhere in comparable regions in the tropics (PENDLETON 1936, STEPHENS 1946, etc.). Another explanation, which e.g. was given for the occurrence of the perdigón layers in the Cuban Nipe profile (MARBUT 1932), regards the concretions as a primary weathering product from ferrallitic material, developed under the influence of *good drainage,* the iron segregations merely being *indurated residual concentrations* brought about by the leaching out of silica and bases.

It was not investigated whether there was in the Mapane region any relation between the occurrence of concretionary layers and the kind of parent rock, as the latter, owing to the very deep weathering, is mostly difficult to ascertain in the field.

N of the Mapane Cr. lateritic clays occur as isolated patches, which further southwards become more frequent and larger in extent. On the schistose hills S of the Mapane, like elsewhere in the hilly upland in N Suriname, the lateritic soil types predominate. The lateritic upland soils bear a type of rain forest which differs markedly from the lowland type (cf. III.4). On the lateritic soils in the Mapane region a luxuriant rain forest was found, which did not differ significantly (at least with the analytical methods used) from the surrounding rain forest on well-drained red soils which contained no concretions. For instance, along the line transect shown in fig. 48 no statistically significant differences in the floristic composition of the forest were found between the quadrats situated between 375 and 650 m on the one hand and those situated between 800 and 1900 m on the other hand.

A similar *overlapping of the predominating forest type over relatively small areas with a different soil type,* will be mentioned below for patches of bleached white sand, which normally bear savanna forest, but which may become overlapped by rain forest. Chemical analyses of the lateritic clays in the Mapane region are available only for one profile (9/0), indicating that the base status probably does not differ much from that in the other soil types. The organic matter content in the upper layers seems to be considerably higher than in the other soil types (viz. up to 4 %) which is in accordance with findings in the concretionary soils of the schistose hills (cf. II.4).

The *reduction of the rooting space* by the presence of iron-oxide concretions, which may make up 50 % or more of the total amount of mineral soil, might have important consequences for plant growth. If the values found for organic matter content, exchangeable bases, etc. (the computation of which is based on fine earth) are expressed as percentages of the total mineral soil, including particles of 2 mm and over, they prove to be considerably lower than they are in the other soil types.

(e) *excessively drained soils*

The higher ridges and terraces in the N half of the area pictured in fig. 46, are almost invariably capped with a layer of coarse, bleached, nearly pure sand, usually several meters thick. The clay content of the bleached sands is less than 5 %. Above that value the soils show a red colour. This soil type was described by VAN DER EYK (1957) as "*Zanderij series*", the dry variant of the "bleached dek soils".

As shown by the vegetation map given in fig. 46, the central parts of the larger sand plateaux bear *open savanna* (consisting of groups of low woody and herbaceous plants, predominantly *Clusia*, *Byrsonima*, *Curatella*, etc., separated by patches of bare sand), surrounded by a fringe of *savanna forest*. The smaller white-sand areas are wholly covered with forest and small patches of white sand even may bear rain forest. For a description of these xeromorphic types of vegetation reference is made to the first parts of "The Vegetation of Suriname" (LINDEMAN 1953, 1959).

In the W part of Suriname extensive areas of *wallaba* forest are found on the white-sand terraces, similar to those described by DAVIS *et al.* (1934) for E Br. Guiana. Such *white sands* have a wide distribution in the tropical rain forest region, and were regarded by RICHARDS (1941) as tropical *lowland podzols*. The possible influence of a biotic factor on the development of the white sands in Suriname will be discussed below (p. 126).

The boundaries of the areas which bear these types of xeromorphic vegetation, as mapped in fig. 46, coincide exactly with those of the excessively drained white-sand areas, the edges both of the white-sand areas and of these types of vegetation always being very sharp.

This is, for instance, shown in the cross-sections presented in figs. 48 and 49, and in the descriptions of two profiles of this soil type (prof. at 0 m in fig. 48 and prof. C/0 and D/0 in fig. 49) which are appended to these figures. Just as with the non-bleached "dek" soils, at the base of the transported deposit a layer containing a considerable amount of very coarse sand and angular quartz gravel is found (cf. prof. C/0 and D/0 in table VI) which marks the boundary with the sedentary kaolinized rock; this boundary is shown in fig. 48 between 0 and 375 m by a broken line. In these profiles found near the S boundary of the Zanderij formation, the white-sand layer is relatively thin (3–4 m). That the sandy layers really are adventitious, and have originated from parent material differing from that of the kaolinitic layers, finds support in the heavy-mineral profiles set out in table VI. The heavy-mineral associations of the upper layers appear to be totally different from those of the kaolinitic subsoil. Frequently a rather sharply defined stratification is found in the bleached sands, as shown e.g. by the descriptions appended to fig. 48 (prof. at 150 m) and to fig. 49 (prof. C/0 and D/0). These yellowish or reddish layers are characterized by a somewhat higher clay content and by a different mechanical composition of the sand fractions (cf. in table VI: in prof. D/0: 260–280 cm, and in prof. C/0: 100–110 cm). These layers might be considered to be illuviated horizons, but this would be in contradiction with the heavy-mineral analyses (cf. table VI) which make it more probable that the zonation is not a matter of pedogenesis but is due to difference in stratification caused by variations in the settling velocity during sedimentation.

As mentioned above, small patches of bleached sands may bear high forest, the physiognomy and floristic composition of which is closely related to that of true rain forest. Profile D/0 was situated in such a forest, the composition of which was studied in sample plot 2 discussed in III.2.2. This particular case of *overlapping* of high forest over a soil type which normally bears savanna forest is presumably due to the fact that the rootlets of the trees extended down to a depth below 5 m, i.e. in the rotting rock.

Under forest cover the bleached sands are coloured greyish-brown by organic matter to a depth of 1 m or over. The upper horizons often are markedly darker than in the more heavily textured red soils. Although it is a well-known fact that the effect of organic matter on soil colour is more marked in sandy than in more heavily textured soils, the laboratory analyses (cf. table VII) show that the upper horizons of sands and sandy loams under forest cover nevertheless contain less organic matter than the heavier soils.

Often one or more ill-defined illuvial horizons are recognizable (cf. e.g. description of prof. D/0 below fig. 49) by a slightly darker colour. The somewhat darker horizon between 60 and 70 cm in prof. D/0, is characterized also by a different composition of the heavy-mineral content (cf. table VI). The toplayer (0–10 cm) of the sand soils contains much bleached sand in the form of coarse grains.

In the Mapane region only very seldom a *hardpan* was found, though such indurated layers are common elsewhere in the bleached Zanderij sands (e.g. BAKKER 1954, 1957, VAN DER EYK 1957, COHEN *et al.* 1953). In profile D/0 (cf. fig. 49) situated in the centre of a sand-capped plateau where relief is at dead-level, a coffee-brown, indurated humic layer is found at a depth of 4 m, in the very coarse sand layer which forms the boundary with the underlying impervious pipe-clay (cf. table VI). It is uncertain whether this "*ortstein*" was formed under the present vegetation (and may still be formed) or not. Probably the hardpan is a *relict B-*

horizon formed by intensive leaching following the removal of the forest at some distant period. This view is supported by the fact that charcoal and fragments of primitive Indian pots were found in the pit.

Biological activity (rooting, traces of animal activities, etc.) penetrates deepest in the very loose, pervious sand soils under forest cover. Soil moisture probably is at a minimum during drought periods (cf. II.6).

As shown by the results of the laboratory analyses presented in table VII the base status of the bleached sands and loamy sands is lower than that of the more heavily textured soils, though the difference is less than would be expected from the sterile appearance of these sands. It should be noted, however, that only sands under high forest were sampled, the xerophytic types of vegetation falling outside the scope of this study.

In table VII the results of the *laboratory analyses* of a number of selected profiles in the area under consideration have been summarized. In the second column the number of sampled profiles upon which the averages are based has been given.

As might have been expected from the extreme age of the soils and the high rainfall (which exceeds evaporation nearly throughout the year) the soils are invariably acid and intensively leached, leaving the clay-complex strongly dominated by H ions. The rather low humus content, the acidity and the deficiency in bases are features which those soils share with the majority of rain-forest soils elsewhere in the tropics.

The *organic matter* content (which may be computed by multiplying the carbon-percentage with 2.2, i.e. by assuming a 45 % C content of the soil organic matter which is determined with the wet-combustion method used) seldom was large and varied between 0.8 and 6 % (mean: 1.9 %) in the upper 40 cm of the red soils. This value is in accordance with the rather low values found elsewhere under tropical rain forest.

CORBET (1935) reported an average of 1 % in Malayan rain forest soils; RICHARDS (1939) found values of 2 and 5 % in the upper 40 cm under mixed forest in the Shasha and Okomu forest reserves (after multiplying the C percentage with 1.7), whereas JONES (1955) in the Okomu-plateau forest found an average of only 0.8 % C (= about 1.4 % org. matter). DAVIS *et al.* (1933) reported in *mora* forest in Br. Guiana 0.8 % org. matter (0–15 cm), in *morabukea* forest 5 % (0–20 cm), in mixed forest 1 % (0–60 cm); in *greenheart* forest on sand they found 1.6 % (0–20 cm), and in *wallaba* forest on bleached sand 1.4 % (0–25 cm).

In the well-drained soils humic penetration was found to be rather deep with indefinite lower limit; at 1 m depth generally 0.5 % organic matter or more was found. Owing to the well-known fact that the effect of organic matter on soil colour is more marked in sandy than in more heavily textured soils, organic-matter content and humus penetration in the field seemed greatest in the bleached sands, and appeared to decrease with the density of the texture. This, however, was disproved by the laboratory analyses.

TABLE VII

Summary of results of the analysis of rain forest soils of the Mapane and Coesewijne region. The data were obtained by averaging over the individual results of the samples, the numbers of which are given in the second column.

	number of samples	depth(cm)	% sand	% clay	% C	% N	C/N	pH (H₂O)	pH (KCl)	Exchangeable plant nutrients (Na-acet. extract.) in p.p.m.									NH₄-acet. (p.p.m.)	
										Ca	Mg	K	P	NH₄	NO₃	NH₄/NO₃	Fe⁺⁺	Al	Na	K
Mapane region: free-draining red sandy clay-loam → clays	8	2–10	66	25	1.4	0.11	12	4.3	3.5	tr	7.5	50	tr	28	52	0.6	180	163	–	28
	12	10–25	59	31	1.0	0.08	12	4.5	3.8	tr	1.2	53	tr	20	40	0.5	102	220	–	60
	6	25–40	51	41	0.5	0.05	10	4.7	3.9	tr	3.7	25	tr	23	17	1.2	60	170	–	15
	6	40–60	51	36	0.4	0.04	10	4.6	3.8	tr	4.5	37	tr	22	15	1.5	60	193	–	40
	5	60–100	49	38	0.3	0.02	9	4.7	3.9	tr	5.5	28	tr	12	10	1.2	24	185	–	15
	32	2–60	55	34	0.7	0.07	11	4.6	3.8	<50	4.1	41	tr	24	26	1.0	90	186	–	33
Mapane region: excessively drained sands → loamy sand	3	2–10	83	6	0.6	0.04	10	4.5	3.6	tr	3.2	35	tr	20	15	1.5	120	122	–	35
	4	10–25	71	10	0.8	0.08	10	44	3.7	tr	2.2	30	tr	87	25	2.9	90	152	–	28
	3	25–40	72	11	0.8	0.08	15	4.7	3.9	tr	tr	35	tr	22	12	1.9	60	198	–	20
	3	40–60	73	10	0.6	0.06	11	5.0	4.1	tr	tr	33	tr	8	7	1.0	30	190	–	38
	–	60–100	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	13	2–60	74	10	0.7	0.07	11	4.6	3.8	<50	1.5	34	tr	33	14	1.8	60	171	–	30
Mapane region: mottled soils (sandy clay → clay)	3	2–10	63	27	1.9	0.16	12	44	3.7	tr	10.0	82	tr	50	95	0.6	150	254	–	60
	4	10–25	58	31	0.9	0.08	11	44	3.8	tr	tr	44	tr	24	52	2.7	9.0	205	–	38
	2	25–40	48	44	0.7	0.06	11	4.6	3.8	tr	2.5	22	tr	28	25	1.7	78	254	–	15
	5	40–60	47	49	0.4	0.04	9	4.6	3.8	tr	2.2	29	tr	17	15	1.3	42	192	–	25
	4	60–100	41	45	0.4	0.02	11	4.7	3.8	tr	tr	30	tr	14	9	1.4	30	150	–	40
	14	2–60	53	40	0.8	0.08	11	45	3.8	<50	3.5	40	tr	27	40	1.6	78	221	–	35
Mapane region: soils of "bruinhart" stands	2	2–10	63	28	1.8	–	–	5.2	4.3	tr	12.5	52	3	22	53	0.4	92	92	17	80
	2	10–25	59	31	1.3	–	–	5.4	4.6	42	17.7	47	5	22	40	0.6	115	115	17	60
	2	25–40	57	32	0.7	–	–	6.0	4.9	75	225	37	5	20	22	0.9	140	140	17	37
	2	40–60	61	34	0.5	–	–	5.3	4.4	tr	10.0	22	5	20	10	1.7	105	105	13	30
	–	60–100	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	8	2–60	58	32	1.0	–	–	54	4.5	30	155	37	5	21	28	1.0	114	114	16	48
Coesewijne region: sandy loam → clay-loam	4	2–40	64	13	0.9	–	–	5.6	5.0	tr	7.5	28	2	37	20	3.0	120	120	17	33
	4	10–25	85	10	0.9	–	–	5.9	4.8	tr	5.0	25	5	25	10	2.8	115	162	7	32
	3	25–40	61	18	0.8	–	–	5.4	4.6	tr	2.0	28	4	25	12	4.1	87	173	17	43
	4	40–60	61	19	0.6	–	–	5.6	4.7	tr	1.6	20	4	25	12	3.0	65	160	15	40
	4	60–100	62	20	0.3	–	–	5.6	4.8	tr	1.2	5	4	27	10	3.5	50	102	15	40
	15	2–60	68	15	0.8	–	–	5.6	4.7	<10	3.5	24	4	27	13	3.2	111	157	14	37

Note: sand: particles of 2 mm–50 μ; clay: particles $< 2\,\mu$; the difference between the sum of the figures and 100, gives the % of silt (50–2 μ).

Carbon and nitrogen content (in % of oven-dry soil) determined, using the Walkley–Black (wet combustion) and standard-Kjeldahl method respectively. Easily extractable ions estimated using Morgan's technique for rapid microchemical soil tests (as modified by Venema) in the extract obtained after shaking one part of soil in 2.5 parts of Na-acetate in acetic acid (pH 4.8) during 30 min.; results expressed as parts per million (mg/kg soil).

Last two columns: exchangeable Na and K, determined after shaking with NH_4-acetate in acetic acid (pH 4.8).

The *total-nitrogen* content is rather high, higher than in the corresponding horizons in the S-Nigerian forest, where RICHARDS (1939) mostly found a percentage of 0.03 in the upper 40 cm. Accordingly the *C/N ratio* under the Mapane rain forest is markedly lower (9–12) than in the Nigerian forest soils, where this ratio averaged about 17. The C/N ratio in the Mapane forests is only slightly above the value of C/N = 10, which is tentatively accepted as denoting complete humification.

The rate, at which organic debris are incorporated into the mineral soil, is rapid, as indicated by the thin discontinuous layer of undecomposed plant material overlying the topsoil. A thin layer of loose *litter*, generally less than 3 cm thick and leaving small patches of mineral soil uncovered, overlies all soil types. Below the litter and mixed with the upper few centimeters of the topsoil (which generally contains much coarse, bleached sand grains) some completely desintegrated material (leaf mold) is found. The analyses showed that at 5–10 cm depth the C/N ratio already had narrowed to an equilibrium at about 11 : 1.

The amount of readily *available nitrogen* (both as NH_4 and as NO_3) also was found to be rather high for a tropical forest soil. In the well-aerated red soils the NH_4/NO_3 ratio generally did not considerably exceed unity. In the sands and in the mottled profiles a few complexes were encountered which showed higher values (NH_4/NO_3 up to 5). Yet the average ratio in the profiles in these soils was not significantly higher than in the well-drained red soils. It should be noted, however, that during the drying and the storage of the soil samples under tropical conditions the ratio may have altered considerably.

The *acidity* varied little from the average value of 4.6 for pH(H_2O) [pH(KCl): 3.8]. The analyses show a positive correlation between acidity and organic-matter content (cf. fig. 51). Consequently in the majority of the profiles acidity tended to *decrease with depth.*

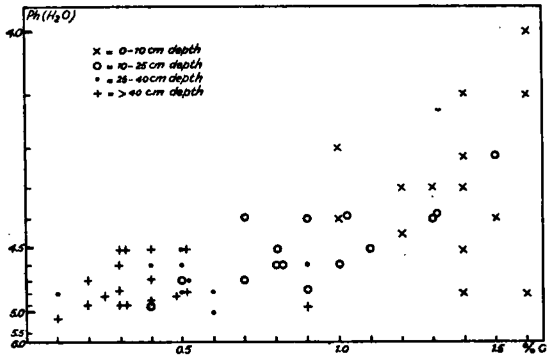


Fig. 51. Relationship between organic matter content and soil acidity in 60 samples from different types of rain-forest soils in the Mapane region. Organic-matter content determined using Walkly–Black's method.

As might have been expected, the quantity of *exchangeable bases* was low to very low. With the method used (shaking with sodium acetate) only the quantities of the *readily available plant nutrients* were determined. In the last two columns of table VII the total quantity of exchangeable sodium and potassium has been given as determined after replacement by ammonium ions. The latter value especially is of interest for long-living plants like trees. The quantity of exchangeable potassium does not look unsatisfactory (as compared with the data given for other tropical soils), but the soils appeared to be *extremely deficient in calcium and phosphorus*, a feature shown by the majority of tropical forest soils. The quantity of exchangeable ions decreased steadily with depth. These ions presumably are adsorbed for the greater part to the humus colloids. The clay minerals in the soils under consideration practically entirely belong to the *kaolinite* group, which shows a very low base exchange capacity (3–15 m.e./100 g). Moreover, the cations presumably are largely replaced by hydrogen, leaving a *highly base-desaturated clay complex.* Especially for the amount of exchangeable iron ions a very close correlation was found with organic-matter content. Exchangeable aluminium, on the other hand, did not vary with depth, and was presumably for the greater part held by the clay colloid. The very high quantity of exchangeable aluminium is another indication of the highly advanced stage of development reached by the soils and of the degradation of the clay-colloids. The averages given in table VII show that the exchangeable bases did not tend to accumulate in an illuviated horizon. An eluviated horizon (being poor in organic matter and plant nutrients) was found exceptionally in very sandy profiles.

The bleached sands and loamy sands with excessive drainage were somewhat poorer in plant nutrients than the more heavily textured soils. Though the difference was much less than would have been expected. It should be noted, however, that samples only have been analyzed from soils bearing rain forest. Probably the leached sands carrying xeromorphous savanna forest are considerably poorer.

As was mentioned above, the highest figures for exchangeable plant nutrients were found in the upper horizons of the mottled soils on the slopes (where drainage is not altogether free throughout the year), although the averages given in table VII fail to show this tendency.

As might have been expected from their old age, the soils are practically devoid of *fresh mutable minerals*; in the sand fraction of some 100 samples which were taken from different horizons in various soil types at best traces of felspars were found. In a few samples muscovite was found (max. 1 %), and heavy minerals (cf. table VI) were found in maximal amounts of less than 1 %.

The distribution of *tree roots* as seen in the soil pits, showed that these roots have a strong tendency to concentrate in the upper horizon between 5 and about 30 cm; in this zone the main skeletal roots were found, but thinner roots were frequently met with at a much greater depth, and fibrous roots generally extended in small numbers as deep as 1 m or deeper. Depth of root penetration increased with decreasing heaviness of texture, and consequently was deepest in the bleached sands, where fibrous roots sometimes were found at 5 m depth, in the kaolinitic rotting rock. As might have been expected, the depth to which the root systems penetrated proved to be the smallest in the hydromorphic soils. The tendency of the tree roots to concentrate in a horizon just below the surface, was observed in the sands too. This fact presumably stands in relation to the competition for water and plant nutrients in these excessively drained soils. JONES (1955) has already pointed out that the root systems of trees in the tropical rain forest may in general be superficial, but that the distribution of the roots as seen by him in soil pits in a S-Nigerian rain forest appeared to be very similar to that which is observed in similarly well-drained forest soils in temperate regions.

An important feature is that species with *stilt roots* seem to be more frequent in the wet vegetation types on poorly aerated soils and in the xeromorphic savanna forest on loose, excessively drained soils than on other soil types. In savanna forests for instance *sabana-mangro* (*Clusia*) often is abundant and especially in low savanna forest it is a striking feature. The relative frequency of species with stilt roots in forest on poor, dry soils might be an *adaptation* to this habitat, because just below ground level the stilt roots give rise to many secondary and tertiary roots and rootlets, thus adding materially to the total extent of the root system. This also might explain why stilt roots are in the Hylaea more common in smaller trees than in tall trees. RICHARDS (1952, p. 62) already pointed to the last mentioned fact, which seems to be in contradiction with the explanation that stilt roots are of great survival value because they provide a better anchorage.

Anthropogeneous factors

From the majority of the pits and borings *fragments of charcoal* were reported, although the amount varied greatly. Minute flecks and larger pieces of charcoal were found as a rule thinly scattered in the upper horizons, between 0 and 40 cm (exceptionally below 60 cm), sometimes forming a conspicuous, continuous layer. The charcoal fragments point unmistakebly to disturbance of the forests of the Mapane region by fire during some distant period, even though the structure and floristic composition of the rain forest may indicate that the forests have been left undisturbed at least during the last, say two, centuries.

That the disturbance by fire was caused by human interference is strongly supported by the finding of fragments of primitive Indian pots in a pit dug in bleached sand (prof. C/0, on top of the sand plateau, cf. fig. 49). Considerable quantities of fragments of pots were found elsewhere in the region during the construction of the truck road. The traces of Indian settlements invariably were found in the bleached, white-sand profiles. There are also other arguments in favour of the opinion that the Amerindian population was formerly less sparse than it is nowadays; already a comparatively scarce population is able to destroy relatively large areas of forest, when they use the bushfallow system of shifting cultivation, as it is still practised to this very day by the Amerindian population.

It is uncertain what might be the causal relation between the ancient Amerindian settlements and the bleached-sand areas. It is possible that the latter are soils, strongly leached and degraded as a consequence of the long-continued practice of burning the vegetation, the bleached white sands being the sites where destruction of the vegetation (and accordingly of leaching) was most intensive (e.g. in the settlements themselves and in their direct surroundings). The original, coarse sandy parent material already may have been rather poor in clay and clayforming minerals. The hypothesis of a leaching of bases and of an eluviation of the finer fractions by biotic causes, is supported by the sharp boundaries found between the white sands and the more heavily textured, red soils.

The question may be raised where the clay fraction has got to. Even if the parent material initially was relatively poor in clay, the assumption has to be made that large amounts of clay have been removed by lateral eluviation. It is possible that the clay minerals have split up into the mobile component oxides, according to HARDY's hypothesis (1940), that the clay minerals are stabilized by bases, but are split up when substitution by hydrogen (hydrolysis) has proceeded far enough to deplete the minerals of their structural bases.

On the other hand it is also possible that the bleached sands were deposited as such, and that the present distributional pattern of the differently textured soils already existed at the time of the arrival of the Amerindians, who chose the bleached sands for their settlements.

Similar bleached sands have a wide distribution elsewhere in the tropical rain-forest region and were regarded by RICHARDS (1941) as *lowland tropical podzols*, derived from parent materials which were probably initially poor in bases and clay-forming materials. In such extremely base-deficient soils there seems to be a tendency for raw humus to accumulate, which in its turn leads to the preferential removal of sesquioxides (iron and aluminium) rather than of silica. The white sands in the Moraballi Cr. region (Br. Guiana), which bear *wallaba* forest (*Eperua falcata*) were also regarded by RICHARDS as podzolic, though no B-horizon was found in borings extending down to a depth of about 2 m. A yellow layer found by DAVIS (quoted by RICHARDS 1941) in another white sand profile in Br. Guiana is not necessarily a B-horizon; such horizons were found also in the white sands of the Mapane region, but these differences in colour are, as discussed above (p. 121), presumably due to differences in the parent material. Indurated illuvial horizons in the *forests* of the Mapane region were but seldom encountered, though such horizons are of common occurrence in the savannas of Jodensavanne, Cassipora, Zanderij, etc. A paper by P. C. Heyligers dealing with this region is in preparation. As will be expounded below (II.3), hardpans in statu nascendi were found in white-sand soils bearing creek-margin forest or rain forest in sites where drainage was impeded, due to depressed topography and/or an impermeable subsoil (pipe-clay). In the Wayombo region extensive areas of *wallaba-dakama* forest (*Eperua falcata-Dimorphandra conjugata*) were found on poorly drained white sand soils with a humous hardpan in statu nascendi at ½–1 m depth.

II.2.3. *Correlations between soil factors and vegetation*

In the Mapane region the aeration of the soil and its power of supplying the plants with water are evidently by far the most potent ecological agents. The main types of vegetation in this region (cf. fig. 46) are determined by these edaphic factors. The swamp- and marsh-forest are found on hydromorphic soils where drainage is impeded owing to topographical conditions. Savanna forest (i.e. xeromorphic rain forest or dry evergreen forest) is the climax vegetation on excessively drained, bleached sands (the other types, such as shrub savanna and open savanna being fire-subclimaxes). Mesophytic (rain) forest is found on the mesic sites, where both aeration and water-supply are adequate throughout the year.

Both composition and physiognomy of the hydro- and xeromorphous formations differ strongly from those of mesophytic forest, although there are many examples of transgressive species, as will be pointed out in part III. A few species show no preference at all, such as *wallaba* (*Eperua falcata*), which is found along the whole gradient from xeric to moist sites. This species even shows a conspicuous preference for the two extreme ends of the gradient, showing a tendency to single-dominance both in xeromorphous forest and in forest on moist sites. In mesophytic forest too this species may locally be rather frequent, although it is absent in other places.

As will be discussed in IV.5, most species of the rain-forest trees show a non-random distribution. It seems most likely that the heterogeneity within the rain forest is caused by differences in edaphic factors, although the differences in composition of the rain forest are regarded by some authors as entirely accidental.

Although it is a well-known fact that tree species (at least those from temperate forests) generally have a rather wide environmental tolerance, and hence are not regarded as the most suitable edaphic indicator plants, I examined the distributional maps of the tree species (some of which are shown in figs. 47, 50, 52 and 69) in order to find out whether it would, nevertheless, not be possible to find some relation with differences in the soil factors. However, the systematic sampling of the soil and the mapping of the trees belonging to 10 selected species overlapped only in one area, and the latter was but 50 ha in extent. Moreover, only a restricted number of soil factors was studied (cf. table VII).

As was expounded on p. 116 (cf. figs. 47 and 51), for the Lauracea *wanapisie* (*Ocotea* sp.) a significant correlation between the degree of

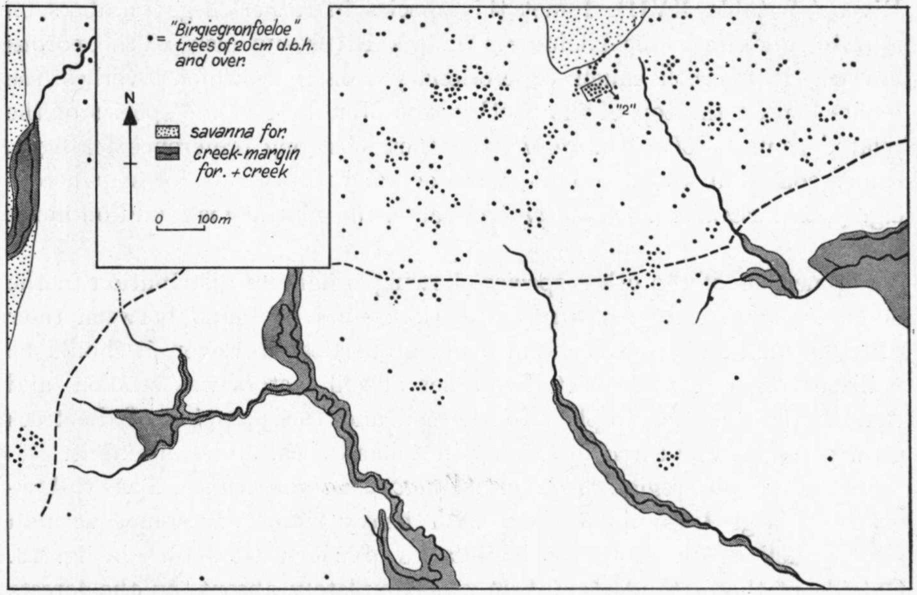


Fig. 52. Distributional pattern of trees of *Qualea rosea* (*birgiegronfoeloe*, Vochysiaceae) in a small area in the Mapane region (for location cf. fig. 46) demonstrating the preference shown by this species for the soils derivated from the Tertiary Zanderij-sediments. The approximate boundary between the latter and soils derived from Old Basement rock weathered in situ, is denoted by a broken line.

drainage and the occurrence of trees of more than 20 cm d.b.h. could be demonstrated.

For another species which clearly showed a non-random distribution, a strong preference was found for soils derived from a definite parent material: *birgiegronfoeloe* (*Qualea rosea*) was found to be most abundant on the sandy soils (varying from brown loamy sands to sandy clay-loams) derived from the sediments of the Zanderij formation, although small nests of trees of this species were found also on soils derived from Old Basement rock weathered in situ. Elsewhere in the Mapane region *birgiegronfoeloe* shows a preference for rain forest near its ecotone to more or less xeromorphous forest. It is possible that this species needs room for the development of its long tap-root; a similar explanation was suggested by SYKES (1930) for the distribution of the dominant species of a *Gossweilerodendron-Cyclicodiscus* type of rain forest in Nigeria, which is confined to deep sandy soils. The presence of this long tap-root of *Qualea rosea* probably explains why this species sometimes is found also and even very abundantly on leached white sand underlain at not too great depth by rotting parent rock, as in profile C/0 (fig. 49) in sample plot 2 (cf. p. 175), where part of the fibrous roots were found in the rotten rock.

A puzzling fact is the complete absence of *Qualea rosea* in the rain forest on non-bleached Zanderij soils in the region of the Upper-Coesewijne

River (cf. table XVII). I met this species in rather large numbers on granite sands near the Kleine Saramacca River and also on the porous lateritic loam with much concretionary ironstone which overlies the ferrite cap on the top of the Stofbroekoe Mountain. Some species of the related genus *Vochysia* (*kwarrie*) too show a strong preference for light, sandy soils and are abundant in the ecotone to savanna forest, whereas e.g. *Qualea coerulea* (*laagland gronfoeloe*) on the contrary is found on moist sites.

For neither of the other species showing a definite distribution in the 50-ha experimental area, any correlation could be found between their distributional pattern and definite soil properties. However, it should be realized that only a restricted number of soil factors was studied, and that the systematic sampling of the soil and the mapping of the trees growing on it, was carried out only in a small area, 50 ha in extent.

In the Mapane region *bruinhart* (*Vouacapoua americana*), a very slow-growing, large Leguminous tree with heavy timber, was met with in sharply delimited stands, the boundaries of which are shown in fig. 46. Outside of these stands *bruinhart* was completely absent. In the forests which cover extensive areas of lateritic earths on the cristalline basement south of Mapane Creek, *Vouacapoua* is almost invariably found as an associate of the leading canopy species. The composition of three of these stands was studied by means of sample plots 3, 4 and 5 (cf. p. 177). A preliminary comparison with the composition of the surrounding forest as assessed by means of the 5.6-ha sample plot 1 (cf. p. 167) failed to show a clearly recognizable correlation between this tree and other species occurring in the *bruinhart* stands, although it is not impossible that the *Eschweilera* species may prove to be more abundant in the latter.

In the three *bruinhart* stands studied, soil samples were taken, the analyses of which (averaged over the three soil pits) are given in table VII. Each of the 8 soil samples shows a higher pH than is found on the average in the samples from the three soil types under rain forest where *Vouacapoua* was absent. It appears that there is also a significant difference in the amount of readily extractable magnesium and in the amount of less readily available potassium (as determined after shaking with ammonium-acetate in acetic acid, cf. last column in table VII). Although there were differences between the soils of the *Vouacapoua* stands and those of a small area of rain forest in which this species did not occur, this does not necessarily mean that they are the (direct) cause of the difference in floristic composition (which, moreover, only concerns this one species).

The peculiar distribution pattern shown by the *Vouacapoua* stands in the Mapane region, viz. an almost ubiquitous distribution in the forests on Old Basement rock and an occurrence in isolated patches in the transitional zone to soils derived from the late Tertiary or early Quarternary Zanderij-deposits, might suggest a distributional correlation with (Holo-) Plistocene physiography. The results of heavy-mineral analyses made in the soils of three stands, do not contradict this hypothesis, but it must be admitted that our present knowledge of the petrography and of the heavy-mineral associations is too fragmentary to allow a fruitful discussion of the problem.

II.3. SOILS OF THE UPPER-COESEWIJNE REGION

According to the geological map of Suriname (SCHOLS *et al.* 1950), the area of the region S of the Upper Coesewijne R. where the phytosociological studies were carried out (i.e. the area shown in fig. 53), belongs to the Zanderij formation. The same opinion is held by COHEN *et al.* (1953, p. 207) and by VAN DER EYK (1957). The second author published a soil map upon which the majority of the soils in that part of the Upper-Coesewijne region considered in the present study are marked as "cover soils". The vegetation map reproduced in fig. 53 may serve also as a soil map; the soils of the mesophytic forest vary from well-drained brownish/yellow-red clay loams to rather excessively drained loamy sands (the "*non-bleached cover soils*" of VAN DER EYK), whereas the xeromorphous vegetation types (savanna forest and shrub-savanna) cover the excessively drained, bleached, coarse quartz sands which contain less than ca. 5 % clay and silt ("*bleached cover soils*"). The majority of the hydromorphic soils (which fall outside the scope of this study) along the creeks are bleached sands. They often are covered with a thick A_0-layer that may attain a depth of one meter. These soils belong to the "*Blakkawatra series*" of VAN DER EYK.

A cross-section of the area under consideration has been reproduced in fig. 54, showing that in this region the bleached sands often are found in the depressions along the creeks, whereas farther southwards and E of the Costerie Cr., the white sands are – on the contrary – capping the flat tops of the low hills (as they also did in the Mapane region; cf. fig. 48).

The average texture of the soils covered with high (sub-)mesophytic forest (which is provisionally called "rain forest", though it is less luxuriant than the Mapane rain forest) is shown in table VII. These figures are averaged over a number of samples which were taken at random in soils of different texture. The texture of the "non-bleached" cover soils of the Coesewijne region resembles that of the corresponding sedimentary soils of the Mapane region (e.g. the soils between 300 and 650 m in fig. 49). But, the first-named soils contain a considerably smaller number of particles belonging to the class of the coarsest sand (2–0.6 mm), as appears from comparison of the mechanical composition given in tables VI (first 5 profiles) and VIII.

The mechanical composition of a typical example (profile 1) of the *heaviest type of the sedimentary cover soils* found in the Upper-Coesewijne region has been recorded in detail in table VIII. This profile shows the following characteristics:

0 – 5 cm: thin layer of partly decomposed forest litter, overlying loose, brown sandy loam, and containing many bleached quartz grains at the top; abundant mild humus; conspicuous concentration of roots and rootlets in the topmost 5 cm (colour at 5 cm: 7½ YR 3/2).

5– 40 cm: (*main rooting zone*): brownish-yellow sandy clay loam, becoming more compact with depth containing much mild humus, but the amount of the latter decreasing with depth; rootlets frequent; occasional flecks of charcoal (10 cm: 10 YR 4/3; 25 cm: 10 YR 5/3; 40 cm: 10 YR 5/4); gradually passing into:

40– 70 cm: rather compact, brownish-yellow clay loam; fragmentated/nutty structure, becoming coarser with depth; humus 0.6–0.4 %; rootlets frequent; gradually merging into:

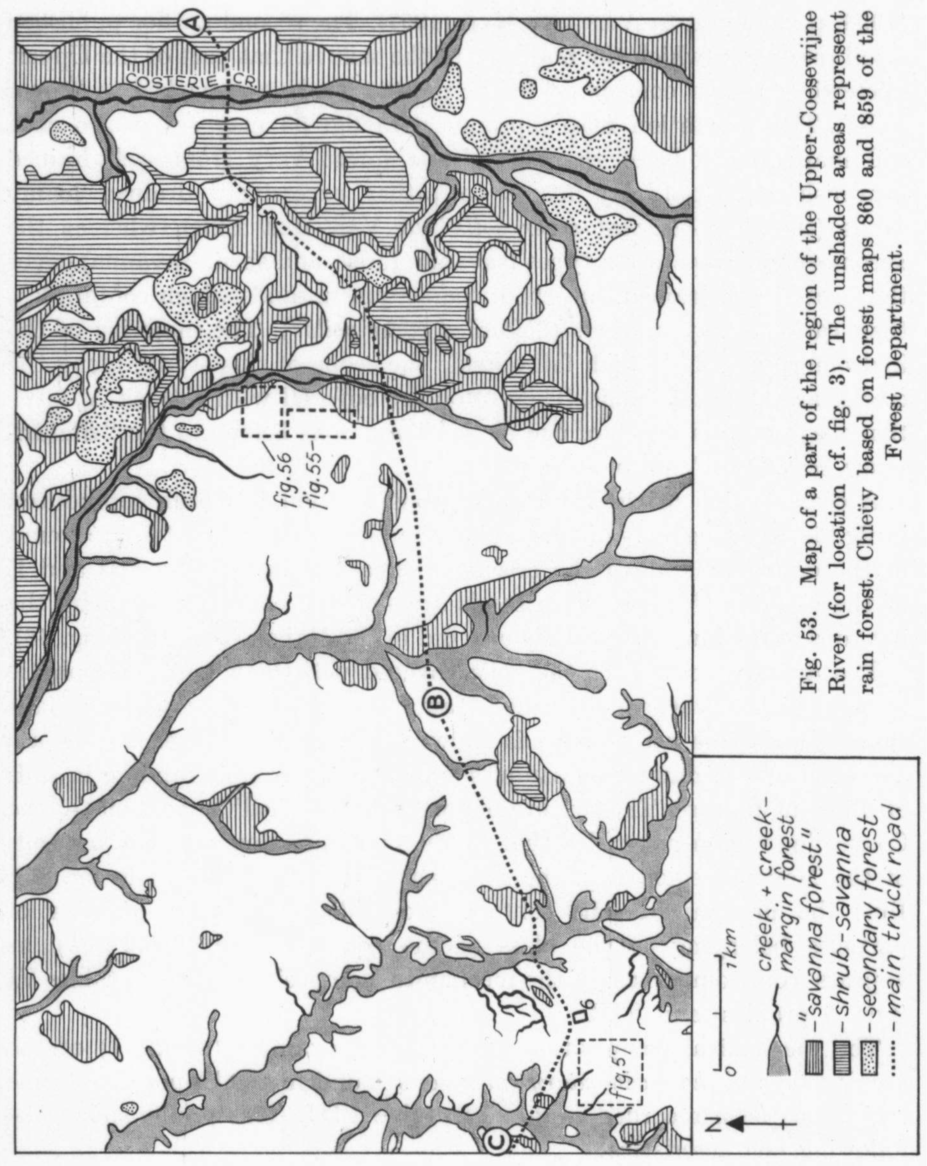


Fig. 53. Map of a part of the region of the Upper-Coesewijne River (for location cf. fig. 3). The unshaded areas represent rain forest. Chiefly based on forest maps 860 and 859 of the Forest Department.

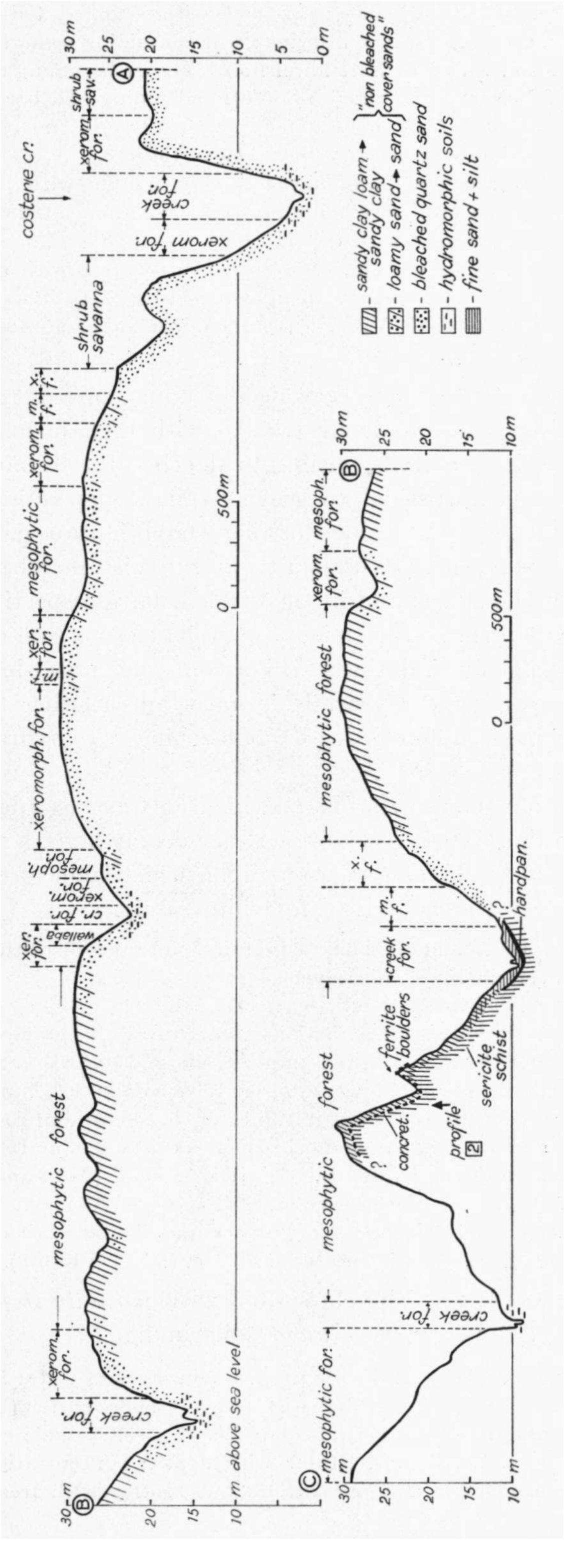


Fig. 54. Transect along the line A–B–C through the area shown in fig. 53.

70–150 cm: brownish-red/light-red clay loam; compact, with fragmentated structure; hardening considerably on drying; still containing some humus (0.2 % at 100 cm, with indefinite lower limit); colour becoming redder to a depth of 100 cm (100 cm: 5 YR 5/6), and fading and becoming more yellowish below that depth (150 cm: 10 YR 5/6); no rootlets and no traces of animal activity seen below 150 cm.
150–280 cm: sandy clay loam; colour becoming gradually lighter with depth: nearly white at 280 cm; very faint mottling beginning at 280 cm; texture becoming coarser with depth.
280–400 cm: greyish white sandy clay loam, sand becoming coarser with depth.
400–460 cm: greyish-white sandy clay loam with light-red (10 R 7/4) flecks.
460–490 cm: yellow-red coarse sand (5 YR 7/6); *groundwater* table at 460 cm.
below 490 cm: clay (rotten schist?).

The soils with a lighter texture are very deeply homogenized, rather excessively drained sandy loams to loamy sands, with organic matter, rootlets and traces of animal activity visible to depths of 100–150 cm; their colour varies from yellowish-red to greyish-yellow, depending on topography, the soils at higher altitudes having the brightest colours (5–7½ YR) whereas the yellowish (10–12½ YR) and greyish members of the catena are found on the slopes and in the creek valleys respectively. The latter soils, which often show a conspicuous eluvial (A) horizon overlying a dark brown, slightly indurated B-horizon, are water-logged throughout the greater part of the year. It is uncertain whether these differences in colour are due to different degrees of leaching or to hydration of the iron compounds.

The following description refers to profile 4 which may be regarded as a good example of the rather excessively drained very deeply homogenized non-bleached sands, i.e. of the *lightest* soil type upon which high forest is found (LS in fig. 55, near the boundary to white sand):

0 – 5 cm: coarse sand with abundant bleached grains, intermixed with raw humus and overlain by a thin layer of forest litter,
5–150 cm: brownish-red/yellowish-red sand (8 % clay and 86 %–90 % sand between 5 and 90 cm); humus well-distributed over the profile to a great depth (0.9 % humus between 5–30 cm and 0.5 % between 60 and 90 cm), with indefinite lower limit (at 150 cm still 0.1 % humus); conspicuous concentration of roots in top layer (5–15 cm), but rootlets frequent to a depth of 100 cm, and occasional rootlets seen at 150 cm; sand becoming coarser with depth: 53 % coarse sand (2–0.2 mm) at 20 cm and 71 % at 75 cm; occasional flecks of charcoal; colour at at 10 cm: 10 YR 6/4–5/8, becoming redder and lighter with depth and decreasing % of organic matter (at 60 cm: 7½ YR 6/8).

Profile 5 is an example of a greyish-yellow sand with *partially impeded drainage* due to depressed topography (*humid* soils in fig. 56):

0 – 3 cm: bleached coarse quartz sand, overlain by a thin layer of forest litter.
3– 70 cm: black-brown sand (up to 5 YR 3/2) with much organic matter (3.4 % at 30 cm); containing 4 % clay and 88 % sand (2–0.05 mm); colour becoming more yellowish and lighter with depth; concentration of roots most conspicuous in upper 20 cm, but rootlets still frequent at 50 cm.

70–120 cm: yellowish-grey sandy loam/loamy sand (3 % clay, 19 % silt and 78 % sand); colour becoming lighter with depth (10 YR 6/2 at 70 cm, 10 YR 8/2 at 100 cm); organic matter with indefinite lower limit (0.9 % humus at 80 cm, 0.2 % at 120 cm); very wet during rainy season; water table at 120 cm depth at the height of the wet season.

In the lower lying, *podzolic bleached-earth,* soils (*wet* soils in fig. 56) the A- and B-horizons become more pronounced (e.g. prof. 6 : 0–10 cm brownish sand with 3 % clay and 2 % humus; 10–40 cm light-grey bleached quartz sand; 40–70 cm black/dark-brown sand with 8 % humus and 3 % clay; 70–100 cm: light-brownish sand with 0.8 % humus and 4 % clay, ground-water table at 90 cm at the height of the dry season).

In most profiles of the non-bleached soils the clay content increases with depth, as is shown by the average figures given in table VII and by the data for profiles 1 and 3 in table VIII.

TABLE VIII

Texture and mineralogical composition of three selected profiles in the Upper-Coesewijne region. For the methods used, see table VI.

Depth in cm	MECHANICAL COMPOSITION												MINERALOGICAL COMPOSITION								
	2 – 1 mm	1 – 0.6 mm	0.6 – 0.3 mm	0.3 – 0.21 mm	210 – 150 μ	150 – 105 μ	105 – 75 μ	75 – 50 μ	50 – 20 μ	20 – 2 μ	2 – 1 μ	< 1 μ	opaque	tourmaline	zircon	rutile	staurolite	kyanite	andalusite	"alterites"	
5 – 12	tr	1	20	16	10	1	tr	tr	34	1	3	14	30	9	56	8	14	1	1	11	PROF. 1 clay loam
110 – 120	tr	2	21	13	9	tr	tr	tr	30	1	2	22	–	–	–	–	–	–	–	–	
330 - 365	–	–	–	–	–	–	–	–	–	–	–	–	37	15	32	4	18	1	3	27	
25 – 45	tr	4	17	13	5	tr	tr	tr	19	14	8	20	28	5	16	17	1	–	–	61	PROF. 2 colluvial
55 – 75	tr	2	14	10	8	tr	tr	tr	23	18	2	23	–	–	–	–	–	–	–	–	
130 – 160	27	8	15	17	2	tr	tr	tr	19	7	3	12	29	3	14	48	–	–	–	35	
240 – 260	tr	tr	tr	tr	tr	tr	tr	tr	24	63	5	8	2	1	–	67	–	–	–	31	rotten sericite schist
2 – 10	1	3	30	18	5	tr	tr	tr	36	1	1	5	–	–	–	–	–	–	–	–	PROF. 3
25 – 50	tr	2	25	17	6	tr	tr	tr	34	1	1	14	33	9	41	35	1	1	4	9	
80 – 100	tr	3	25	14	6	tr	tr	tr	26	2	2	22	35	8	36	44	1	–	1	10	

As appears from the laboratory analyses (the average data of which are reproduced in table VII), the soils of the Upper-Coesewijne region are on the average somewhat poorer in readily extractable ions than the average soils of the Mapane region. These laboratory analyses did not reveal any significant differences in the amount of exchangeable bases between non-bleached cover soils with different texture. This is quite understandable, because the exchangeable ions must be largely absorbed to the humus complex (the amount of which was practically independent of the clay content of the soil, and was approximately the same in the various types of well-drained non-bleached soils), whereas the cations of the highly base-desaturated clay complex have largely been replaced by hydrogen.

The soils were found to be practically devoid of weatherable minerals, the maximum percentage being 1 %.

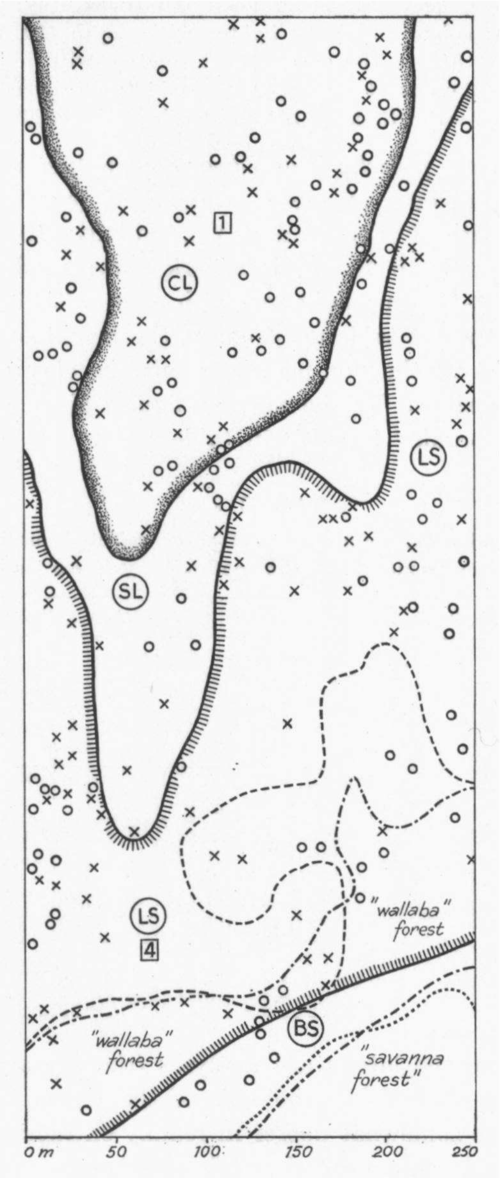


Fig. 55. Map of a small area in the Upper-Coesewijne region (for location cf. fig. 53), showing the distributional pattern of individuals of *wana* (*Ocotea rubra:* crosses) and *basralokus* (*Dicorynia guianensis:* circles) of 20 cm d.b.h. and over, in dependence of the texture of the soil. CL: clay loams (cf. prof. 1: p. 132) to sandy clay loams; SL: sandy loams; LS: loamy sands to non-bleached sands (containing ca. 4–10 % clay + silt: cf. prof. 4, p. 134); BS: bleached sands (containing less than ca. 4 % clay + silt). The drainage varies from good to excessive. Broken line: S boundary of *boegroemakka* palms (*Astrocaryum sciophilum*). Dot-dash line: boundary of *wallaba* (*Eperua falcata*) forest, i.e. sub-mesophytic/sub-xeromorphic forest in which *wallaba* forms ca. 25–80 % of the canopy trees. Dotted line: boundary of xeromorphous savanna forest.

Great differences were found in the *water-holding capacity* of the soils with different texture, as clearly appears from the determinations of soil moisture which were carried out in two different sites (clay loam and sand respectively) at the end of the very dry season of 1957 (cf. table XIV).

The non-bleached cover soils bear mesophytic (rain) forest, although the latter tends to be sub-mesophytic in comparison with the somewhat more luxuriant forest of the Mapane region, where the soils on the average have a more heavy texture and are less poor in plant nutrients. The differences in floristic composition will be discussed in III.3.3.

Notwithstanding the large differences in texture (and accordingly in water-holding capacity, etc.) in the well-drained non-bleached soils, the preliminary phytosociological investigations failed to reveal any distinct relationship between the floristic composition of the mesophytic forest of the Upper-Coesewijne region and the mechanical composition.

Although the composition of the forest was found to be far from homogeneous, no clear correlation could be found between the various textural classes and the floristic composition of the 100 quadrats which were laid out in various transects along gradients reaching from clay loam to loamy sand (together forming sample plot 5, cf. III.3.2). For a number of predominant canopy species, viz. *kopie* (*Goupia glabra*), *fomang* (*Chaetocarpus schomburgkianus*), *basralokus* (*Dicorynia guianensis*) and *wana* (*Ocotea rubra*) the distribution of trees of more than 20 cm diameter was mapped in two areas, the location of which is shown in fig. 53. For *basralokus* and *wana* part of the distributional maps are reproduced in figs. 55–57, which show the wide ecological amplitude of these species, and the fact that, within wide limits, the distribution was practically independent of the texture and the water economy of the soil. The distributional pattern of both species in the small areas under consideration, did not differ significantly from a random distribution, the development of local aggregates being accidental. As appears for instance from the map shown in fig. 55, both *wana* and *basralokus* showed approximately the same average density in the various texture classes reaching from clay loam to sand (with ca. 4 % clay). Only near the ecotone to true xeromorphous forest (savanna forest) these species, and the other species of the mesophytic forest too, disappear to make place for species that are characteristic for subxeric sites (excessively drained, bleached quartz sands). *Boegroemakka* (*Astrocaryum sciophilum*), which forms the conspicuous palmlayer in the undergrowth of the Upper-Coesewijne mesophytic forest, becomes rather scarce on the loamy sands and totally disappears (cf. the broken line in fig. 55) in the ecotone; *wallaba* (*Eperua falcata*) becomes the predominant canopy tree on the soils with the lightest texture. This species, which is rather abundant on the more mesic sites too, tends once more to single dominance (up to 80 % of the canopy trees) when it approaches the other end of the gradient, viz. on the podzolic

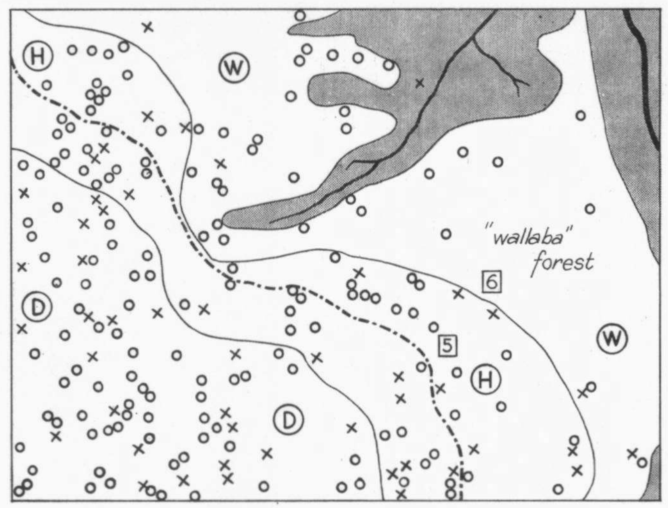


Fig. 56. Map of a small area in the Upper-Coesewijne region (for location cf. fig. 53), showing the distribution of individuals of 20 cm d.b.h. and over of *wana* (*Ocotea rubra:* crosses) and *basralokus* (*Dicorynia guianensis:* circles) in dependence of drainage. D: clay loams—loamy sands with (rather) good drainage (colours 5–10 YR); H: sandy loams—sands with partially impeded drainage, due to depressed topography (cf. profile 5, p. 134); colours 10 YR to light greyish-yellow; ground-water table at 150–100 cm depth during wet season; W: podzolic bleached earths, waterlogged during the greater part of the year and ground-water table less than 100 cm below the surface in the dry season (cf. prof. 6, p. 135). Dot-dash line: boundary of *wallaba forest* (*Eperua falcata*). Shaded area: marsh-forest.

bleached (loamy) sands where drainage is more or less impeded during the greater part of the year (cf. fig. 56).

For a number of species I have arranged the *size-class distribution* according to the texture classes of the soils of the enumeration plots; but – owing to the great variability of the material – the number of the data which have been gathered so far, proves to be too small to allow reliable conclusions. Yet for some species, such as *basralokus* and *wana*, the diameter-class distribution tends to show a shift to the larger diameters on the sands near the ecotone to xeromorphous forest. If this should actually be so, it might mean that these species are retreating from these soils; however, other explanations of these differences in the size-class distributions are not excluded.

In fig. 58 B an example is shown of a case in which the *regeneration of basralokus* is significantly better on a certain soil type. In the small area which is reproduced in this figure, the absolute as well as the relative number of young trees (5–20 cm d.b.h.) of *basralokus* is greatest on the soils which are marked with a S, viz. on the loose sandy soils with optimal drainage and very deep penetration of biological activity (although the water-holding capacity may be rather low: cf. site 6 in table XIV). The soils of this area (i.e. in the SW corner of the region shown in fig. 53) differ from the above mentioned cover soils of Zanderij origin; as will be pointed out below, they belong to a N extension of the "schist-hill landscape".

Although with a number of species the density appeared to be independent—within wide limits—of the texture and of the drainage of the soils, for the two commercially most important species in this region (*wana* and *basralokus*), both the *height* of the trees and the *girth increment* appeared to be significantly lower on the sub-xeric sites than on the (sub-)mesic ones. That in *wana* trees the maximum height of the centre of the crown becomes lower near the ecotone to xeromorphous forest, is illustrated by measurements which were made on different soils along the transect shown in fig. 54. The differences in girth increment will be discussed in IV.4 (cf. fig. 67: Coesewijne).

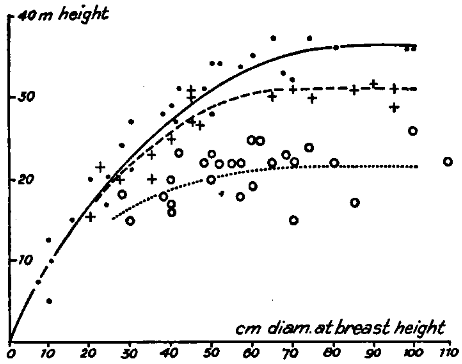


Fig. 57. Height-diameter relation for *wana* (*Ocotea rubra*) trees in the Upper-Coesewijne region. Dots: height of the centre of the crown for trees on clay loams/sandy loams. Crosses: idem on coloured sands and bleached sands. Open circles: clean bole length on clay loams/sandy loams.

As was mentioned above, between the cover soils of the Zanderij formation (which form the majority of the soils of the area that we have studied) N extensions and relic-hills of the Old Basement are found. In the SW corner of the area shown in fig. 53 such a relic-hill of the "*schist-hill landscape*" is clearly distinguishable by the dendritic drainage pattern, which differs conspicuously from that of the "cover landscape" of the Zanderij formation. For a schematic cross-section reference is made to fig. 54. The soil is ferrallitic clay loam/silt clay, and belongs to the "*schist-laterite soils*" and the colluvial "*foot-plain soils*" distinguished by VAN DER EYK (1957). Drainage is less free than in the loose cover soils, which is due partly to the lesser permeability of the subsoil, especially where the impervious rotten rock occurs at a relatively shallow depth.

The schist-laterite soils contain varying amounts of iron concretions, ranging from angular gravel to large, slag-like sandstones and claystones, in which the quartz and clay particles are cemented to each other by iron oxide. These concentrations of iron oxide vary from slightly indurated, friable spots to real, concretionary iron stone. Where the overlying horizons have been eroded, and the horizons with iron concretions crop out, ferrite gravel and boulders are found on the surface (e.g. 50 m E of profile 2 in fig. 54).

In table VIII the mechanical composition has been given of a profile (profile 2, for location cf. fig. 54) of a ferrallitic, colluvial silt clay, overlying sericite schist weathered in situ; the boundary between the colluvial soil and the kaolinitic weathering product of the schist is marked by a layer of very coarse sand and quartz gravel (ca. 180–200 cm). The quartz gravel presumably originated from the numerous quartz veins which are found in the parent rock. The mineralogical composition and the comparatively high percentage of silt found in the top soil (0–200 cm), make it plausible that these top layers consist of colluvially transported material, which, however, originated from the same sources as the subsoil (below 200 cm); the latter is a residual schistose weathering product.

The following is a brief description of *profile* 2:

0 – 5 cm: coarse sand with abundant bleached quartz grains, intermixed with semi-decomposed forest litter.

5– 30 cm: main rooting zone; loose brownish-yellow clay loam (10 YR 5/4–12½ YR 5/4), containing ca. 2 % humus; conspicuous concentration of roots in top 30 cm; charcoal flecks abundant.

30– 50 cm: compact, brownish-yellow clay loam (12½ YR 6/6) with occasional rootlets and with faint *red flecking* (5 R 3/6–10 R 5/8); humus ca. 0.3 %; gradually merging into:

50–130 cm: very compact silt clay, light yellowish-brown (12½ YR 8/3); soil particles cemented by iron oxide to dark red, irregularly formed, vesicular masses reaching a diam. of 1 m, friable to hard (colour: 5 R 3/6–10 R 5/8); becoming very hard on exposure.

130–200 cm: greyish-yellow sandy clay loam; sand becoming coarser with depth (cf. table VIII!) and colour fading to greyish-white; faint flecking (10 YR 5/4–5 YR 3/6); compact and structureless; rootlets occasional; moist/very moist, even at the height of the dry season, becoming very hard on exposure; 180–200 cm: much angular *quartz gravel.*

below 200 cm: rotten *sericite schist,* bluish-grey; fibre roots, and red streaks of iron oxide, occasionally penetrating along the cleavage planes of the schist.

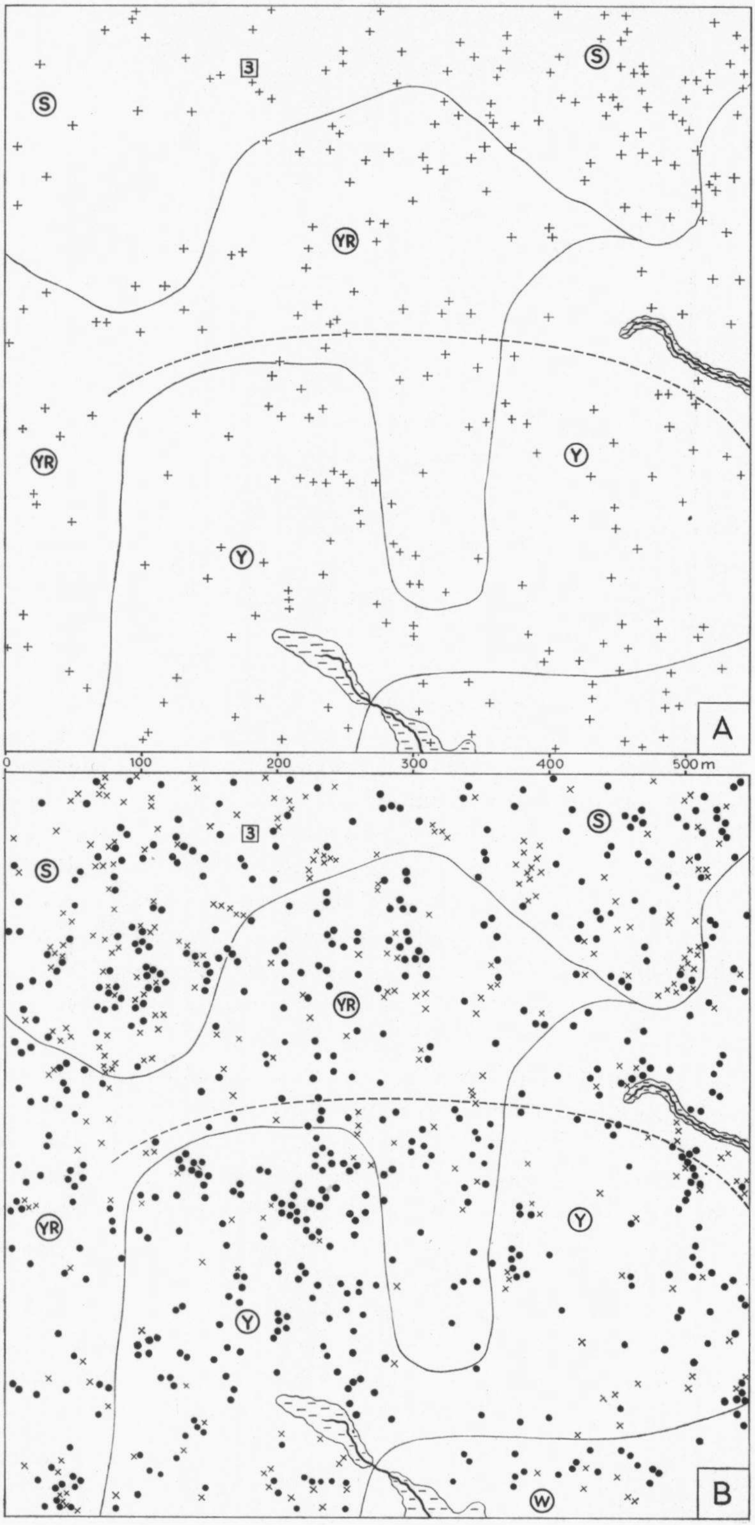
This is a typical case of *laterite in statu nascendi* that is found just above a horizon which, owing to the imperviousness of the weathered schist, is nearly completely water-saturated during the greater part of the year, and which is very moist even during a very dry season, such as that of 1957. This fact might lend support to the opinion of those authors who consider the horizon above which an irreversible deposition of ferric oxide is found, to be determined – at least in certain cases – by the proximity of a (fluctuating) level of complete saturation. It is also an example of the formation of ferrite in a moist climate without a severe dry seaon.

In the forest found on the lateritic soils of the schistose relic hills (for which profile 2 is representative) the *floristic composition,* especially that of the lower storeys, differs significantly from that of the surrounding forest on the cover-soils of the Zanderij formation. These differences in composition will be discussed in III.3.2 (plot 6).

Lower down the slopes of the schistose hills, (sub-)hydromorphic colluvial/alluvial soils ("foot-plain soils" of VAN DER EYK) may be found, consisting of compact silt loams, silty clay loams or silty clays, and often containing much fine sand (200–50 μ) in the top layer. At the boundary with the impervious kaolinitic weathering product of the schistose parent rock these soils often are underlain by a *hardpan*, which consists of coarse sand and gravel cemented by organic matter (cf. fig. 54: in the creek valley, E of profile 2).

In the transitional zone to the cover soils of the Zanderij formation, the upper layers consist of a mixture of the two soil series (schist-laterite soils and cover soils). The floristic composition of the forest is approximately the same as that of the forest on the loose cover-soils, although some elements may be present (especially in the undergrowth) which are characteristic for the station on ferrallitic schist-soils. Such a transitional area is shown in fig. 58; this figure is given in the first place to illustrate the distributional pattern of the trees of more than 20 cm d.b.h. belonging to two species. In this small area the soils marked Y and W are mottled, heavy sandy clay(-loams), differing in colour from yellowish-brown (10–12½ YR) to greyish-white, according to the degree of drainage; their profile is similar to the above mentioned profile 2, but the concretions are much smaller and less abundant, whereas the colluvial top soil is much deeper (3–4 m); their development from the same schistose parent material appears from their mineralogical (rutile!) and mechanical composition. The soils which are marked YR and S, are porous, well-drained, yellowish-red (7½–10 YR), deeply homogenized sandy clay loams/loamy sands, which show no signs of mottling in the upper 2 m. In their mechanical composition they resemble the non-bleached cover-soils (e.g. in the absence of fine silt and in the position of the maximum in the 0.6–0.3 mm fraction); this appears from the figures given in table VIII for profile 3 (for location cf. fig. 58), which is representative for the rather excessively drained sands overlying (sandy) loam, i.e. for the soils in the northern strip of the area (marked S). The mineralogical composition of these sandy soils shows that they are a mixture of the cover soils (zircon-staurolite-tourmaline association) and the schist-soils (rutile!). These light-textured soils often show a conspicuous B-horizon, in which illuviation of organic matter and of easily available plant nutrients has taken place; this is shown by the following results of the laboratory analyses of samples from *profile 3* (for the methods used, cf. the notes to table VII):

Figure 58 has in the first place been given because it shows that for the two species under consideration (as for a number of other species) the distributional pattern of the trees of more than 20 cm d.b.h. is nearly independent of that of the soil types which were encountered in this small


S
3
S
YR
YR
Y
Y
A
0
100
200
300
400
500 m
S
3
S
YR
YR
Y
Y
W
B

	sand %	clay %	pH(H_2O)	org.matter %	exchangeable in p.p.m.			plant nutr. (Na-acet.)			
					Ca	K	P	NH_4	NO_3	Fe	Al
0–10 cm; bleached sand (10 YR 4/3)	**57**	6	**6.2**	0.9	< 25	42	2	**45**	**22**	150	80
25–50 cm; yellowish-brown loam (10 YR 4/3)	50	15	6.0	**1.1**	< 25	**53**	**10**	35	10	**156**	**235**
80–100 cm: sandy clay loam (10 YR 6/4)	48	**24**	5.6	0.3	50	20	1	17	12	70	127

area. As was mentioned above, in the case of *basralokus* the young trees (5–20 cm) were considerably more abundant on the lightest soil type (S). The considerable difference in water-holding capacity between the loose sands/sandy loams and the ferrallitic soils with their heavier texture is shown by the results of an analysis of the moisture content shown in table XIV (sites 6 and 7).

In the next part the influence of *biotic factors* on the development of the vegetation will be discussed. Both the vegetation and the soil bear witness of former disturbances, e.g. by forest fires. The soil does this in the presence of fragments of charcoal and pots (although for the majority of the forests in the Upper-Coesewijne region sufficient time has elapsed to allow a regeneration to climax forest). In II.2.2 the question has been raised to what extent human influences are to be held responsible for the development of the bleached-sand areas, and there the hypothesis was put forward that these bleached sands are to be regarded as lowland tropical podzols derived from parent soils which were initially poor in bases and clay-forming materials; and that leaching – and, consequently, degradation to bleached quartz sands – was strongly accelerated by the repeated burning of the vegetation practised by the natives.

This hypothesis is supported by the fact that the bleached sands W of the Costerie Cr. are especially found along the creeks (cf. figs. 53 and 54), where lateral leaching is most intensive, and where the Amerindians preferably practise their bush-fallow system of cultivation (as appears, e.g., from the location of secondary forests shown in fig. 53, which mark rather recent disturbances of the forest).

Fig. 58. Distribution of trees of *Ocotea rubra* over 20 cm d.b.h. (A) and of *Dicorynia guianensis* (B) (crosses: 5–20 cm, and dots: over 20 cm d.b.h.) in a small area in the Upper-Coesewijne region. The continuous lines mark the boundaries between the soil types (for description, see text: p. 141). The broken line marks the northern boundary of a distinct palm layer, formed chiefly by *Astrocaryum sciophilum*.

II.4. FERRALLITIC SOILS OF THE SCHIST-HILL AND SCHIST-MOUNTAIN LANDSCAPE

Behind the unconsolidated sediments of the Coastal Sedimentary series and the Zanderij formation, the older Basement rocks are found; the latter are of complex composition and structure consisting of basic or acidic gneiss, schists and foliated volcanic rocks intruded by granite, dolerite, etc. The surface of the Basement complex, which is the remnant of a very old peneplain, is undulating or irregular to fairly flat, with prominent ridges, hills and – farther inland – even low mountains which may attain an elevation of some 1200 m.

The soils of the Mapane region, which were described in II.2, are situated in the transitional zone between the old Basement and the Zanderij sediments. Phytosociological studies were made also farther inland, viz. in the upland forests covering the hilly country of the *"schist-hill landscape"* (VAN DER EYK 1957) found S of the Upper-Coesewijne region (in the Goliath Cr.–Saramacca R. watershed) and in the region of the Upper-Suriname R. near Bergendal and Remontcourt. The physiography of both areas is rather steep and rugged; the low rounded hills and hilly ridges, which in these areas attain heights of 50–150 m above sea level, are sharply indented and dissected by many gullies and creeks. The dendritic drainage pattern, which is characteristic for the schist-hill landscape and differs conspicuously from that of the granitic hills, is easily recognizable on aerial phtographs. The soils of the above mentioned regions largely consist of bright-red/yellowish ferrallitic (sandy)(clay-)-loams, silt loams, (silt-)clays, etc., *with abundant pisolithic ironstone gravel* in the upper layers. Locally they are underlain by a sheet of lateritic ironstone (ferrite/ferrobauxite). Where this sheet approaches the surface, the forest becomes a xeromorphous pole forest with abundant lianes.

The residual soils of the schist-hill landscape were described by VAN DER EYK as *"schist-laterite soils"*, and the colluvial/alluvial soils at the foot of the hills and at the valley bottom as *"foot-plain soils"*.

In the present study only the forests on the well-drained soils of the hills and the plateaux were investigated. These soils are classified as "residual" soils, although the upper layers obviously have undergone colluvial transport over some distance.

South of the "cover-sands" of the Upper-Coesewijne region, which were discussed in the foregoing section (II.3), phytosociological studies (cf. III.4.1) were made in the upland forests covering the *hilly country between the Goliath Cr. and the Saramacca R.* (cf. fig. 3: sample plots 1–4).

The parent rocks underlying most of the profiles are unknown, but presumably it are highly metamorphous rocks of Pre-cambrian age. The majority of the soil profiles in the Saramacca R.–Goliath Cr. watershed resemble those of the ferrallitic earths found in the Mapane region (cf.

description of profiles between 350 and 550 m in fig. 48 and profile 9/0 at 1200 m in fig. 49). The texture varies between silty clay(-loam), silt loam, (clay-)loam and sandy (clay-)loam, sometimes with loamy fine sand in the top 10 cm. The silty soils presumably have developed from schistose (sericite) parent material. In the majority of the profiles a horizon with much ironstone gravel is found, varying in depth from 10 cm to one meter. It is not clear whether these iron concretions have been formed in situ and under a vegetation cover similar to the existing one, that is under high upland (rain) forest. Where at the surface a layer of ironstone gravel is found, it is either of colluvial origin or it represents part of a truncated profile. Locally continuous sheets of *ferrite/ferro-bauxite* are found; they attain their strongest development on the Goliath Hills, W of the Goliath Cr. The colour of the soils varies from brownish-red (5 YR) to yellowish (12½ YR), according to the physiography: the brightest colours are found in the best-drained sites. Humic penetration, and depth of rooting and other biological activities vary from 30 cm to about 1 m; on the whole, homogenization is less deep than it is with the majority of the lowland cover-soils. The upper layers are well-aerated throughout the year, owing to the porous structure of the gravelly soils; even after heavy showers no standing water was observed in the soil pits on the plateaux and on the slopes. Below the zone of biological activity the kaolinitic weathering product of the parent rock is found, viz. friable, rather impervious mottled kaolinite, which feels dry even at the height of the wet season. Where the topsoil contains much gravel, and/or where a ferrite cap is found near to the surface, the rooting space and the water-supply is considerably reduced. Nevertheless high forest was found on sites where only 30 cm of soil covered the ferrite cap. Drainage is in the majority of the ferrallitic schist-hill soils more thorough than on the mesic sites of the lowland soils, owing to the greater porosity and the relatively lower capillary-pore space, and locally to the higher elevation. The wet soils lower down the slopes and at the valley bottom, which bear hydromorphous forest, fall outside the scope of this study.

As is shown in table IX, the top layer of the ferrallitic soils may contain more organic matter than the lowland soil types described in the foregoing sections; organic matter averaged about 3 % in the samples taken at 2–30 cm. The comparatively *high C/N ratios* (average: 28!) may be caused by the presence of much partly decomposed plant material, which would mean that mineralization is here significantly less intensive than in the soils of the Mapane and Upper-Coesewijne region, where the C/N ratio seldom exceeded a value of 20 (average: 10–15). The wide C/N ratio in the top layers may be partly caused by the presence of elementary carbon, as pieces of charcoal are rather abundant in some profiles.

As might be expected from the age of the soils, the exchange capacity of the colloidal complex (T-value) proved to be low to very low, whereas the exchangeable base content (S-value) was still lower. This high saturation deficit is in accordance with the low pH. Unfortunately, no data on the amount of available plant nutrients are at our disposal, but these amounts presumably are as low or even lower than those found in the lowland cover-soils.

TABLE IX

Results of laboratory analyses *) of soil samples from various sites in the Goliath Cr. region (sample plots 1–4, cf. fig. 3).

Texture class	Depth in cm	Number of samples	pH (H_2O)	pH (KCl)	Org. ¹) matter %	N ²) %	S- ³) value	T- ⁴) value
(silty) clay	0– 25	2	4.4	4.0	3.0	0.13	2	12
	25– 50	1	5.0	4.1	0.5	0.03	4	11
	50– 65	1	5.1	4.4	<0.1	<0.01	3	9
	90–110	1	4.8	3.9	<0.1	<0.01	3	10
silt loam	0– 25	3	4.3	3.6	5.3	0.17	2	17
	25– 50	1	4.9	4.0	4.3	0.08	2	12
sandy loam/ loamy sand	0– 25	2	4.2	3.5	2.2	0.07	<2	7
	25– 50	1	4.5	3.9	1.6	0.06	<2	6
	75–100	2	4.7	4.0	0.2	0.02	<2	5

¹) total-carbon determined by a wet combustion method (Kurmies), and converted to organic matter by multiplying with a conventional factor (1.7).

²) Kjeldahl.

³) *exchangeable base* content expressed in mg equivalents per 100 g air-dry soil; determined after shaking with 0.1 N HCl.

⁴) *exchange capacity* in mg equival./100 g soil; determined after treatment of the soil with calcium carbonate.

The preliminary phytosociological studies of the forests covering the ferrallitic soils of the Goliath Cr. region failed to show any relation between the composition of the forest and the quite distinct differences in such soil features as depth, texture, etc. As will be discussed in III.4.1, the average composition of the forest differed significantly from that of the lowland rain forest on mesic sites found some 25 km farther northward on the cover-soils of the Upper-Coesewijne region.

The ferrallitic soils of the area near *Bergendal and Remontcourt* where phytosociological studies were carried out (for location, cf. fig. 1), are bright red, rather heavy soils with very abundant ironstone and quartz gravel. The parent rocks are of the metamorphous kind, such as (quartzose) sericite schists (phyllites), which geologically belong to the *Bonnidoro*

---

*) The analyses were carried out in the soils laboratory of the Agricultural Experiment Station at Paramaribo.

(*Taffra* group) and *Paramacca* series; these series are part of the Precambrian *Orapu-* and *Balling* formation respectively. The physiography of the Taffra group is steep and rugged, whereas that of the Paramacca series is more undulating, with low rounded hills and hilly ridges, and with broad valleys.

A soil-survey map which includes the area under consideration, was published by Dost *et al.* (1957). The colluvial/alluvial soils of the valleys fall outside the scope of this study. The majority of the residual soils of the schistose hills are well-drained, ferrallitic, sticky, plastic (silty-)clays and silt loams, with (very) much ironstone gravel, and in places overlain by a thin layer of bleached fine sand. The colour of the soil varies from brick-red to ochrous, presumably according to the degree of drainage; often a *catenaous series* is found with brick-red coloured profiles at the top of the hill and yellowish-grey colours in the more or less hydromorphic soils at the foot of the latter.

The following is a description of a profile of a soil which had been developed from a *sericite schist* of the Taffra group (located in the sample plot near Remontcourt, cf. III.4.3):

0 – 2 cm: loose (silt) loam, with much bleached fine sand in the top ½ cm; intermixed with partly decomposed forest litter; conspicuous *root-mat* in the top 2 cm, partly overlying the surface of the soil.

2–100 cm: red clay, tinged brownish with humus (5 cm: 7½ YR 5/4; 80 cm: 10 R 4/7); plastic and sticky, becoming more and more compact with depth; containing much ironstone gravel, with stones up to 3 cm in diam.; 55–70 % gravel (> 2 mm); coarse + very coarse sand (0.3–2 mm) less than 10 %; silt (2–50 μ) 15–20 %; clay 50–65 %; roots frequent to a depth of ca. 35 cm and still occasional at 100 cm.

Notwithstanding the heavy texture of the profiles, *homogenization is rather deep* (50–100 cm), and internal drainage is fairly good in most profiles. The water supplying power presumably is sufficient throughout the year. Unfortunately the results of the laboraty analyses of the soils of this region are not yet available.

Only some preliminary phytosociological studies were carried out in the upland forests covering the ferrallitic soils of this area (cf. III.4.3); it would be interesting to investigate, by more systematic sampling than was done in the present study, possible correlations between the observed differences in floristic composition of the forest and differences in the parent material of the soils (e.g. the Taffra schists and the soils of the Paramacca series).

Some phytosociological studies were carried out on the plateau and the slopes of *Stofbroekoe Mountain*, a *schist mountain* in the region of the Little Saramacca R. (cf. fig. 1). The parent rock of the mountain is *amphibolite schist*. The soil on the plateau (at 500 m above sea level) is a red sandy (clay-)loam with more than 60 % iron stone gravel (> 2 mm), overlying a *very thick sheet of lateritic iron stone*. In the sample plot on the plateau which is described in III.4.2, the ferrite cap was found at a depth of ca. 150 cm, and according to informations supplied by the Geological Department it has a thickness of 3–5 m. The soil overlying the ferrite cap is yellowish-brown sandy clay loam, becoming redder with depth (e.g. in one profile: 25 cm: 5 YR 5/4; 40 cm: 10 YR 6/6; 100 cm: 2½ YR 5/6; 150 cm: 10 R 4/4). The mechanical composition of three samples from one profile has been set out in table X, showing a high proportion of silt in the upper layer. It should be noted, however, that the results of the conventional methods of mechanical analysis when applied to lateritic clays which contain abundant ironstone gravel, do not give a true picture of the real texture of such soils. The results of the chemical analyses of the plateau profile (which are directly comparable with those given in table VIII, because the same methods were used), show that the amount of organic matter increases with depth, and thus appeared to be highest just above the ferrite cap. The readily available amounts of various plant nutrients are approximately similar to those found in the lowland cover- and residual soils of the Mapane and the Upper-Coesewijne region, except for the comparatively high amount of easily extractable sulphate. In the majority of the soils internal drainage is good; humic penetration is very deep, as shown by the amount of organic matter at 135–155 cm (1 %), at which depth also occasional rootlets were found.

The soil of the sample plot half-way down the slope was similar to that on top of the mountain, but the ferrite cap already was found at a depth of 75 cm. The surface of the soil was strewn with ferrite and ferro-bauxite boulders.

In the sample plot at the foot of the mountain a very shallow layer of sandy loam is present which covers the ferrite. As will be discussed in III.4.2, notwithstanding this very thin layer of soil (15 cm or less in depth) which, moreover, contained ca. 70 % of gravel (of which more than ¾ consisted of stones that were 5 mm and over in diam.), it bore a rather high upland forest, with a few outstanding trees (*Couratari*) reaching a height of ca. 40 cm. Perhaps the roots of the larger trees may have spread through crevices in the ferrite cap to a greater depth and this may have enabled these trees to reach such large dimensions. Another important factor is that the amount of available plant nutrients (especially of *calcium*!) proved to be very high (cf. table X) in comparison with the figures that were obtained in other sites. Apart from the comparatively high amount of calcium, the high figures for easily extractable potassium and magnesium ions (in contrast to the rather low amount of iron) are striking features. However, it should be noted that these ions are concentrated in a layer of 15 cm depth only, and that the amount is of the same order of magnitude as that of the total amount of nutrients which in the other profiles are distributed over a rooting zone of considerably greater depth (30 to 80 cm).

Notwithstanding the very low water-supplying power of the shallow gravelly soil, the latter remains moist during the greater part of the dry season; this is due to seepage water received from the slopes of the mountain.

For sake of comparison a sample plot was laid out in the broad, flat *valley of the Little Saramacca R.*, at a distance of about 1 km from the foot of the mountain in a forest on a totally different soil. As will be discussed in III.4.2 this forest differed significantly from that on the ferrallitic soils of the schist mountain. The soil of the sample plot was a rather compact, yellowish loam, containing much fine silt (cf. table X). The parent rock probably was a granite, near its contact zone with the neighbouring schists. This is suggested by the mineralogical composition of the soil (5–50 cm depth) – for it contained 44 % rutile, 20 % zircon, 3 % staurolite, 1 % tourmaline, 1 % epidote and 30 % limonite – and by the abundance of large pieces of vein-quartz (which may attain diameters of more than 1 m).

TABLE X

Results of laboratory analyses of soil samples from Stofbroekoe Mnt. and the neighbouring river valley, and from a profile in the Wayombo region (cf. III.6). For the methods used, see table VII.

location		depth (cm)	mechanical composition					% C	pH		easily extractable ions. (Na-acet.extr.) in p.p.m.												id.(NH_4 acet.) in p.p.m.	
			2mm-200μ	200-50μ	50-20μ	20-2μ	<2μ		H_2O	KCl	Ca	Mg	K	P	NH_4	NO_3	NH_4/NO_3	Fe	Al	Mn	SO_4	Cl	Na	K
Stofbroekoe Mnt.	top (500m)	5–40	22	15	**39**	7	17	0.4	5.5	5.5	< 10	2	20	5	25	10	2.5	37	55	tr	**375**	tr	12	25
		90–120	26	36	1	8	29	0.6	5.4	5.1	< 10	3	30	2	25	20	1.3	65	77	tr	**158**	tr	25	37
		135–155	39	33	5	2	21	1.0	4.8	4.2	< 10	5	25	5	30	18	1.7	58	**187**	tr	tr	tr	10	35
	foot :	2.–15	30	45	10	1	14	**2.1**	5.2	4.2	**212**	**78**	**72**	8	**55**	20	2.7	**17**	92	tr	tr	tr	**48**	**138**
Saram. r. valley		5–35	**7**	34	1	7	**51**	**4.5**	4.7	4.0	< 10	**40**	**68**	3	**113**	**100**	1.1	55	**165**	tr	tr	tr	**70**	**165**
Wayombo		20–35	27	16	17	**24**	16	0.4	5.2	4.4	< 10	5	12	2	20	**5**	**4.0**	90	**195**	tr	tr	tr	5	22
		45–55	26	12	8	**35**	19	0.2	5.2	4.2	< 10	tr	12	2	30	**10**	**3.0**	67	**205**	tr	tr	tr	5	22

The upper layers of the soil are perhaps mixed with colluvially transported material from the schist mountain. The laboratory analyses show comparatively high amounts of available nutrients, especially of nitrate and ammonium ions and of potassium ions. The latter were estimated after shaking with ammonium acetate in acetic acid. This ***high amount of available plant nutrients*** goes parallel with a comparatively high percentage of organic matter.

It should be noted, however, that the number of trees found per ha in the sample plot (cf. table XXI) was not higher than that found in the lowland forests where the soils were definitely poorer in readily available plant nutrients.

II.5. GRANITE LATERITE SOIL IN THE REGION OF THE VOLTZ MOUNTAIN

Two sample plots (cf. III.4.4) were laid out in the high forest occurring in the vicinity of the Voltz Mountain, a granite "inselberg" in the

Coppename R. basin (some 20 km S of the bottom line of the map shown in fig. 1). As will be discussed in III.4.4, the forest covering the deeply weathered ferrosiallitic/ferrallitic soils is high upland forest. The other sites (e.g. the shallow soils covering laterite caps and outcrops of unweathered granite), which bear more or less xeromorphic types of vegetation, were described recently by Bakker (1957). The deeply homogenized soils of the high forest are yellow-red/red (5 YR–10 R) sandy soils, varying in texture from sandy loam to clay, with occasional (friable) iron concretions.

In table XI the results of the analyses of two profiles are given. The soil pits were situated in forest sample plots 1 and 2 (cf. table XXII) respectively, near the foot of the mountain. The upper layers probably are colluvially transported. Professor J. P. Bakker kindly allowed me to make use of his field data and of the results of the analyses which were carried out at the Laboratory for Physical Geography (Amsterdam).

TABLE XI

Descriptions and analyses of two profiles of high-forest soil in the Voltz Mnt. region (obtained from Professor Dr. J. P. Bakker, Amsterdam).

Depth in cm	Particulars	Colour	sand		silt		clay	% org. matter	pH H_2O	pH KCl	S-value 4)	T-value 5)
			2–0.2 mm	210–50 μ	50–16 μ	16–2 μ	< 2 μ					
Profile 1:												
3– 15	sandy clay loam with abundant roots . . .	5 YR 5/4	48	19	5	3	24	2.8	4.5	3.8	—	—
50– 70	loose sandy clay; frequent roots 1)	2½ YR 5/8	36	14	5	5	40	0.5	5.1	4.4	—	—
100–120	comp. clay; rootlets occasional 2)	10 R 5/7	33	12	4	5	46	<0.1	5.9	5.2	—	—
150–170	clay; rotten granite; no roots	10 R 4/8	32	12	6	7	43	<0.1	6.0	5.3	—	—
170–180	transit. zone to unweathered granite . .	10 R 4/8	41	18	9	8	24	<0.1	5.8	4.5	—	—
Profile 2:												
3– 10	sandy loam with rootmat	5 YR 5/7	43	21	3	6	17	4.6	4.4	3.6	2	26
55– 65	rather loose clay; roots frequent	2½ YR 5/8	23	11	4	6	56	1.5	5.1	4.2	0.9	12
90–100	id.; rootlets occasional 1)	10 R 5/7	33	12	5	7	43	<0.1	5.6	4.7	0.6	12
150–270 3)	rotten granite; no roots	10 R 5/8	44	15	7	12	22	<0.1	5.8	4.9	1.2	8

1) with few friable red iron concretions;

2) abundant idem, up to 4 cm in diam.

3) mean of 3 samples (150–160, 185–200, 235–270 cm).

4) exchangeable base content in mg equival./100 g soil.

5) exchange capacity in mg equival./100 g clay (< 1 μ).

4) and 5) determined after shaking with NH_4-acetate 1 N (pH 7).

The figures for cation-exchange capacity and for the exchangeable-base content determined for the second profile are extremely low; they are of the same order of magnitude as those obtained for the ferrallitic soils of the Goliath Cr. region (cf. table IX). The highly degraded clay-complex largely consists of kaolinite (95–100 % of the fraction $< 1\ \mu$).

For the second profile the amount of exchangeable ions, expressed in mg equivalents/100 g soil, varied between 0.1–1 for Ca + Mg, 0.1–0.3 for K and tr.–0.3 for Na. Owing to the intensive tropical weathering, easily corruptible minerals, such as felspars, were found to have disappeared already at a short distance from the unweathered parent rock (cf. BAKKER 1957).

Rooting and penetration with humus are rather deep (on the average approximately 75 cm). Just as in the other soil profiles, the roots showed a conspicuous concentration in a layer a few centimeters thick at the top of the profiles. As is shown by the figures in table XI, both the top layers and the layers overlying the unweathered bedrock are very rich in coarse sand. In the extreme top bleached quartz grains are abundant.

Drainage of the sites under consideration is moderate to rather good.

The red forest-soils of the Voltz Mnt. region belong to the "*granite-laterite soils*" as distinguished by VAN DER EYK (1957) from the "*granite yellow earths*". The first perhaps have developed from less acid granites.

II.6. SOIL MOISTURE AND AIR

Combined data on pore space and soil moisture are of paramount ecologic interest, because they enable us to estimate the degree of aeration (free air space = difference between total porosity and water content) as well as the water-supplying power of the soil. These two edaphic features are even considered by some students of tropical forest soils to be the main factors of ecological importance.

In the present study pore space was determined at different depths of the soil profiles for a range of soil types varying from loose coarse sands to silty clay, in order to gain a preliminary impression of the order of magnitude which the variation of this factor shows under forest conditions.

When comparing the various *free-draining soil* types in the regions the *water-supplying power* during the dry periods presumably is the main differential factor, because these soils probably are throughout the year well aerated to full depth. Hence these soils were chiefly sampled during the course of the dry season.

For the *partially-impeded* and impeded soil types on the contrary the degree of *aeration* that is still maintained during the wettest periods, presumably is the differential factor. Lack of time prevented a systematic investigation in these soil types during the wet season. Yet a few samples taken in the beginning of the wet season at a site where the occurrence of mottling at a relatively low depth seemed to indicate a not altogether free drainage, confirmed our supposition.

In order to investigate the porosity, the site profiles were sampled by means of constant-volume brass rings, which, when forced into the soil, cut out an approximately undisturbed sample of known volume (ca. 100 cm^3). Volume weight was determined by weighing the constant-volume samples after they had been desiccated to constant weight at 105° C.*) Percentage pore space was calculated as follows: $\%\text{ pore space} = 100 - \left(\frac{\text{Vol. weight in g/cm}^3}{\text{real s.g.}} \times 100\right)$, a mean value of 2.5 being accepted for the real specific gravity (= s.g. of the mineral soil particles).

In practice the volume of the metal rings proved to be too small, as the soil, on account of the irregular distribution of quartz fragments, roots, cavities dug by earth worms, etc., proved to be insufficiently homogeneous. Therefore it was decided to take 5 samples in each horizon, providing a total sample of about 500 cm^3 per layer.

The samples (200–800 g) used for the determination of soil moisture were procured with a trowel (a fresh pit being dug for each sample), and put at once in plastic bags, which were closed airtight for transport to the laboratory.

By using the porosity constants derived from the measurements made on the constant-volume samples, the moisture data (found by drying and weighing, the result being expressed as a percentage of the oven-dry weight of the soil) could be interpreted in terms of volume-percentage of water and free air-space.

In table XII the data on the porosity of 8 selected profiles are set out, together with some laboratory data characteristic for the profiles.

TABLE XII

Porosity in selected profiles of forest soils. Sites 1–5: Mapane region; 6 and 7: Coesewijne region; 8: Wayombo region.

Depth (cm)	site 1				site 2				site 3				site 4			
	sand a)	clay b)	organic matter c)	porosity (vol.-%) d)	sand	clay	organic matter	porosity (vol.-%)	sand	clay	organic matter	porosity (vol.-%)	sand	clay	organic matter	porosity (vol.-%)
5	89	7	0.3	50 e)	76	20	1.6	45	75	20	1.2	45	66	25	–	45
10-20	90	7	–	44	70	25	1.2	45	70	36	–	43	60	32	–	43
25	91	6	0.8	44	–	–	0.7	47	65	42	–	43	–	–	1.0	43
35	91	6	0.8	44	–	–	0.6	–	60	32	0.6	39	52	40	0.6	40
55	90	7	0.2	44	54	37	0.3	42	54	26	0.4	39	52	40	0.4	38
90	91	7	0.1	41	–	–	–	–	55	26	0.2	38	–	–	–	–
115	–	–	–	–	50	40	0.1	35	–	–	–	–	–	–	–	–
	site 5				site 6				site 7				site 8			
5	64	29	1.6	39	78	15	0.9	–	64	21	1.0	–	–	–	–	–
10	50	40	0.9	–	79	17	0.7	40	63	26	0.7	45	50	15	0.6	49
25	44	51	0.7	41	71	22	0.6	40	63	29	0.6	37	43	16	0.4	39
55	40	48	0.2	38	70	26	0.4	40	58	35	0.4	37	38	19	0.2	30
90	–	–	–	38	65	29	0.2	42	57	36	0.2	–	–	–	–	–

a) 2 mm–50 μ; b) $< 2\ \mu$; c) total carbon as a % of dry soil (Walkley–Black); d) total porosity $= 100 - \left(\frac{\text{vol. weight}}{2.5} \times 100\right)$; e) unreliable owing to the difficulty of obtaining constant-volume samples in the very loose sand of the top layer.

---

*) The weighing of the samples was carried out at the Soils Dept. of the Agricultural Experiment Station, Paramaribo.

Sites 1–5 represent 5 soil types occurring in the Mapane-forest experimental plot; the corresponding profiles were described in the text below fig. 49.

Site 1 (profile C/0) was a loose coarse sand, excessively drained and strongly bleached, and overlying white pipe-clay at a depth of 3 m. The forest was rain forest but it showed some affinity to high savanna forest as appears from the results of the enumeration in sample plot 2 (cf. III.2) in the centre of which site 1 was situated.

Sites 2 *and* 3 are representative for the deeply homogenized yellow-red light soils, varying in texture from sandy clay loams to sandy clays, showing free drainage due to its topography (i.c. the situation on top of the terrace) as well as to the characteristics (high content in coarse sand) of the parent material. Site 3 was described in profile 8/1.

Site 5 was situated 100 m W. of site 3 on a gentle slope leading to a creek, and 7 m below the sites 2 and 3. The profile 8/0 is representative for the relatively heavy soils (sandy clay merging into clay at about 50 cm depth), and shows partially-impeded drainage due to topography (i.c. to its situation on a slope draining a terrace) as well as to the restricted perviousness of the material of the parent soil, which presumably was a granite or a gneiss weathered in situ. As has been discussed already in II.2, the relative importance of the impeded drainage in such profiles is indicated by the occurrence of *mottling*, which begins at a relatively shallow depth. Such profiles were found also in the transect shown in fig. 49 between 1100–1250, 1300–1400 and 1775–1900 m. The profile was described as a humic sandy clay loam merging at 35 cm into a compact red/yellow mottled clay.

As was mentioned before (II.2.2.b), this mottling was taken to be an indication of *inadequate aeration*. Rooting at this site appeared to be shallower than in the foregoing sites: main root zone 2–10 cm, moderate rooting at 10–35 cm, and rare below 35 cm. Signs of the activity of burrowing animals (earthworms, termites, ect.) were rare below 35 cm. Hence the zone of biological activity was markedly shallower than in the foregoing, deeply homogeneous profiles (1–3), in which roots and activity of the soil fauna penetrated to depths of 75 cm and more.

Site 4 (profile 8/2) is intermediate between sites 2 and 3 on the one hand and site 5 on the other hand. Mottling began below 200 cm, but the upper layers were less permeable, due to heavier texture (sandy clay below 40 cm) than in sites 2 and 3.

Sites 6 *and* 7 represent the lightest and the heaviest textured soil types met with in the *Upper-Coesewijne* region.

Site 6 (rain forest) is a (sandy) clay loam, merging at 40 cm into a sandy clay, showing weak mottling below 60 cm. This profile belongs to the relatively heavy, yellowish-brown (12½ YR 6/5 at 50 cm) soil type Y in fig. 58 (similar to the soil of enumeration plot 6, cf. III.3.2). Drainage is not altogether free, owing to the relative imperviousness of the parent-soil material and also to topography.

Site 7 is an excessively drained, bleached coarse sand, which represents the lightest soil type on which high forest was met with in this region (soils marked S in fig. 58).

Site 8 represents a heavy silty clay such as found in the Old Coastal Plain, south of the Wayombo R. The profile was described in III.5. Drainage is partially impeded during the greater part of the year.

The porosity figures given in table XII clearly show that *the total pore volume in the upper horizons of soils under forest cover is within wide limits independent of the mechanical composition of the soil, and varies between* 39–47 % *in the main zone of biological activity.*

In the heavier soil types pore space shows a marked decrease below this zone.

The figures given in this table represent total pore space, comprising both *capillary* and *non-capillary* pore volume. For the light-textured, free draining Mapane soils (sites 1–4) an impression of the proportion between the two values can be obtained from the moisture values set out in table XIII, which were determined two days after a short period of heavy rainfall at the beginning of the short wet season, when these pervious soils presumably had been drained from all gravitational water, but when the capillary space was still filled at storage capacity.

As is shown in fig. 59, in various sites approximately the same moisture figures were found when after the last heavy showers of the long wet season (22–9–'56) the gravitational water had been drained away. This probably did not hold for site 5, where drainage was very slow and where part of the moisture content represents non-capillary, gravitational water. Accordingly the moisture figures in table XII for sites 1–4 are thought to represent approximately the *field capacity*, which to be sure is mainly determined by capillary pore volume.

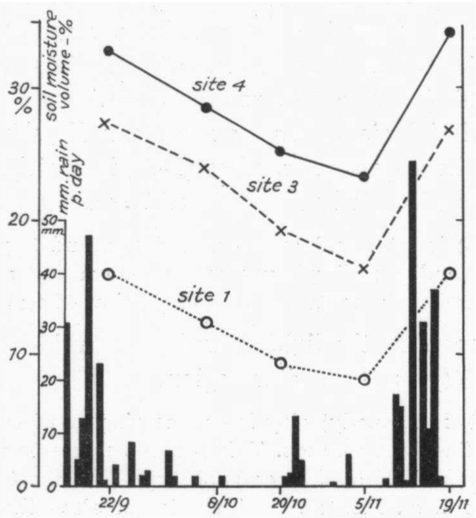


Fig. 59. Total soil moisture content (expressed as volume-percentages) in 3 soil types in the Mapane rain forest. Values averaged over main rooting zone (5–60 cm). Site 1 and 3 (sand and sandy clay loam respectively) are situated on top of the terrace. Site 4 (sandy clay loam merging into sandy clay) in a position a few meters lower. For detailed analyses of samples taken on 5 and 19 Nov. 1956, compare with table XIV and XIII. The columns at the base of the figure represent daily rainfall as recorded at Mapane camp, 500 m from the sites (cf. fig. 7).

In table XIII *free air-space* is given assessed as the difference between total pore volume and total moisture content (expressed as volume-%).

TABLE XIII

Soil moisture content (loss of weight after desiccation at 105° C, expressed as a volume percentage) and free air-space in 4 selected soil types in the Mapane region. Determined on 19 Nov. 1956, after the first winterrains: 177 mm rainfall during the preceding 9 days (cf. rainfall distribution for Mapane camp shown in fig. 7). Compare with values set out in table XIV, taken 14 days previously (5 Nov. 1956), i.e. at the end of the dry season. Values in bold type (less than 10 % air-space) might, according to CHENERY *et al.* (1945) and HARDY (e.g. 1946), be regarded as denoting *unsatisfactory aeration.* Soil moisture at the time of sampling approximately represents field capacity, except for site 5 (for explanation see text).

Depth (cm)	site 1		site 3		site 4		site 5	
	moist.	air	moist.	air	moist.	air	moist.	air
5	13%	37%	26%	19%	30%	15%	30%	**9%**
10	-	-	-	-	31	12	-	-
25	16	28	27	16	31	12	34	**7**
35	16	28	27	16	31	**9**	35	-
45	16	28	27	12	31	**8**	35	**3**
85	14	27	-	-	-	-	35	**3**

The figures for free air-space, which may be taken as representative for the greater part of the wet season, confirm the impression obtained by studying the soil profiles, viz. that the deeply homogenized profiles on the terraces and on the crests of the hills are well aerated throughout the year, whereas the lower lying soils, showing mottling at rather shallow depths, are less well aerated. Soils like that of site 5 are poorly aerated during the greater part of the wet season, i.e. during at least 8 months of the year.

The values given in table XIV illustrate the differences in soil moisture in various soil types at the end of a dry season. Because the actual rainfall in the period preceding the sampling was not identical for the three regions, only the data for sites in the same region can be compared with each other.

As might have been expected, soil moisture appeared to be strongly correlated with the mechanical composition of the soil, the light-textured soil types showing considerably lower values. The very low figure found in site 1 at a depth of 175 cm refers to the very coarse sandy horizons found in this profile between 145 and 300 cm.

A rough estimate of the *"growth water"* (readily available water in excess of the permanent-wilting percentage) during the yearly drought period might be obtained by comparing the figures given in table XIV with some calculated value for the *wilting coefficient.* This value may be assessed, for instance, at 0.6 times the moisture value set out in table XIII,

TABLE XIV

Soil-moisture content (expressed as volume-%) at the end of the dry season. 1–4: Mapane region (sampled at 5 Nov. 1956). 6–7: Coesewijne region (11 Nov. 1957). 8: Wayombo region (5 Nov. 1957). For the last station no rainfall data were available, but precipitation during the preceding 30 days was certainly less than 50 mm and during the preceding 7 days 0 mm.

site no.	1	3	4	6	7	8
Depth (cm)	Mapane			Coesewijne		Way.
5	9%	17%	24%	–	–	–
10	9	17	22	7%	14%	18%
25	9	17	22	–	19	16
35	8	16	24	10	21	16
45	8	16	–	12	–	17
60	8	19	24	13	22	19
85	8	–	–	–	–	–
175	2	–	–	–	–	–
rainfall during preced. 30 (7) days:	32 (8) mm[*]			10 (0) mm		<50 (0) mm

[*] cf. fig. 7.

which approximates field capacity. But because this ratio, especially for light-textured soils, may vary considerably, the calculation of available water based on percentages of non-available water which have not been determined by direct observation of the permanent-wilting percentage, may be highly untrustworthy.

PART III

FLORISTIC COMPOSITION OF THE FOREST

III.1. INTRODUCTION

The proper classification of a forest area into a set of homogeneous phytosociological units is the first step towards practising forestry on a scientific basis. Silvicultural techniques can be given precision only when they are viewed in relation to such units. Although the phytosociological data presented in this chapter are utterly insufficient for such a classification, our sampling records are nevertheless not without interest as they reveal the order of *magnitude of the differences in composition* found in lowland and upland mixed forest in the central part of N Suriname, over small as well as over greater distances. The significant differences found between the lowland mesophytic forests in the Mapane region (Suriname R.-Commewijne R.) and the Upper-Coesewijne region (Saramacca R.-Coppename R.) and between these lowland forests and the forests on ferrallitic soils, might be regarded as an indication that this formation in the N half of Suriname consists of discrete vegetational units. These preliminary studies of the floristic composition of the Suriname rain forest provide an argument against the opinion of some students of tropical rain forest, that the possibility of a phytosociological subdivision of this formation in a definite region is nothing but a chimera.

The lowland rain-forest of Suriname is typical mixed forest in that it shows the same pecularities in the distribution of the constituent species as have been described by many authors for other equatorial countries. On mesic sites this forest seldom shows any tendency towards single-species dominance. The composition of the forest shows distinct variations from place to place; each of the sample plots described in the following sections shows a different assemblage of relatively abundant, "leading", species. The latter do not exceed 20 in number, although in the whole of Suriname there are in this formation at least some 200 species of large trees. Some species are found throughout the country and even far beyond its boundaries; others are more local. Some are limited to a single compact area, others have discontinuous areas. Commonness of a species in one place may go with rarity or even absence of the same species in a neighbouring site. Some species are not confined to the mesophytic lowland forest, but show a much wider ecological amplitude. As will be discussed in more detail in III.7, in other tropical countries where extensive phytosociological studies have been carried out, a similar state of affairs has led to a divergence of opinion on the possibility of subdividing the local rain-forest formation in phytosociological units of lower rank.

In the present study the floristic composition was studied by means of *quadrats*. It may appear from further investigations that the "random pairs method" which has largely replaced quadrating in the sampling of North American forests, is also useful in tropical rain forest. Qualitative or semi-quantitative studies based on ocular estimates of certain vegetational characteristics as are used in less complex types of vegetation, are usually unsuitable for phytosociological studies in the tropical rain forest. Even for experienced foresters it is practically impossible to obtain reliable estimations of abundance (e.g. HEINSDIJK 1953), even for the few tree species which are easily distinguishable at first sight. Accordingly quantitative methods based on counting and measuring the individual trees in sample plots, had to be used for collecting field data which can be handled by regular mathematical and statistical procedures. The most important vegetational attributes which may be measured readily, are *number*, *size* and *distribution* of the component plants. For the investigation of these attributes a 10 × 10 m quadrat was used as the basic unit. The number of 100 m^2 quadrats per sample plot depended primarily on the amount of time available and on the type of forest. This size of the basic sampling unit has proved the most convenient one for sampling trees of 5 cm diameter and over, and was used also by LINDEMAN (1959) in the Suriname forest. In most cases the sample plot was one hectare in area and square in shape, and was subdivided by cut lines into 100 quadrats, the boundaries of which were demarcated by posts. In one case the quadrats were arranged in sampling strips (sample plot 1 in the Mapane region). Personal bias in placing the plots was excluded as much as possible by rigidly adhering to the sampling plan, once it was made.

I am fully aware of the fact that the size of the sample plots was arbitrarily chosen and that the sampling technique did not come up to the standard required for a statistical analysis of the floristic composition, but it should be understood that the present investigations are no more than a preliminary study, which is meant to give a first insight in the order of magnitude of the variability existing in the composition of the forest in a small area (Mapane region) as well as over larger distances. Further investigations of the distributional pattern of the individual species and of the assemblages are needed before it will be possible to take a decision with regard to the most favourable size, shape (e.g. squares or long and narrow rectangular plots) and distribution (e.g. one large plot or several small plots, and plots distributed at random or in a definite pattern) of the sample plots. Moreover, before the various sampling techniques can be tested and before the most effective type of sampling unit for the purpose of a phytosociological classification of the rain forest in Suriname can be determined, at least the broad principles of such a classification should be defined and the criteria determined upon which the distinction of the vegetational units is to be based.

Only then it will be possible to define exactly what should be understood by an *adequate slampe* and to decide how such a sample can be obtained with a minimum of effort. If, for instance, the classification is to be based on the composition of the assemblage of, say 10, *leading* (most abundant) tree species, the present study shows that a relatively small sampling area (50–100 quadrats) is amply sufficient, as it provides the minimum of floristic data needed for the classification of a certain phytocenose. If, on the contrary, it should appear that the vegetational units will have to be defined by species groups which include rather rare ones, or such which show contagious distribution, much larger sampling areas would be needed.

As quadrating in order to obtain vegetational data in tropical rain forest takes a lot of time, the total area of our sampling quadrats runs to about 17 ha only, 10 ha of which were confined to a relatively small area in the Mapane region.

In the sample plots girth and vernacular name of the trees were recorded with the help of Mr. Jan Elburg, a trained "tree-spotter". The counts were made for each quadrat separately, thus enabling the computation of quantitative structural characteristics like quadrat-frequency, and providing data for species/area curves. The trees of 5 cm d.b.h. or more were counted in all quadrats of the sample plots. Trees of 2–5 cm were usually noted in 10 % of the quadrats only.

The Creole names used by the assistant, who had a many years' experience as "tree-spotter" on the enumeration surveys of the Forestry Department, were found on the whole to be constant and reliable, as was proved by cutting down and identifying various trees to which he gave the same name. For a discussion of the reliability of the vernacular names, reference is made to LINDEMAN (1953). In cases where one vernacular name was known to correspond to more than one species (e.g. *tingiemonnie* and *salie*, which include several genera and a large number of species of Burseraceae and even of Meliaceae; *pisie*, used for many genera and species of Lauraceae, etc.) and if identification in the field was impossible, specimens were collected and sent to the Utrecht herbarium for identification. This was also done with trees that were unknown to the enumerator. Sometimes flowering material was collected outside the plot. The identifications given in the following tables apply only to the areas under consideration; the vernacular names may be applied in other parts of Suriname to different species. Where the identification of the specimens collected was impossible, the collector's number is given instead of the botanical name.

The majority of the material was identified by Dr. J. C. Lindeman and other members of the staff of the Utrecht Herbarium (director Professor Dr. J. Lanjouw). In the following sections *nomenclature* follows generally that of the "Flora of Suriname".

The diameters of the trees and saplings were measured with a rule or a calliper, either at *breast height* or abov ethe buttresses. For irregularly formed trunks the average was taken of two measurements, perpendicular to each other.

The enumerations included woody plants only. Other members of the phytocenoses, like ferns, mosses, herbs, lianas and epiphytes were not counted. Herbaceous species of the undergrowth and of the groundflora were noted only if there was a special reason for paying attention to them.

The most important vegetational attributes which can be readily measured in areal plots, are *number*, *distribution in space*, and *size* of individuals of the component species.

As was mentioned above, the diameter of all trees either of 2 or of 5 cm d.b.h. and over was measured; this enabled us to compute for the constituent species the (areal) *density* (in the sense of Anglo-American students, i.e. the number of individuals per unit area) of different diameter-classes.

In the tables which appear in the following sections, average densities per hectare are given for the diameter-classes of 25 cm and over (i.e. for the upper- and middle-storey species), of 5–25 cm (lower-storey species) and of 2–5 cm (undergrowth species). This procedure is to some extent liable to interpretative errors in the event that the sample plots are small (e.g. plot 2 in the Mapane region and the sample plots in the Wayombo region, cf. table XVII); in that case the use of a standard unit of 1 ha involved that figures which were determined in small areas were accepted as representative for a much larger area. The choice of the diameter limits upon which the densities were based, was more or less arbitrary. For the emergent and canopy species 25 cm d.b.h. was taken as the lower limit because in their case it was found that the greater part of the individuals with a trunk diameter of 25 cm or more had reached the main canopy and the reproductive stage.

It appeared, moreover, that for most sample plots the use of a *lower diameter limit* caused no very significant shifts in the list in which the preponderant tree species are arranged in the order of their densities. Admittedly, the difficulty which is inherent in the choice of a rather arbitrary lower diameter limit for the individuals that are to be taken into account for the relative densities of the species could have been avoided by taking total (trunk) *basal area* per ha as a criterion of their relative importance, as is sometimes done in phytosociological forest studies; total basal area is taken in addition as a substitute for the degree of cover. As the diameter was recorded for all the trees of each species, the basal area could easily be computed. However, I did not use this value in the tables, because I am not sure that its classificatory value is really greater than that of the *number of individuals*. For most sample plots the use of the basal area as an *importance value* for the upper- and middle-storey species would have resulted in an arrangement of the leading species which differed considerably from that based on their number, as is shown by the data for the basal area given in table XV. In the Mapane forest, for instance, the basal area is considerably higher for *Goupia glabra* (*kopie*) than it is e.g. for *Eschweilera odora* (*hoogland manbarklak*), although the latter species (which seldom attains a diameter of more than 30 cm) is highly characteristic for the composition of this forest type, which is well reflected in the density figure found for the mature trees ($\geq$ 25 cm d.b.h.). The same holds true for *rode salie* (*Tetragastris altissima*), a canopy species which seldom attains a large diameter, and for which basal area would not show the relatively strong prominance of this species in the Mapane forest so clearly as the density figure does.

If basal area is used as a criterion of relative importance, too much weight is given, in my opinion, to the diameter of the trees, the squares of which are used for computing the basal area. For instance, a species which is represented only by a single tree of 100 cm d.b.h., would rank as

Xeromorphous (savanna) forest on bleached coarse sand in the Mapane region
The tree with stilt roots is a *sabana-mangro (Clusia fockeana)*.

high as a species of which 25 trees of 20 cm d.b.h. occur in the same unit area. Yet, at least in the Suriname mixed forest, in most cases the latter species will have a much greater diagnostic value than the first, how impressive the dimensions of its single representative may be.

The most decisive criterion for an evaluation of the relative importance of a species in a given stand is the *number of individuals* which, by reaching a certain size, show that they have succeeded in overcoming the principal obstacles in the struggle for existence.

For the canopy species it seemed reasonable to take a size of 25 cm d.b.h. as the average lower limit, because, as mentioned above, the greater part of the trees which have attained this size, may be considered to have definitely made their way to the dominant layer. As I have observed in several undisturbed rain-forest types in Suriname, it is primarily the specific character of the tree, and but in a minor degree the nature of the site, that determine what size the tree may reach, once it has reached the canopy. In other words, for most species there proved to be a close correlation between the total basal area and the density of the trees of 25 cm d.b.h. and more. In a few cases a species could show a considerable departure from the "normal" specific size-class distribution (e.g. *Goupia*, cf. fig. 64). As will be discussed in IV.2 such pecularities in the diameter-class distribution indicate differences in the recent *history* of the forest stand. So I found, for instance, in a rain forest stand in the Mapane region in an area of about 1 ha five *Goupia glabra* (*kopie*) trees of more than 25 cm d.b.h., and these trees had a total basal area of 3.5 m^2, whereas in a neighbouring stand for this species about the same density was recorded (6 trees of more than 25 cm d.b.h.), but a total basal area of no more than 1.5 m^2. For comparing the composition of the two stands, the basal area (or still better: the size-class distribution) of *kopie* has to be considered side by side with the density value; the—for this species—*abnormally* high proportion of middle-sized trees (25–50 cm) in the second stand indicates a relatively recent disturbance of the forest (say 50–100 years ago), whereas the large proportion of large-sized trees (50–120 cm) in the first stand shows that here the influx of the strongly light-demanding *kopie* has taken place at a far more distant date.

For the computation of the densities of the lower storey and of the undergrowth species a lower diameter limit of 5 and 2 cm respectively was chosen. Further study of the phytosociology of the Suriname rain forest will probably show that the 5 cm limit is too low.

Admittedly, for undisturbed forest the total basal area of all the species together may be of considerable ecological value as an indication of the productivity of the site, though it may give a false impression of the latter in forest types (like the xeromorphous variants of rain forest) which are rich in species with deeply fluted trunks (e.g. *ijzerhart*, *Swartzia* spp. and *bruinhart*, *Vouacapoua americana*).

In two tables the (quadrat-) *frequency* data have been given for a few selected species; this value indicates in what percentage of the unit-quadrats a species occurs in the sample plot; when used in combination with density it proves to be a very useful feature, for then not only the number of individuals is known, but also the way in which they are distributed in the stand. Fuller reference to the distributional pattern of some tree species will be given in IV.5. These two characters, density and frequency, are of prime importance in determining community structure, especially in forests. Taken together they have a variety of uses far beyond the scope of other quantitative values. Because frequency values can only be compared when they are computed on a standard unit, a constant quadrat size (10 × 10 m) was used. Our phytosociological data are insufficient to decide whether absolute or relative frequency figures should be used for the Suriname rain forest. For the moment absolute quadrat-frequency percentages are used. The distributional pattern was studied only for a few tree species of the Suriname rain forest (and that only in a few sites) but I nevertheless got the impression that the mode of distribution is no very reliable characteristic; a species which shows a random distribution in one type of forest, may grow in groups in other forest types. This would mean that for classificatory purposes the relative importance of a species in a stand should not be based on a combined *importance value* (frequency plus density), but only on density. This holds true also for strongly light-demanding species, for which the quadrat-frequency depends on the accidental circumstances under which the influx of seedlings has taken place. The occurrence in groups e.g. of *kopie* trees is due to regeneration in rather large openings, whereas random distribution of the individuals (causing a relatively higher frequency-percentage) indicates that regeneration took place in the randomly distributed, rather small gaps that are caused by the death of large trees.

The *degree of cover* is a characteristic which can hardly be used in tropical forests. In the large sample plots that are required in the heterogeneous tropical forests, estimating the cover of the individual trees in the highly complicated tangle of overlapping crowns would take too much time. Moreover, estimating the area of the horizontal projection of the tree crowns gives no adequate picture of the real cover, as it gives no weight to the density of the crowns, which varies considerably from one species to another. The shading effect which the very thin and irregularly formed crowns of *Goupia* and other Celastraceae (*zoutoemetiehoedoe, Maytenus* spp.) and of some species of Mimosaceae exercise on the subordinate layers is much less than that of the dense crowns of many Papilionaceae (*Mora*!), though the vertical projection on the ground may have the same area. For classificatory purposes, the degree of cover is, like the basal area, of minor importance, because it is largely determined by the nature of the species, and to a much lesser degree by that of the site.

Recently desperate attempts have been made to apply to the tropical rain forest the ocular estimations upon which the original methodology of the French-Swiss school of phytosociology was based, and even tables containing estimations of combined cover-degree plus abundance and of sociability have been published (e.g. GERMAIN *et al.* 1956).

If we wish to estimate the degree of cover of the tree layers in order to obtain an idea of the degree in which they may influence the lower layers, it is the density of the tree layer as such which is important, and it is immaterial which particular species is the dominant one. In that case the percentage of light which is transmitted by the tree layer, is an objective and easily obtainable measure.

III.2. Rain forest of the Mapane region

III.2.1. *General remarks*

In the Mapane region rain forest is found on *mesic* sites, viz. on the well-drained soils, varying from brown loamy sands to red sandy clays, which were described in detail in part II.2.2. The other types of vegetation that are found in this area, viz. xeromorphic formations (like savanna forest and open savanna) on more freely draining sands, and creek-margin forest on the hydromorphic soils occurring in depressions and alongside the forest streams, fall outside the scope of this study. The distribution of the main types of vegetation were shown in figs. 2 and 46.

A short description of the rain forest as found between the Suriname River and the Commewijne River, in the region North of the Mapane Creek, was given in the General Introduction. It is locally called *high, firm-ground forest* and forms the natural climax on mesic sites, where both soil moisture and soil air are nearly always adequate to the requirements of the trees. The physiognomy of this climax formation (cf. Lindeman 1959: right part of profile V) is the same as that of the rain forest in the neighbouring countries, as this has been described for British Guiana by Davis *et al.* (1933, cf. fig. 6: *Mixed forest*) and by Fanshawe (1952, 1954) and for the *terra firme* areas in Amazonia by Cain *et al.* (1956). Here and there, on the slopes to the forest streams, it is magnificent forest, but it seldom gives "the impression of the vault of cathedral aisles" (Beard, 1944), as the luxuriant rain forests in Malesia do. The trees have long clean straight boles, with a maximum diameter varying from 100 to 150 cm.

As was stated before, no well-marked tree strata were readily distinguishable in this forest. I am inclined to agree with Mildbread (1922), who stated – with reference to the forest of the Cameroons – that any grouping of the trees according to their height is arbitrary, although the space can indeed be thought as consisting of certain height intervals, and the woody plants might be grouped into a corresponding number of classes, according to the height level which they reach when full grown. I have divided the woody species into four groups, viz. *upper storey, middle storey, lower storey* and *undergrowth* species, but this is to be regarded as a classification justified by its convenience for a division of the large mass of tree species, and not as one based on differences of fundamental importance.

For the sake of convenience, the forest may be divided into corresponding layers, each having a distinct floristic composition, although e.g. in the *lower storey* (about 8–18 m) young individuals of species which when full-grown reach the higher strata may occur side by side with the mature individuals of lower-storey species.

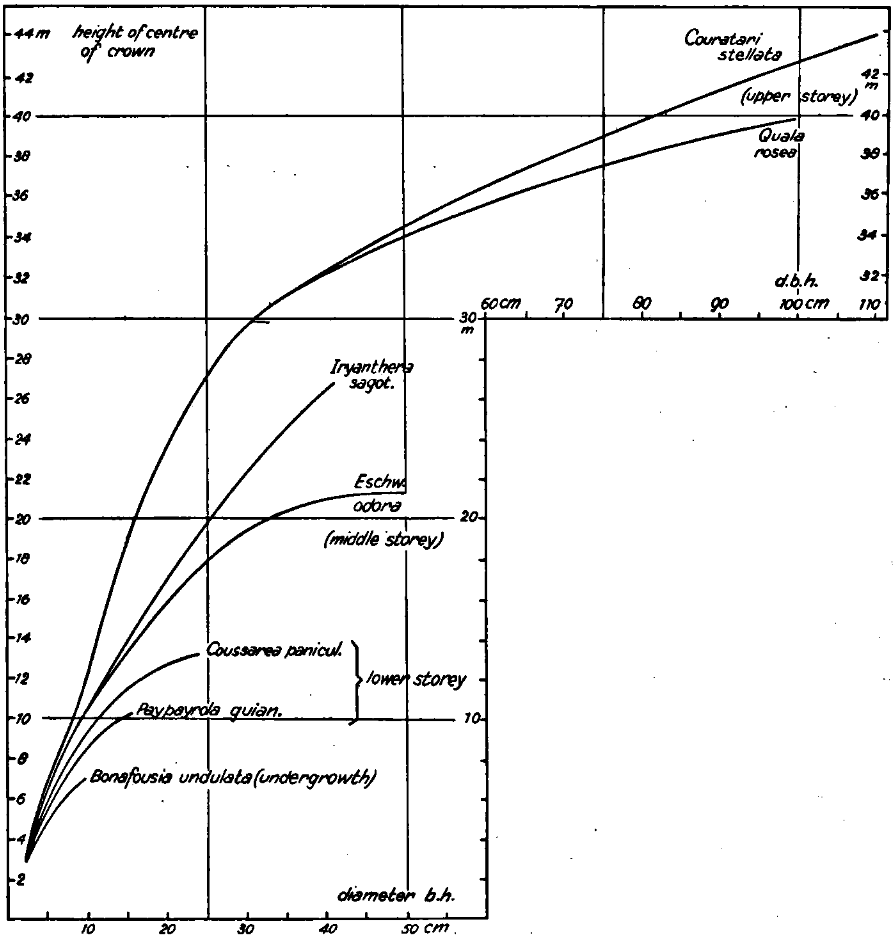


Fig. 60. Height/diameter diagrams for 7 rain-forest species, each based on 1000 readings (except *Couratari:* 200 measurements). With height is meant the distance to the middle of the crown. Diameter is diameter at breast height or just above the buttresses.

The *upper storey* (or *emergent storey*) comprises those species which, when full-grown, form the irregular main canopy, and which reach a height of about 28–45 m (total height). It also includes such species as *ingipipa* (*Couratari* spp.), whose crowns are sometimes lifted clear above the real canopy (*outstanding trees*). In fig. 60, which shows some of the results of comprehensive height/diameter measurements, the trend lines for *Couratari* and *birgiegronfoeloe* (*Qualea rosea*) illustrate the height-diameter relation for such an *outstanding* species and an ordinary *emergent* species respectively. Attention is drawn to the fact that in this diagram the height of the centre of the crown has been taken instead of the "total" height. The majority of the dominant species of the upper storey show a similar relation between height and diameter. In mature trees belonging to the upper-storey species the diameter of the crown is usually larger than their height. These crowns sometimes (Mimosaceae!) even tend to become more or less umbrella-shaped, although true umbrella-shaped crowns are largely confined to emergents in the xeromorphous forest (savanna forest). The crowns of the upper storey, which approximately corresponds with the highest (A) stratum of other authors (e.g. RICHARDS 1952, p. 25–34), form a discontinuous canopy. The canopy dominants tend to occur in groups between which the crowns of trees of species of a lower storey form the continuation of the canopy, thus giving the forest roof seen from above a more or less uneven appearance. Though the canopy is more continuous than it is in the mixed tropical rain forest in Africa, as described by RICHARDS (1952, fig. 6), it is less continuous and lower than that of the taller and more luxuriant rain forests, such as the mixed *Dipterocarp* forest in Malaysia. The canopy has the same height (32 m on the average) and about the same appearance as mixed rain forest in British Guiana.

The predominant leaf-size is mesophyllous, more than 90 % of the species and the individuals having leaves which belong to this leaf-size class. About one-quarter of the individual trees of the upper stratum have compound leaves (Leguminosae, Meliaceae).

The arbitrariness of this classification of the species in height-classes is necessarily accompanied by the inconvenience that a comparatively great number of species form transitions between the groups. In fig. 60 *broedoehoedoe* (*Iryanthera sagotiana*) appears to be intermediate between the species of the highest stratum and those of the *middle storey*. *Broedoehoedoe*, like many other species, such as various representatives of the genera *Couepia*, *Trichilia*, *Pouteria*, etc., seldom attain diameters of more than 35 cm, but their crowns form a large proportion of the canopy, where they appear between individuals or groups of trees of the tallest species, and they will accordingly be classified as upper-storey species.

The trees of the species belonging to the *middle-storey* ones, seldom attain a total height of more than 25 m, but they may form the roof of the forest in gaps in the upper storey. *Hoogland-manbarklak* (*Eschweilera odora*) and other *Eschweilera* species are typical representatives of this group. In the tables the species of the upper- and middle storey were grouped together. The height of the mature trees of the middle-storey species in the Mapane forest (and in other rain-forest types in Suriname) approximately corresponds to that of the B-storey in mixed rain forest in the Moraballi Creek region in British Guiana (about 20 m: DAVIS *et al.* 1933). *Eschweilera* species (*barklak*) often form the majority of the true middle-storey species.

To the middle-storey species also belong two palms, viz. *koemboe* (*Oenocarpus bacaba*) and *maripa* (*Maximiliana maripa*), which may be rather abundant near the ecotone to xeromorphic forest (cf. sample plot L in table XVII), but are rare in true rain forest in the Mapane region.

The mature trees which are reckoned to the *lower-storey* species attain heights between 8 and 18 m. In the Mapane forest typical representatives of this group are *boskoffie* (*Coussarea paniculata*) and *tajahoedoe* (*Paypayrola guianensis*) (cf. fig. 60). The majority of the trees belonging to this storey have conical crowns which are larger in diameter than in height.

Dwarf trees, tall shrubs and stemless palms are classified as ***undergrowth*** species; they reach a maximum height of 3–10 m. In the Mapane forest stemless palms mainly *paramakka* (*Astrocaryum paramaca*) are abundant, and form the only easily recognizable stratum. The undergrowth is relatively poor in true undergrowth species, and consists for the greater part of saplings of the trees belonging to the higher storeys. The majority of the undergrowth species are dwarf trees, and possess a distinct, straight stem. Some species, such as various Rubiaceae (e.g. *Cephaëlis* and *Rudgea* spp.), *Abuta grandifolia* (Menispermaceae) and *mirkitikie* (*Bonafousia undulata*, which is abundant in the Mapane forest) tend to a more or less shrubby form; they branch not far above the ground level and possess no distinct stem; they may have a very irregular form. Giant herbs such as tall Musaceae (*Ravenala*) and Marantaceae (*Ischnosiphon*) also belong to the undergrowth species, but are absent in the Mapane rain forest. Piperaceae are occasional to frequent. Large Zingiberaceae (*Costus*) are found only in openings in the ecotone to xeromorphic forest.

Many woody species of the undergrowth and in the lower storey belong to families which have no representatives in the higher strata: Rubiaceae, Annonaceae, Violaceae, Sapindaceae, Monimiaceae, Dichapetalaceae, Hippocrateaceae, etc. (cf. table XVIII).

In the sample plots 2 cm diameter was taken as the lower limit for the recording. Hence the true shrubs, like *Cephaëlis* species and Piperaceae, although locally abundant in the Mapane forest, were not noted.

The species of the lower storey and the miniature trees in the undergrowth attain heights (ca. 2.5–18 m) which correspond to those found in the lower (C) stratum (20–4.6 m) and the upper part of the shrub stratum (D) which DAVIS *et al.* (1933) and RICHARDS (1952, p. 27) distinguished in the mixed rain forest in British Guiana.

Below the dwarf trees and the shrubs of the Mapane forest an uneven ***herb stratum*** is found, corresponding to the lowest shrubs and the ground or field layer (E-stratum) in the Moraballi Creek forest. This herb- and seedling-layer consists largely of seedlings of woody plants; the true herbs are relatively rare and belong to few species.

Terrestrial ferns and grasses (e.g. *Pariana campestris* and *Olyra* spp.)

are scanty, and this applies also to the smaller Marantaceae (e.g. *Monotagma*) and Zingiberaceae (*Renealmia*). Terrestrial Bromeliads are absent in the Mapane forest, in contrast to other rain-forest types (Wayombo!) where the abundance of *Bromelia alta* (*bosananas*) may be a conspicuous feature of the lowest stratum.

The density of the herb- and seedling-layer (as well as that of the lowest tree stratum) varies greatly from one place to another, and mainly depends on the amount of light penetrating through the upper strata. Under undisturbed forest large patches of the forest floor may be almost completely bare, whereas under gaps in the canopy the lower strata may become almost impenetrable.

To the ground layer also belong Angiospermous *saprophytes*, such as *Leiphaimos* and other Gentianaceae, which are confined to shaded sites with an abundance of decaying organic matter. *Mosses* are limited to tree trunks, to decaying wood, and to earth heaps, thrown up by uprooted trees and by digging animals such as *armadillos*. In shade and moist places epiphyllous mosses and lichens are conspicuous on the older leaves of the plants belonging to the lower storeys.

In these preliminary studies no more than superficial attention was paid to the herbs, the lower shrubs and the lianes and epiphytes. Canopy lianes are moderately frequent. Epiphytes are occasional and are chiefly confined to the upper branches of the canopy trees. The commonest epiphytic plants are Bromeliads, Orchids (over 40 spp. collected in the Mapane forest) and Araceae. The strangling *Clusia* and *Ficus* spp. (*abrasa*) are occasional, other hemi-epiphytes (Cyclanthaceae and some Araceae) are rather frequent.

III.2.2. *Composition of the forest*

Sample plot 1, situated approximately in the centre of compartment 836, is a 5 % sample of the rain forest in the area pictured in fig. 52. It consisted of 560 quadrats, situated along parallel lines which were cut at unequal distances in the E–W direction. The enumeration in this sample plot was undertaken primarily to provide the data for the height/diameter relations (as shown for a few selected species in fig. 60) and the girth-class frequency-diagrams. In table XV the densities of the leading species are given, averaged over the total area of 5.6 ha. Because the sampling strips were divided into unit quadrats (10 × 10 m), the enumeration data can be used for statistical analysis, such as tests of homogeneity, and quadrat-frequency percentages could be computed. Because of the patchy distribution of many species (cf. IV.5), which also appears from a comparison of the figures for density and quadrat-frequency given in table XV, these 560 quadrats situated along transects, provide better average data than one square sample plot of the same size would have done. The transects crossed all types of rain-forest soils found in this region (cf. II.2.2), varying from loamy sands to clays, and including also red ferrallitic earths with concretionary ironstones.

The following table gives for the leading species density, frequency-percentage and basal area. Of the canopy species only those represented by one or more trees per ha of 25 cm d.b.h. or over have been considered.

TABLE XV

Density (number of individuals per ha), quadrat-frequency percentage (% of 10 × 10 m quadrats in which one or more individuals of a species were noted) and total basal area (surface of the cross-sections measured at breast height of all the individuals) for the most abundant species in Mapane rain forest. Based on enumerations in 560 quadrats (5.6 ha) of sample plot 1. The list of less abundant species appears in the next table,

Vernacular name and scientific name	Number of trees per ha				Basal area in dm^2/ha	Frequency %	
	≥2 cm	≥5 cm	≥25 cm	≥35 cm		≥2 cm	≥25 cm
I. UPPER- AND MIDDLE-STOREY SPECIES:							
hoogl. manbarklak (*Eschweilera odora*) (Lecyth.)	98	62	11	2	140	62	11
rode salie (*Tetragastris altissima*) (Burs).	89	40	10	7	165	56	10
broedoehoedoe (*Iryanthera sagotiana*) (Myrist.)	45	35	6	<1	70	21	5
tingiemonnie (chiefly *Protium*) (Burs.) 1)	100	45	5	2	76	59	4
ingipipa (*Couratari stellata*) (Lecyth.)	30	16	4½	4	180	30	4
hoogl. baboen (*Virola melinonii*) (Myrist.)	35	18	4	1	45	23	4
kopie (*Goupia glabra*) (Celast.)	4	4	3	3	132	3	2
fomang (*Chaetocarpus schomburgkianus*) (Euph.)	13	8	3	2	44	3	1
birgiegronfoeloe (*Qualea rosea*) (Vochys.)	33	19	3	2	94	3	<1
anaura (*Couepia versicolor*) (Rosac.) 2)	47	26	3	1½	50	35	1
doifisirie (*Guarea guara* + *G. gomma*) (Mel.) 3)	44	16	3	1½	61	21	3
switieboontje (*Inga* spp.) (Mimos.) 4)	?	?	3	1½	?	?	2
hoogl. oemanbarklak (*Eschweilera corrugata* Lecyth.)	36	26	2	1	34	35	2
teteihoedoe (*E. poiteaui* + *E. simiorum*) (Lecyth.) 5)	16	7	2	1	62	16	2
krappa (*Carapa guianensis*) (Mel.)	23	13	2	1	28	23	2
jakanta (*Poraqueiba guianensis*) (Icac.)	40	24	1	<1	29	30	1
jakanta (*Dendrobangia boliviana*) (Icac.)	14	6	1	1	24	9	1
wanapisie (*Ocotea* sp.) (Laur.)	20	7	2	2	71	7	1
aprahoedoe (*Pouteria gonggrijpii*) (Sapot.)	29	12	2	<1	20	20	1
zwart riemhout (*Pouteria engleri*) (Sapot.)	12	4	2	1	39	11	2
zwart riemhout (*Micropholis* sp. nov.) (Sapot.)	10	5	1	1	27	10	1
wallaba (*Eperua falcata*) (Papil.)	13	11	2	2	50	13	2
okrohoedoe (*Sterculia pruriens*) (Sterc.) 6)	13	6	2	1	41	12	2
pikienmisikie (*Piptadenia suaveolens*) (Mimos.)	8	5	2	2	55	7	2
prokonie (*Inga alba*) (Mimos.)	4	4	1	1	16	4	1
mansalie (*Guarea kunthiana*) (Mel.) 7)	22	10	1	1	26	20	1
djaditja (*Sclerolobium melinonii*) (Papil.)	15	4	1	1	23	4	1
basralokus (*Dicorynia guianensis*) (Papil.)	6	3	1	1	33	1	1
gandoe (*Swartzia tomentosa*) (Papil.)	3	2	1	1	14	3	1
kwassiba (7424) (Sapot.)	4	4	1	1	28	4	1
witte foengoe (*Drypetes variabilis*) (Euph.)	35	14	1	<1	24	25	1
goebaja (*Jacaranda copaia*) (Bignon.)	5	3	1	<1	21	5	1

TABLE XV *(continued)*

Vernacular name and scientific name	Number of trees per ha				Basal area in dm²/ha	Frequency %	
	≧2 cm	≧5 cm	≧25 cm	≧35 cm		≧2 cm	≧25 cm
II. Lower Storey species:							
tajahoedoe (*Paypayrola guianensis*) (Viol.)	142	70	—	—	—	57	—
switieboontje (*Inga* spp.) (Mimos.) 8)	93	40	—	—	—	52	—
boskoffie (*Coussarea paniculata*) (Rub.)	50	36	1	—	—	42	1
blaka oema (*Diospyros melinonii* + *D.* sp.) (Eben.)	43	21	½	—	—	30	—
koni-konihoedoe (*Gustavia hexapetala*) (Lecyth.)	33	20	—	—	—	24	—
melisalie (*Trichilia surinamensis*) (Mel.) 7)	50	26	2	—	—	44	2
III. Undergrowth species:							
lèlètikie (*Rinorea* sp.) (Viol.)	77	23	—	—	—	59	—
mirkitikie (*Bonafousia undulata*) (Apoc.)	72	26	—	—	—	53	—
pakiratikie (*Tapura guianensis*) (Dichap.)	66	21	—	—	—	29	—
— *Siparuna decipiens* (Monim.)	49	20	—	—	—	44	—
— *Cheiloclinium cognatum* (Hippocrat.)	25	8	—	—	—	20	—
paramakka (*Astrocaryum paramaca*) (Palm.)	abundant				—	82	—

1) chiefly *Protium polybotryum, P. insigne, Tetragastris panamensis*, and other unidentified species of Burseraceae; the lower diam. classes also include lower-storey species, such as *P. aracouchini, Hemicrepidospermum rhoifolium.* 2) probably also *C. caryophylloides.* 3) probably including other spec. of *Guarea.* 4) chiefly *I. rubiginosa* + *I. pezizifera;* numbers of lower diam. classes unknown, because no distinction was made between different *Inga* spp. 5) possibly also *E. chartacea.* 6) probably incl. *S. excelsa.* 7) the lower diam. classes may include also a few individuals of *Trichilia roraimana.* 8) in this plot under this name are included *I. capitata, I. thibaudiana* (on sands), *I. heterophylla* (id.), *I. coriacea, I. marginata, I. acrocephala, I. splendens, I. stipularis, I. bourgoni* and other species; a few of these species probably may grow into the canopy.

TABLE XVI

List of less abundant species (with less than one tree of 25 cm d.b.h. or over per ha) in sample plot 1 in Mapane rain forest, averaged over the total area of the sample plot (5.6 ha).

I. Upper- and Middle-Storey Species (between brackets the number of individuals of 5 cm d.b.h. and over per ha):

Papilionaceae: *Clathrotropis brachypetala* (< 1) — *Swartzia benthamiana* (3) — *Vouacapoua americana* (< 1) — *Vataireopsis speciosa* (1) — *Vatairea guianensis* (< 1) — *Copaifera guianensis* (1) — *Pterocarpus rohrii* (1) — *Andira* cf. *villosa* (1) — *Ormosia* cf. *paraënsis* a.o. spp. (< 1) — *Platymiscium trinitatis* var. *durum* or *P. ulei* (< 1) — *Hymenolobium flavum* (< 1) — *Hymenolobium* sp. (< 1) — *Alexa wachenheimii* (1) — *Martiusia parviflora* (11) — *Peltogyne* sp. (< 1) — *Sclerolobium albiflorum* (2) — *S. micropetalum* (2) — *Andira surinamensis* + *A. coriacea* (1) — *Diplotropis purpurea* (1) — *Dipteryx odorata* + *D. punctata* (3).

Mimosaceae: *Parkia nitida* + *P. ulei* var. *surinamensis* (< 1) — *P. pendula* (< 1) — *Pithecellobium corymbosum* (< 1) — *P. jupunba* (< 1) — *P. racemosum* (< 1) — *P. pedicellare* (< 1).

Sapotaceae: *Manilkara bidentata* (< 1) — *Pouteria melanopoda* + *P. minutiflora* + 7851 (1) — *P. guianensis* + *P.* aff. *cladantha* (8026 and 8027) (7) — *P. ptychandra* (< 1) — *P.* aff. *reticulata* and *P.* spec. nov. (< 1) — *P. cladantha* + *P. sagotiana* + *P. surinamensis* (2) — *Chrysophyllum cuneifolium* (< 1) — *Micropholis gyuanensis* (7) — *Ecclinusa guianensis* (< 1).

Moraceae: *Cecropia*, mainly *C. sciadophylla* (5) — *manbospapaja* (*Pourouma mollis, P. aspera* and *P. laevis*) (1) — *Bagassa tiliaefolia* (< 1) — *letterhout* (*Piratinera* spp., *Trymatococcus* vs. *amazonicus*, etc.) (4) — *manletterhout* (*Piratinera* spp., *Perebea laurifolia, Clarisia ilicifolia*) (7) — Mor. 7887 (< 1) — *Brosimum paraense* (< 1).

Lauraceae: *Ocotea glomerata* (2) — *O. rubra* (2) — *O. petalanthera* (6) — *Nectandra grandis* (4) — *N.* cf. *kunthiana* (4).

Vochys.: *Qualea coerulea* (2) — *Q. albiflora* (3) — *Q. dinizii* (< 1) — *Vochysia densiflora* (1) — *V. tomentosa* (1) — *V. surinamensis* (1) — *V.* sp. nov. (< 1).

Apocyn.: *Geissospermum sericeum* (< 1) — *Parahancornia amapa* (< 1) — *Aspidosperma album* + *A. megalocarpon* (2) — *A. marcgravianum* (4) — *A. oblongum* (2) — *A. vargasii* (< 1) — *Couma guianensis* (1).

Other families: Lecyth.: *Couratari pulchra* (1) — *C. fagifolia* (< 1) — *Lecythis* sp. (< 1) — Burs.: *Trattinickia rhoifolia* ssp. *willdenowii* — *Tetragastris* sp. (7304) (1) — Bomb.: *Bombax globosum* (1) — *B.* cf. *spectabile* (< 1) — Til.: *Lueheopsis* sp. (< 1) — *Apeiba echinata* (< 1) — *A. tibourbou* (1) — Elaeoc.: *Sloanea eichleri* + *S. dentata* + *S. guianensis* (2) — Myrist.: *Virola surinamensis* (< 1) — *Iryanthera paraënsis* (< 1) — Myrt.: *Campomanesia aromatica* (< 1) — Myrt. 7717 (1) — Ros.: *Parinari campestris* (2) — *Licania micrantha* (< 1) — *L. ovalifolia* (3) — *kwepie* (*Hirtella manigera, Licania apetala,* a.o.) (1) — *Prunus myrtifolia* (< 1) — Simar.: *Simarouba amara* (1) — Mel.: *Cedrela odorata* (< 1) — Hum.: *Sacoglottis guianensis* var. *sphaerocarpa* (1) — Linac.: *Hebepetalum humiriifolium* (2) — Combr.: *Terminalia amazonia* (< 1) — *Terminalia* sp. (< 1) — Ulm.: *Ampelocera edentula* (1) — Nyctag.: ?*Pisonia* sp. (< 1) — Olac.: *Minquartia guianensis* (3) — *Chaunochiton kappleri* (< 1) — Rub.: *Capirona surinamensis* (< 1) — *Duroia aquatica* (1) — Flac.: *Casearia javitensis* (2) — *Laetia procera* (< 1) — Ochn.: *Ouratea castaneifolia* (< 1) — Bign.: *Tabebuia serratifolia* (< 1) — *T. capitata* (1) — Melast.: *Mouriria crassifolia* (3) — Bor.: *Cordia* spp. (2) — Celast.: *Maytenus* sp. (2) — Malp.: *Byrsonima coriacea* var. *spicata* (< 1) — Styr.: *Styrax glabratus* (< 1) — Anac.: *Anacardium giganteum* (< 1) — *Thyrsodium schomburgkianum* (< 1) — *Tapirira guianensis* (4) — *Loxopterygium sagotii* (1) — Euph.: *Maprounea guianensis* (< 1) — *Croton matourensis* (< 1) — *Alchorneopsis trimera* (1) — Aral.: *Schefflera paraënsis* (< 1) — *Didymopanax morototoni* (< 1) — Caryoc.: *Caryocar nuciferum* and *glabrum* (3) — Annon.: *Xylopia* vs. *aromatica* (< 1) — *Xylopia* spp. (< 1) — Gutt.: *Symphonia globulifera* (8) — *Rheedia macrophylla* (< 1) — *R. benthamiana* (< 1) — *Platonia insignis* (< 1).

II. LOWER-STOREY SPECIES (between brackets: individuals of 5 cm d.b.h. and over per ha):

Papil.: *Swartzia arborescens* (3) — *S. longicarpa* (1) — Lecyth.: *Gustavia augusta* (< 1) — *Eschweilera longipes* (1) — Ros.: *Hirtella* vs. *triandra* (2) — Laur.: *Licaria cayennensis* + *L. guianensis* (4) — Laur. 7522 (1) — aff. *Aniba riparia* (< 1) — Rub.: *marmeldoos* (*Duroia eriopila* and/or *Amajoua guianensis*) (4) — *Palicourea guianensis* (< 1) — Mel.: *Trichilia roraimana* (4) — Myrt.: *Eugenia patrisii* and/or *P. coffeifolia* (1) — Ochn.: *Ouratea* cf. *flexuosa* (10) — Elaeoc.: *boskoesoewe* (*Sloanea grandifolia, Sloanea* 7956 and possibly other spp.) (3) — *raverienja* (chiefly *S. guianensis*) (4) — Sapind.: *gauetrie* (*Matayba opaca, M. camptoneura, M. arborescens, Cupania* vs. *scrobiculata* var. *guianensis*) (4) — Gutt.: *Vismia* sp. (< 1) — *V. angusta* (< 1) — *Tovomita* spp. (3) — Viol.: *Leonia glycycarpa* (< 1) — Apoc.: *Ambelania* *acida* (1) — Bor.: *Cordia* spp., on this plot chiefly *C. hirta* (15) — Euph.: *Sagotia racemosa* (< 1) — *Mabea piriri* (12) — *mirkiehoedoe* (*Sapium klotzschianum* and/or *S. obtusilobium*) (1) — Annon.: *Anaxagorea dolichocarpa* (< 1) — *boszuurzak* (on this plot chiefly *Duguetia calycina*) (1) — *jarijari* (on this plot *Fusaea longifolia, Unonopsis rufescens, U. guatteroides, Duguetia inconspicua, Guatteria chrysopetala,* etc.) (15).

III. UNDERGROWTH SPECIES (between brackets: individuals of 2 cm d.b.h. and over per ha):

Burs.: *Hemicrepidospermum rhoifolium* (± 5) — Ros.: *Hirtella racemosa* (22) — Laur.: *Systemonodaphne mezii* (2) — Eben.: *Diospyros martinii* (26) — Sapind.: *Cupania hirsuta* (13) — *Talisia* spp., on this plot chiefly *T. megaphylla* and *T. pedicellaris* (5) — *bosgujave* (under this name are included several genera of Myrtaceae: *Myrcia, Myrciaria, Calycolpus,* etc.) (10) — Myrt. 7478 (14) — Rub.: *Palicourea nicotianaefolia* (< 1) — *Rudgea cornigera* (2) — *Mapouria opaca* (< 1) — *Posoqueria latifolia* (< 1) — Olac.: *Heisteria cauliflora* (± 8) — *mispel* (different spp. of Melastomataceae, mainly *Miconia*) (< 1) — *Mouriria sagotiana* (5) — Borag.: *Cordia nodosa* (3) — Monim.: *Siparuna guianensis* (2) — Icac.: *Discophora guianensis* (5) — Quiin.: *Lacunaria crenata* (8) — *L. jenmani* (1) — *L.* sp. (1) — *Quiina oblanceolata* (2) — *Touroulia guianensis* (1) — Menisp.: *Abuta grandifolia* (2) — Opil.: *Agonandra* sp. (4) — Logan.: *Strychnos* sp. (1).

The foregoing tables clearly illustrate the great floristic richness of the Mapane forest; in looking at these tables it should be borne in mind that only the woody species have been recorded. The enumeration in sample plot 1 was carried out first of all in order to obtain an estimate of the density of the prominent tree species. Only in a part of the plot, and here only for the larger trees (viz. for those of more than 10 cm diam.), a distinction was made between the species of the difficult groups (such as the *tingimonnie's*, the *Inga* spp., the *Annonaceae*, etc.) in order to arrive at a more or less reliable estimate of the *number of species*. For an area of 3 ha the *species/area curve* for individuals with stems of more than 10 cm and with stems of more than 25 cm diameter is given in fig. 61; it shows that on a total sampling area of 3 ha 87 canopy species were found of which individuals had reached a stem diameter of 25 cm or more. Trees of 168 species had reached a stem diameter of more than 10 cm (upper-, middle- and lower-storey species). For the diameter-class 5 cm and over an estimate of the number of species would have been too unreliable, because for a number of small trees a sufficient distinction between closely related species was as yet impossible.

For those important tree species which have been recorded in the evaluation-survey reports of the Forest Department, the average densities for rain forest in compartment 836 (being the area shown in fig. 46) are given in the first column of table XVII. These figures are based on enumerations which were carried out in 10 m wide strips along lines which were cut in E–W direction at 500 m intervals, thus providing a 2 % sample of the forest.

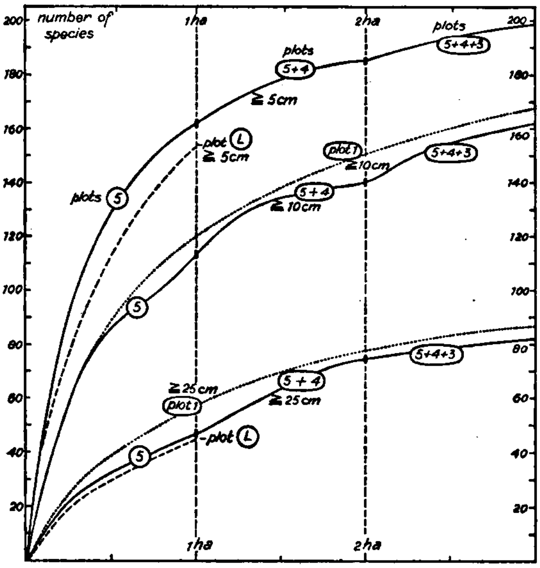


Fig. 61. Species/area curves for 3 ha of sample plot 1, and for plots 3, 4 and 5 (mesophytic forest with *Vouacapoua americana* as the leading species, cf. p. 177) in the Mapane region. The plots in the *Voucapoua* stands were 1 ha in extent and the results of the enumerations were combined in a single curve by adding the new species found in plot 4 to the species encountered in plot 5, and the new ones of plot 3 to those of 5 and 4.

Table XVII gives for a few species the results of the above mentioned enumeration survey which was carried out by the Forestry Department in compartment 836. These data show that for most of the large tree species (in so far as recorded in the evaluation-survey reports) the average densities obtained for the individuals of 25 cm d.b.h. and more in sample plot 1 are more or less representative for compartment 836. Only for *wallaba* (*Eperua falcata*) the abundance in the forest surrounding the camp (2 trees of 25 cm d.b.h. or more/ha) is considerably lower than in the rest of the Mapane forest (12 trees/ha). Otherwise the data show that the relative prominence of Burseraceae (especially of *Tetragastris altissima*) and of *Eschweilera odora* in the small area sampled by means of plot 1 applies also to the whole compartment. The comparatively low percentage of *wallaba* trees in sample plot 1 is due to the fact that the sampling strips did not include stands of forest on more or less hydromorphous soils where drainage, however, is not so much impeded that the rain forest is replaced by swamp- or marsh-forest. It is for soils of this kind that *wallaba* shows a strong preference. Moreover, for the computation of the results of the evaluation survey in compartment 836 part of the ecotone to xeromorphous forest on leached white sand (where *wallaba* is abundant too!) was reckoned to belong to the rain forest, whereas in sample plot 1 the delimitation of what had to be regarded as mesophytic (rain) forest was more restricted.

Apart from sample plot 1 by means of which the average composition of a part of the lowland rain forest on mesic sites in the Mapane region was estimated, a few sample plots were laid out in rain forest on soils where drainage is more intensive than on the mesic sites (sample plot L on brown loamy sand/sandy loam and plot 2 on white sand to brown loamy sand, both near the ecotone to savanna forest) and in three stands of mesophytic forest which were noticeable by a tendency to single dominance (plots 3, 4 and 5, where *bruinhart*, *Vouacapoua americana* was the prominent canopy species) (for location see fig. 46).

Sample plot L was situated in rain forest, near the ecotone to xeromorphous forest (*high savanna forest*).

The soil varied from rather excessively drained loamy coarse sand to well-drained coarse sandy clay (-loam), similar to the profiles "150 m" (in fig. 48) and 7/0, B/0 and 8/1 (in fig. 49). The part of the transect between 90 and 190 m, shown in fig. 48, ran some 100 m south of the southern border of sample plot L. The sample plot was 1 ha in extent (100 × 100 m) and was subdivided in 100 quadrats, which were listed separately. The enumerations were carried out under the direction of Dr. J. C. Lindeman, who introduced me here to the forest-sampling methods, and to whom I am indebted for his permission to publish some of the results.

For the most abundant species the number of individuals per unit area (1 ha) is given in table XVII; it shows that the list of the most abundant species is approximately identical with that drawn up for the samples which show the average composition of the rain forest in this region (samples 1 and 836); the relative importance of these *dominant* species, however, appears to be influenced considerably by the habitat, which is near the *edaphic limit* of true rain forest. The influence of the soil manifests itself amongst other things in the abundance of *hoogland anaura* (*Couepia versicolor*), which forms about one-fifth of the trees with a diameter of more than 25 cm; the latter proved to be less numerous here (51 per ha as against an average of 66–69 for the rain forest of this region). Other points in which plot L differs from the average composition of rain forest on heavier soils are the preponderance of *birgie-bébé* (*Swartzia benthamiana*), *pikienmisikie* (*Piptadenia suaveolens*) and *parelhout* (*Aspidosperma marcgravianum* and *A. oblongum*) in the canopy and of *boskoffie* (*Coussarea paniculata*) and *Hirtella racemosa* in the under-storeys. A striking feature is the *absence of mature trees of rode salie* (*Tetragastris altissima*), which is highly characteristic for the rain forest on mesic sites in the Mapane region. The structure of the forest in this sample plot was that of true rain forest. The tree species were largely evergreen and the percentage of deciduous and semideciduous trees as well as that of the species to which they belong, was similar to the corresponding percentages found in forest on less drained, heavier soils. Neither in the tree strata nor in the undergrowth, species were found which are characteristic for *savanna forest*.

TABLE XVII

		Mapane region					Coesewijne region			Goliath cr. region	Stofbroekoe Mnt.	Remont court	Voltz Mnt.	Wayombo-region	
sample plot		836	1	L	2	3-5	859 860	5	6	1-4				1	2
sampled area in ha		92	5.6	1.0	0.3	3.0	150	1.0	0.4	1.5	1.2	0.4	0.6	0.2	0.2
										← lateritic clay →					
A. UPPER-and MIDDLE-STOREY SPECIES (number of trees ≧ 25 cm d.b.h./ha															
Couratari spp. (1)	*Lec.*	?	5	1	5	3	?	1	2	2	5	6	10	+	+
Eschweilera amara (2)	„	?		} +	–	4	–	–	–	+	10	–	–	+	–
E. corrugata (3)	„	?	2		5	5	3	3	+	+	1	–	11	–	–
E. odora (4)	„	8	11	1	2	12	0.3	+	+	+	7	12	+	–	–
Eperua falcata (5)	*Pap.*	12	2	3	–	2	16	16	–	7	–	–	–	–	–
Dicorynia guianensis (6)	„	1.5	1	1	+	0.5	12	21	25	7	3	9	–	36	10
Swartzia benthamiana (7)	„	?	1	5	–	1	?	–	–	1	–	12	+	10	22
Piptadenia suaveolens (8)	*Mim.*	2	2.5	6	5	4	?	1	2	0.5	1	6	–	–	–
Inga alba + I. pezizifera (9)	„	?	2	5	+	3	?	+	2	3	2	–	8	5	–
„*tingiemonnie*" (10)	*Burs.*	6	3	5	+	1	4	+	13	1	1	12	10	5	56
Tetragastris altissima (11)	„	7	10	+	1	3	–	–	–	–	–	–	25	–	–
Couepia versicolor (12)	*Ros.*	3	3	19	5	2	5	3	5	3	+	3	7	–	–
Parinari campestris (13)	„	3	3	1	5	2	} 12	7	20	1	+	3	+	15	30
Licania micrantha (14)	„	–	±?	–	–	–		2	8	11	1	6	2	–	–
Carapa guianensis (15)	*Mel.*	3	2	+	5	3	1	1	+	0.5	+	–	+	–	–
Virola melinonii (16)	*Myrist.*	3	4	2	5	3	0.5	+	+	3	1	6	3	+	+
Iryanthera sagotiana (17)	„	5	6	6	5	4	?	+	–	1	–	–	–	+	+
Chaetocarpus schomb. (18)	*Euph.*	4	3	–	+	5	?	15	12	14	1	9	–	+	+
Manilkara bidentata (19)	*Sapot.*	0.3	+	+	+	+	1.5	+	+	0.5	1	–	–	–	–
Micropholis guyanensis (20)	„	±2	1.5	2	–	0.5	±9	9	+	+	3	+	–	–	–
Ocotea rubra (21)	*Laur.*	1.5	0.5	–	+	2	7	11	18	3	–	–	–	–	–
Ocotea spec. (22)	„	?	2	+	5	1	?	–	–	+	3	–	–	–	–
Vouacapoua americana (23)	*Pap.*	1.5	–	–	–	21	0.5	–	–	16	11	–	–	–	–
Swartzia remigifer + S. schomburgkii (24)	„	?	–	–	–	–	?	–	–	5	7	+	6	–	–
Swartzia prouacensis (25)	„	?	–	–	–	–	?	–	+	5	+	12	+	–	–
Qualea rosea (26)	*Voch.*	±3	3	+	85	2	–	–	–	–	3	–	–	–	–
Aspidosperma spp. (27)	*Apoc.*	?	0.5	5	+	0.5	?	4	+	1	3	3	–	+	+
Catostemma fragrans (28)	*Bomb.*	?	–	–	–	–	?	–	–	–	–	–	–	5	5
B. LOWER STOREY SPECIES (number of trees ≧ 5 cm d.b.h.)															
Inga spp. (29)	*Mim.*	not recorded	36	45	80	31	not recorded	22	10	23	15	18	10	10	–
Paypayrola guianensis (30)	*Viol.*		70	18	55	85		–	125	40	12	165	–	–	–
Gustavia hexapetala (31)	*Lec.*		20	11	20	19		6	8	7	12	9	4	–	–
Coussarea paniculata (32)	*Rub.*		36	109	15	13		–	–	–	11	–	15	–	–
Ambelania acida (33)	*Apoc.*		1	2	–	4		7	68	2	–	–	–	180	10
Sagotia racemosa	*Euph.*		–	–	–	3		–	–	4	90	21	–	–	–
Eschweilera labriculata (34)	*Lec.*		–	–	–	–		–	–	41	42	–	–	–	–
Oxandra asbecki (35)	*Annon.*		–	–	–	–		–	–	66	121	6	–	–	–
Diospyros spp. (36)	*Eben.*		24	52	10	10		–	–	–	1	–	14	+?	–
C. UNDERGROWTH SPECIES (number of trees ≧ 2 cm d.b.h.)															
Bonafousia undulata (37)	*Apoc.*	not recorded	72	180	135	75	not recorded	–	370	12	45	10	60	+	–
Tapura guianensis (38)	*Dichap.*		66	100	100	60		250	180	195	75	10	16	120	200
Siparuna decipiens	*Monim.*		49	40	260	50		15	10	5	10	20	15	–	–
Hirtella racemosa (39)	*Ros.*		5	130	60	10		190	280	30	–	–	10	5	375
Cheiloclinium cognatum	*Hipp.*		25	110	260	150		10	+	–	15	–	5	–	–
Posoqueria latifolia (40)	*Rub.*		–	–	–	–		–	–	–	–	–	–	20	100
Erythroxylum amazon.	*Eryth.*		–	–	–	–		–	–	–	–	–	–	450	460
Astrocarum sciophilum (41)	*Palm.*		–	–	–	–		a	–	a	r	f	a	–	–
A. paramaca (42)	„		a	f	f	a		–	a	–	–	f	–	–	–
trees per ha of (43):															
35 cm d.b.h. and over		69	66	51	85	68	70	53	82	80	66	100	100	37	45
25 cm „ „ „		135	120	105	140	125	136	140	140	151	175	155	155	126	154
5 cm „ „ „		?	990	1150	1330	1060	?	880	1685	1020	1110	1150	670	1780	1410
2 cm „ „ „		?	2000	3300	3400	2000	?	1750	4100	2200	1900	2100	975	4600	3600

TABLE XVII. Density (average number of individuals per ha) for a few selected species in different sample plots in rain forest.

(1) *ingipipa* (chiefly *C. stellata*); (2) *birgie-oemanbarklak*; (3) *hoogl.-oemanbarklak*; (4) *hoogl.-manbarklak*; (5) *wallaba*; (6) *basralokus*; (7) *gandoe*; (8) *pikienmisikie*; (9) *prokonie*; (10) chiefly *Protium* spp.: *P. polybotryum*, *P. insigne*, etc.; (11) *rode salie*; (12) *hoogl. anaura*, probably including other Rosaceae; (13) *foengoe*; (14) *zwarte foengoe*; (15) *krappa*, probably including a few *C. procera*; (16) *hoogl. baboen*; (17) *broedoehoedoe*; (18) *fomang*; (19) *bolletrie*; (20) *zwart riemhout*; (21) *wana*; (22) *wanapisie*; (23) *bruinhart*; (24) + (25) *ijzerhart*; *boegoe-boegoe*, etc.; (26) *birgie-gronfoeloe*; (27) *parelhout*: *A. oblongum* + *A. marcgravianum*; (28) *barmanni*; (29) *switieboontje*, also including a few individuals, belonging to upper- and middle-storey spp., cf. note below table XV; (30) *tajahoedoe*; (31) *hoogl. konikoni-hoedoe*; (32) *boskoffie*; (33) *batbati*; (34) *oeman-barklak*; (35) *pikapika*; (36) *blakaoema*, *D. melinonii* and *D.* sp.; (37) *mirkitikie*; (38) *pakiratikie*; (39) *kleine foengoe*; (40) *pipa-hoedoe*; (41) *boegroemakka*; (42) *paramakka*; (43) without palms.

\+ means species present, but only represented by trees of less than 25 cm d.b.h.

For the trees of more than 5 and 25 cm d.b.h. respectively the species/area curve is given in fig. 61; it shows that the number of species per unit area is lower than it is in average rain forest on more favourable sites.

Sample plot 2 (0.3 ha) was located on rather exessively drained, bleached sand/loamy sand, and was chosen in a stand of rain forest, strongly dominated by *birgie-gronfoeloe* (*Qualea rosea*). The trees of this Vochysiacea, which shows a strong tendency to patchy distribution (cf. fig. 53), formed in this sample plot about 2/3 of the canopy trees (cf. table XVII). About 50 m away from the plot the rain forest merged into savanna forest. The soil of this plot was described in detail as profile C/0 (fig. 49). That during the dry season the moisture content was rather low, appeared from the calculations given in II.6 (table XIII: site 1). The content of available plant nutrients in this soil is lower than in the heavier soil types (cf. table VII: excessively drained soils). Yet, apart from the strong dominance of *Qualea rosea*, the floristic composition of the forest was largely that of true rain forest, although individuals of xerophytic species characteristic for the savanna forest, were found in the lower storeys (e.g. *Inga heterophylla* and/or *I. lateriflora* and Myrtaceae like *Myrcia sylvatica*). Moreover, the enumeration showed a relatively high proportion of thin stems, another feature that is characteristic for the savanna forest. On the other hand the number of large trees exceeds the average number found for the rain forest; this is shown by the data given in table XVIII.

The relative luxuriance and the floristic composition of this forest on leached sand (which elsewhere in this region bears savanna forest) may probably be accounted for by the fact that the roots of the *Qualea* trees reach to within the rotting rock (cf. profile C/0 in fig. 49). *Qualea rosea* shows in this region a preference for rain forest on light textured sandy deposits (as appears from fig. 53), although "nests" of trees of this species are found also on well-drained residual soils. On the other hand, fig. 53

TABLE XVIII

Relative dominance (number of trees per ha) of selected families in the upper and lower storeys of forests on different sites.

Forest type	Mapane Cr. region				Coesewijne R. region			Suriname R.		Voltz Mt.	Wayombo R.	
	average	ecotone to xeromorph. forest		*bruinhart* stand			upland forest on laterite					
Sample plot	1	L	2	3–5	5	6	1–4	Stofbroekoe Mt.	Remoncourt		1	2
UPPER- AND MIDDLE-STOREY SPECIES (trees ≧ 25 cm d.b.h./ha):												
Papilionaceae	10	14	1	30	45	35	48	34	42	12	46	44
Mimosaceae	8	14	5	10	7	7	5	4	9	12	15	+
Eschweilera (Lec.)	14	4	5	25	3	+	+	19	12	13	5	+
Lecythidaceae 1)	19	5	10	28	4	3	3	23	18	23	5	+
Burseraceae 2)	14	2	+	7	+	13	5	1	15	33	5	25
Rosaceae 3)	5	24	5	7	14	32	20	5	18	7	15	35
Lauraceae 4)	5	2	5	6	13	18	7	5	3	+	+	+
Euphorbiaceae	5	4	+	7	17	2	20	+	3	11	+	+
Myristicaceae 5)	9	8	10	7	+	+	2	1	6	3	+	+
Vochysiaceae 6)	3	1	85	3	1	2	—	3	+	+	5	10
Sapotaceae 7)	8	7	4	7	9	5	8	17	3	+	5	10
Other families	34	25	15	13	30	23	33	48	38	54	30	30
Total ≧ 25 cm d.b.h.	120	106	140	125	140	140	151	141	155	155	126	154
LOWER-STOREY AND UNDERGROWTH SPECIES (trees ≧ 5 cm d.b.h./ha):												
Papilionaceae	4	5	10	2	2	—	3	52	3	1	5	—
Mimosaceae 8)	32	25	70	25	15	10	20	10	15	2	10	—
Lecythidaceae 9)	16	15	25	20	10	10	50	17	9	3	—	—
Burseraceae 10)	?	10	30	20	10	90	70	15	35	20	110	120
Apocynaceae 11)	28	45	55	31	6	235	2	18	3	21	175	20
Rubiaceae	38	123	30	18	4	15	14	25	24	23	10	130
Violaceae 12)	86	18	55	85	+	125	40	27	165	13	5	—
Annonaceae	20	37	35	27	18	15	80	170	30	4	50	130
Rosaceae 13)	4	11	2	4	27	60	52	2	—	—	5	35
Sapindaceae 14)	9	30	20	29	9	38	27	30	21	30	70	10
Monimiaceae 15)	20	23	15	23	3	+	2	4	6	8	—	—
Dichapetalaceae 16)	24	3	10	19	73	106	12	34	3	+	25	30
Guttiferae 17)	20	3	20	12	2	2	22	13	3	2	+	+
Boraginaceae 18)	15	2	45	18	10	15	14	10	9	2	+	+
Quiinaceae 19)	6	8	15	5	11	13	6	1	12	—	—	—
Olacaceae 20)	?	+	20	1	—	20	1	3	—	+	10	—
Myrtaceae	5	3	+	13	10	5	9	27	12	30	30	10
Hippocrateaceae 21)	?	39	65	19	2	+	—	3	—	2	—	—
Ochnaceae 22)	?	26	—	—	—	—	25	—	—	—	—	—
Rhizophoraceae 23)	+	—	+	+	23	22	—	2	—	—	—	—
Palmae 24)	a	f	a	f	a	f	a	f	f	a	r	r
Other fam. 25)	?	24	81	52	30	45	2	—	—	—	—	—
Total ≧ 5 cm d.b.h. (undergr. + lower-storey species)	400	460	673	450	282	1016	451	555	393	204	630	710
Total ≧ 5 cm d.b.h. (all species)	990	1145	1335	1060	880	1685	1020	1110	1150	670	1780	1410

Mesophytic forest in the Upper-Coesewijne region. The palms are *Astrocaryum sciophilum.*

also shows that there are areas of "dek" soils bearing rain forest in which *Qualea rosea* is but sparingly represented (e.g. sample plot L).

Sample plots 3, 4 and 5 were chosen in three stands of rain forest, all rich in *bruinhart* trees (*Vouacapoua americana*). The peculiar distribution of this Papilionacea in this region as well as the soil of the plots was discussed in II.2.3. In the rain forest of this region *bruinhart* occurs in sharply delimited stands, outside of which no trees of this species are encountered. In these stands *Vouacapoua* forms from 1/6 to 1/3 of the canopy trees. Each of the three sample plots in *bruinhart* stands consisted of a 100 × 100 m square. The stands were sampled to ascertain whether any association between *bruinhart* and other woody species could be detected. Only for the 7 *Eschweilera* species occurring in this region the countings suggested a positive association with *bruinhart*; this is shown by the data given in tables XVII and XIX (25 *Eschweilera* trees of 25 cm d.b.h. and over per ha, averaged over plots 3, 4 and 5, as compared with an average of 14 trees in plot 1). This high proportion of *Eschweilera*, together with the relative abundance of *bruinhart*, account for the strong family dominance of the Papilionaceae and Lecythidaceae (cf. table XVIII) and the community might be called a *bruinhart-barklak* (*Vouacapoua-Eschweilera*) forest, the two genera (8 species) forming about one-half of the canopy trees. Before any generalization can be made, more *bruinhart*-islands will have to be studied. It should be noted that the difference in the abundance of the *Eschweilera* species is merely one of degree; they are also found with high constancy, though less abundant, in the rain forest surrounding the *bruinhart* stands.

All the species listed in the *bruinhart* plots were found in the surrounding rain forest too.

As was mentioned before, *Vouacapoua* forms a more or less abundant, but always highly constant character species of the *hill forest* occurring on the lateritic soils which cover large stretches in the inland, farther southwards (cf. sample plots in the Goliath Cr. region and on Stofbroekoe Mt., the data of which also appear in tables XVII and XVIII). None of the other species which are characteristic for this forest (e.g. *Swartzia*

---

1) *Eschweilera* + *Couratari*; 2) *Protium* + *Tetragastris*; 3) chiefly *Couepia*, *Parinari* and *Licania*; 4) chiefly *Ocotea*; 5) chiefly *Virola melinonii* + *Iryanthera sagotiana*; 6) *Qualea* + *Vochysia*; 7) chiefly *Pouteria* + *Micropholis*; 8) *Inga*; 9) *Eschweilera longipes* + *E. labriculata* + *Gustavia hexapetala*; 10) *Protium* + *Tetragastris* + *Hemicrepidospermum rhoifolium*; 11) chiefly *Ambelania acida* + *Bonafousia undulata*; 12) chiefly *Paypayrola guian.* + *Rinorea* sp.; 13) *Hirtella racemosa*; 14) *Talisia* + *Cupania* + *Matayba*; 15) *Siparuna*; 16) *Tapura guian.*; 17) *Vismia* + *Tovomita* + *Rheedia*; 18) *Cordia*; 19) *Quiina* + *Lacunaria*; 20) *Heisteria cauliflora*; 21) *Cheiloclinium cognatum*; 22) *Ouratea*; 23) *Cassipourea guian.*; 24) *Astrocaryum paramaca* or *A. sciophilum*; 25) a.o. Ebenac., Elaecarp., Opiliac., Menisperm., Melastom., Rutac., Lacistem., Icacin., Meliac., Polygon., etc.

+ means species represented only by small individuals with diam. below the limit.

remigifer, *S. schomburgkiana*, *Oxandra asbecki*, etc.) was found in the *bruinhart*-islands N of Mapane Cr., with the exception of *Sagotia racemosa*, which was found in sample plot 3, but not in the other two stands.

Eschweilera species were abundant in the sample plots on Stofbroekoe Mt., but were rare in the canopy in the Goliath Cr. region (cf. table XVII).

In table XIX for a few selected (most abundant) species the number of individuals of 25 cm d.b.h. and over occurring per ha is given. The three plots are listed separately to show the constancy and the variability in density of the species in the three stands. This table illustrates the fact that, although each of the sample plots shows the *Vouacapoua-Eschweilera* dominance, there are considerable differences in the density of the other species (cf. *Eperua falcata*, *Piptadenia suaveolens*, *Inga*, *Iryanthera sagotiana*, etc.!). The most conspicuous feature is the prominence of *Eschweilera amara* in plot 3 (forming one-fifth of all trees ≧ 5 cm d.b.h.), and the absence of this species (even as seedlings!) in the two other plots. As shown by table XVII, this species is rare in the Mapane rain forest (cf. sample plots 1, 2, L and 836).

The species/area curve for the three *bruinhart* plots is given in fig. 61. The curves have been constructed by adding the new species which were met with in the quadrats of plot 4, to those found in plot 5, etc. Naturally another sequence of the plots could have been chosen, but this would have resulted in an only slightly different shape of the curves. This figure shows that the number of woody species that are found per unit area in the *bruinhart* stands, approximates the number found in sample plot 1. The slightly lower figure for the *bruinhart* plots is due to the relatively large number of *Vouacapoua* trees, which leave less room for the other species.

Additional reconnaissance surveys were made in various areas of the lowland rain-forest in the Suriname R.–Mapane Cr. region. These reconnaissances, as well as the data provided by the 2 % samples that were taken by the exploration parties of the Forest Department in a part of this region, convinced me that the enumerations which were made in the 5.6 ha sample (plot 1), give a fairly good estimate of the average composition of the lowland forest in this region.

As would be expected in a vegetation that is so extremely rich in species, the composition of the forest in this region is far from homogeneous; as appeared already from the small sub-area which was studied in detail, the composition of the forest varies continuously. All possible combinations of *leading species* were met with. However, nearly everywhere in the lowland rain-forest of this region the leading species proved to belong to the rather limited group of leading species found in sample plot 1 (cf. table XV), a group which is small in comparison with the total number of tree species occurring in this region; the majority of the latter never becomes codominant. The relative densities of these leading

TABLE XIX

Density and constancy for a few selected species in 3 plots (each 1 ha in extent) in rain forest stands (in the Mapane region) in which *Vouacapoua americana* (*bruinhart*) is the leading dominant.

+ means species represented only by trees of less than 25 cm d.b.h.

Species	Density (number of trees of ≧ 25 cm d.b.h. per ha)				Constancy (≧25 cm)
	plot 3	plot 4	plot 5	Average	
Vouacapoua americana (Papil.) . . .	15	34	14	21	3/3
Eschweilera odora (Lecyth.)	9	17	10	12	3/3
„ *corrugata*	3	7	6	5	3/3
„ *chartacea*	—	3	1	1	2/3
„ *poiteaui*	+	2	4	2	2/3
„ *amara*.	11	—	—	4	1/3
Couratari stellata (Lecyth.)	2	3	3	3	3/3
Chaetocarpus schomburgkianus (Euph.)	8	1	7	5	3/3
Drypetes variabilis (Euph.)	+	3	2	2	2/3
Eperua falcata (Papil.).	6	—	1	2	2/3
Inga spp. (Mimos.)	+	6	5	4	2/3
Piptadenia suaveolens (Mimos.) . . .	+	3	8	4	2/3
Virola melinonii (Myrist.)	2	3	3	3	3/3
Iranthera sagotiana (Myrist.)	8	1	3	4	3/3
kwassiba (8031, Sapot.)	2	2	3	2	3/3
Pouteria spp. (Sapot.)	1	4	5	3	3/3
Tetragastris altissima (Burs.)	1	4	4	3	3/3
Tetragastris sp.	6	+	3	3	2/3
Licania ovalifolia (Rosac.)	2	+	6	3	2/3
Parinari campestris (Rosac.)	2	1	1	1	3/3
Couepia versicolor (Rosac.)	4	2	+	2	2/3
Qualea rosea (Vochys.).	2	1	2	2	3/3
Ocotea rubra (Laur.)	5	1	+	2	2/3
Nectandra cf. *kunthiana* (Laur.) . .	3	1	3	2	2/3
Total number of trees ≧ 25 cm d.b.h.	123	135	116	125	—

	Density (≧ 5 cm d.b.h. per ha)				Constancy (≧5 cm)
Vouacapoua americana (Papil.) . . .	26	40	30	33	3/3
Eschweilera odora (Lecyth.)	95	130	104	110	3/3
Eschweilera amara (Lecyth.)	226	—	—	72	1/3
Bonafousia undulata (Apoc.)	17	25	49	30	3/3
Siparuna decipiens (Monim.)	5	32	30	22	3/3
Cheiloclinium cognatum (Hippocr.) .	7	34	15	19	3/3
Tapura guianensis (Dichap.)	31	23	2	19	3/3
Guarea kunthiana (Mel.)	52	3	—	18	2/3
Sagotia racemosa (Euph.)	11	—	—	4	1/3
Total number of trees ≧ 5 cm d.b.h.	1200	830	1150	1060	—

species vary considerably from one place to another, as is clearly shown by the sample plots which were laid out in the *Vouacapoua* stands (plots 3–5, cf. table XIX). Nevertheless, the forest as a whole is well-characterized by the *numerical preponderance of various Lecythidaceae* (*Eschweilera* and *Couratari*) and *Burseraceae* (especially *Tetragastris*) and by the relative abundance of Myristicaceae (*Virola* and *Iryanthera*) among the canopy trees. The composition of the lower storeys as recorded in sample plot 1 (*Astrocaryum paramaca*, *Coussarea paniculata*, *Paypayrola guianensis*, *Bonafousia undulata*, *Rinorea* sp., etc.), may also be taken as fairly representative for the type of forest that is characteristic for this region.

It cannot be questioned that the variations in composition of the rain forest in this region are in some measure accidental. Sometimes they are due to differences in history (e.g. in stands with *disturbance indicators* such as *Goupia glabra* and other light-demanding species), but I am convinced that variations in edaphic factors too may often play a part. Sample plots L and 2 are examples of *association segregates* wich have been derived from the true mesophytic forest by a sorting of the species (e.g. *Couepia*, *Piptadenia* and *Swartzia* in plot L and *Qualea rosea* in plot 2) due to changes from mesic to sub-mesic and even to sub-xeric conditions. Other *consociations* (*Eperua falcata*!) are found as association segregates near the ecotone to hydrophytic forest. In II.2.3 examples were given of species whose distribution appeared to be correlated with edaphic variations.

III.3. Rain forest of the Upper-Coesewijne region

III.3.1. *General remarks*

Rain forest was studied also in the country lying between the Saramacca River and the Goliath Creek, south of the Upper Coesewijne River (cf. figs. 1 and 3), i.e. approximately 70 km W of the area discussed in the foregoing sections. Detailed studies of the composition of this forest were confined to a small area shown in fig. 53, which gives a detailed map of the main types of vegetation occurring in this region.

As was discussed in II.3 rain forest is found on mesic, well-drained sites (i.e. "non-bleached dek-soils"), whereas xeromorphic forest forms the climax on the excessively drained bleached sands, and marsh- and swamp-forest occur on the hydromorphic soils (white sands and alluvial silts) in the creek valleys.

Although falling outside the scope of this study, passing reference is made to the fact that the composition of most of the *creek-margin forests* in the Upper-Coesewijne R. area differs from that of the forests found in the Mapane region; in the swamp forest bordering Costerie Cr. and some of the creeks feeding the Upper-Coesewijne R., the *troelie* palm (*Manicaria saccifera*) partly replaces *pina* (*Euterpe oleracea*), which elsewhere is characteristic for hydromorphic forest. Another conspicuous feature is the frequent occurrence of a dense herb layer, largely consisting of *Rapatea paludosa* (*ansiwawai*). This species appears to be characteristic for peaty soils with a deep A_0-layer ("*Blakkawatra series*" of VAN DER EYK, 1957, p. 81), such as are found in forested swamps and marshes which are fed by the extremely oligotrophic water of the "blackwater" streams draining the bleached sand areas. Along the Costerie Cr. the most eastern station of *Mora excelsa* was noted.

Passing reference is made also to the occurrence of patches of *dakama* forest (*Dimorphandra conjugata*), which is rather frequently found on the white-sand plateaux between Saramacca River and Goliath Creek. On the maps given in figs. 3 and 53 no distinction was made between this *Dimorphandra conjugata* consociation and mixed xeromorphic forest, both being mapped as *savanna forest*. One gets the impression that in the Suriname lowland *Dimorphandra* forest becomes more frequent in the direction from east to west. I have met large stretches of this consociation on white sands west of the Coppename River (S of the Wayombo River) and it is still more frequent on white sands in the lowland region of British Guiana, W of the Mazaruni River, where it has been described as a distinct faciation of "Dry Evergreen *Wallaba* Forest" (FANSHAWE 1952, p. 63). In the white-sand savannas N of the Mapane region, scrub savanna as well as savanna woodland are locally dominated by *dakama* coppice, but it should be realized that in this region the repeated burning which took place in relatively recent years, did not allow sufficient time for the development of full-grown *Dimorphandra* forest, which may reach a height of more than 25 m, but which is here kept in a seral stage by burning. It is the unusually thick layer of raw humus accumulating under *dakama* (as mentioned already by RICHARDS, 1952), which forms a potential fire hazard during the long dry season.

There is another Leguminous species which tends to single dominance in the Coesewijne region; viz. *wallaba* (*Eperua falcata*), encountered as the leading dominant of *wallaba* forest in the ecotone between rain forest and xeromorphic forest (on excessively drained soils) as well as in that between rain forest and the hydromorphic forest bordering the creeks. In the Upper Coesewijne region the second ecotone often occurs on bleached-sand podzols, which are moist during the greater part of the year, but which may become dry during the long dry season (cf. fig. 54). *Eperua falcata* is abundant on mesic soils too, as appears from the data obtained in sample plot 5, and from the estimation of the average density of this species in the whole Upper-Coesewijne region computed for compartments 859+860 (see table XVII). In the maps shown in figs. 3 and 53, *wallaba* forest has been mapped as *savanna forest*. West of the Coppename River extensive *wallaba* forests are met with on the white-sand plateaux, in which *Eperua falcata* itself forms more than 75 % of the canopy trees.

The *mesophytic forest* of the Upper-Coesewijne region has approximately the same physiognomy and structure as the Mapane forest found on mesic sites, but on the whole it makes a somewhat more xeromorphic impression. The latter undoubtedly is due to the fact that the soils in this region show a greater porosity than those of the Mapane forest, which – on the average are of a heavier texture. Nevertheless, it is a rather luxuriant, well-stocked forest; this is shown e.g. by the number of large trees (more than 25 cm d.b.h.) per ha given in table XVII (cf. columns 836 and 859+860). The forest is of great economical value, owing to the relative abundance of individuals of commercially valuable timber species, such as *basralokus* (*Dicorynia guianensis*), *wana* (*Ocotea rubra*) and *kopie* (*Goupia glabra*) (cf. table XVII). It belongs to the most valuable forests of Suriname, and after the enumerations were concluded, exploitation on a large scale was started in the concessions alongside the main truck road. A number of forest compartments were reserved for further studies on regeneration under natural conditions. Up to 1957 timber working had been confined to places from which the timber could be easily extracted by hand, i.e. in the sites near the Saramacca and Coesewijne River and near the larger creeks, e.g. near the Costerie Creek.

At present the population in this region is confined to a few dozen Amerindian families living in the village of Gran-Poika; at present they visit the country S of the Upper-Coesewijne R. for fishing and hunting only. Yet, traces of farming (bush-fallow) are found in many places. As shown in the map given in fig. 53, scattered patches of secondary forest, in different stages of development up to climax forest (mesophytic as well as xeromorphic forest), are found chiefly in the eastern part of the area. The absence of transition between the patches of secondary forest and the climax forest, and the location of these patches on light-textured soils (brown sands to sandy loams) in the vicinity of the creeks (which are the sites preferred by Amerindians for practising their shifting cultivation), prove that they have developed an abandoned farm land. Under the bushfallow system large stretches of forest can be kept in a seral stage by a relatively sparse population.

Traces of an old Bush-negro village (Jacksonkondre) were found along the upper course of the Costerie Creek. In this region also large stretches of secondary forest are met with.

The unshaded parts of the map given in fig. 53 represent rain forest, although it is presumably not primary forest if we use this term in the sense of fully undisturbed by man. The frequent occurrence of *kopie* (*Goupia glabra*) (cf. table XVII), a strongly light-demanding species which is considered to be a *disturbance-indicator*, is one of the arguments in favour of the opinion that, at some time in the past, the greater part of the Upper-Coesewijne forest has been disturbed by man. Yet, the floristical composition of the forest, the dimensions of the stems of typical climax forest species and the size-class distribution of *kopie* indicate that the greater part of the rain forest of this area has been left undisturbed during at least two centuries (cf. p. 222).

The rain forest in the Upper-Coesewijne region shows approximately the same structure as that of the Mapane forest on mesic sites described in III.2.1, though perhaps it contains a smaller number of *outstanding* trees elevating their crown above the main canopy (such as *Couratari* species). Consequently, the canopy has a somewhat more regular appearance. The most conspicuous difference, at first sight, with the Mapane rain-forest is the replacement of the stemmless *paramakka* by the shortstemmed *boegroemakka* palm (*Astrocaryum sciophilum*), which forms here the palm layer. Locally the dense foliage of this palm layer may intercept so much light that the other plants of the undergrowth are partially suppressed, which results in a more or less *open* appearance of the forest. The average illumination at the forest floor nevertheless tends to be somewhat higher than it is in the Mapane forest.

III.3.2. *Composition of the forest*

The floristic composition was studied by means of a number of sample plots (each consisting of 10–30 unit-quadrats) laid out in a stand which may be taken as representative for this type of forest in its optimal development. 100 quadrats were laid out in the area shown in fig. 55 and 56. Part of the results of this one-hectare sample are listed under the heading *plot* 5 in table XVII. The estimation of the average of a number of canopy species (as recorded in the forest-evaluation reports) based on a 2 % sample of forest compartments 859 + 860 (of which the area shown in fig. 53 forms a part), has been added for comparison.

The figures given in table XVII clearly show the significant difference in composition with the Mapane forest. The chief characteristic of the Coesewijne rain forest is the *higher degree of dominance of a few leading canopy species*; the trees of the 5 leading species in sample plot 5 (*Dicorynia guianensis*, *Eperua falcata*, *Goupia glabra*, *Chaetocarpus schomburgkianus* and *Ocotea rubra*) form more than one-half of the total number of the larger trees (25 cm d.b.h. and more), whereas in sample plot 1 in the Mapane rain forest the 5 most abundant species (*Eschweilera odora*, *Tetragastris altissima*, *Couratari stellata*, *Iryanthera sagotiana* and *Virola melinonii*) contribute less than one-third to the total number of canopy trees. This difference probably depends ultimately on the nature of the soil. As was noticed already by RICHARDS (1952, p. 242 and 262), the principle that the most mixed type of forest is found on the best soil and that a tendency to single-species dominance depends on less favourable soil conditions of one kind or another, appears to be of wide application, and extends to the composition of rain forest generally. In the case of the Coesewijne forest the selective effect of the soil depends presumably in the main on the less favourable water-supply on the rather porous soils. Moreover, it appeared from the laboratory analyses discussed in II.2 (cf. table VII) that the amount of exchangeable plant nutrients showed a lower average in the samples from the Coesewijne soils.

The preponderance of two Leguminous species (*Dicorynia guianensis* and *Eperua falcata*) in the Coesewijne forest is responsible for the numerical preponderance of the Papilionaceae, which family (as appears from table XVIII) produces about one-third of the canopy trees (as compared with less than one-tenth in the Mapane plot). It is interesting to note that this is in accordance with the experience that in tropical rain forest on less favourable soil (especially in S America) the dominant tree species frequently belong to the Leguminosae (cf. RICHARDS 1952, e.g. p. 221).

The Lecythidaceae and the Burseraceae, which are the numerically preponderant families in the Mapane forest, are represented in the Coesewijne forest per ha by a few trees only, which is due to the total absence of *rode salie* (*Tetragastris altissima*), the leading species in the lowland rain-forest between the Suriname R. and the Commewijne R., and the relative scarcity of *Couratari* (*ingipipa*) and *Eschweilera*. For instance, of *Eschweilera corrugata* (*hoogl. oemanbarklak*) 11 trees of more than 25 cm d.b.h. and over per ha were found in sample plot 1 in the Mapane area, and only one small sapling (which, moreover, could not be identified with absolute certainty) was noted in sample plot 5 in the Coesewijne forest.

The relative importance of the Lauraceae in the Coesewijne forest is chiefly due to the abundance of *wana* (*Ocotea rubra*). Myristicaceae, which are rather abundant in all plots in the Mapane forest, are rare in the Coesewijne forest.

The Rosaceae rank third in the list of leading families (arranged according to the number of individuals of 25 cm diam. and over), which is due to the relative abundance of *foengoe* (*Parinari campestris*).

Noticeable is the absence of *birgiegronfoeloe* (*Qualea rosea*) in the whole Coesewijne region. As was demonstrated in the foregoing section and in part II.2.3 (cf. fig. 52), in the Mapane region this species showed a strong preference for the porous soils derived from the sedimentary "cover-sands". If this preference would rest primarily on the physical properties of the soil, this species would be expected to occur abundantly in the Coesewijne forest which grows on the loose, porous loamy sands and sandy (clay-) loams derived from the Coesewijne "cover-soils". The other Vochysiaceae, which in the Mapane region are typical for the ecotone to xeromorphic forest, appeared to be absent or very rare in the physically similar soils in the Upper-Coesewijne region.

No complete list of the canopy species found in sample plot 5 is given. In addition to the species listed in table XVII, in sample plot 5 one or more trees of 25 cm d.b.h. or over of the following species of the upper- and middle storey were counted:

Papil.: *Sclerolobium albiflorum*, *Swartzia* sp., *Andira surinamensis*, *A.* cf. *villosa*, *A. coriacea*, *Diplotropis purpurea* — Mimos.: *Parkia nitida* and/or *P. ulei*, *Piptadenia suaveolens*, *Pithecellobium racemosum*, *P. pedicellare* — Elaeocarp.: *Sloanea eichleri* — Tiliac.: *Lueheopsis flavescens*, *Apeiba echinata* — Euphorb.: *Pera bicolor*, *Mabea piriri* — Sapot.: *Pouteria engleri*, *Micropholis* spec. nov. — Olac.: *Minquartia guianensis* — Bomb.: *Bombax globosum* — Humir.: *Sacoglottis guianensis* — Bignon.: *Jacaranda copaia* — Vochys.: *Qualea albiflora* — Icac.: *Dendrobangia boliviana*, *Poraqueiba guianensis* — Laur.: *Licaria* spp. — Ros.: 7954 — Meli.: *Carapa guianensis* and/or *C. procera* — Logan.: *Antonia ovata* — Annon.: *Xylopia* sp. — Flacourt.: *Laetia procera* — Simar.: *Simarouba amara* — Anac.: *Loxopterygium sagotii*, *Tapirira guianensis* — Apocyn.: *Aspidosperma marcgravianum*, *A. oblongum*.

The composition of the *under storeys* too differed considerably from that in the Mapane forest (cf. table XVII). Some of the most conspicuous features are the total absence of *Coussarea paniculata* (*boskoffie*) and the rarity of the Violaceae *Paypayrola guianensis* (*tajahoedoe*) and *Rinorea* sp., resulting in the negligible role played by the Violaceae in the Coesewijne forest, as compared with the preponderant position occupied by this family in the lower storeys of the Mapane forest on mesic sites. *Paypayrola* too was less abundant, e.g. in sample plot L on light-textured soil in the Mapane region. *Mirkietikie* (*Bonafousia undulata*) is extremely rare in the Coesewijne forest, whereas *pakiratikie* (*Tapura guianensis*) and *Cassipourea guianensis* are abundant in the undergrowth. The latter species, a Rhizophoracea, is characteristic for sub-mesic sites.

For the relative abundance of the other genera of lower storey and undergrowth, reference is made to the list of families given in table XVIII.

The *species/area* curves given in fig. 62 show that the number of species in the group comprising trees of more than 10 cm, as well as in that comprising trees of more than 25 cm d.b.h., are in sample plot 5 in the Coesewijne forest somewhat smaller than in plot 1 in the Mapane forest. The curve for the Coesewijne forest closely resembles that for sample plot L in the Mapane forest, which was laid out in forest on a sub-mesic site, viz. on a "non-bleached" cover-sand, which in its physical properties closely resembles the soil of the Upper-Coesewijne forest.

As is noticeable from the figures given in table XVIII, both the absolute and the relative *number of individuals by which the species of the under storeys are represented* is in the Coesewijne forest lower than in sample plot 1 in the Mapane forest (respectively 282 and 400 individuals of lower-storey and undergrowth species of 5 cm d.b.h. and more per ha).

That the result of the enumeration in sample plot 5 is fairly representative for the average composition of the whole area, is shown by the average values of a 2 % enumeration in about 7500 ha of mesophytic forest in compartments 860 a and 860 c and 859 (the greater part of which is shown in fig. 53) given in table XVII. The differences with the results of the countings in sample plot 5 are partly accidental, but they are also partly due to the fact that the one-hectare sample was by purpose chosen in a patch of forest showing optimum development, whereas the 2 % evaluation of the whole area also included the ecotones to secondary and to xeromorphic forest.

Sample plot 6: As was mentioned in II.3, the flat plains of the "cover"-sands of the Upper-Coesewijne region merge to the S and to the W into the schistose hills of the old crystalline basement (which in the transitional zone may be capped with white-sand plateaux). Tongues and isolated low relic-hills extend northward to within the "cover-sand" plains of the Upper-Coesewijne. Such an extension of the schistose hills was found e.g. in the SW corner of the area shown in fig. 53 (corresponding to the W end of the cross-section given in fig. 54). On this map it is recognizable by the dendritic pattern of the forest streams, the upper parts of which are found in rather sharply incised gullies. In the forest growing on this deviating soil type, a small rectangular sample plot, 0.4 ha in extent,was laid out (plot 6, for location cf. figs. 3 and 53). The soil was deeply weathered sericite-schist, overlain by coarse sandy clay(-loam) which was locally rich in masses of slaglike concretionary ironstone. It was described in II.3 as profile 2.

As is clearly shown by the data given in tables XVII and XVIII the composition of this patch of forest differed significantly from that of the surrounding forest on non-bleached "cover"-soils. The most striking difference was the greater number of trees, both in the larger (≧ 35 cm) and in the small (≧ 5 cm) diameter classes, the appearance of *Paypayrola guianensis* (*tajahoedoe*) and *Bonafousia undulata* (*mirkietikie*) in the under storeys, and the replacement of the *boegroemakka* palm by *paramakka*. Each of these species was absent or extremely rare in the surrounding forest on more lightly textured soils, but was frequent in the Mapane rainforest; the first two species were found also in the sub-mesic forest that occurs farther to the S on the lateritic soils of the schistose hills (cf. III.4.1). The affinity with the latter type of forest appears also in the relative abundance of *Licania micrantha* (*zwarte foengoe*), a Rosacea which is very abundant in the *hill forest* and has infiltrated also in the neighbouring forest on the "cover-sands" of the Upper-Coesewijne region (cf. table XVII), but which is very rare or absent in the forest N of Mapane Cr. (the sign ±? in the column of sample plot 1, refers to one small specimen which could not be identified with certainty). The occurrence of *Licania micrantha* in the Upper-Coesewijne forest, which lies N of the forest region where this tree is rather abundant, is another example of affinities in floristic composition occurring in the direction S–N between neighbouring forests on highly different soils. These affinities may be much greater than the affinities between forests on similar sites in the direction E–W if the latter are separated from each other by one or more barriers (such as the Suriname R. and Saramacca R. between the Mapane and the Upper-Coesewijne region). Below, this point will be discussed in more detail (III.3.3).

Noteworthy is the occurrence of large numbers of saplings of *Swartzia prouacensis* (*ijzerhart*) and another, unidentified kind of *ijzerhart*. These, and other species of this genus, are very characteristic for submesic upland forest on lateritic (ferrallitic) soils. On the outcropping slag-like blocks of ferrite a fern, *Amphidesmium blechnoides* (Polypod.), was found, which occurs exclusively on such sites.

A conspicuous element of the herb layer in the region of sample plot 6 is *Diplasia karataefolia* (Cyperaceae), which may reach a height of 1½ m, and which is absent or very rare in the surrounding forest. From the creek-valley forest on hydromorphous soil *Rapatea paludosa* (*anansiwawai*) has invaded this high-ground forest. The occurrence of this hydrophilous herb presumably is an indication of the slow drainage of the soil, which is due to the rather low permeability of the comparatively heavy soil, which, moreover, overlies the impermeable kaolinitic weathering product of the sericite schist. That this soil has a high water content, in comparison with the loose "cover-sands" of the surrounding forest, appears also from an analysis of soil moisture made at the end of a very dry season (cf. table XIV: site 7, which was chosen in this sample plot).

In the lower and middle storey, besides *Astrocaryum paramaca*, various other palms were rather abundant (ca. 50–100 stems per ha), e.g. *birgie-maripa* (*Attalea* sp.), *koemboe* (*Oenocarpus bacaba*), *maripa* (*Maximiliana maripa*).

For the rest, the floristic composition of plot 6 closely resembled that of the surrounding forest. A similar overlapping of the woody species of the surrounding forest over a deviating site of relatively small extent, was repeatedly observed in the Suriname forests, e.g. on the small white-sand pockets in the Mapane region. The "socions" (in the sense of the Uppsala school of phytosociology) of the lower storey and undergrowth species, which need a smaller minimum area for their development, react much sharper on differences in habitat (as shown by *Paypayrola*, *Bonafousia* and *Astrocaryum paramaca* in plot 6).

III.3.3. *Comparison with the composition of the Mapane forest*

The floristic composition of the mesophytic (rain) forest occurring on mesic sites in the Upper-Coesewijne region, differs significantly from that of the lowland rain forest N of the Mapane Cr.; the numerical preponderance of Lecythidaceae (*Eschweilera*!), Burseraceae (*Tetragastris*!), Papilionaceae and Myristicaceae amongst the canopy species in the Mapane forest, appears to be replaced by that of species belonging to the Papilionaceae (*Dicorynia* and *Eperua*!), Euphorbiaceae (*Chaetocarpus*!), Rosaceae (*Parinari*) and Lauraceae (*Ocotea*) in the Coesewijne rain forest. In the under-storeys the *boegroemakka* palm replaces *paramakka*, and many species, which are more or less abundant in the forest N of the Mapane Cr., are (very) rare in the Upper-Coesewijne rain forest, where the under-storeys are dominated by species which are much less abundant in the Mapane region.

The difference in floristic composition of the two types of rain forest is largely one of degree: with a few exceptions (e.g. *Tetragastris altissima*, *Qualea rosea* and *Astrocaryum sciophilum*) the leading species in one of the two forests were found also in the other one, be it with a much lower density. With the exception of the *boegroemakka* palm, each of the species found in the Coesewijne rain forest, was encountered also in the Mapane forest. On the contrary, a number of tree species of the latter were not noted during the surveys in the Coesewijne region, although this is no proof that they really do not occur in this area, because the registration of the species in the lowland forest W of the Saramacca R. is still less exhaustive than that in the region N of the Mapane Cr. Only for *Qualea rosea* and *Tetragastris altissima*, two species which are common in the lowland forest E of the Suriname R., it is very likely that they are really absent in the Upper-Coesewijne area, although the first species showed in the Mapane area a strong preference for light-textured soils exhibiting approximately the same physical properties as most of the soils found in the Upper-Coesewijne region do.

The Coesewijne forest clearly showed a greater tendency for *single-dominance*, which means that it shows a greater degree of dominance of relatively few leading species (as compared e.g. with the forest on mesic sites in the Mapane region), a feature which is characteristic for forests on less favourable sites and which was observed also in forest on sub-mesic sites in the Mapane region (e.g. sample plots L and 2). The greater relative density of a few leading species results in a comparatively lower number of woody species per unit area (as shown by the species/area curves in figs. 61 and 62), although this does not necessarily mean that the Upper-Coesewijne forest is poorer in woody species.

Naturally the question arises to what extent the *differences in edaphic factors* may be responsible for the considerable differences in composition found between the two types of forest. As was shown in table VII there are differences, both chemical and physical ones, the second amongst other things resulting in a smaller water-supply during the dry seasons (cf. table XIV). Indeed, two of the leading species in the Coesewijne rain forest (*wallaba* and *basralokus*) showed in the Mapane region a preference for light-textured soils. But, as mentioned before, a number of species which were rather abundant in the ecotone on light-textured soils in the Mapane region (e.g. in plots L and 2) were not abundant in the Coesewijne forest. Yet, in their physical properties the "non-bleached cover-soils" of the latter closely resemble the "non-bleached cover-sands" in the Mapane region, although it must be admitted that they are poorer in some plant nutrients.

It is impossible to evaluate the role which differences in *historical development* may have played in the difference in composition between the rain forest of the two areas. As mentioned before, the relative abundance of a *disturbance-indicator* like *Goupia glabra* (*kopie*) might indicate that in the Coesewijne area more recently disturbances on a rather large scale have taken place.

Apart from the possibility of differences in the degree of biotic influences during sub-recent times, other differences in historical development since the deposition of the Zanderij sediments and the subsequent recolonization of the plain from the refuges on the relic-hills and the old basement are not unconceivable. The recolonization presumably followed the Quaternary physiographic pattern, which probably may explain, at least to some extent, the conspicuous S–N affinity in the composition of the forests, as was noted in various watersheds between the great rivers, the main direction of which is northward. The peculiarities in the distributional pattern of a number of species in British Guiana are imputed by DAVIS (1941) to peculiarities of late Tertiary or Quaternary physiography. By this author examples are given of tree species whose known range is confined to a single river valley; such examples are known in Suriname also. Hence, it is very likely that the rivers act for various species with large seeds as barriers for an E–W dispersal, thus causing the S–N affinities within the watersheds, even between forests on very different soils. This affinity sometimes may be greater than that between forests on similar soils which are separated by one of the larger rivers. For instance, attention is drawn to the phytosociological affinity (so far as the woody species are concerned) between the Upper-Coesewijne forest and that of the submesophytic forest found on the lateritic residual soils in the hilly country farther southward. (Goliath Cr. region: cf. tables XVII and XVIII, and section III.4.1).

III.4. COMPOSITION OF UPLAND RAIN-FORESTS (HILL FORESTS)

In this section are gathered a small number of miscellaneous observations made on the floristic composition of the upland forests that are found behind the belt of lowland forests of which two examples were described in the foregoing sections.

The upland region varies in physiography from fairly flat and undulating to rather steep and rugged. Two examples were studied of the upland forest covering the gravelly, ferrallitic soils of the rugged schistose hills and hilly ridges that are found respectively in the region S of the Upper-Coesewijne lowland (viz. in the Goliath Cr.–Saramacca R. watershed, cf. figs. 1 and 3) and in the region of the Upper-Suriname R. (Bergendal-Remontcourt, cf. fig. 1). A third forest complex was studied on a schist mountain (Stofbroekoe Mnt., cf. fig. 1) covered by a sheet of lateritic ironstone. Finally, in the valleys of the Saramacca R. (near the Stofbroekoe Mnt.) and the Coppename R. (near the Voltz Mnt.) examples were studied of forest covering ferrosiallitic upland soils which have developed from acid parent rocks (such as granites and acidic gneisses).

The soils of these sites were discussed in II.4. Although complexes of high, well-developed forest were chosen, the *upland forests on gravelly, lateritic (ferrallitic) soils* often are somewhat less luxuriant than the examples of true mesophytic lowland rain-forest which were described in the foregoing sections. The main canopy is more open (and here and there somewhat lower), undergrowth and especially ground vegetation are less abundant. This is due to the fact that the soils of the "schist-hill-" and "schist-mountain landscape" (VAN DER EYK 1957) are generally more freely draining (in connection with their topography), and may have a considerably lower water capacity (depending on the amount of ironstone gravel and the resultant reduction of total pore space).

But, although being sub-mesophytic in comparison with lowland rain-forest in its optimum development, the physiognomy of the upland forests which will be discussed below, is not so that it would justify their inclusion in the xeromorphous series to which the "dry evergreen forest" belongs. Only on exposed rocks, and where the soil, overlying sheets or bolders of concretionary ironstone, becomes very thin, a type of forest is found which physiognomically resembles the "*xeromorphic rain forest*" that was described by BEARD (1944) and by FANSHAWE (1952) on similar sites in Tobago and in British Guiana respectively.

Physiognomically the upland forests on the gravelly hills of the "schist-hill landscape" resemble the "*evergreen seasonal forest*" described by these two authors.

In contrast to BEARD's "evergreen seasonal forest", in which about 25 % of the species among the large emergent trees are deciduous, our forest type may be regarded as almost entirely evergreen, as less than 5 % of the species are deciduous.

According to FANSHAWE, the "evergreen seasonal forest" in British Guiana is characterized by the fact that only 5 % of individuals with a stem diameter of over 10 cm are Leguminous, whereas our forest type is characterized by the high numerical preponderance of Leguminosae (cf. table XVIII). The "evergreen seasonal forest" in British Guiana probably is equivalent to our "high savanna forest", or to its transition to rain forest; the "evergreen seasonal forest" in the lowland of British Guiana occurs on the light coloured sands of the eastern district, and the "high savanna forest" in Suriname is found on similar soils belonging to the Zanderij formation.

The type of forest on ferrallitic soils, that will be described in the following sections, will provisionally be called "*upland rain-forest*".

The floristic composition of the three complexes of this forest type (which, on purpose, were chosen at rather great distances from each other) appeared to show considerable differences. The enumerations nevertheless demonstrate the occurrence of a few character species which were found with fairly great constancy in each of the three complexes (e.g. *Vouacapoua americana*, certain *Swartzia* species, *Sagotia racemosa*, *Oxandra asbecki*, etc.).

III.4.1. *Upland forest of the Goliath-Creek region*

Some 15 km S of the Upper-Coesewijne forest on the Zanderij sediments, in the hilly country, which was described in II.4, five sample plots, each 0.3 ha in extent, were laid out in the upland rain forest. The location of the sample plots appears from fig. 3 (the plots 4a and 4b, which were only 100 m apart, are indicated by one and the same cross). The physiography is rugged, the steep hills and "kopjes" attaining heights of about 100 m. The soils consist of a yellow-red ferrallitic earth, varying from sandy loams to silty clay, and containing much ironstone gravel. They have developed from deeply weathered, highly metamorphous rocks (schists), and have been described by VAN DER EYK (1957) as "schist-laterite soils". In the

TABLE XX

Density, frequency and constancy of a number of selected species in 5 square sample plots of 0.3 ha each, located in high upland forest on lateritic clay in the Goliath Creek region. Each 0.3 ha plot consisted of thirty 100 m^2 quadrats. *Density:* number of individuals per ha, averaged over the total area sampled (i.e. 1.5 ha). *Constancy:* the occurrence of one or more individuals (of more than 1½, 4½ and 24½ cm d.b.h. respectively) of a species per plot, expressed as a vulgar fraction of the five 0.3-ha plots. *Quadrat-frequency:* expressed as the percentage of quadrats in which a species occurs, out of the total of 150 quadrats. Species which are considered to be differential for the forest type under consideration, are in spaced type.

A. UPPER- AND MIDDLE-STOREY SPECIES	Average density		Quadrat-frequency		Constancy	
	≧ 5 cm	≧ 25 cm	≧ 5 cm	≧ 25 cm	≧ 5 cm	≧ 25 cm
Chaetocarpus schomburgkianus (Euph.)	28	14	25%	14 %	5/5	5/5
Licania micrantha (Rosac.)	48	11	34%	10 %	5/5	5/5
Vouacapoua americana (Papil.)	23	17	21%	16 %	5/5	4/5
Swartzia cf. *prouacensis* (Papil.)	44	7	37%	7 %	5/5	4/5
Pouteria cf. *cladantha* (Sapot.)	17	4	15%	4 %	5/5	4/5
rode kwepie (Rosac.)	7	4	7%	4 %	5/5	4/5
Dicorynia guianensis (Papil.)	12	7	12%	7 %	5/5	3/5
Eperua falcata (Papil.)	32	7	22%	7 %	4/5	3/5
Swartzia remigifer (Papil.)	13	5	13%	5%	3/5	3/5
Inga alba (Mimos.)	19	3½	13%	3 %	3/5	3/5
kwassiba (Sapot.)	5	3½	5%	3½%	3/5	3/5
Virola melinonii (Myrist.)	10	2½	10%	2½%	5/5	3/5
Sterculia sp. (Sterc.)	7	2½	7%	2 %	5/5	3/5
Pourouma sp. (Morac.)	18	3½	17%	3 %	5/5	2/5
Goupia glabra (Celast.)	5	3	5%	3 %	3/5	2/5
Ocotea rubra (Laur.)	5	3	5%	3 %	3/5	2/5
Jacaranda copaia (Bignon.)	4	2	4%	2 %	4/5	2/5
Inga coriacea (Mimos.)	11	2	10%	2 %	3/5	2/5
Trattinickia sp. (Burs.)	6	2	6%	2 %	4/5	2/5
Martiusia parviflora (Papil.)	5	1½	5%	1½%	4/5	2/5
Couepia sp. (Rosac.)	13	2½	13%	2½%	5/5	1/5
Byrsonima aerugo Malp.)	7	3	5%	2½%	1/5	1/5
Geissospermum sericeum (Apoc.)	3	2	3%	2%	2/5	1/5
Iryanthera sagotiana (Myrist.)	9	1	9%	1 %	5/5	1/5
Couratari gloriosa (Lecyth.)	1	<1	1%	—	1/5	<1/5
B. LOWER-STOREY AND UNDERGROWTH SPECIES:	≧ 2 cm	≧ 5 cm	≧ 2 cm	≧ 5 cm	≧ 2 cm	≧ 5 cm
Oxandra asbecki (Annon.)	315	66	82%	35%	5/5	5/5
Protium spp. (chiefly *aracouchini*) (Burs.)	120	70	60%	47%	5/5	5/5
Eschweilera labriculata (Lecyth.)	120	41	48%	38%	5/5	5/5
Ouratea cf. *flexuosa* (Ochn.)	45	11	40%	9%	5/5	4/5
Rheedia benthamiana (Gutt.)	25	20	23%	18%	5/5	5/5
Paypayrola guianensis (Viol.)	130	40	30%	26%	4/5	4/5
Tapura guianensis (Dichap.)	95	15	52%	15%	4/5	4/5
Sagotia racemosa (Euph.)	4	10	4%	7%	4/5	3/5
Rinorea sp. (Viol.)	60	3	26%	2%	1/5	1/5
Astrocaryum sciophilum (Palmae)	250		100%	100%	5/5	5/5

transitional zone to the Zanderij formation, some of the plateaux are capped with leached quartz sands; these are covered with xeromorphous (savanna) forest, (e.g. mixed *savanna forest*, the *wallaba* consociation and the *dakama* consociation) as shown by the map in fig. 3.

On the plateaux on the top of the schist hills and ridges, drainage is free to rather excessive. Although the water-holding capacity of the clayey and silty soils is presumably fairly high, it is not impossible that the large amount of ironstone gravel may reduce this capacity to such an extent that the water supply may sink in dry years (which are, as was shown in I.1, by no means uncommon in Suriname) below the requirements of the vegetation. This circumstance may explain the more or less xeromorphic aspect of the forest. The forest on the slopes which drain the plateaux, looks somewhat more luxuriant, which may be due to a more favourable water supply during the dry season.

The forest in which the sample plots were laid out, is high forest, the main canopy reaching a height of approximately 30–35 m, which is about the height of the canopy in mesophytic lowland forest. Outstanding trees (such as *Swartzia* and *Couratari*) may reach a height of 40 m. Small stands of *"liane forest"* occur (as a seral stage of secondary forest, and as an edaphic climax on colluvial deposits and truncated horizons of ironstone gravel), but on the whole, lianes are not frequent in this forest. Epiphytes were scarcer than in the lowland rain-forests of the Mapane and Upper-Coesewijne region.

The upper storeys are more open than in true mesophytic lowland forest. The sub-mesophytic character of the upland forest reveals itself perhaps also in the occurrence of some species of *Swartzia* (*ijzerhart*), as various species of this Leguminous genus are in the Guianas characteristic for sub-mesic and xeric sites.

Some of the results of the enumerations which were carried out in the sample plots have been set out in tables XVII and XX. In the second table for the most abundant woody species the density, quadrat-frequency and constancy are recorded. The difference between the figures for density and quadrat-frequency give an impression of the way in which the individuals of a given species are distributed in the plots. For instance, if the frequency-percentage is low in comparison to the density, this indicates that the individuals occur in more or less distinct groups (*over-dispersion*). For instance, of *Oxandra asbecki*: 66 individuals of more than 5 cm d.b.h. per ha were found in 35 % of the quadrats of 100 m^2, which means that they must occur in groups, whereas 41 trees per ha of *Eschweilera labriculata* were distributed over 38 % of the quadrats, a more or less even distribution. The constancy values give an idea of the distributional pattern on a larger scale: for instance *Vouacapoua americana* was the most abundant tree (in average number of trees of more than 25 cm d.b.h. per ha), but the *non-homogeneous distribution* appears from the fact that trees of this size-class were absent in one of the sample plots.

With the exception of the species that are in bold type in table XX, all woody species which were noted in the sample plots in the upland forest of the Goliath Cr. region, were found also in the Upper-Coesewijne and/or in the Mapane region.

The affinities with the neighbouring Upper-Coesewijne rain forest on "non-bleached cover-sands" were discussed already in III.3 (viz. the abundance of *Chaetocarpus schomburgkianus*, the preponderance of Papilionaceae, the scarcity of individuals of canopy species of *Eschweilera* and Burseraceae and the absence of *Coussarea* in the lower storey, etc.; cf. tables XVII and XVIII). On the other hand, the appearance of *Paypayrola guianensis* (*tajahoedoe*) and of another Violacea (*Rinorea* sp.: *lèlètikie*), and also of *Bonafousia undulata* (*mirkitikie*), *Ouratea* cf. *flexuosa*, *Virola melinonii* (*hoogl. baboen*), etc., which are very rare or absent in the neighbouring lowland forest of the Upper-Coesewijne, are points of resemblance with the lowland forest N of the Mapane Cr.

Basralokus (*Dicorynia guianensis*) and *wallaba* (*Eperua falcata*), which are common co-dominants in the majority of the forests on "schist laterite soils" (although by no means characteristic for this type of forest alone, as is shown e.g. in table XVII), were rather abundant in this region too (and also in the neighbouring lowland rain forest of the Upper-Coesewijne region!).

The species which are supposed to be *characteristic* for the upland forest on ferrallitic soil, are rather few in number. Among the canopy species *Vouacapoua americana* was the most abundant one. The occurrence of isolated stands of this species in the Mapane lowland forest was discussed already in detail in II.2.2 and III.2.2. Although *bruinhart* stands are said to occur also on white sands, I did not meet this species on such sites; I found it, on the other hand, on the majority of "schist laterite soils", and for this type of soil this species is, in my opinion, a reliable indicator species. *Licania micrantha* (*zwarte foengoe*) too shows perhaps a preference for upland forest (cf. table XVII), although this species was found also in the lowland forest of the Upper-Coesewijne forest; except for one uncertain finding the species was not encountered in the Mapane lowland forest.

Byrsonima aerugo (*hoogl. lontoekassie*) was met with in aggregated stands (which is reflected in the low constancy value). Other species of this genus, such as *Byrsonima crassifolia* are common co-dominants in white-sand savannas in the Guianas.

Among the canopy species, the big trunks of two *Swartzia* species (*boegoeboegoe*, *ijzerhart*) are noticeable. These (and other) species of this genus, with their extremely deeply fluted trunks, are very characteristic for all the upland forests on lateritic soils which I visited. They are sometimes named *parelhout*, because of the close resemblance of their trunks with those of the *Aspidosperma* species indicated by this vernacular name. Other representatives of this genus (e.g. *Swartzia bannia*, *savanne ijzerhart*) are characteristic for high savanna forest on bleached quartz sands in Suriname and British Guiana. Some species (e.g. *S. tomentosa*, *gandoe* and *S. benthamiana*, *birgiebébé*), which have no deeply fluted trunks, prefer mesic sites.

Eschweilera labriculata was rather abundant in the lower storey. Later it was found also in the upland forest on the ferrallitic soils of the slopes of Stofbroekoe Mnt. This species is probably absent in the lowland forests of Suriname. *Couratari gloriosa* was collected for the first time in Suriname in the ecotone to hydromorphic sites (on moist "foot-plain soils" and "creek-valley soils", according to the terminology of VAN DER EYK). Later it was found in similar sites on the hills near Bergendal and Remontcourt. *Oxandra asbecki* (*pika-pika*) was the most abundant species in the undergrowth; it was found, with varying abundance, in other upland forests on ferrallitic soils (cf. e.g. Stofbroekoe Mnt. and Remontcourt), and is also very abundant in "mountain savanna forest" on ferrite and ferro-bauxite caps.

The palm layer consisted exclusively of *boegroemakka* (*Astrocaryum sciophilum*). The many spiny stems of this palm, which may reach a height of approximately 5–8 m, are a common feature in the majority of the forests on the old basement, behind the Zanderij formation. West of the Saramacca R. this palm replaces its close relative, *Astrocaryum paramaca* (*paramakka*) in the lowland rain forest on sedimentary soils too; the palm layer of the mesophytic lowland forest between Saramacca R. and Coppename R. consists nearly everywhere of *boegroemakka*. I do not know how the situation is W of the Coppename R. On the alluvial silty clays and silty loams of the river terraces bordering the Coppename R., the Wayombo R. and the Nickerie R., *boegroemakka* locally forms nearly pure stands. The two *Astrocaryum* species occupy areas which are in part overlapping, (e.g. in the upland forest near Remontcourt (cf. table XVII) where *paramakka* was met with some 20 km S of the N boundary of the old basement. It is uncertain, whether the distribution of the two species is determined by edaphic or other environmental factors, or whether the difference in their area of distribution is determined by historical factors, *boegroemakka* (which seems to be the most aggressive one) invading the area of *paramakka* or vice versa. Howsoever this may be, it is one of the many examples of ecological problems which are encountered already during a first, reconnoitring study of the Suriname forests. How puzzling the situation is in this particular case, may appear from the fact that on the schistose rest hills in the Upper-Coesewijne region (e.g. in sample plot 6, cf. table XVII) i.e. on soils upon which elsewhere exclusively *boegroemakka* is found, *paramakka* occurred, whereas *boegroemakka* formed the palm layer in the surrounding lowland rain forest on "non-bleached cover sands", that is on soils upon which *paramakka* forms the palmlayer in the lowland forest between Suriname R. and Commewijne R.!

III.4.2. *Upland forest on Stofbroekoe Mountain* *)

Stofbroekoe Mnt. is a *schist mountain* range, running closely parallel to the Little Saramacca R. (cf. fig. 1). On three places, viz. on the flat plateau which forms the southernmost top (ca. 500 m above sea level), midway down the slope (at ca. 250 m height and at a distance of 5 km from the first plot), and at the foot of the mountain, sample plots of 0.5 ha each, were laid out. The ferrallitic soil of this mountain range, a yellow-red or red loam, sandy clay loam or silty loam, containing much ironstone gravel, and overlying a very thick (bauxo-) ferrite cuirass, was described in II.4.

For comparison also a sample plot was laid out in forest growing on a very different soil (alluvial and/or residual soil, presumably developed from a granitic weathering product) found in the flat, broad valley of the Kleine Saramacca R.

On those sites of the mountain where the soil overlying the thick ferrite cap is of sufficient depth (say, at least 75 cm), a well-developed upland rain-forest is found. In this forest the two first sample plots (viz. on the top and halfway down the slope) were laid out. The relatively open upper storey is rather irregular, the height of the main canopy averaging 28–35 m, with a few scattered emergents (e.g. *Couratari* and *Manilkara*) reaching a height of 35–45 m. The forest is almost entirely evergreen.

The feature in which this forest differs most conspicuously from the other forests described in this study, is the comparatively *sparse ground cover* and the more or less open appearance of the lower storeys. The latter is caused not so much by a lower number of small trees (as is shown by the figures given in tables XVII, XVIII and XXI), as by the fact that the foliage of the understoreys is less dense than in the other forest types and, especially, by the fact that the palm layer is nearly absent. Only a few scattered individuals of *paramakka* (*Astrocaryum paramaca*) and *boegroemakka* (*A. sciophilum*) are found in the forest on the Stofbroekoe Mnt. Lianes and epiphytes are not abundant. The number of buttressed trees is not larger than in the other types of forest studied. More or less deeply fluted stems (*Vouacapoua, Swartzia*) are a conspicuous feature, just as in the other types of upland forest on ferrallitic soils.

The physiognomy of this forest, with its rather great number of large stems (cf. tables XVII and XVIII), shows a closer resemblance with the ordinary rain forest than with the "xeromorphic rain forest" that was described from lateritic ironstone-capped ridges in Tobago (BEARD, 1944) and British Guiana (FANSHAWE, 1952).

Where the ferrite cuirass approaches the surface, and where the soil layer accordingly is very thin, the high forest may become xeromorphous forest or woodland, a "pole forest" with many lianes, and comparatively rich in individuals of Myrtaceae and Sapotaceae ("mountain savanna forest", LINDEMAN 1959).

---

*) This region could be visited owing to the friendly co-operation of the Geological and Mining Department, which service placed at my disposal its camps, means of transport, etc.

The third sample plot was laid out in rather poor transitional forest near the foot of the mountain, where the thick sheet of concretionary ironstone lay close to the surface. The thin (2–30 cm) layer of soil, moreover, contained much ironstone gravel. The roots of the larger trees tended to spread along the rocky surface. In this plot, the upper storeys were still more open, and the undergrowth was still sparser than in the other two plots. Yet, the number of large stems ($\geqq$ 25 cm d.b.h.) was in view of the inhospitable aspect of the site unexpectedly high; even *Couratari* trees of 40 m height were encountered. The development of such a relatively large number of tall trees on this site, notwithstanding the very shallow soil, is probably made possible by the circumstance that throughout the greater part of the year seepage water is received from the slopes. With this seepage water presumably also plant nutrients are brought down; as was shown by the figures in table X (Stofbroekoe Mnt., foot), the amount of readily available plant nutrients was remarkably high in this shallow soil. For calcium ions this amount was even exceptionally high!

Although traces of charcoal were found at various depths in the soil borings, it is practically certain that for a considerable time no disturbance of any significance has taken place in this forest. The many "balata" trees (*Manilkara bidentata*) are periodically tapped, but this is of nearly negligible influence upon the forest. Farming and timber working by the Bush-negroes are confined to a narrow strip along the Little Saramacca River.

In table XXI the densities per ha for a number of the most abundant species have been recorded. These figures have been given for the three sample plots separately to show the considerable differences in composition existing between these plots.

But besides these differences, the first two plots, at 500 and 250 m height also have a number of common features, which apply to the greater part of the forest on ferrallitic soils in this region (provided that the soil is not too shallow), viz. the relative abundance of *Eschweilera* species (*E. amara* and/or *E. odora*), *Swartzia* species and *Vouacapoua americana* in the canopy, and of *Oxandra asbecki*, *Tapura guianensis*, *Swartzia apetala* and *Sagotia racemosa* in the lower storeys. In the upper and middle storey *Papilionaceae and Lecythidaceae play a dominant role* (cf. table XVIII).

The numerical preponderance of Lecythidaceae (*Eschweilera* and *Couratari*) is characteristic for the majority of the upland forests on ferrallitic soils in the N half of central Suriname (except, e.g. in the forest of the Goliath Cr. region) as it is also for the lowland forest on the Suriname R.–Commewijne R. watershed.

As species which are considered characteristic for forest on schist hills, were noted: *Swartzia* species (*S. remigifer* and/or *schomburgkii*, *S. prouacensis* and *S. apetala*), *Vouacapoua americana*, *Eschweilera labriculata*, *Oxandra asbecki*, *Sagotia racemosa* and *Amphirrhox surinamensis*.

The comparatively large number of *wanapisie* (*Ocotea* sp.) is a remarkable feature of the forest on the plateau at the top of the mountain. This species also was met with on well-drained sites in the Mapane region (cf. II.2.2), but it is absent or very rare in the other forests that were studied.

A remarkable fact is the absence of *wallaba* (*Eperua falcata*). I did not meet a single individual of this species in the whole region, and it was absent or very rare also in the other upland forests which were visited (except in the Goliath Cr. region in the transitional zone to the sedimentary soils of the Zanderij formation).

The total number of woody species found per unit area did not differ significantly from that found in the other forest types.

The undergrowth was rather open. Palms (*Astrocaryum*) were rare, which is in contrast to the situation found elsewhere in the upland forests. A very conspicuous feature of the lower storeys was the fact that *Tapura guianensis* (*pakiratikie*) was found to reach unusually large dimensions (cf. table XXI) as compared with the usual size this undergrowth species reaches in other sites. In the plateau forest mature individuals were found to reach the middle storey. It is still uncertain whether this vigorous growth is due to the habitat, or that the individuals on Stofbroekoe Mnt. belong to another biotype or even to another sub-species.

The ground flora was very sparse, but locally the fern *Stigmatopteris guianensis* was abundant (especially on outcrops of concretionary ironstone). On ironstone boulders another fern, *Amphidesmium blechnoides* was found, which was noted also in similar sites in sample plot 6 in the Upper-Coesewijne region. A root parasite, *Helosis cayennensis* (Balanophoraceae), which is widely distributed in tropical America, was just flowering (August) on moist gravelly and rocky sites.

The composition of the third plot, in the forest on the gravelly, shallow soil near the foot of the mountain, differed considerably from that on the deeper soils, as appears from table XXI; e.g. *Eschweilera* is replaced by *Alseis longifolia*. It was the first time that this species was found in Suriname.

For sake of comparison, a sample plot was laid out in the well-developed high forest on different soils in the flat, broad valley of the Little Saramacca R. This forest closely resembles lowland rain forest in physiognomy. The laboratory analyses (cf. table X) of one sample of this soil (which is rather compact clay, containing much very fine sand), presumably developed from alluvial material of granitic or gneissose origin), showed comparatively high amounts of readily available plant nutrients.

It should be noted, however, that notwithstanding these high figures for available nutrients, the *number of trees per ha* was approximately the same as that found in the sample plots on the lowland soils, for which the laboratory analyses showed much lower values for available nutrients.

The affinities with the neighbouring forest (such as the occurrence of

TABLE XXI

Density (number of individuals of ≧ 25 cm or ≧ 5 cm d.b.h. per ha) of selected species in 4 sample plots (each 0.5 ha in extent) on Stofbroekoe Mnt. (upland rain-forest on ferrallitic sandy (clay-)loam) and in the valley of the Little Saramacca R. (on alluvial and/or residual loam, presumably derived from granitic parent rock)

A. UPPER- AND MIDDLE-STOREY SPECIES	Mountain			River-valley
	top	slope	foot	
	(trees ≧ 25 cm d.b.h./ha)			
Vouacapoua americana (Papil.)	6	10	16	6
Dicorynia guianensis (Papil.)	—	10	+	12
Sclerolobium melinonii (Papil.)	4	—	+	+
Sclerolobium albiflorum (Papil.)	—	5	2	+
Swartzia remigifer (and *S. schomburgkii?*) (Papil.)	6	15	—	—
Swartzia sp. (7927) (Papil.)	4	+	—	4
Hymenolobium sp. (Papil.)	4	5	—	+
Martiusia parviflora (Papil.)	—	5	+	—
Inga spp. (Mimos.) (*I. alba*+8062+8063)	+	2	5	6
Eschweilera amara (Lecyth.)	4	25	+	—
„ *odora*	20	—	—	—
„ *corrugata*	4	—	+	+
„ *poiteaui*	2	+	2	—
(*Eschweilera* total) [1])	(30)	(25)	(2)	(+)
Couratari stellata (Lecyth.) [2])	4	5	4	2
Micropholis guyanensis (Sapot.)	8	—	+	2
kiemboto (*Pouteria ptychandra?*) (Sapot.)	2	5	2	+
kwassiba (*Pouteria* cf. *egregia*) (Sapot.)	2	+	8	+
Pouteria cf. *cladantha* (Sapot.)	4	+	+	+
Micropholis spec. nov. (Sapot.)	4	+	—	—
pientobolletrie (*Pouteria* sp.) (Sapot.)	+	5	—	—
Manilkara bidentata (Sapot.)	+	5	4	—
rode kwepie (Rosac.)	4	+	6	+
Couepia versicolor (Rosac.)	+	+	+	4
wanapisie (*Ocotea* sp.) (Laur.)	10	—	—	—
Bombax globosum (Bomb.)	2	—	2	2
Apeiba echinata (Tiliac.)	—	+	8	+
bosamandel (*Terminalia* sp.) (Combr.)	—	5	—	—
Pourouma sp. (Morac.)	—	5	—	4
Brosimum paraënse (Morac.)	—	—	6	—
Bagassa tiliaefolia (Morac.)	—	—	4	—
Qualea rosea (Vochys.)	2	—	8	10
Myrtaceae (7999 and/or 8047)	2	+	4	+
zoutoemetiehoedoe (*Maytenus* sp.) (Celast.)	2	10	+	+
Chaetocarpus schomburgkianus (Euph.)	+	—	—	22
Mabea piriri (Euph.)	+	—	—	2
Aspidosperma album (Apoc.)	—	5	+	6
Aspidosperma oblongum (Apoc.)	2	—	—	2
Geissospermum sericeum (Apoc.)	2	—	6	4
Carapa guianensis and/or *C. procera* (Mel.)	+	—	—	2
Jacaranda copaia (Bignon.)	—	—	2	2
Tabebuia capitata (Bignon.)	2	5	+	—
(*Tapura guianensis*: Dichap.) [3])	10	+	+	4
Mouriria crassifolia (Melast.)	4	+	+	2
Virola melinonii (Myrist.)	2	+	+	10
Alseis longifolia var. *pentamera* (Rub.)	+	—	14	—

TABLE XXI *(continued)*

B. Lower-storey and undergrowth species:	Mountain			River-valley
	top (500 m)	slope (250 m)	foot	
	(trees ≥ 5 cm d.b.h./ha)			
Eschweilera labriculata (Lecyth.)	2	35	90	18
Coussarea paniculata (Rub.)	28	5	20	—
Oxandra asbecki (Annon.)	152	110	102	148
Fusaea longifolia (Annon.)	18	35	50	12
Bonafousia undulata (Apoc.)	28	10	10	2
Rinorea sp. (Viol.)	—	—	62	—
Paypayrola guianensis (Viol.)	10	25	—	—
Amphirrhox surinamensis (Viol.)	20	25	—	—
Tapura guianensis (Dichap.)	74	25	2	216
Swartzia apetala (Papil.)	12	135	4	—
Swartzia prouacensis (Papil.)	6	20	—	—
Sagotia racemosa (Euph.)	184	80	4	—
Astrocaryum sciophilum (Palmae)	r	r	v r	—
Astrocaryum paramaca (Palmae)	—	—	—	f
Total number of trees ≥ 25 cm d.b.h.	172	145	132	114
Total number of trees ≥ 5 cm d.b.h.	1160	1325	1082	1056
Total number of individuals of lower storey and undergrowth species ≥5 cm d.b.h.	645	680	390	480

1) also including *E. simiorum*, *E. longipes*, *E. chartacea*.

2) possibly also including *C. fagifolia?*

3) a lower storey species, reaching unusually large diameters in this forest.

+ only individuals of < 25 cm d.b.h. observed.

Vouacapoua, *Swartzia* spp., *Oxandra asbecki*, and other species which are considered to be characteristic for upland forest on gravelly, ferrosiallitic soils on schistose hills), must be due partly to the circumstance that an influx of seeds was possible. In the foregoing attention was drawn repeatedly to this effect of a neighbouring site.

The abundance of *Chaetocarpus schomburgkianus* (*fomang*) and *Dicorynia guianensis* (*basralokus*) in this plot, and the scarcity of individuals of *Eschweilera* are points of resemblance with the northerly lying upland and lowland forests, i.c. those of the Saramacca R.–Upper-Coesewijne R.–Goliath Cr. watershed.

The occurrence of *birgiegronfoeloe* (*Qualea rosea*) on this relatively heavy soil may serve as an example of the complexities which are related to the autecology of the tree species; for in the Suriname R.–Commewijne R. (Mapane) region this species actually showed a strong preference for porous "cover-soils" with a light texture (cf. II.2.3)! Noteworthy is the appearance of *paramakka* (*Astrocaryum paramaca*) in the undergrowth. For further details reference is made to table XXI.

III.4.3. *Upland forest of Bergendal-Remontcourt*

The floristic composition of the forests in the hilly country of the "schisthill landscape" near Bergendal and Remontcourt, along the Upper-Suriname R. (cf. fig. 1) could as yet be studied only in broad outline. Detailed analyses of the soils are not yet available at this moment; a few general remarks, however, were made in II.4. The majority of the soils in this region, which is formed by low steep hills and hilly ridges, are rather compact, brick-red clays, containing varying amounts of fine sand and silt, and much ironstone gravel. Here and there, where the hills are capped with a slag-like sheet of concretionary ironstone, overlain by a thin layer (2–25 cm) of gravelly clay, the vegetation approaches rather low "dry evergreen forest" (with an irregular, open canopy at a height of ca. 20 m), but usually it is high, well-developed forest with a rather open main canopy at ca. 30 m. Provisionally it is classified as upland rain forest.

In this region timber-working and farming at a comparatively large scale have taken place since the 18th century; only with some difficulty forest stands could be found in which the floristic composition and the age-class distribution of the canopy species approximated that of primary forest, and even here the relative abundance of *disturbance indicators* ("long-lived nomads" in the sense of VAN STEENIS, 1958 b), such as *Goupia glabra* (*kopie*) and *Laetia procera* (*pientokopie*), indicated that formerly large-scale disturbances must have taken place too. The age-class distribution of *Goupia* trees, however, made it certain that the stands which were studied, had been left untouched for at least one century.

The composition of the forest appeared to vary considerably from one place to another. For one of the sample plots (Remontcourt, 0.4 ha) the densities for the most abundant species have been recorded in table XVII. For a tabular survey of the individuals per family reference is made to table XVIII. The numerical preponderance of Papilionaceae found in this sample plot is a characteristic feature of all the stands visited in this region. This preponderance is chiefly due to the relative abundance of *Dicorynia guianensis* (*basralokus*) and *Swartzia* species (e.g. *ijzerhart* and *boegoeboegoe*: *S. prouacensis*, *S. remigifer*, *S. schomburgkii*, etc., and *birgiebébé*, *S. benthamiana*). *Wallaba* (*Eperua falcata*) is absent, just as in the forest of the Stofbroekoe Mnt. region.

The scarcity of *bruinhart* (*Vouacapoua americana*), a species that is characteristic for all upland forests on ferrallitic soils which were visited by me, is presumably due to the fact that the *bruinhart* trees have in this region been felled for centuries. The relatively large number of individuals belonging to the Burseraceae (cf. table XVIII) found in the 0.4-ha plot near Remontcourt, is characteristic for the forests of the whole region. Rosaceae were rather abundant in this plot (especially *zwarte foengoe*, *Licania micrantha* and *rode kwepie*, cf. *Licania* sp.), in contrast with other stands. Individuals of *Eschweilera* species were found in varying numbers. *Eschweilera labriculata*, which was a characteristic species in the lower storey of upland forests on lateritic soils in the Saramacca region, (cf.

table XVII), was not met with in the hill forests of the Bergendal region. *Sagotia racemosa* was fairly frequent, but other species which were characteristic for the under storeys in the upland forests on lateritic soils described in the foregoing sections (such as *Oxandra asbecki*), were very scarce in this upland forest. Locally, e.g. in the Remontcourt plot, *Paypayrola guianensis* (*tajahoedoe*) formed the greater part of the individuals of the lower storey species, but elsewhere this species was very rare, and, especially on the ferrite caps, it was replaced by *gauetrie* (*Matayba* sp.) and/or *Poecilanthe effusa* and *Lacistema grandifolium.* The latter species was found also on sandy loams in the Upper-Coesewijne region.

N of Bergendal the palm layer generally is formed by *paramakka* (*Astrocaryum paramaca*) and *boegroemakka* (*A. sciophilum*). This region is a part of the zone where the distributional area of *paramakka* (which forms the palm layer in the mesophytic lowland forest farther northwards) overlaps that of *boegroemakka,* which forms the palm layer South of Bergendal.

III.4.4. *Upland forest of the Voltz Mountain region*

In tables XVII, XVIII and XXII have been brought together some of the results of the enumerations that were made in two sample plots which were laid out in high forest in the vicinity of the Voltz Mnt., a granitic "inselberg" in the basin of the Upper-Coppename R., near the Raleigh Falls (about 20 km S of the bottom line of the map shown in fig. 1). Some details concerning the soil profiles of these two sites were given in II.5.

In the present study only the high forest on the deeply weathered, ferrosiallitic soils will be considered. The xeromorphous types of vegetation found on shallow soils, on bare granite, on laterite caps, etc. (cf. BAKKER 1957) will be discussed in due time in separate publications.

The high forest is characterized by the open appearance of the lower storeys, especially of the undergrowth. This fact is shown also by the comparatively low number of individuals in the smaller diameter classes (about 500 trees per ha in the diameter class 5–25 cm, which is approximately half the number found in the other types of forest studied). The irregular main canopy has a height of ca. 30 m, with emergent *Couratari* trees reaching a height of ca. 40 m. The ground flora is very sparse;locally it may consist largely of *Selaginella* (*S. radiata* and *S. epirrhizos*) or of a Polypodiacea, *Adiantum latifolium.* The relative scarcity of individuals in the lower storey and the undergrowth perhaps is due to the abundance of *boegroemakka* palms (*Astrocaryum sciophilum*), the leaves of which form a fairly continuous layer at ca. 8 m height.

Although the forest of the Voltz Mnt. region may offer a somewhat poorer appearance than the lowland rain forest in its optimal develop-

TABLE XXII

Density (number of individuals per ha) of a number of selected species in two sample plots of 0.3 ha each in upland rain-forest in the Voltz Mnt. region.

Scientific name and vernacular name	Fam.	Plot 1	Plot 2
UPPER- AND MIDDLE-STOREY SPECIES:		(number of trees $\geqq$ 25 cm d.b.h./ha)	
Swartzia schomburgkii (*zwarte boegoeboegoe*)	(Papil.)	8	3
Pterocarpus rohrii (*Hoogl. bébé*)	(Pail.)	4	6
Diplotropis purpurea (*zwarte kabbes*)	(Papil.)	—	3
Couratari stellata (*ingipipa*)	(Lecyth.)	8	3
Couratari pulchra (*ingipipa*)	(id.)	8	+
Eschweilera corrugata (*hl. oemanbarklak*)	(id.)	16	6
Eschweilera longipes (*hoogl. manbarklak*)	(id.)	+	+
Eschweilera poiteaui (*teteihoedoe*)	(id.)	4	—
Inga alba (*prokonie*)	(Mimos.)	4	13
Protium hostmannii (*tingimonnie*)	(Burs.)	+	10
Tetragastris altissima (*rode salie*)	(id.)	20	30
rode kwepie (cf. *Licania* sp.)	(Ros.)	4	3
Couepia versicolor (*hoogl. anaura*)	(id.)	8	6
Guarea sp. (*doifisirie*)	(Mel.)	24	—
7816	(Euph.)	+	13
Conceveiba guianensis	(id.)	+	3
Drypetes variabilis	(id.)	+	3
Ecclinusa guianensis (*batamballi*)	(Sapot.)	—	3
Bagassa tiliaefolia (*kauhoedoe*)	(Mor.)	4	3
7848	(id.)	+	6
Virola melinonii (*hoogl. baboen*)	(Myrist.)	+	6
Geissospermum sericeum (*birgiebita*)	(Apoc.)	4	—
Sterculia sp. (*okrohoedoe*)	(Sterc.)	4	6
Diospyros melinonii (*blakaoema*)	(Eben.)	4	+
7852 (*prasarahoedoe*)	(Nyct.)	4	+
Siparuna surinamensis	(Monim.)	4	+
LOWER-STOREY AND UNDERGROWTH SPECIES:		(number of trees $\geqq$ 5 cm d.b.h./ha)	
Coussarea paniculata (*boskoffie*)	(Rub.)	20	10
Eugenia cf. *patrisii* (*boskers*)	(Myrt.)	16	17
Bonafousia undulata (*mirkitikie*)	(Apoc.)	32	10
Talisia cf. *hemidasya* (*mankrappa*)	(Sapind.)	—	23
Trichilia surinamensis (*melisalie*)	(Mel.)	8	23
Amphirrhox surinamensis	(Viol.)	4	13
Astrocaryum sciophilum (*boegroemakka*)	(Palm.)	80	84
total number of trees $\geqq$ 25 cm d.b.h.		137	166
total number of trees $\geqq$ 5 cm d.b.h.		622	686
total number of trees of lower-storey species $\geqq$ 5 cm d.b.h.		200	210

+ means that only individuals of < 25 cm d.b.h. were observed.

ment, I think it still should be called "rain forest". The term "evergreen seasonal forest" would be misleading, as the water supply apparently meets the needs of the vegetation practically throughout the year.

As appears from the figures given in table XXII the composition of the forest shows significant differences from one place to another. The two sites which were chosen for the sample plots, were about 2 km apart. It does not seem very likely, that differences in edaphic factors are responsible for the differences found in floristic composition, as the soil in the two sites has developed from identical parent material and as the laboratory analyses show no significant differences.

But notwithstanding these differences between the two plots, they both show a number of features which are characteristic for the mesophytic forest on the granitic weathering products of this region; amongst other things this forest is marked by the relative abundance of *rode salie* (*Tetragastris altissima*) and of *ingipipa* (*Couratari pulchra* and *C. stellata*) in the upper storey, species that are also a characteristic feature in the lowland rain-forest on ferrosiallitic soils in the Suriname R.–Commewijne R. watershed (Mapane region). As shown in table XVII, the first species was absent in the other forest complexes described in this study. The same holds true for *blakaoema* (*Diospyros melinonii*) and for the lower storey species *boskoffie* (*Coussarea paniculata*), which are also characteristic associates in the Mapane forest. Conspicuous features of the forest are the *absence* of *wallaba* (*Eperua falcata*), of *basralokus* (*Dicorynia guianensis*) and *kopie* (*Goupia glabra*) in the upper storey, and of *tajahoedoe* (*Paypayrola guianensis*) in the lower storey. Locally *doifisirie* (*Guarea* sp., perhaps *G. guara* or *G. gomma*) is abundant (e.g. in the first sample plot); probably this Meliacea is a disturbance indicator, just like *kopie*. This is suggested by the fact that in sample plot 1 only trees of more than 25 cm d.b.h. were found.

Except *Swartzia schomburgkii* (*zwarte boegoeboegoe*) and *Amphirrhox surinamensis* no species were found which are characteristic for upland forests on ferrallitic soils of the schist-hill landscape.

III.5. LOWLAND RAIN-FOREST OF THE WAYOMBO REGION

In tables XVII and XVIII the results have been set out of the enumerations made in two small sample plots, 0.2 ha each. The location of the plots, S of the Wayombo R., is shown in fig. 1. Plot 1 was laid out in high forest on (silt) loam which belongs to the "moist soil phase" of the "Wayombo soil series" ("old clay-" or "Para-landscape") (cf. VAN DER EYK 1957, and VAN DER VOORDE 1957, chapt. 8, 3.5). Geologically the "Para landscape" belongs to the old coastal sediments of the "*Coropina series*" and it forms the transition to the "cover landscape" ("Zanderij series"). The second plot (2) was laid out some 5 km farther to the S, in high mesophytic forest on well-drained red sandy (clay) loam, which has developed from old basement rock and/or sediments of the "Zanderij series".

The very compact soil of plot 1 ("schol" soils of VAN DER EYK) is very moist throughout the year, owing to impeded drainage, as also appears from the greyish-yellow colour, mottling and the hogwallowed surface. During the dry season the soil may become very hard. Notwithstanding the bad structure, the total pore space in the upper 25 cm is not significantly lower than in other forest soils; rooting and animal activity (earth worms, etc.) are practically confined to the upper 20–30 cm. The soil is extremely poor in extractable plant nutrients, and the clay complex is strongly degraded as also appears from the very low values for the exchange capacity and total amount of exchangeable bases given by VAN DER VOORDE (1957).

The results of the enumerations in these two sample plots are given exclusively to illustrate the large difference in composition of this forest with that of the stands which were discussed in the foregoing sections. The forest of plot 1 is high forest which shows many signs of rather recent disturbance, presumably by shifting cultivation (cf. the high proportion of *Goupia glabra*, *Xylopia* spp., etc.). The even-aged, young population of *Goupia* (cf. IV.2) is a strong indication that disturbance took place rather recently. The forest of this region is of great economical importance because of the relative abundance of *basralokus* (*Dicorynia guianensis*), which locally may form nearly pure stands, in which it forms more than 50 % of the trees over 10 cm diam. Regeneration of this species is very abundant as shown by the diameter-class distribution (fig. 65). It is clear that this local gregariousness of a single species which, moreover, is of great commercial importance, is highly interesting from a silvicultural point of view. The situation is the more puzzling, because growth of *basralokus* appeared to be considerably slower on this site than in other stands where the species was less abundant (cf. IV.4 and fig. 67). In this region *basralokus* is not confined to the silty soils of the "Wayombo series", but it was found to attain local dominance on a great variety of soils, viz. e.g. on hydromorphous white cover sands together with *dakama* (*Dimorphandra conjugata*) and/or *wallaba* (*Eperua falcata*), and in luxuriant forest on well-drained red sandy (clay-)loam (such as in sample plot 2). The forest in which plot 1 was laid out was markedly lighter than mesophytic forest of e.g. the Mapane region (cf. fig. 18); it is not impossible that this stronger illumination favours regeneration of *basralokus* more than that of other species. Probably the latter (in co-operation with edaphic factors) also is the cause of the local abundance of *bosananas* (*Bromelia alta*) which in places may form an almost impenetrable thicket. In the forests of this region another species is found, viz. *moraboekea* (*Mora gonggrypii*) which may form rather small nearly pure stands, a feature which is very seldom met with in tropical forest on mesic sites. In this region the natural areas of the two Papilionaceae overlap: *Dicorynia guianensis* becomes very scarce W of the Nickerie R., whereas *Mora gonggrypii* is not found E of the Coppename R. It is interesting to note that two other Papilionaceae, viz. *Eperua falcata* and *Dimorphandra conjugata*, are found as single dominants over extensive areas (especially on white sands) in NW Suriname (just as in Br. Guiana).

A more detailed analysis of the composition of the rain forest of this region better can be postponed till more enumeration data have been collected. Yet, the data given in tables XVII and XVIII already show the large differences with the other stands which were studied.

Lecythidaceae only play a minor part; *Eschweilera* is represented by *E. glandulosa* (*manbarklak*), which is characteristic for some of the forests of the coastal plain and the river-margin forests. Leguminosae play a preponderant part in the canopy, together with Rosaceae (*Parinari campestris*) and Burseraceae (*tingiemonnie*, unidentified species of *Tetragastris* and/or *Protium*). Particularly the composition of the lower storey and the undergrowth differs strongly from that of the other forest types. *Erythroxylum amazonicum* is the most abundant dwarf-tree of the undergrowth; this species which is widely distributed in the hylaean forest, was not met with in any of the other stands. *Ambelania acida* (*batbati*) may be very abundant in the lower storey. A striking feature is the total absence of Violaceae in this storey (just as in the Upper-Coesewijne forest). A characteristic species of the upper storey of the Wayombo forest, viz. *Antonia ovata* (*likahoedoe*), happened to be scarce in plot 1.

The striking similarities between the two plots which were laid out in neighbouring stands on very different sites, illustrate a phenomenon to which attention was drawn repeatedly in the foregoing sections. Although the soil of plot 2 is similar to that of the well-drained sandy loams in the Mapane and Upper-Coesewijne region, the floristic composition of the forest shows stronger affinities to that of the neighbouring forest on a very different site.

III.6. COMPARISON WITH THE FLORISTIC COMPOSITION OF RAIN FORESTS IN NEIGHBOURING COUNTRIES

It has already been mentioned that the structure of the mesophytic lowland forests of central Suriname closely resembles that of the stands of rain forest on similar sites in British Guiana (DAVIS *et al.* 1933, 1934; FANSHAWE 1952, 1954; RICHARDS 1952).

The mixed forest of the low hilly land of the Moraballi Cr. region, some 350 km W of the lowland forest areas described in the present study, occurs on soils which presumably are comparable to the soils with medium texture, found in the Mapane and the Upper-Coesewijne region. Comparison of the composition of the 1½-ha sample plot in the mixed forest of Moraballi Cr. (DAVIS *et al.* 1934, table IV) with that of the sample plots in the Suriname mesophytic lowland forest, show many points of resemblance, e.g. in the large number of dominants; although there is never a single dominant on the mesic sites, there is – just as in the Suriname mesophytic forest – a small group of leading canopy species, belonging to a few genera only, and which together make out more than one half of the canopy trees. For instance, in the *mixed forest* sample plot of the Moraballi Creek, there were 330 trees of 20 cm d.b.h. and over, and 178 of them belonged to 6 species and to 4 genera (*Licania laxiflora, L. venosa,* *Eschweilera sagotiana*, *E. decolorans*, *Pentaclethra macroloba*, *Ocotea rodiaei*). As shown by the tables given in the present study, trees belonging to *Eschweilera* species also reach a numerical preponderance in various stands in the Suriname mesophytic forests (and, it may be added, elsewhere in the hylaean forest too). However, the *Eschweilera* trees which prove to be comparatively abundant in the majority of the Br. Guiana lowland forests on mesic sites (the "*Eschweilera-Licania* association" of FANSHAWE), belong to species (e.g. *E. sagotiana*, *E. decolorans*, *E. confertiflora*, *E.* sp. nov., etc.) that are absent or very rare in the Suriname forest. In this connection it is interesting to note that in the Br. Guiana forests *Eschweilera* disappears on submesic sites, viz. in the ecotone to more or less xeromorphous types; e.g. in what FANSHAWE called the "*Goupia glabra* faciation" found on the rather excessively drained cover-sands of the Corantijn-Canje R. region, i.e. on soils that are similar to the lightest soils of the Upper-Coesewijne region in Suriname, where the forest also showed a conspicuous scarcity of *Eschweilera* trees (cf. e.g. tables XVII and XVIII).

Another genus which is well represented in nearly every faciation distinguished by FANSHAWE in the Br. Guiana lowland rain forest, viz. *Licania*, is seldom abundant in the Suriname mesophytic lowland forests of the areas studied, where other Rosaceae too seldom attain numerical preponderance, except in some sub-mesophytic forests, such as those on the cover-soils of the Upper-Coesewijne region (cf. plot 5 in tables XVII and XVIII) and in the Mapane region (cf. plot L: *Couepia versicolor*).

Although the majority of the genera which are listed by DAVIS, RICHARDS and FANSHAWE for the Br. Guiana sample plots in mesophytic forest, are also met with in the Suriname plots, many species are different, and several leading species of the Br. Guiana rain forest communities are apparently endemic in Br. Guiana (DAVIS 1941). Except for the numerical preponderance of *Eschweilera*, which apparently is a common feature in many stands of the hylaean forest (as shown also by the sample plots in the Brazilian rain forest which will be discussed below), the assemblages of leading dominants in the sociological units which were distinguished by FANSHAWE in the lowland rain forest of Br. Guiana, differ considerably from those that were found in the Suriname sample plots discussed in this study. In the areas of the Suriname forest investigated during the present study, none of the sociological units of FANSHAWE were found, although various species which attain numerical preponderance in the Suriname sample plots, also occur in Br. Guiana rain forests, and reversily.

This may partly be due to differences in climate, as the total amount and the distribution of the rainfall in some of the lowland stations of Br. Guiana appear to differ considerably from the total amount and the distribution in N Suriname. Partly it must be due to historical factors; this may be concluded from the fact that the flora of the two countries shows many differences in taxonomic composition. For instance, in a

5.2-acre sample plot situated in the NW district in a stand of the "*Alexa imperatricis* faciation" of the "*Eschweilera-Licania* association" and occurring on soils that are of common occurrence in Suriname too, 52 canopy species (over 10 cm d.b.h.) were listed by FANSHAWE (1954), and of these 52 only about 25 were collected in corresponding sites in Suriname (although 51 of the species belong to genera which are also common in Suriname). For the Moraballi Cr. sample plot in mixed forest, of the 56 identified species with individuals over 10 cm diam. listed by DAVIS and RICHARDS, 33 are known from Suriname (54 of the species belong to genera which are common to the two countries). For a 2-ha sample plot in, what FANSHAWE called the "*Goupia glabra* facies of evergreen seasonal forest", 53 canopy species were listed, of which 25 were collected in Suriname too. The composition of this last sample plot, which was laid out on brown sand in the Corantijn-Canje R. area, i.e. near the Suriname border, shows some resemblance with that of stands of sub-mesophytic/sub-xeromorphous forest (*high savanna-forest*) found on similar sites, viz. on *non-bleached cover sands*, in W Suriname. (The latter are not discussed in the present study).

Although presumably none of the specific combinations which characterize the sociological units distinguished by FANSHAWE in the rain forest in Br. Guiana, are met with in the lowland rain forest of central and E Suriname, it should be noted that among the vegetation types which are found in more extreme habitats, viz. on xeric and hydromorphic sites, there are closer affinities between the two countries; for instance both in Br. Guiana and in Suriname *wallaba* (*Eperua falcata*) and *dakama* (*Dimorphandra conjugata*) attain single-dominance on excessively drained white sands (although the associated species may differ), whereas a number of communities which were distinguished by FANSHAWE in the marsh forests and swamp forests, are distinguishable in the Suriname coastal plain too (cf. LINDEMAN 1953).

123 of the 132 species of more than 8 m height listed by CAIN *et al.* (1956) for a 2-ha sample plot in the apparently primeval *terra firme* rain forest of Mucambo (near Belém, Pará), are known from Suriname. Only 5 of the species of the Mucambo plot belonged to genera which are unknown from Suriname. 58 species were noted also in the 5.6-ha plot in mesophytic lowland forest in the Suriname-Commewijne R. region (plot 1 of the Mapane area), and 122 of the 132 species of the Mucambo plot belonged to genera which occurred in the Mapane plot too. Notwithstanding the ca. 1000 km distance between the two forests, and the differences in the local floras the resemblance in floristic composition is apparent, and to my opinion, is greater than that between the Mapane forest and the majority of the Br. Guiana lowland rain forests. This resemblance becomes particularly striking when the leading species of the two sample plots are arranged by families; *the Brazilian plot shows among the canopy trees a numerical preponderance of Lecythidaceae, Burseraceae, Vochysiaceae,*

Sapotaceae, and Myristicaceae, families which also rank high in the Mapane forest; the only exception being the Vochysiaceae, which rank high in the Mucambo plot because of the abundance of *Vochysia guianensis.* The latter species (*wiswis-kwarrie*) is only occasionally met with in the Suriname forests. The family of the Lecythidaceae owes its preponderance in the first place to the relative abundance of *Eschweilera odora,* a species which also belongs to the leading canopy species in the Mapane forest. The numerical preponderance of the Burseraceae in the Mucambo plot is due to the abundance of canopy species of *Protium* and *Trattinickia,* but these species are unknown in Suriname.

An arrangement by families of the canopy trees of the mixed forest plot in the Moraballi Cr. region (Br. Guiana) according to the density of trees with a d.b.h. of more than 25 cm (estimated after interpolation of the diameter-class distributions given by DAVIS and RICHARDS), shows the following order: 1. Lecythidaceae (ca. 20 trees over 25 cm d.b.h./ha); 2. Leguminosae (ca. 15); 3. Rosaceae (ca. 15); 4. Lauraceae (ca. 10); 5. Sapotaceae (ca. 4). These 5 families account for more than 2/3 of the trees with a diameter of more than 25 cm. Comparison with the data given in table XVIII clearly shows the difference with the Mapane forest on mesic sites (plot 1); if we leave the preponderance of Lecythidaceae (*Eschweilera*) in the Moraballi Cr. plot out of consideration, the list of the leading families shows some resemblance with that found in the Upper-Coesewijne forest on cover soils (plot 5), where Leguminosae, Rosaceae and Lauraceae also ranked high. No details are given of the soil of the Brazilian plot; that of the Moraballi Cr. plot in mixed forest is a yellowish-brown light loam, of which DAVIS and RICHARDS suppose that it has been derived from the underlying granite and/or gneiss.

The *species/area curve* of the Mucambo plot is significantly steeper than those of the two Suriname plots set out in fig. 62. Perhaps the greater floristic richness of the Brazilian plot is only apparent, due to a greater thoroughness of the field identifications carried out by CAIN and co-workers.

In fig. 62 the species/area curve has been set out also for another sample plot in the Amazonian rain forest (Castanhal); it closely resembles the trend lines for the Suriname sample plots.

The Castanhal sample plot (3.5 ha) was described by MURÇA PIRES *et al.* (1953). It was virgin, luxuriant *terra firme* forest. Just as in the Mucambo plot, the Suriname plots and the majority of the Br. Guiana communities, the family Leguminosae was represented by the largest number of species (about 25 spp. with a diameter of more than 20 cm). The next most diversified family of canopy trees was that of the Sapotaceae with about 20 species with a diam. of more than 20 cm on 3.5 ha.

According to the number of trees per unit area the leading families are: 1. Lecythidaceae (ca. 50 trees with a diam. of over 20 cm/ha); 2. Sapotaceae (ca. 30); 3. Leguminosae (ca. 26); 4. Burseraceae (ca. 17). This strong

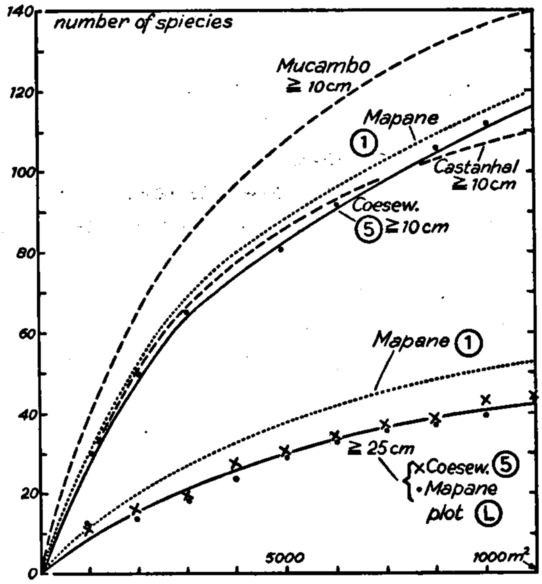


Fig. 62. Species/area curves for 2 diameter classes in samples of mesophytic forest in the Upper-Coesewijne region (plot 5: solid lines) and the Mapane region (part of plot 1: dotted lines). For plot L in the Mapane region (dots) the curve for the trees of 25 cm diam. and over is nearly identical with that of the Upper-Coesewijne region (crosses) and the two curves are represented by one line. The curves for samples of Amazonian *terra firme* forest in the region of Mucambo (Belém) and Castanhal are taken from CAIN *et al.* (1956) and MURÇA PIRES *et al.* (1953).

numerical preponderance of Sapotaceae was not met with in the Suriname forests. Among the commoner genera and species in the Castanhal plot are *Eschweilera krukovii* (ca. 30 trees of over 20 cm diam./ha), *E. odora* (ca. 15), *Protium* (ca. 17), *Pouteria* (ca. 15), *Sterculia* sp.?, *Micropholis guyanensis* and *Vouacapoua americana*. The commonest lower-storey tree proved to be *Rinorea passourea*; in this connection it is interesting to note that one or more members of the family Violaceae (such as *Rinorea* and *Paypayrola* spp.) are often relatively abundant in the lower storey of the hylaean forest.

III.7. DISCUSSION

The enumerations were made in the first place to obtain some idea of the floristic composition of stands on different sites, and also of the order of magnitude of the variation in composition, both over small and over larger distances. As a matter of course, the material which was collected, is much too scanty to justify an attempt at even a preliminary classification of the forests of the region studied. Such an attempt would be premature before more detailed analyses are made of this region. Moreover, such a classification would certainly have to be modified when sociological studies are extended over a much wider area, as is intended for the near future.

The preliminary studies reveal the need for classification, if it were only for the sake of convenience. Moreover, the forests differ very strongly in the number of individuals by which commercially important species are represented, and accordingly a proper classification of the forests into more or less homogeneous sociological units (*forest types*) necessarily would be the first step towards practising scientific forestry. Silvicultural techniques can be given a scientific status only when they are viewed in relation to such ecological units.

The present studies were carried out in stands on mesic sites belonging to the same "floristic" (e.g. RAUP 1947) or "natural" area (CAIN 1947), which means that every species which was encountered in the sample plots has a natural range which is greater than the region under consideration. In other words, all stands had equal *chances* of containing the same species. Yet, as was clearly demonstrated in the foregoing sections, the floristic composition of the forests which were sampled showed marked differences.

Tables XVII and XVIII are a good illustration of the results of some of the enumerations, in that they demonstrate – for a few stands only – the complexity of the floristic composition with which the sociologist is confronted. It should, moreover, be realized that these tables are confined to a few tree species which showed numerical importance in one or more of the stands. The complete lists, of which one has been reproduced in table XVI, are still more discouraging, as they show an endless display of variation, in which at first sight little or no order can be discerned. The heterogeneity of what is supposed to be a single stand on homogeneous (?) soil, as this appears from the tables in which the results of enumerations in neighbouring sample plots are given (e.g. tables XIX, XX, XXI and XXII), adds still further to the difficulties with which the sociologist is faced. It seems as if each of the sample plots is an example of a merging or continuously varying series with all possible combinations and permutations among the tree species.

Each of the stands which was described in the foregoing sections showed a different group of *leading species* and a very large number of associates which never become codominant. As was shown in the foregoing sections, each of the stands of mesophytic forest which was studied, showed a (relatively small) group of such leading (i.e. numerically preponderant) tree species, which together formed the greater part of the total number of individuals per unit area. Our preliminary study of the mesophytic forest in Suriname indicates that it is possible to distinguish geographic regions, within which the forest on the mesic sites shows approximately the same group of leading species, although within such a region the relative numerical importance of each of the leading species shows considerable fluctuations from one place to another (because, e.g., of differences in site or of the patchy distribution which is characteristic for many species of the tropical forest, cf. IV.4). Moreover, within such a general area *association segregates* are distinguishable (sociations?) which are characterized for instance by:

(a) the scarcity or even absence of one or more of the characteristic leading species (e.g. *Vouacapoua americana* in the upland mesophytic forest on ferrallitic soils, cf. tables XVII and XX), or

(b) the local abundance of a species which is absent or relatively scarce in the greater part of the area; such *peripheral association segregates* especially are found when the environment becomes less favourable, such as, e.g., near the ecotone to forest on sub-mesic or sub-xeric sites; examples are *Vouacapoua americana* stands in the Mapane region (cf. fig. 46, and sample plots 3, 4 and 5 in section III.2.2 and in table XVII); the aggregation of *Eperua falcata* (both on sub-xeric and sub-hydric sites!) and of *Qualea rosea* (cf. sample plot 2 in III.2.2 and in table XVII), *Vochysia* species and *Couepia versicolor* (cf. sample plot L in III.2.2) on sub-mesic sites on excessively drained sandy soils in the Mapane forest.

Notwithstanding these heterogeneities in the composition of the forest the *average* floristic composition remains more or less the same in such a geographic region and differs sufficiently from that in other regions, so that the various parts of such a region may be regarded as belonging to one phytosociological unit, although the latter has as yet somewhat arbitrary boundaries. In this connection reference may be made to the striking differences between the mesophytic forests of the Upper-Coesewijne region and those of the Suriname R.-Commewijne R. region (Mapane area) which are discussed in III.3.3.

The extent to which the differences in the soil are responsible for these differences in floristic composition between the two last-named regions is uncertain. The existence also of differences in *history* was discussed in the foregoing sections. For the forests on the ferrallitic soils which were discussed in III.4, it is highly probable that their composition—at least partly—is due to site factors.

Although the results of the preliminary studies presented in the foregoing sections are too few to serve as proof for such a hypothesis, it seems unlikely that the mesophytic forests of Suriname are chance aggregates in an amorphous collection of plants in which no pattern is discernible, and that the stands of trees are chance combinations of species without relation to their environment, so that unlimited variations, combinations and permutations (CAIN 1947) would be possible. Such a situation also was denied for the complicated continua of deciduous forests in N America (e.g. CURTIS *et al.* 1951).

Although I am convinced that some sort of classification of the types of mesophytic forests found in Suriname is necessary—if it were only for the sake of convenience, both for the silviculturist and the botanist—, and also that it will be possible after much more data have been collected, the *vegetational continuity* (which is the general condition also in the mixed tropical forest) will render any classification of the forests highly arbitrary.

A grouping dependent on man's choice of what constitutes sufficient similarity and difference in floristic composition and environment in the Suriname forest inevitably will be a highly artificial one.

Indeed the boundaries between different communities can only be distinct when several species of each one do not occur as important members in the others. Although they are still scanty, the results of the preliminary studies and the general observations which I have made in various forests in N. Suriname, seem to indicate that in this region such a *discrete* grouping (association) of species does not occur within the forest on mesic sites. Even the boundaries between the mesophytic forest (rain forest) formation and the wet and dry formation series are far from distinct. There are many species which may be characteristic for one of these formation series and also are found as minor associates in mesophytic forest. That which passes best as an *association* in the Suriname forest is a series of stands in a local area where there is an overlap of the areas of a series of species. If so, this situation would closely resemble that which was described for the mixed eastern hardwood forests in the U.S.A. (e.g. WHITTAKER 1957). In fact, I think that the extensive hylaean forests, where *man-made discontinuities* are still of rather rare occurrence, form the best illustration of the principle of *species individuality* (i.e., that each species responds uniquely to external factors and enters the community as an independent member) and of the principle of *community continuity* (i.e. that the composition of the plant cover changes continuously in space), which ideas are familiar as GLEASON's (e.g. 1926) "*individualistic concept* of the plant association".

The preliminary sociological studies in the mesophytic forest of N Suriname have scarcely brought us nearer to the crux of the matter, i.e., to the methodology upon which some sort of classification – artificial as though it may be – should be based. The enormous floristic diversity forms a practical impediment to the tabulation of species and the establishing of diagnostic species groups into a single synthesis table, which would be the first thing required by the standard methodology of the Zürich-Montpellier school of phytosociology. There are other serious difficulties attached to an application of its way of analysis (on the assumption that the fundamental ideas underlying the concepts of this school would be applicable to the mixed tropical forest). There is, for instance, the practical impossibility to make ocular estimates of cover of the tree species. A more serious difficulty is the technical problem of finding characteristic species of high fidelity, as the latter usually are rather rare species. Although it might be possible to ascertain the presence of a very sparsely distributed species (and many tree species in mixed tropical forest belong to this category!), it is in an extensive stand of tropical forest practically impossible to establish the *absence* of such a species. Moreover, fidelity can be determined only if a sufficient wide array of different plant communities has been sampled and compared, and it will take a long time before this condition will be fulfilled in the extensive forests of Suriname. The results obtained with standard Z.-M. methodology in W- and Central-African forests (EMBERGER 1950, EMBERGER *et al.* 1950, HEIM 1950, MANGENOT 1950 a+b, GERMAIN *et al.* 1956) suggest that such difficulties perhaps have not been encountered in the vegetation types that were studied in that continent, although their conclusions have been bitterly contested (e.g. CHEVALIER 1953, AUBRÉVILLE 1950–'51).

Although classifications based on *dominance* have often been regarded as unsatisfactory, for a first, rough characterization of the composition of the mesophytic forest types in Suriname *abundance* (relative number of individuals above a certain diameter per unit area, i.e., *density* according to N-American ecologists) might prove to be the best single expression indicating the *relative importance* for each species. Hence, in my opinion, for a preliminary classification of these forest types should be chosen the *leading* species of the various strata which show their preference for a certain community by a comparatively high degree of numerical abundance.

As was shown in the foregoing sections, each of the stands which was studied, was characterized by such a group of *leading* (i.e. numerically preponderant) tree species, which together formed the greater part of the total number of individuals (cf. also table XVII).

Such a classification, which is based primarily on *dominance* (in so far as this term can be used in connection with the mixed rain-forest!) was also used succesfully by FANSHAWE (1952) for the forests of Br. Guiana.

Further study will almost certainly reveal that among these *leading* species there are many indifferents of no or small diagnostic value, whereas among the species which (owing to their specific idiosyncracies) are unable to achieve an ecological success which reveals itself in numerical preponderance, there may be some which actually are of much greater diagnostic value. Therefore, great caution should be observed in the choice of species for classificatory purposes. *Goupia glabra*, for instance, may attain a high degree of abundance in some stands (cf. table XVII), and HEINSDIJK (1953) accordingly distinguished a "*Goupia* type" within his "*Eschweilera-Dicorynia* association"; but, as will be discussed in detail in IV.2, this species is a strong light-demander and as such merely a disturbance indicator and highly indifferent to the kind of soil: in fact it only marks a *successional* stage.

Another question is what criterion should be used for the determination of the relative importance of a species in a certain stand. In my opinion, for reasons which were discussed on p. 159–161, the characterization of the relative importance of a species at least at the present stage of investigations – should be based upon a simple analytical character like the *number* of (established) individuals over some complex index. Such an index was used e.g., by CAIN *et al.* (1956) for enumerations in the Brazilian rain forest. Such a combined *importance index* might give undue weight to basal area or to some other factor concerned with the size, bulk, or space-demands of a species, i.e., to characters which are to be regarded primarily as specific ones.

As a matter of fact, abundance should be calculated using different lower diameter limits for the various species groups (*socions*) of the forest. As was mentioned in III.1, for the species of the upper storeys a lower limit of 25 cm d.b.h. was proposed (rather arbitrarily!) whereas for the lower storey and undergrowth species a lower limit of 5 and 2 cm, respectively was chosen. Presumably it will appear that the 25 cm threshold is too high for the first group, and that individuals of these species might be considered already as *established* if their crowns have reached the lower storey, which would correspond to an *average* diameter of ca. 10 cm.

Perhaps in the future, in a more advanced stage of the phytosociological studies of the Suriname forests, and when more intensive forest management requires finer methods for classification, it will be necessary to replace a single measure of relative importance by a more complex importance value which is weighted towards density, but which also takes account of one or more other quantitative expressions of *ecological success.*

It is evident that the data supplied by the preliminary studies which were represented in the foregoing sections are by far too scanty to allow any discussion on the very important problem of the *size of an adequate sample* and the *method of sampling* the Suriname mesophytic forest, although it is true that the rather nebulous concept of the *minimal area* of the association in mixed tropical forest has been discussed on the basis of still more limited data (e.g. MIJER DREES 1954). It will be clear that it would be next to useless to discuss the problem of adequate sampling in the Suriname forest before at least a rough idea has been gained about the phytosociological classification, the boundaries of the communities (if any are distinguishable!) and the characteristics distinguishing them from each other. The criterion of what should be called an *adequate sample* depends on the purpose intended with the sampling done. Let us assume for the sake of argument that the mesophytic forest of the Suriname R.-Commewijne R. area (of which the Mapane region forms a part) represents one sociologic unit, which is characterized by the group of leading species consisting of *Tetragastris altissima, Couratari stellata, Eschweilera amara* and/or *E. odora, Iryanthera sagotiana, Coussarea paniculata, Cheiloclinium cognatum, Paypayrola guianensis* and *Bonafousia undulata,* regardless of their order of numerical importance. In that case it appears from our data that a *sample plot of one hectare*—provided that it is laid out adequately—in which all individuals over 10 cm diam. are counted (and which is sub-sampled at 10 % for the undergrowth species over 2 cm diam.), may be sufficient to establish whether a certain stand belongs to this community or not. The same holds true for the forest of the Upper-Coesewijne region, where a one-ha plot (5) was quite sufficient to reveal the preponderance of the group of leading species which are characteristic for the forest region, and the scarcety of other species which are characteristic for other areas! (compare in table XVII sample plot 5 with the 2 % enumeration in compartments 859 + 860).

If, on the other hand, an *accurate* measurement of the relative abundance of a larger number of tree species would be required, the number of quadrats for even reasonable accuracy might become impossibly great in a tropical rain forest with its very large number of species per unit area, as may appear from the statistical studies of e.g. COTTAM *et al.* (1953). It should be noted, moreover, that the calculations of these authors are based on *random* populations, whereas the majority of the tree species in tropical rain forest show non-random (i.e. aggregated) distribution, which adds still further to the difficulties connected with sampling such forests for phytosociological purposes.

It was largely because of this perplexing heterogeneity and patchy distribution in mixed tropical forests that VAN STEENIS (1958 a) recently stressed the impossibility of applying "temperate methods" of analysis to tropical vegetation types in general. The heterogeneity of tropical rain forest also was established by various other students of this formation (e.g. JONES 1955–'56), although EMBERGER (1954) in vain tried to prove the contrary by using RAUNKIAER's quadrat-frequency curve as a test for homogeneity.

It is certain that in the Suriname mesophytic forest a community cannot be characterized by means of the results of enumerations of the trees in only one very small quadrat of only some 200 m² or less in extent, as was asserted positively by some phytosociologists of the French-Swiss school with reference to W-African rain forest (e.g. EMBERGER 1950, MANGENOT 1949, HEIM 1949). It should be noted, however, that these students counted *all* individuals (including seedlings, lianas, epiphytes, etc.). Perhaps a characterization of communities in Suriname mesophytic forest also will prove to be possible if the small species in the undergrowth also are included in the phytosociologic studies. Indeed, there are some indications that in the Suriname forest the undergrowth may provide better indicators than the upper storeys.

It is clear, therefore, that in the extended collecting of phyto-sociological data, the necessity of which was stressed in previous pages, adequate account of the undergrowth should be taken.

PART IV

REGENERATION OF THE FOREST

IV.1. INTRODUCTION

One of the aims of the ecological studies carried out in the years 1955–1957 was to find a base for investigations concerning some aspects of the regeneration of the mesophytic forest under natural as well as under controlled conditions. The regeneration studies which were started during these years, are preliminary to a research program on a larger scale, which will be carried out in the next future in order to obtain part of the scientific background needed for forest management and for the application of silvicultural techniques on a commercial scale.

The process of natural regeneration in tropical rain forest is exceedingly complex because of the enormous wealth of species and the complexity of the structure and of the floristic composition of the forest, both in the vertical and in the horizontal plane. It is very unlikely that the ecological study of the Suriname rain forest will ever provide the silviculturist with more than some general information; the large number of local communities and the manysided interrelations between the numerous associates found in the latter as well as between them and the environmental factors, are by far too complex to allow an exact *prediction* of the effects of far-reaching regeneration operations.

As was pointed out by RICHARDS (1952, p. 40), some of the first problems which suggest themselves to the rain-forest ecologist who is interested in regeneration, are: What is the normal *age-class* representation of the leading dominants, and how does the *growth rate* of the trees vary during the successional stages of development? At what stages does the heaviest *mortality* (and hence the most intensive natural selection) occur? To these questions may be added some of those which were recently put by JONES (1956): To what extent are the species regenerating and reproducing a forest, which is of substantially the same form and composition as those that now exist? Are the emergents regenerating periodically or continuously? How do the emergents regenerate and attain their position?

Some of these problems are to be seen in connection with a theory which has become known as AUBRÉVILLE's "*Mosaic* or *Cyclic theory*" of regeneration. On the base of this theory an area of mixed forest may be regarded as a kind of mosaic, groups of species succeeding each other periodically in every part of it. How attractive this kaleidoscopic concept may look a first sight, it was doubted already by RICHARDS (1952, p. 52), that it can be applied to the Guiana mesophytic forest. Moreover, as was pointed out by JONES (1955), AUBRÉVILLE's exposition is accompanied by scarcely any indication with regard to the extent of the observations on which it was based, nor of the size of the individual patches in the supposed mosaic. As far as Aubréville's views are based on the observation that there is a great deficiency of medium-sized trees among the canopy species (a well-known feature, which apparently is of general occurrence in the majority of African rain forests), they rather seem to indicate that the stands which he studied, did not represent normally developed climax communities. Nevertheless, Aubréville's repeated insistence (c.q. AUBRÉVILLE 1950–'51) upon the important role which *chance* plays in regeneration and, accordingly, in the floristic composition of the rain forest, deserves serious consideration. Moreover, it carries a strong warning against an uncritical application of European phytosociological methods in the irregular patchwork of the tropical rain forest.

During the preliminary regeneration studies in the Suriname rain forest in the first place attention was paid to the *diameter-class representation* of the trees, especially of the canopy species (emergents), because an appreciation of the fundamental laws governing balanced uneven-aged crops which may be regarded as capable of giving sustained yields in perpetuity (the class to which the majority of the mesophytic climax forests in Suriname belong), was thought to be fundamental for an efficient working plan. As will be discussed in IV.2, the diameter-class distribution of most leading emergents in the areas studied differs from that of many of the principal emergent species in the African rain forests. The latter show a conspicuous deficiency in the middle and/or smaller girth classes.

For a number of "economics" additional *growth measurements* were made over a period of two years. The results of these careful measurements also allow a rough conversion of the size-class into *age-class distributions.*

Unfortunately the available time did not allow a study of one of the fundamental problems mentioned above, viz. that of the mortality of the trees during the various stages of development and the establishment of the suppression period. Because the syn-ecological concept of succession is an important guiding principle in the successful application and control of any natural regeneration technique, permanent quadrats were laid out in several openings in the mesophytic forest of the Mapane region (Suriname–R. Commewijne R. area). The results of the microclimatic observations made in one of the extensive clearings, have been given in part I.

IV.2. DIAMETER-CLASS REPRESENTATION OF TREES

The following table gives some typical examples of the manner in which the representatives of the more important species in the mesophytic forest of the Suriname R.–Commewijne R. area are distributed over the various size-classes.

TABLE XXIII

Diameter-class representations of a number of common canopy species in the Mapane forest (sample plot 1, cf. III.2.2). The figures give the number of trees in an area of 5.6 ha.

	Average number under 2 m high *)	Diameter classes in cm									
		<5 >2 m high	5– 15	15– 25	25– 35	35– 45	45– 55	55– 65	65– 75	75– 85	>85
Qualea rosea		81	61	11	5	1	1	1	1	1	4
Dicorynia guianensis	5500	14	9	3	1	—	1	1	1	1	—
Iryanthera sagotiana		70	77	54	28	1	—	—	—	—	—
Guarea sp.		171	50	11	7	2	1	3	2	—	—
Parinari campestris		11	6	3	2	1	—	—	—	—	—
Chaetocarpus schomburgkianus .		73	30	9	7	6	3	1	—	—	—
Tabebuia serratifolia	900	3	1	—	—	2	—	—	—	2	—
Jacaranda copaia		11	6	4	—	3	1	1	—	—	—
Couepia versicolor		120	80	22	9	6	1	—	—	—	—
Virola melinonii		85	51	15	11	6	1	—	—	—	—
Eschweilera odora		200	169	76	38	6	3	1	—	—	—
Eschweilera corrugata.		66	80	32	7	1	1	—	—	—	—
Couratari stellata		99	53	10	2	4	6	3	2	1	8
Goupia glabra	**6**	**1**	**4**	—	—	**1**	**1**	**4**	**2**	**2**	**7**
Carapa guianensis	650	54	44	10	1	3	3	—	—	—	—
Piptadenia suaveolens		16	12	5	1	4	1	2	1	2	—
Ocotea sp. (*wanapisie*)	1350	80	22	—	—	1	2	3	1	3	1
Eperua falcata		13	28	11	3	3	2	3	—	—	—
Vochysia guianensis	6000	7	3	3	—	1	—	—	—	—	1
Vochysia tomentosa		1	1	—	1	—	—	—	—	—	3
Tetragastris altissima		235	135	26	11	15	14	6	2	1	—
Ocotea rubra	700	17	7	2	—	1	2	—	—	—	1

*) The seedlings and saplings of this size-class were counted for a few species in strips which together were equal to one-tenth of the total area, and the figure obtained was multiplied by 10.

The upper-storey species of the Mapane forest which have not been recorded in table XXIII, as well as the middle- and lower-storey species, show a size-class distribution similar to that of the species which are given in this table. The great majority of the species show a *normal* distribution, which is to say that the number of individuals decreases logarithmically as the diameter increases. This kind of curve is typical, in mixed stands of primary forest, of species which are (comparatively!) shade-tolerant, and which are regenerating rather continuously in the climax forest. Only a few species, of which *kopie* (*Goupia glabra*) was included in table XXIII, clearly show another behaviour. Seeds of such strongly *light-demanding* species (to which also belong *soemaroepa, Simarouba amara,* and *pientokopie, Laetia procera*), apparently require a considerable amount of light for *germination,* and these species show some other features of the *secondary forest species* too (such as rapid growth, especially during the first stages of development).

For some other species viz. *Jacaranda copaia* (*goebaja*) and *Tabebuia serratifolia* (*groenhart*) the data given in table XXIII might suggest a somewhat abnormal trend of the diameter-class distribution, but the sample upon which the figures are based, is too small to warrant any definite conclusion. Seedlings of *goebaja* are often rather abundant in small openings and this species perhaps is intermediate between the strongly light-demanding and the more shade-tolerant species. Seedlings of the other Bignoniacea, *groenhart*, are more frequent under a closed canopy, at least in the vicinity of seed-bearers.

For *wanapisie* (*Ocotea* sp.) the absence of trees in the classes 15–35 cm in table XXIII presumably is accidental; the enumeration in the neighbouring 50-ha sample plot (cf. fig. 63) showed that the number of individuals regularly decreased with increasing diameter.

In fig. 63 for a number of commercially important species the results have been set out of the enumerations which were performed in the 50-ha experimental plot in the Mapane forest. The diagrams of *krappa*, *rode salie*, *birgie-gronfoeloe*, *wanapisie* and *basralokus* agree with those obtained from the majority of the upper-storey species in the primary rain forest in N Suriname, in that they show a regular decrease of the number of trees with increasing diameter. The irregularity in the frequency distribution of *basralokus* may be regarded as accidental.

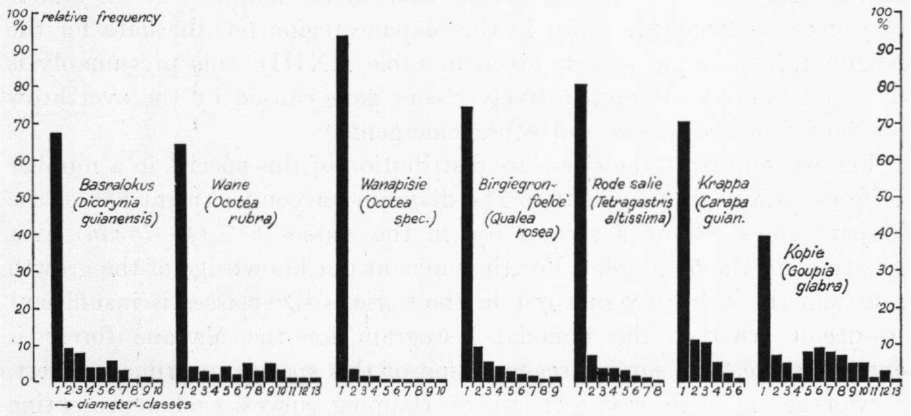


Fig. 63. Diameter-class representation of 7 canopy species in a 50-ha sample plot in the Mapane region (i.e. the area shown in fig. 50). Diameter class 1: 2–14½ cm d.b.h., class 2: 15–24½ cm, class 3: 25–34½ cm, etc. For *wana* and *kopie* see also figs. 64 and 65.

Two species, viz. *wana* (*Ocotea rubra*) and *kopie* (*Goupia glabra*), show a different frequency distribution of the diameter classes. In the 50-ha plot in the Mapane forest *wana* shows a marked deficiency in the middle classes, which appears more clearly in the diagram for the diameters from

25 cm upwards given in fig. 65. Yet, this frequency distribution is not representative for the whole area; the diagram for compartment 836 (in the centre of which the 50-ha plot was laid out) given in the same figure, shows a different form, though it is also more or less irregular in that it shows a secondary maximum in class 6 (55–65 cm diam.) (classes 1–2 have been left out in this figure). *Wana* shows a similar bi- or multimodal frequency distribution in other compartments in the Suriname-Commewijne R. region too.

These peculiarities in the size-class distributions, which are not explained by the growth curves (cf. IV.4), may perhaps be connected with the occurrence of years during which climatological and biological conditions for germination and/or the first growth of the seedlings were unusually favourable for this species. *Wana* trees fruit rather profusely every two years, but only a very small percentage (much less than 1 %) of the seeds were seen to germinate during the period of observation. These irregularities in the size-class distribution were not found in the Upper-Coesewijne region (cf. fig. 65: compartments 859 and 860), where this commercially important species belongs to the leading dominants.

In the foregoing already mention was made of the size-class distribution of the *strongly light-demanding species* such as *kopie* (*Goupia glabra*) and *soemaroepa* (*Simarouba amara*) which in primary forest generally show a marked deficiency in the lower and/or middle size-classes. The smaller size-classes (especially 2–5 cm in diam.) of *kopie* in the 50-ha plot in the Mapane forest are better represented than in the majority of the stands of primary mesophytic forest in the Mapane region (cf. the data for the neighbouring sample plot 1, given in table XXIII); this presumably is due to a number of comparatively recent gaps caused by the overthrow of giant *Couratari* trees and other emergents.

Fig. 64 represents the size-class distribution of this species in a number of forest stands in N Suriname. The diagram for compartment 836 of the Mapane forest shows a second top in the classes 5–7 (45–75 cm), just like that for the 50-ha plot. For the moment our knowledge of the growth rate and the mortality of *kopie* in the various size-classes is insufficient to decide whether the bimodal histogram for the Mapane forest is characteristic for a *normal* regeneration of this species in primary forest, or whether it is the result of two overlapping curves, each representing a distinct population. In the first case (i.e. if the *kopie* trees in the Mapane forest have developed in their normal way in the natural gaps in the primary forest), the pecularities in the size-class distribution might be caused, e.g., by pecularities in the growth rate, the deficiency in certain classes being apparent only, and arising because the trees are not growing through equal intervals of girth in equal intervals of time. However, the discontinuities in the size-class distribution might also be due to discontinuities in the environmental conditions (light!) which promote the germination and the development of *kopie* into the middle sizes (e.g.,

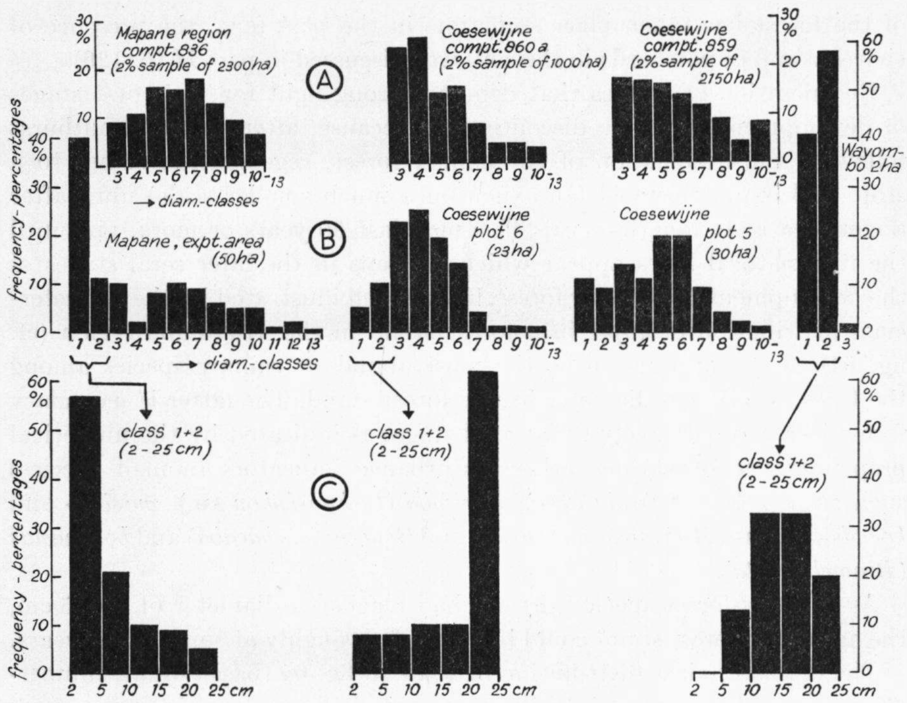


Fig. 64. Diameter-class representation of *kopie* (*Goupia glabra*) in different forests. A and B: for class limits cf. fig. 63. C: classes 1 + 2 of B subdivided in diameter-classes of 5 cm. The 23-ha plot in the Upper-Coesewijne region was located in compt. 860 a (in the E part of the region shown in fig. 53), in the vicinity of plot 6 (cf. III.3); the 30-ha plot (i.c. the area shown in fig. 57) was laid out near sample plot 5 in compt. 859.

the occurrence – at great and irregular intervals – of violent winds which are responsible for the formation of large gaps in the forest, cf. p. 15).

A second possibility is that the *kopie* trees in the Mapane forest represent *two populations:* an old one, more or less even-aged population (diam. cl. 5 and upwards) and a new population of younger trees (diam. cl. 1–4). The old population might date from a large-scale disturbance (e.g., destruction by the native population), which from the scanty data on girth increment of *kopie* might have taken place some 150–200 years ago; large differences in the rate of growth of the individual trees might be responsible for the spreading of the even-aged crop over a great number of diameter classes shown by the diagrams. During the development of the secondary to climax forest and during the growth of the emergent primary-forest species to maturity, the regeneration of *kopie*, which can establish itself in comparatively large gaps only, must have been practically nil, because such large gaps are comparatively scarce in the secondary forest and in young climax forest. They apparently do not occur until the emergents have grown to such age and dimensions that they become apt to be blown down. Evidence that in the Mapane area locally destruction of the forest has taken place sometime in the past (e.g., the presence of charcoal and of potsherds in the soil) was discussed in part II (p. 126).

Regeneration of species that demand strong light for their first stages of development, must be discontinuous because, after an initial outburst following the destruction of the climax forest, regeneration comes to a stop, and is not resumed (and then on a much smaller scale) until after a comparatively long interval. This may last 50 years or more, viz. until the first natural holes appear which happens in the later seral stages of the development to primary forest. This is well illustrated by the diameter-class distribution of *kopie* in a forest stand in the Wayombo region (cf. fig. 64). *Kopie* appears to be the most abundant canopy species among the trees over 10 cm diameter in this forest stand. The latter is secondary forest in a comparatively early seral stage, as indicated by the numerical preponderance of various other disturbance indicators (nomad species) such as *pegrekoe* (*Xylopia* spp.), *warimbo* (*Ischnosiphon* sp.), *maripa-* and *koemboe*-palms (*Maximiliana maripa* and *Oenocarpus bacaba*) and *bosananas* (*Bromelia alta*).

As primary-forest species already had reached a diameter of 10–15 cm, the age of the forest stand could be estimated roughly at some 20–30 years.

The diameter-class distribution of *kopie* in fig. 64 (based on an enumeration in a 2-ha plot) clearly illustrates that its regeneration came to a stand as soon as a covering of closed vegetation prevented further germination of this species (the *invasion stage* lasts less than 1 year, as could be observed in many recent clearings); not a single individual of less than 7 cm diam. could be found in this forest, where openings are characteristically absent.

Moreover, the diameter-class distribution of the 2-ha plot in the Wayombo stand shows that the even-aged population of *kopie* had spread already during the relatively short period over the diameter classes 5–35 cm. This must be due to the large differences in increment which appeared in our measurements of the growth rate (cf. fig. 66). During the future development of the population the range of diameters will be drawn out over more size-classes, because the smaller trees which are captured under the canopy, will grow at a much slower rate than those of the larger diameter classes which succeeded in reaching the upper storey.

In the high mesophytic forest on the cover-soils of the Upper-Coesewijne region (cf. III.3.2), *kopie* belongs to the leading dominants (cf. table XVII). This fact in itself is already an indication that this forest has undergone large-scale destruction in a rather near past. From the diameter-class distributions given in fig. 64 A it may be concluded that this disturbance has taken place more recently than in the Mapane region. That the influx of *kopie* did not take place simultaneously in the whole region appears from the difference in the histograms for the compartments 860 a and 859. The greater number of trees in the larger diameter classes in the second area suggest that this forest is *on the average* in a later seral stage than that of 860 a. This supposition is supported by the fact that in compt. 860a recent traces of abandoned cultivation are more frequent (cf. the distribution of secondary forest in the E part of the map in fig. 53). The forest in the 30-ha plot in compt. 859 probably represents an older successional stage than the average forest of the whole compartment; this may be concluded from the fact that in the histogram the top is found at a larger diameter.

Comparison of the enumeration in the 23-ha plot in compt. 860 a with that in the 50-ha Mapane plot also illustrates the above mentioned fact that the smaller diameter classes of a strongly light-demanding species are comparatively less well represented in a younger developmental stage than in later stages.

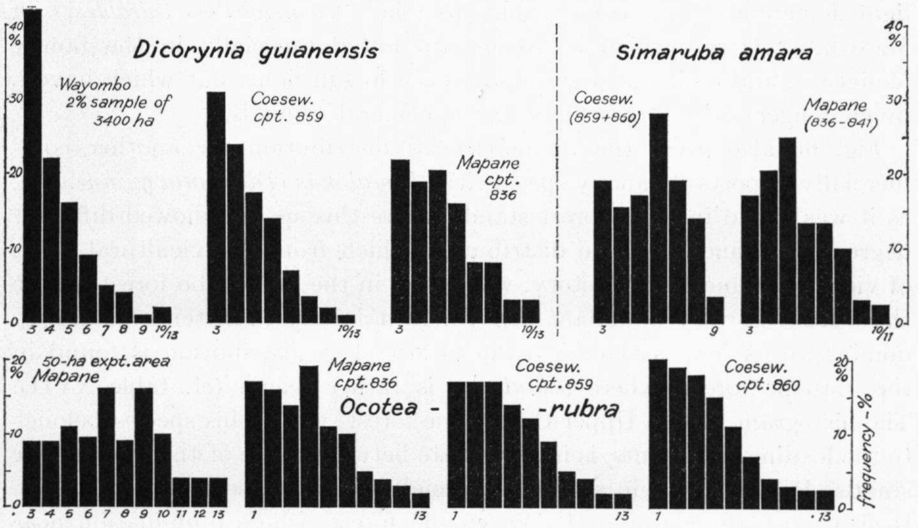


Fig. 65. Diameter-class representation of ***basralokus*** (***Dicorynia guianensis***), ***wana*** (***Ocotea rubra***) and ***soemaroepa*** (***Simarouba amara***) in various stands of mesophytic forest.

Note: In the basal row class numbers 1 and 13 should be 3 and 12/13 respectively (3 times).

In fig. 65 the size-class distribution of another strongly light-demanding species, viz. *soemaroepa* (*Simarouba amara*) has been set out; the histograms agree with those for *kopie* in that they show a top in the larger diameter-classes and a deficiency in the smaller ones.

It is a matter of personal preference whether strongly light-demanding species such as *kopie* and *soemaroepa* are included among the *secondary-forest species* ("nomad" species of VAN STEENIS, 1958) or not. This group of trees (to which a few other species belong, such as the Flacourtiacea *pientokopie*, *Laetia procera*) shares with the typical *weed species* a number of features which VAN STEENIS (1941) has described as "pioneer qualities", viz. the requirement of a considerable amount of light for the germination of their seeds, efficient means of seed dispersal (small, wind- or bird-dispersed seeds), a large output of seeds, and *rapid growth* (at least during the first stages of development) which enables them to establish themselves before they are shaded out by other species. Some, such as *soemaroepa*, have a light wood and continue to grow at a fast rate, others, such as *kopie*, have a heavy wood, and grow in a later stage of development very slowly (cf. fig. 66). *Kopie* flowers and fruits every year profusely, and the viability of its very small seeds apparently lasts much longer than that of the seeds of the majority of the typical primary-forest species. But the above mentioned group of strongly light-demanding species differ from the typical, short-lived secondary-forest species in their much longer span of life: the age of the large stems of *kopie* trees can be estimated roughly at some 150 years and it may even be higher. These long-living light-demanders are comparable to the "*cicatricielles durables*" of MANGENOT (1958) which in Africa are found especially in the family Meliaceae, and which also germinate only in full light, but which have a much longer span of life than the ephemeral nomads.

Fig. 65 also gives the diameter-class distribution for another commercially important canopy species, viz. *basralokus* (*Dicorynia guianensis*), as it was found in three forest stands where this species showed different degrees of abundance. The distribution which from a silvicultural point of view is the most satisfactory, was found in the Wayombo forest, where this species is very abundant and where it locally even tends to single-dominance. A less favourable form of size-class distribution is found in the Mapane forest, where *basralokus* is rather scarce (cf. table XVII). The histogram for the Upper-Coesewijne forest, where this species belongs to the leading dominants, is intermediate between those of the two former stands. Regeneration in size-classes smaller than those given in fig. 65, is also most abundant in the Wayombo forest, where illumination near the ground is markedly higher than in the Mapane forest (cf. fig. 18). As shown in fig. 67, the girth-increment at least of the trees with a diameter of over 5 cm – quite unexpectedly – was slowest in the Wayombo stands, where the species was most abundant, whereas the most rapid growth was found in the Mapane forest.

IV.3. GERMINATION AND DISTRIBUTION OF SEEDLINGS IN CLOSED FOREST

In the foregoing section our attention was confined to the larger diameter classes (over 2 cm or 25 cm diam.), the frequency distribution of which appeared to show significant differences, which appeared to be due partly to a specific idiosyncracy and partly to historical factors and to habitat factors. As might have been expected, the specific and local differences in the relative abundance of the seedlings proved to be still greater. For a few canopy species the numbers of seedlings and small saplings are given in table XXIII; these figures illustrate once more the well-known feature of mixed tropical rain forest, viz. that the relative abundance of various species may differ strongly in various strata; a species which forms a relately large proportion of the upper storey, may be very poorly represented or even absent as seedling and sapling, and seedlings of a species which is quite rare as an adult, may be very abundant. Examples of the first kind of species are few in number in the mixed forest in Suriname; their seeds can germinate in full light only. On the contrary, seedlings of e.g. *Vochysia guianensis* (*wiswiskwarrie*) and of *V. tomentosa* (*wanakwarrie*) are extremely abundant, although mature trees are scarce, as is shown in table XXIII. In this connection it is perhaps interesting to note that *V. guianensis* which—as far as is known—never attains prominence in the tree strata in the Suriname forests, may belong to the dominants in the *terra firme* forest in Brazil (cf. III.6). In small openings and places with a thin canopy the seedlings of these Vochysiacea (which under a closed canopy do not advance beyond the unfolding of the first pair of leaves) show vigorous growth, and locally their saplings may form dense thickets. Further observation of the development in the openings (cf. IV.6) will have to make out at what stage (and, if possible, why) this profuse regeneration must leave the field to other canopy species; that this must be so follows from the fact that adults of these *Vochysia* species are very scarce, notwithstanding the fact that natural openings are numerous in the climax forest. There are a few other emergent species, e.g. *ingipipa*'s (*Couratari* spp.), *gronfoeloe* (*Qualea coerulea*), *ceder* (*Cedrela odorata*), *groenhart* (*Tabebuia serratifolia*), etc., which produce successive waves of rather short-lived (½–1 year) crops of seedlings, which suffer a heavy mortality, and are doomed, unless there happens to be a suitable gap. But for the majority of the tree species (and especially for those of the middle and the lower storey, which are naturally more shade-tolerant than many of the emergents), the relative numbers of the individuals in the various age-classes show much smaller differences; e.g. *Eschweilera* spp., *Paypayrola guianensis* and *Coussarea paniculata*, which belong to the leading middle- and lower-storey species in the Mapane forest (cf. table XVII), are also best represented among the seedlings. This approximately is the same state of affairs as that described by BEARD (1946) for the regeneration in the "Evergreen Seasonal Forest" in Trinidad; there too the species which are most common in the tree storeys, are also most common among the seedling population.

Thus, in a few species, a comparatively large percentage of the seeds germinates on the forest floor, and the relative scarcity of poles and adults of these species (as compared with the abundance of seedlings) is due to the very small proportion of seedlings which survice even long enough to become established saplings.

On the contrary, for the *majority* of the middle- and upper-storey species (including most of the "economics"), *germination is the critical stage* in the establishment of regeneration, and the seedlings and saplings may survive very long (and even show some growth; cf. fig. 66) under a closed canopy. For a few species, such as *kopie* and *soemaroepa*, this is due to their need for strong light as stimulus for germination, but for the other emergents the reason of the enormous wastage of seeds is still obscure. The forest floor is seldom too dry for germination, and the seeds of 30 canopy species, which were tested on nursery beds, showed a high germination percentage (50–95 %) and no dormancy. The proportion of seeds which decay or are destroyed on the forest floor without germinating, is enormous. For instance, the annual crop in one stand of *bruinhart* (*Vouacapoua americana*) in the Mapane forest was estimated at more than 20.000 seeds, but during the three years of observation in the whole stand not more than 20 seedlings per year were counted of which, moreover, the greater part afterwards fell a victim to rodents and deer. Already three months after seedfall careful search was needed to find some of the large *bruinhart* seeds: they had been eaten by animals or had rotten away. If, on the contrary, the seeds were *pressed in the ground* (either on the nursery beds or in the forest), germination was practically 100 % after two weeks. The same holds true for the other emergents of economic importance, although the wastage of seeds is not as extreme as with *Vouacapoua.* In the 30 species (including all economics) on whose germination closer observations were made, it appeared that the latter was strongly stimulated by pressing the seeds into the ground or by covering them with earth or leaves. It is still a point of investigation whether this is due to the fact that they are withdrawn from the direct influence of light, or to some other factor(s).

Under natural conditions, i.e. on the forest floor, the *viability* of the seeds produced by the majority of the tree species of the primary forest (even the thick-coated ones) lasts but a very short time. Within a few weeks (or, often even days) they are attacked by insects and/or by microorganisms. For this reason of most economics the seeds needed for the nurseries have to be collected every day.

The majority of the canopy species of the primary forest fruit *every second year* (e.g. all Vochysiaceae, many Lecythidaceae, Burseraceae and Leguminosae). Only a very small proportion of the tree species have seeds or fruits which are wind-dispersed. Some species (e.g. *Couratari, Dicorynia, Aspidosperma,* etc.) have rather light seeds, which may be distributed by wind over short distances. A few species (Papilionaceae such as *wallaba*) have pods which dehisce on the tree and scatter the large flat beens far and wide. The majority of the trees (especially those of the lower storeys) have fruits or seeds which are adapted to animal-dispersal (e.g. the fruits of Burseraceae, Rosaceae and Rubiaceae, the pods of some Leguminosae and the berries of Sapotaceae). The rather heavy seeds of *Eschweilera* species are dispersed by dehiscence of the pyxidia and also by animals.

On the whole, the seeds of most species are dispersed in quantity over very short distances only, and consequently there is a great concentration of seeds and seedlings beneath and around the parent trees. Owing to this *patchiness of the seedling population* (which is a general feature in tropical rain forest, cf. e.g. JONES, 1956) the floristic composition in the small openings in the forest varies strongly from one place to another (cf. IV.6), and presumably is the main cause of the patchy distribution shown by many of the canopy species.

Although the typical primary forest species of middle- and upper-storey are frequently described as *shade-tolerant*, this is true only in a relative sense, as was pointed out already by JONES (1956) and RICHARDS (1952, p. 45). They differ from strongly light-demanding species, such as *Goupia glabra*, *Simarouba amara*, *Laetia procera* and other typical secondary-forest species, only in the fact that they need no light (and partly perhaps even need darkness) for the *germination* of their seeds, and that their growth in the seedling and sapling stage may be (much) slower than that of the typical light-demanders. Hence a partial or total removal of the shelter may be less necessary for their regeneration (or even may be unfavourable for the germination of some of them); however, at some later stage light also becomes essential at least for the majority (and perhaps even for all) of the upper- and middle-storey species. In this respect the differences in light-requirement are *gradual* only. At one end of the series stand the typical, short-lived and fast growing ephemerals ("cicatricielles éphémères" of MANGENOT), which are during their whole life-cycle extremely light-demanding and which also require full light for the germination of their seeds; these species (such as *Cecropia* spp., *Trema micrantha*, *Vismia* spp., etc.) are found in extensive clearings only, and will be mentioned in IV.6. Longer living, strongly light-demanding nomads are e.g. *Pourouma* spp., *Laetia procera*, etc. Some economically important species such as *Goupia glabra* and *Simarouba amara* belong to the long-living trees which show very abundant regeneration in clearings; these species germinate at somewhat lower light intensities (daylight factor ca. 60–80 %), and grow more slowly than the typical weed species: when, at a later stage of development, they become imprisoned under the canopy of the forest, they may survive and even show some growth (cf. fig. 66). On the next step to the typical shade-tolerant primary-forest species are found such species as *Jacaranda copaia* and *Sclerolobium melinonii*, the seeds of which germinate somewhat better in light than in darkness, but which otherwise behave in their growth and light-requirement like the majority of the emergents of the primary forest. Closer study undoubtedly will bring out many more transitional species. Finally there is the large group of typical primary-forest species, which can germinate under a closed canopy, and which even may need total darkness for germination. During the further stages of development their light-requirements vary strongly. Some species (e.g. *Cedrela odorata*, *Vochysia guianensis*, *V. tomentosa*, *Couratari* spp., etc.) produce abundant seedlings, which survive only during a short time under the closed canopy. The seedlings of other emergent species (especially of those which have large seeds) may persist for several seasons in fairly dense shade, and therefore perhaps might be classified as *shade-tolerant*. Some of the emergent species, such as e.g. *wanapisie* (*Ocotea* sp.), even may grow (though very slowly) to the sapling stage, as shown by the relatively large number of individuals of this species found in the diameter class 2–15 cm (cf. fig. 63). Other species show no growth at all after the store of food in the seeds has been exhausted, but they may persist very long in this stage. How long the various stages of the various species may persist in the dense shade prevailing under a closed canopy, and what growth they eventually still may show under these circumstances, is being studied in permanent quadrats which have been laid out in undisturbed forest. Quantitative data will be published later, when the observations cover a longer period.

That the saplings of a number of emergent species (over 7 cm diam.) show some growth under a closed canopy may appear from fig. 66; but as was indicated by the preliminary observations made in a number of experimental plots in which various amounts of light were let in (cf. IV.7), the growth of all middle- and upper-storey species was in all age-classes, without any exception, *strongly stimulated by the extra illumination*. The same was found on nursery beds which received different amounts of light, and where the seedlings of 30 upper-, middle- and lower-storey species showed their optimal growth in full sunlight (probably with one exception, viz. *wana*, *Ocotea rubra*, which perhaps prefers a light shade, at least during part of the day). Among the lower-storey species presumably some examples will be found of trees which prefer at least some shade.

VAN STEENIS (1958) in his "biological nomad theory", which I think very stimulating, stated that he had observed by practical experience in Malaysia a sharp difference between nomads and stationary species, and that "... there is no gradual series of transitions which would blot out the whole nomad concept". For the hylaean forest such a divison of the flora into nomads and other species would tend "... to over-emphasize the first and final members of a successional series" (FOSBERG in the discussion following VAN STEENIS' address).

From the foregoing it appears that in the mesophytic lowland forest in Suriname regeneration of the canopy species differs considerably from that in the majority of the rain-forest stands in Africa. The striking and much discussed disproportion between the number of mature trees of the upper storey species and that of their young stock, was repeatedly observed in African forests (e.g.: Cameroons: MILDBRAED 1930; Nigeria: RICHARDS 1939; JONES 1955–'56; Ivory-coast: AUBRÉVILLE 1938). Even when young trees of canopy species were present, often a great deficiency of medium-sized trees was found. This state of affairs has led AUBRÉVILLE (1938) to his well-known theory of regeneration in the African rain forest, in which he postulates that groups of species are succeeding each other periodically in any given area. The above-mentioned discussion on regeneration in the

Suriname lowland-forest, and the results of the studies of BEARD (1946) in Trinidad and of DAVIS *et al.* (1934) in Br. Guiana showed that such a conception does not hold for rain forest in tropical America. Certainly, in the primary forest here also a few long-lived nomads are found, which for their regeneration exclusively depend on large openings, and which consequently show certain irregularities in the age-class distribution. But in the large majority of the canopy species found in the mesophytic forest, all sizes are adequately represented, increasing progressively in abundance from the upper to the lower storeys, and accordingly suggesting that they are regenerating rather continuously and *maintaining the existing proportions in the population.*

Probably the differences observed in the two continents between the age-class distribution of the upper-storey species of the rain forest is less fundamental than might appear at first sight, and may be due primarily to the fact that the greater part of the African forest is no true climax (in the sense of stable) forest, but old secondary forest which is changing in composition, particularly in respect to the emergents. JONES (1956, p. 112) e.g. concluded for the "High Forest" in the Okomu forest reserve, that "... it is in accordance with all the evidence to regard the forest as secondary forest ... which is now breaking up". In the Guianas where to-day's population on the average is very scarce, on the contrary much larger areas of forest could develop more or less undisturbed by man to a stable climatic climax.

IV.4. GIRTH INCREMENT OF UPPER-STOREY SPECIES

During the years 1956–'57 in the Mapane forest monthly girth-increment measurements were made on 250 trees of various size classes, belonging to 7 economically important species (cf. fig. 66). For the year 1957 the observations were extended over some 300 trees of *Goupia glabra* (*kopie*), *Dicorynia guianensis* (*basralokus*), *Ocotea rubra* (*wana*) in various stands of lowland rain forest and *Virola surinamensis* (*baboen*) in swamp forest, the locations of which are shown in fig. 1.

The method we used, was that of DAWKINS (1956), which during the present study too has proved to be a highly accurate and efficient system of measurement, capable of detecting very small changes in girth-increment (about 1 mm) without involving a costly apparatus. Mr. DAWKINS, when visiting Suriname in 1956, was so kind to inform us on his "ten-ring method". For a more detailed description of the system reference is made to the afore mentioned publication. The method simply consists of painting ten parallel rings on each tree; each measurement consists of a single reading with a steel tape calibrated in millimeters which during the measurement is held flush against the paint-ring. The mean of the readings of the 10 rings is expressed in tenths of millimeters and is likely to be within 0.4 mm of the truth.

As was remarked by DAWKINS, "... the effect is similar to that of a vernier scale except that in this case the scale is interrupted and must be read in ten places." For the present purpose the accuracy obtained with a single measurement per ring (instead of the best-of-three readings in Uganda) appeared to be sufficient. Of course the method which was used does distinguish neither between growth (and shrinkage!) of the extracambial tissues and the wood, nor between true growth and changes in turgidity, dilatation, etc.; the measurements merely represent

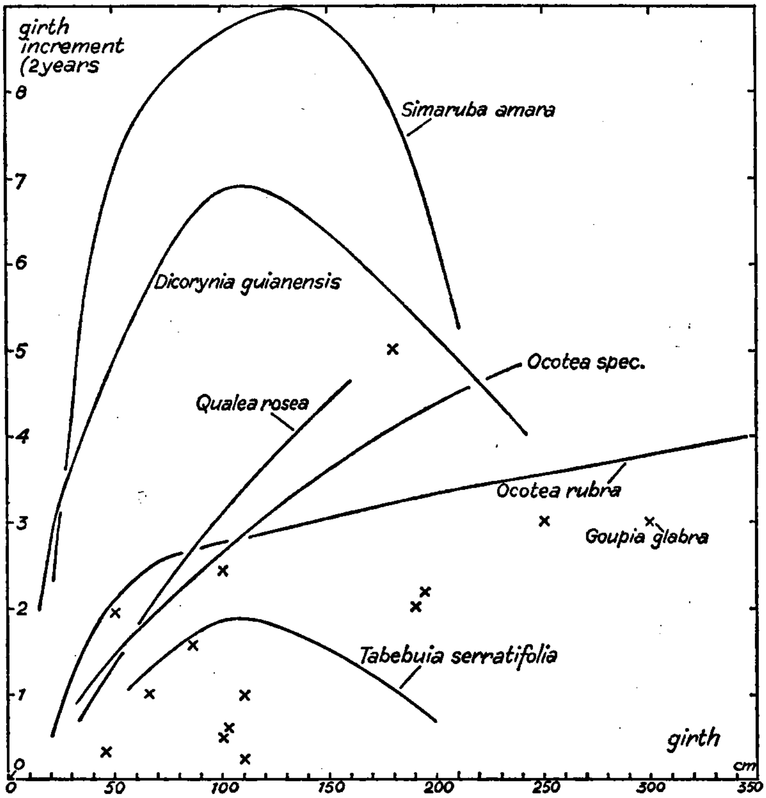


Fig. 66. Girth increment during two years (Jan. 1956–Jan 1958) of canopy species in closed forest on mesic sites in the Mapane region (i.e. the area shown in fig. 47). The curves are based on measurements, made on ca. 40 trees per species (except *Goupia:* 14 trees). For *Goupia* (crosses) the scattering is too great to allow the drawing of a trend line.

fluctuations in *girth* and in *girth increment,* whatever their origin may be; they accordingly reflect the true growth only to some extent. Only when increment data covering a longer period (of, say, 2 years or more, dependent on specific and individual pecularities of the extracambial zone) are compared, the differences may be regarded as representing the true growth of the wood.

After a preliminary study had revealed the comparatively large fluctuations in girth which may appear during a single day (in the dry season a tree of 100 cm girth may show between 8 and 16 hr. a contraction of more than 2 mm!), from then on measurements only were made between 6.30 and 11 hr.

The results obtained in Suriname agree with those from Uganda (DAWKINS 1956) in so far as adjacent and similar trees were found to show vastly different growth rates, which may be of the order of 1 : 3. Sometimes these differences were correlated with apparent differences in vigour and crown position, but often – just as in Uganda – no correlation could be detected between such differences in girth increment and apparent vigour, crown position and form of the trees. The large individual discrepancies in girth increment are illustrated in fig. 66 (crosses) for 14 *kopie* trees (*Goupia glabra*) growing in the Mapane forest.

Owing to this strong variability, a rather large number of stems have been measured to arrive at a more or less reliable increment curve for any given habitat and species.

The 2-years' girth-increment curves which are reproduced in fig. 66 are based on the measurement of some 40 trees per species, and are smoothed lines drawn by free hand through the swarm of points. For sake of clearness only the means for girth-classes of 5 cm have been indicated. Although these trend lines were drawn tentatively, the general trend, e.g. the relative difference in the rate of increment between the

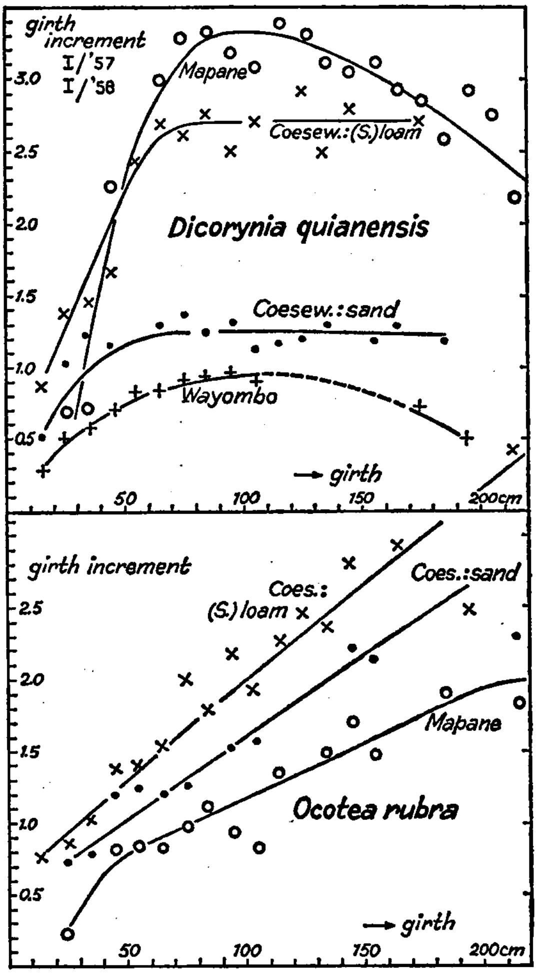


Fig. 67. Girth-increment of *Dicorynia guianensis* (*basralokus*) and *Ocotea rubra* (*wana*) during the year 1957 (Jan. '57–Jan '58) in the Mapane forest and on various sites in the Upper-Coesewijne forest; for *basralokus* also in the Wayombo forest. Curves based on 10-ring measurements of 40–80 trees per species and per stand. Curves are drawn free-hand through means of 5 cm girth-classes.

various species, is real. This appeared from the fact that it was confirmed by observations which were made on a much greater number of trees in the 50-ha experimental plot (cf. IV.7). The two *Ocotea* species and *Qualea* (and perhaps also *Goupia*) showed an increase of the rate of increment with increasing diameter (up to the highest diameters which were measured), whereas *Simarouba*, *Dicorynia* and *Tabebuia* clearly showed an optimum at ca. 30–40 cm, which approximately corresponds with the average girth reached by the canopy species when their crowns have become expanded in or above the main canopy (cf. fig. 60). It should be noted that the boles of the first group of species may attain much larger diameters than those of the second group; e.g. *Simarouba amara* in the Mapane forest was seldom found with a diameter of more than 80 cm (cf. fig. 65). For *Dicorynia* the form of the curves appeared to vary in different sites, as appears from a comparison of the curves shown in fig. 67. In this figure the increment curves for *Ocotea rubra* and *Dicorynia guianensis* have been set out for different habitats, showing significant differences in growth on different soils. Quite unexpectedly, the growth of *basralokus* proved to be best in the Mapane forest, where this species only plays a minor role among the canopy species (cf. table XVII). Growth was slowest in a stand in the Wayombo forest, notwithstanding the fact that illumination was higher (cf. fig. 18, p. 41) and that *basralokus* was the leading canopy species (cf. III.5 and p. 224).

The results of the measurements of the rate of increment clearly illustrate that *growth and abundance of a species are not necessarily correlated.* The growth of *basralokus* in the Upper-Coesewijne forest was intermediate between that in the former two areas. The differences in growth on two different soil types are clearly shown by the curves for *basralokus* and *wana* on sand and (sandy) loam in the Upper-Coesewijne region. Yet, as was shown in figs. 55, 56 and 57, neither the abundance, nor the height of the trees of these two species were affected by these differences in soil!

The majority of the trees showed more or less marked *seasonal variations in girth-increment.* Especially during the very dry season of 1957 (cf. part I) the majority of the trees contracted considerably. The strongest seasonal periodicity was found with *groenhart* (*Tabebuia serratifolia*), one of the exceptional deciduous trees in the Suriname rain forest; it stands bare for 2–4 weeks during the beginning of the long dry season (Aug.). The trees show explosive aestivation, coinciding with the beginning of the bare period, all trees in the same region coming nearly simultaneous into flower. In the Mapane region it was observed that the trees on bleached sand (cf. II.2) (where, in places, *groenhart* may be rather abundant in xeromorphous *savanna* forest) shed their leaves, and came into flower one or more weeks before the population on mesic sites did so. In the pronounced short dry season of 1957 (Febr.–April) part of the trees on the excessively drained white sands also shed their leaves and blossomed.

These observations suggest that drought is the chief factor determining the periodicity of this species. In fig. 68 the curves for the monthly girth-increment have been set out for three trees of *groenhart*; the curves clearly show that the period of strongest activity coincides with the first rains of the short wet season (Dec.–Feb.), i.e. shortly after or during the unfolding of the new leaves. The *groenhart* trees showed a comparatively inert period during the second half of the wet season and during the greater part of the dry season. During the dry season shrinkage sometimes was considerable, especially in 1957. The curve for the large tree (C) showed an abnormal activity during the wet season (June) in 1957, which might be due to the sub-normal amount of precipitation during the preceding period, and which illustrates the fact that for this species activity is induced especially by *rain following a period of relative drought.* Notwithstanding the pronounced periodicity in cambial activity in the stems of *groenhart*, age estimation by means of the growth rings appeared to be very difficult, because the growth rings appeared to be incomplete. The other canopy species also showed a more or less marked correlation of girth increment with rainfall. Nearly all trees showed an interruption of the increment or even a contraction during the long dry season (especially in 1957!), but, owing to the method of estimation, no distinction is possible between shrinkage and a real interruption of the growth. That in many species of the upper storeys a periodic slackening in cambial activity must occur, appears from the fact that their wood shows more or less distinct growth zones, although, as was observed in *groenhart*, but very seldom complete rings are formed, and although it is uncertain whether they are formed annually. From the many available curves, three have been selected at random, and are reproduced in fig. 68. In the upper part of fig. 68 the girth-increment curves for two *basralokus* (*Dicorynia guianensis*) trees and for a *soemaroepa* (*Simarouba amara*) are shown. The second species is the quickest growing canopy species found in the Suriname forest; the tree for which the increment curve is given in fig. 68 (50 cm d.b.h.), showed a diameter increment of 3 cm in 2 years. *Soemaroepa* trees were less affected by the yearly draught than the other species which were studied. All other species showed a markedly stronger shrinkage during the dry season. This difference may be due (a) to the comparatively thin bark of *Simarouba* (which, accordingly, cannot shrink much) or (b) to the fact that this species is better adapted to dry sites (which appears from the fact that it prefers the forest on the dry sand ridges in the coastal plain). The curves for the *basralokus* trees clearly illustrate the strongly stimulating influence which *illumination* exercises on the increment (cf. also fig. 70!). The large amount of data that are already available, were not tested for a possible correlation of the increment to sunshine hours, but for many trees the curves suggest that such a correlation between illumination and growth actually exists, at least above a certain threshold value for rainfall. In the much drier

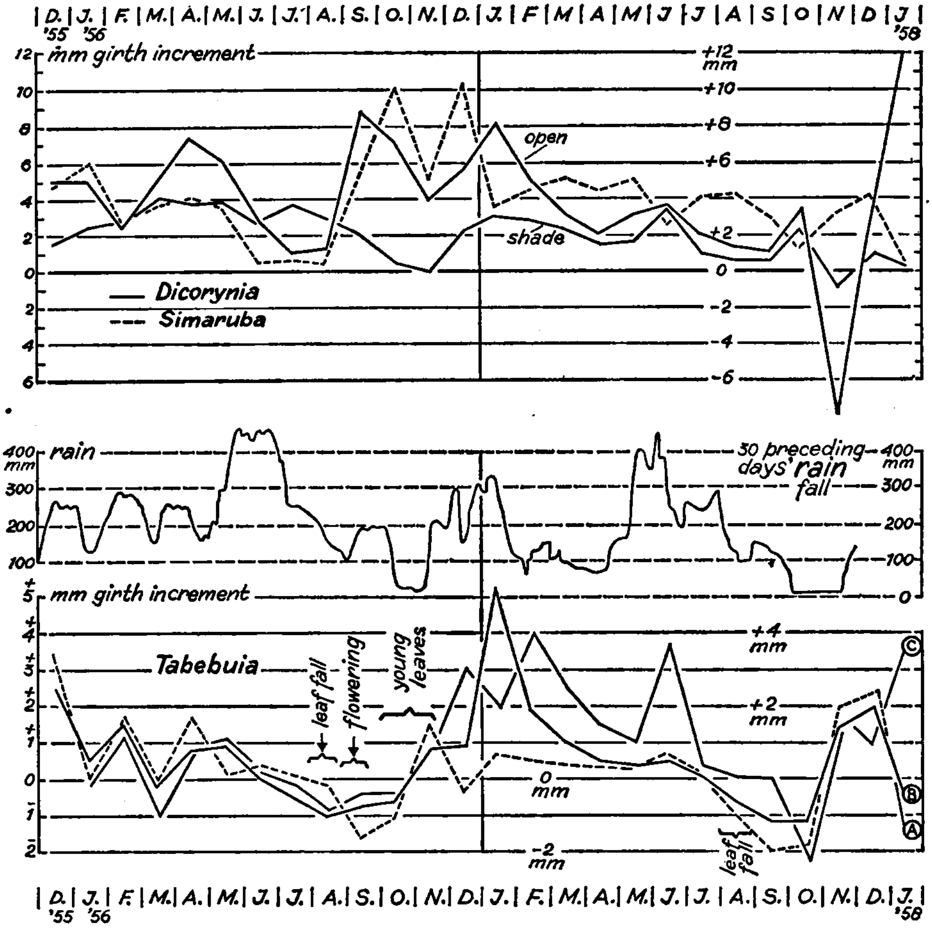


Fig. 68. Monthly girth increment of selected trees in the Mapane forest. The two *Dicorynia* (*basralokus*) trees (one of which stood in the centre of a large clearing) measured ca. 25 cm in diam.; *Simarouba amara* (*soemaroepa*) 50 cm d.b.h. Of the *Tabebuia* (*groenhart*) trees, A and B had a diam. of 25 cm and C of 60 cm. The curve for the rainfall represents the 30-days' moving total for Mapane camp (cf. fig. 7).

climate of Uganda DAWKINS (1956) found a correlation of girth increment and rainfall (provided the tree is in full leaf and not flowering), but no clear correlation with sunshine-hours.

IV.5. HORIZONTAL DISTRIBUTION OF THE SPECIES

The matter of differences in the composition of the mesophytic forest was brought up repeatedly in the two foregoing parts. The presence of a striking variation in the abundance of particular species, even over very small distances and in stands which are supposed to grow on a rather uniform soil, was demonstrated by enumerations which were carried out in neighbouring sample plots in the same stand (part III). Such vagaries in the distribution of many species are the main difficulty for the application of standard phytosociological methods, and, even worse, may form a considerable obstacle to the commercial exploitation of the forests.

From the enumerations in the 560 quadrats of sample plot 1 (cf. III.2.2) as well as from the distributional maps of various canopy species in a 200-ha area in the Mapane region (a few of which are reproduced in figs. 47 and 69), it appeared that in this forest *many species showed a non-random distribution*, even if their distribution on the mesic sites only (viz. the well-drained red earths, cf. II.2.2) was considered. Although the statistical treatment of the available data was not so thorough as that carried out by JONES (1955) in his exhaustive study of the horizontal distribution of the species in a Nigerian forest, a superficial inspection of the horizontal pattern found for the principal species on the mesic sites in the Mapane area already revealed a strong resemblance with the state of affairs described by JONES. The tendency for aggregation was most obvious in the lower storeys; e.g. *Paypayrola guianensis* (*tajahoedoe*) and *Coussarea paniculata* (*boskoffie*), the characteristic trees of the lower storey in the Suriname R.–Commewijne R. region, appeared to be markedly aggregated. The strongest degree of gregariousness was observed with shrubs such as the *bofroekassaba*'s (chiefly *Cephaëlis violacea*). For the upper-storey species the tendency to aggregation appeared to be more pronounced when smaller sizes were included (cf. below). The stronger tendency to aggregation shown by the under-storey species might partly be due, as was pointed out by Jones, to the circumstance that the number of individuals belonging to the upper-storey species is smaller, so that a significant aggregation is less easily observed. It might be due also to a sharper reaction of the smaller species on site differences, but the correlation with soil factors have not yet been tested. In this connection it is interesting to recall the fact that in the Upper-Coesewijne region the composition of the lower storeys appeared to react much sharper on differences in site than that of the upper-storeys (compare in table XVII the composition of plot 6 on a schist-laterite "island" with that of plot 5 on the surrounding cover-soil).

In figs. 47 and 69 for a number of species the distributional pattern of individuals with a diameter of more than 20 cm has been illustrated. Some of the important canopy species in the Mapane region show a rather uniform distribution, e.g. *rode salie* (*Tetragastris altissima*) (cf. fig. 69) and *krappa* (*Carapa guianensis*). Others show departures from randomness in various degrees. The most extreme case is the distribution of *bruinhart* (*Voucapoua americana*), which N of the Mapane Cr. is found in strictly localized stands (cf. II.2.3 and fig. 46); but within these stands this species appeared to be distributed at random. For two species, viz. *Qualea rosea* (*birgiegronfoeloe*) and *Ocotea* sp. (*wanapisie*), it was made plausible (II.2.3) that edaphic factors are responsible for the peculiarities of their distribution in the Mapane forest. On the other hand, for *basralokus*

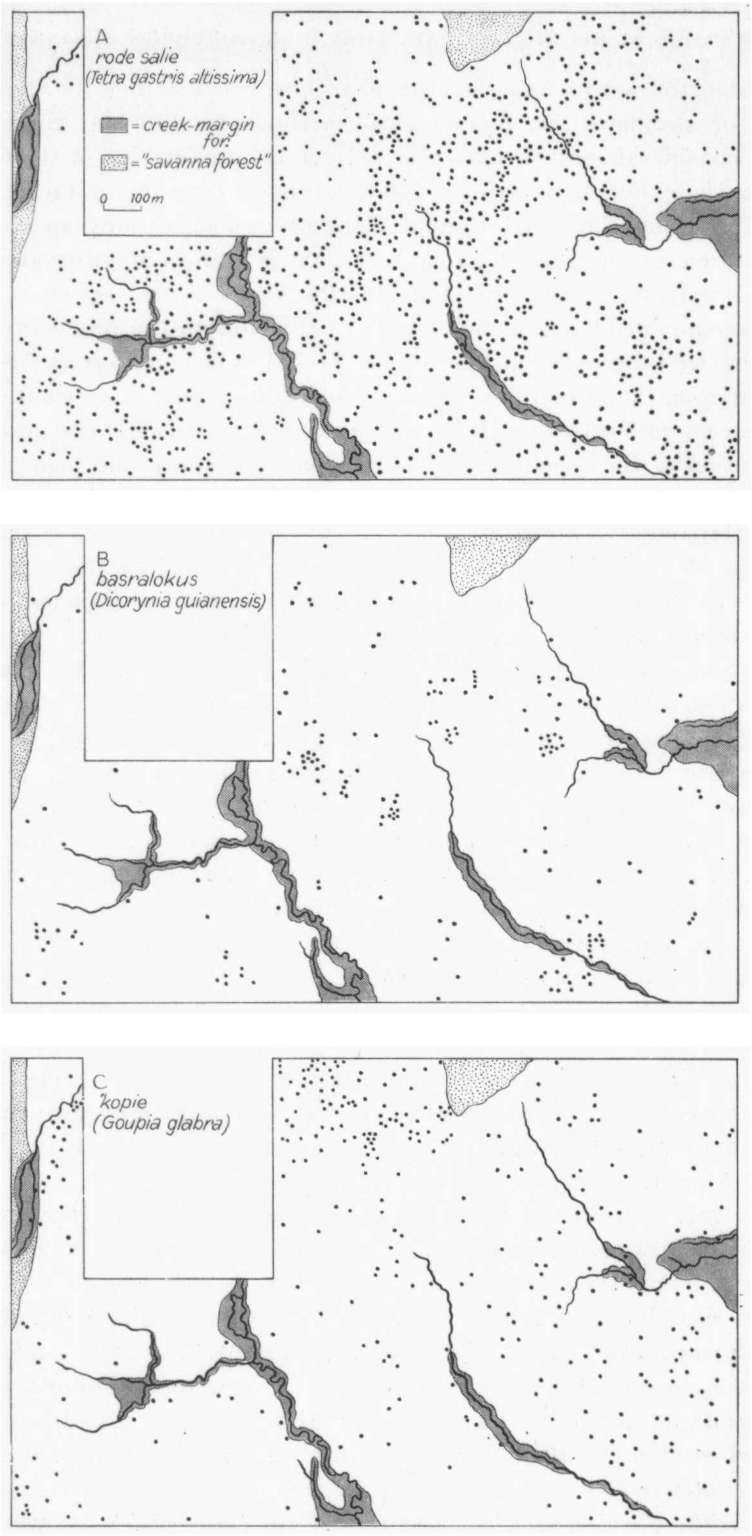


Fig. 69. Distributional pattern of trees over 20 cm d.b.h. of three canopy species in a small area in the Mapane region. For location, cf. fig. 46.

(*Dicorynia guianensis*) and *wana* (*Ocotea rubra*) it was demonstrated that their distribution in the Upper-Coesewijne forest was unaffected, within rather wide limits, by differences in site (cf. figs. 55, 56 and 57), although the map given in fig. 57 shows that for the *basralokus* trees this only applies to individuals over a certain diameter. Undoubtedly, for a number of other species a more thorough study will reveal that the vagarities in their distribution are due to site differences. Nevertheless, in my opinion, the uneven distribution must often be attributed to "*chance regeneration*" as it was called by VAN STEENIS (1958 a). The large role which chance plays in the regeneration of many tree species in rain forest was emphasized also by AUBRÉVILLE (e.g. 1950–'51) and many other students of the W-African rain forest (e.g. MILDBRAED 1930, JONES 1955–'56).

It is beyond doubt that in the Suriname forest too chance (i.e. influences of a stray nature) may play a very important role in the regeneration of the majority of the tree species. The patchy distribution of the young individuals of many species (which often are concentrated near the mother trees) is perhaps the direct cause of the aggregated distribution shown by the adults both in the upper and in the lower storeys. It is decided by chance when and where a hole is formed in the over-storey, and also how the composition of the young population happens to be at that spot. The latter will depend on such factors as the proximity of seedbearers, the season, and the occasional occurrence of seed years. Accordingly, as will be pointed out in the next section (and was likewise observed by VAN STEENIS, 1958 a), the composition of the new vegetation in the openings differs strongly from one place to another.

IV.6. SUCCESSION IN OPENINGS IN THE MAPANE FOREST

Except for a few patches of secondary forest (which is locally called *kapoewerie*, cf. *capoeira* in Brazil!) of unknown age, which are in a late stage on the way back towards climax forest, secondary forest on mesic sites is very scarce in the Mapane area. The extensive stands of *kapoewerie* in various stages of development that are found in the Upper-Coesewijne region, have not yet been studied. Moreover, if the reconstruction of a succession has to be based on comparative studies made in a number of spatially separated seral stages, it will contain so many uncertainties in the form of more or less arbitrary assumptions, that it can not be regarded as an exact picture of what really happens. The details of the succession can only be fully elucidated by careful quantitative observations that are continued over a long period of years, and that are made in openings varying in size and in habitat. Moreover, a rather large number of replications are necessary, because – as also appeared from the present study – the floristic composition of the successive stages is largely a question of chance, viz. distance to seed bearers, occurrence of seed years, composition of the existing regeneration at the moment at which the shelter was removed, etc. Accordingly, the composition may very considerably from one place to another and with the time at which the opening in the canopy arose.

The openings in the Mapane forest in which the successions were studied, can be divided in two groups: (1) those in which varying degrees of light were let in by various degrees of removal of the overhead shelter (by felling or by poisoning the trees), but in which the existing ground flora was left undisturbed as much as possible; (2) clearings of different size, in which practically all vegetation was removed (e.g. old camp sites, collecting-yards for logs, logging tracks and extraction roads, etc.).

Small openings

In the first group of openings, which varied in size from 1/100–1/10 ha, and which were meant as imitations of natural gaps such as are caused by the overthrow of very large trees, the aspect after two years of observation appeared to depend largely on the composition of the seedling population that happened to be present at the moment at which the shelter was removed, and on the seeds which since then had arrived in the site. Owing to the erratic distribution shown by the seedlings and the seeds of the majority of the species, the floristic composition of the regeneration after the first two years differed significantly from one place to another. The short time of observation allows only some general remarks on the first stages of the successions. Publication of the detailed quantitative data (of which RICHARDS 1952, p. 377, remarks, that ... "no aspect of the ecology of the Tropical Rain Forest is of greater practical value or promises results of more theoretical importance") can better be postponed until the study of the successions has been extended to a later stage of their development.

The rate of growth of the seedlings and poles naturally depends on the amount of light which in its turn depends on the width of the openings in the shelter. The growth of the seedlings and saplings of all species, including the more shade-tolerant lower- and middle-storey species, was favoured by the removal of the shelter. Among the most rapid growing species were the *Inga* spp. of the lower storey.

In those openings in which the average daily illumination at ground level (according to the sampling method described on p. 39) was less than 10–20 times that in closed forest, the existing regeneration of the primary forest species made good growth. In those gaps in which the amount of incident light exceeded this value, the regeneration of the primary forest species was strongly inhibited by the development of rapid-growing secondary forest species (the "nomad species" of VAN STEENIS 1958 b), the same which invaded the totally cleared grounds during the first stages of the secondary succession. As a matter of course, no sharp distinction could be made between openings in which the illumination was sufficient for the reproduction of typical secondary forest (nomad) species and those in which this was not so. Generally, below gaps in the upper-storey under which the average daily illumination was less than about 15 times that under a closed canopy (i.e. with a daylight factor of ca. 30 %, cf. p. 47), only a few individuals of strongly light-demanding species such as *Cecropia* spp., *Goupia*, etc. were found, and here the new vegetation largely consisted of primary-forest species.

KRAMER (1933) similarly observed in mountain rain forest in W Java that the young individuals of the primary-forest species that were already present, showed good growth in artificial openings if the latter were less than 1/10 ha in extent, whereas this regeneration was strongly suppressed by the competition of secondary-forest species in openings of more than 1/5 ha.

Under the *larger openings* in the over-storeys and in the larger clearings (daylight-factor 50–100 %) in which practically all vegetation had been removed, a *secondary succession* set in shortly after the removal of the shelter. Although young individuals of the primary-forest species that may be present may also partake in the increase in growth, their further development was soon suppressed by the vigorous growth of the secondary-forest species. Very soon after the increase of the illumination seedlings of herbs, shrubs and trees are coming in. In places, herbaceous weeds, such as several Melastomataceae, *Heliconia* spp., Zingiberaceae (*Costus* spp., especially on sands), may very rapidly form a closed stand, but their dominance is transient, and the part they play in the succession on mesic sites is a very minor one. Locally (especially where the regrowth has been cleared away several times, and/or where part of the topsoil has been removed by erosion or by tractor-logging) the most characteristic plants of the first phases of recolonization are coarse grasses and sedges. The grasses number about 10 species, and include several species of *Setaria*, *Axonopus*, *Panicum*, *Paspalum*, etc.; the sedges include several species of *Cyperus* and *Scleria*. As temporarily predominant shrubs several species of *Piper* and of Melastomataceae (especially on sands) may be found. In the majority of the clearings typical secondary-forest species very soon attain dominance, and may form almost pure stands. Among them the well-known *Cecropia* spp. (*bospapaja*, in the Mapane region chiefly *C. sciadophylla* and *C. surinamensis*), are the most plentiful and the most rapidly growing ones. Locally *Cecropia* spp. (which are the S-American counterpart of the related West-African *Musanga cecropioides*) may form an almost pure, closed stand, which may attain in 2 years a height of more than 10 m. *Pourouma mollis* (*granboesipapaja*, Morac.), *Trema micrantha* (*kopie-kopie*, Ulmac.), certain species of *Inga* (*switieboontje*, Mimos.), *Alchorneopsis trimera* (*manbébé*, Euphorb.), *Vismia* spp. (*pienja*, Guttif.), *Didymopanax morototoni* (*kasabahoedoe*, Aral.), and, especially, *Goupia glabra* (*kopie*, Celast.) and *Palicourea guianensis* (*pinpin*, Rub.) are frequent pioneers. The majority of these genera and species are ubiquists which are found everywhere in tropical America in secondary growth. *Trema* is even a pan-tropical nomad genus. Locally lianes (*Bauhinia* spp.!) and trailing cucurbits (*Gurania*) help to complicate the tangle; razor grass (*Scleria* spp.) being the chief climber. *Scleria* may persist very long in the secondary growth.

From a practical point of view the behaviour of the young populations of the valuable timber species *Goupia glabra* (*kopie*) in the secondary successions is of greatest interest. As was discussed already in the foregoing sections, the seeds of this species are capable to germinate only in full light. In the majority of the extensive clearings seedlings of this species appeared within a few weeks after the removal of the overhead shelter, and saplings of over one meter height locally had formed dense thickets after about one year. It seemed that the regeneration of *kopie*, just as that of the majority of the other secondary-forest species was rather independent of the time of the year at which the openings were formed. This would imply a rather long viability of the seeds of *kopie*, as this species only fruits once in a year (Aug.–Nov.). After two years of observation in many openings the initially very abundant regeneration of *kopie* was strongly suppressed by the quicker growing, large-leaved weed species, such as *Cecropia* spp. and *Palicourea guianensis*. Many saplings and seedlings of *kopie* had died or were strongly suppressed in their growth. Moreover, many individuals were overgrown by climbers. In a patch of secondary growth in an abandoned camp site where *kopie* saplings were very abundant after the first year of regrowth, 4 years later only one, overgrown, individual of *kopie* could be found.

In the Mapane area the quick-growing, large-leaved saplings of *Palicourea guianensis* (*pinpin*) are the chief suppressors of the other species. In a number of experimental plots it appeared that one cleaning which was carried out at the end of the first year, was sufficient to ensure a dense stock of vigorously growing *kopie* poles. In these plots the poles had reached a height of ca. 3 m after 2½ years. Time will show whether this single cleaning is sufficient for *kopie* to retain its lead.

From a silvicultural point of view another important result of the observation of the preliminary stages of the development of the regrowth in the regeneration plots was the fact that *for none of the emergent primary forest species the number of the seedlings was increased* by the removal of overhead shelter.

As was remarked already in the foregoing sections germination of the seeds of these species is inhibited rather than stimulated by exposure to strong light (although for the present it has to be left aside as to whether this inhibition is caused by the direct influence of the light or to changes in other micro-climatological factors which are incident to removal of the upper strata of the forest).

IV.7. A MIXED-FOREST REFINING EXPERIMENT

The results of the preliminary studies on the syn-dynamics of the primary mesophytic forest (based chiefly on age-class distributions and regeneration under various conditions), led to the arrangement of a pre-exploitation refining experiment *) in a 50-ha plot in the Mapane region. The working-plan objective of the silvicultural treatment carried out in this plot, was to make use of the *existing, established young* population of desirable species in the form of *retarded poles and young trees* which have reached a stage of development *at which they are able to compete without further assistance with other species after removal of the shelter.*

The enumerations had revealed that in the majority of the primary mesophytic lowland forests in N Suriname there is a quite sufficient young stock of "economics" in the smaller and intermediate classes. As was discussed in the foregoing pages, the majority of the desirable canopy species are *partial shade bearers,* surviving very long and even making some growth in undisturbed forest, but showing vigorous growth after removal of the overhead shelter. It appeared that growth of *seedlings* and *small saplings* of these economically important species is too slow to allow for succesful competition with other, more quickly growing primary and secondary-forest species. Certainly, repeated improvement cleanings would be necessary to assist these relatively slow growing seedlings and small saplings of the desirables during the first stages of their development after opening of the canopy (at least if so much light is let in, that growth is stimulated materially). In Suriname the relatively high labour costs would prohibit the application of such repeated undergrowth cleanings.

If, on the other hand, the crowns of the saplings and poles which already have reached a height of more than, say, 5 m are freed from lateral and vertical crown competition, it seems likely that such a single operation will appear to be sufficient. As all undesirables of the same or greater height are killed, the young stock of the "economics" presumably will be able to keep ahead of the majority of the saplings and poles of the other species, over which it has an advantage from the moment that the light is let in. Moreover, competition will be less severe because the large group of individuals belonging to species which can not grow higher than the lower storey is practically excluded from the competition for light (and it are exactly these species which appeared to play an important role in the suppression of the seedlings and small saplings of the "economics" after removal of the shelter).

Therefore, for these mesophytic lowland forests of N Suriname where the intermediate classes of the economically valuable species are relatively abundant (and well distributed!) some sort of an approach to natural

---

*) The term "refining" was adopted following a proposal made by DAWKINS (1955).

regeneration seems warranted that attaches greater relative importance to the saplings and poles than to the seedlings and small saplings.

The lower limit of the size-class of desirables which are to be freed should be determined by examination of the *size-frequency curves* of the compartment under consideration, and, accordingly, will be different from one stand to another. For instance, in the Upper-Coesewijne forest, where the very valuable species *basralokus* (*Dicorynia guianensis*) and *wana* (*Ocotea rubra*) are relatively abundant, it is sufficient to free all trees of these two species over 10 cm d.b.h. to guarantee sufficient stocking with trees of these species in the future. In the Mapane forest, where the number of individuals of "economics" is comparatively small (which is one of the reasons why this forest is elegible for pre-exploitational refining), a lower limit should be chosen. Moreover, because of the low number of trees of the most important commercial timbers, in the Mapane forest also less-valuable species have to be included in the treatment.

In a 50-ha area in the Mapane forest (i.e. the area shown in fig. 50), four different treatments were carried out:

(a) all trees of undesirable species over 5 cm d.b.h. poisoned during the first year,
(b) idem over 10 cm d.b.h.,
(c) all undesirable trees over 40 cm poisoned during the first and trees of 5–40 cm d.b.h. in the second year,
(d) idem, but only down to 10 cm d.b.h.

The trees were poisoned by basal application of a contact-arboricide (2 or 5 % butyl 2, 4, 5-T in dieseloil), using the method described by DAWKINS (1953). Large climbers—which are not frequent in the Mapane forest—were killed at the same time. The first leaves of the trees which had been sprayed began to fall a few days after treatment. After one year about 70 % of all treated trees had succombed and stood bare; especially Sapotaceae resisted poisoning. Fuller details on the results of the poisoning will be published separately.

Owing to the heterogeneity of the soil (cf. II.2.2 and fig. 49) and the composition of the forest (as illustrated by the distribution maps in figs. 47, 50 and 69), the experimental area was divided in 50 one-ha plots. The 4 different treatments and the controls of undisturbed forest were divided over the 50 plots according to a Latin Square arrangement, allowing for analyses of variation and co-variation, if necessary. The composition of the forest stand may appear from the enumerations carried out in a 5.6-ha sample plot (plot 1, cf. tables XV and XVI) which was laid out in the direct vicinity.

The most abundant species of economic value encountered in the area are: *rode salie* (*Tetragastris altissima*), *krappa* (*Carapa guianensis*), *basralokus* (*Dicorynia guianensis*), *kopie* (*Goupia glabra*), *wanapisie* (*Ocotea* sp.), *birgiegronfoeloe* (*Qualea rosea*), *wana* (*Ocotea rubra*), *zwarte pisie* (*Nectandra grandis* and *N.* cf. *kunthiana*). Trees of some 15 other valuable species, the majority of which were represented by a few individuals only, also were spared.

For three species which were chosen indiscriminately, the girth-increment curves are given in fig. 70. The curves clearly show the significant response of the trees already during the first year, notwithstanding the fact that the full effects of the treatments (in the form of the leaf fall of the poisoned trees) were not produced until the end of this first year. As would be expected, the strongest stimulation of growth

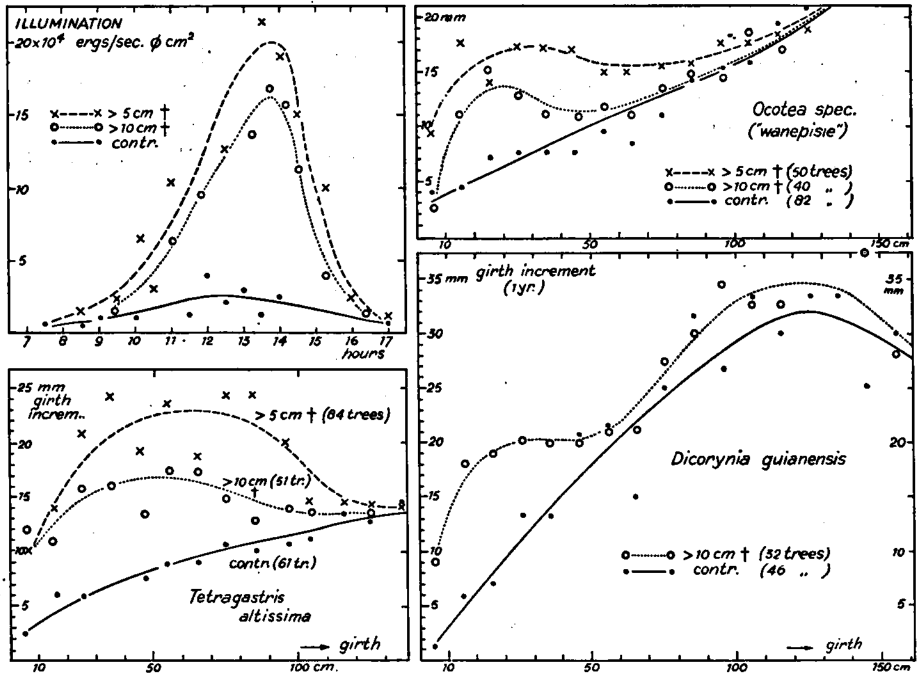


Fig. 70. Forest refining experiment in the Mapane region; girth increment of three species during the first year after poisoning of ca. 70 % of undesirable trees over 5 or over 10 cm d.b.h. Curves for undisturbed controls were added for comparison. The points, through which the curves were drawn free-hand, represent the means for 10 cm girth classes, and are placed at the class-midmarks. Illumination at 1½ m above groundlevel was measured with a spherical lightmeter (cf. I.3.2): each point represents the arithmetical mean of ca. 50 measurements made at the time indicated (for method of sampling, cf. p. 39). Girth increment was measured, using Dawkins' 10-ring method described in IV.4.

during this first short period of observation was noticed in the smallest diameter classes.

The regeneration of valuable light-demanders which can germinate only in full light (such as *kopie*, *Goupia glabra*) will ask for some other system of natural regeneration.

As was mentioned in IV.6, there are indications that opening of the canopy and a single cleaning of the secondary growth in the clearing will be sufficient to provide adequate stocking with *kopie* poles.

The silvicultural treatments which were carried out in the Mapane experimental area, bear some resemblance to the method which is known as "*l'Uniformisation par le haut*" in the Belgian Congo (e.g., DONIS *et al.* 1951), in that it is also a liberation, especially of the intermediate classes, from lateral and vertical competition for light, which is based in the first place on an examination of the age-class distributions. It differs essentially from such methods of improved natural regeneration which are based on the ability of the seedlings of many of the local "economics" to keep pace with the regrowth of weed species after removal of the shelter, such as, for instance, is the case with the light and medium hardwoods in Malaya (LANDON 1955). Moreover, in Malaya and Br. N. Borneo – in contrast to the majority of the timber species in the Suriname mixed forests – the middle sizes are poorly represented (WALTON 1954).

SUMMARY

During the years 1955–1957 ecological data were collected in various types of mesophytic forest occurring in the northern half of central Suriname (fig. 1). Physiognomically as well as floristically these forests correspond with the type of vegetation which in the other parts of tropical America generally is designed as the "rain forest formation".

The main points of investigation were: (1) the environmental factors prevailing in mesophytic forest, more particularly in connection with the regeneration of tree species; (2) the variation in the floristic composition of some stands belonging to this formation; (3) the mode of regeneration of a number of valuable timber species under natural and artificial conditions.

The first chapter deals with the *general climate* in northern Suriname, which is primarily determined by the distribution of the rainfall. Although (except for a narrow drought belt along the coast) the amount of total yearly reainfall is rather high (fig. 10), the distribution of *precipitation* is distinctly *seasonal* (figs. 4–9). The annual march of atmospheric humidity, air temperature and daily amount of sunshine are strongly correlated with that of the rainfall (figs. 4 and 31). Consequently, for a number of tree species flowering, growth and leaf fall also show a distinct periodicity.

From an ecological point of view especially the *length and the severity of the yearly period(s) of drought* are of importance. To that effect the rainfall data obtained from the meteorological stations were worked up according to a method for estimating the climatic effectivity of precipitation as recommended by MOHR. By this method – instead of using long-term monthly averages – for each year of the period of observation the number of dry months is determined separately (fig. 8, table I). The average number of dry months per year obtained in this way provides the ecologist with more reliable figures than e.g. the Köppen method does, which works with long-term averages and which, moreover, gives no weight to the length of the dry season(s). In default of empirical data on water requirements of the vegetation in Suriname, in our provisional classification of the rainfall stations in N Suriname, a month is called *dry* if the total amount of rainfall is less than 60 mm, and *wet* if the latter exceeds 100 mm. These critical values are based on the outcome of studies carried out elsewhere in the tropics. The 100-mm limit is supported to some degree by data on potential evapotranspiration and discharge values in the basin of the Upper-Suriname R. Applying this method to N. Suriname the average number of *dry* months varies for most of the stations (with exception of the narrow coastal belt) between 1.5 and 1.8 per annum, the *short dry season* comprising 0.3–0.5 months, the *long* one 0.9–1.4 months.

A disadvantage attaching to this method is the obscuring effect of the averaging upon the strong variation in the severity of the yearly period(s) of drought with its intendant fluctuations in the yearly total amount of rainfall. The years of great drought, although occurring exceptionally and irregularly (figs. 6 and 8), probably are a differential factor of considerable ecological significance, which strongly accentuates the differences in available soil moisture existing between soils with different texture and drainage. Moreover, these severe drought periods may exercise an indirect influence upon the vegetation because they create conditions favourable to extensive fires due to human activities. Accordingly, for a better characterization of the dry periods a method was used which is described in detail; an essential feature of this method is the calculation of 30-*days' moving totals*, which are set out graphically in figs. 7–9. A day is tentatively called *dry* when in the preceding 30 days less than 60 mm has been recorded. For the station Republiek the length of the longest yearly dry period varied in the last 50 years between 0 and 105 days (fig. 8).

When the narrow coastal belt is left out of consideration, it appears that the differences in over-all climate, viz. air temperature, total rainfall per annum and climatic effectivity of rainfall (as determined by each of the above mentioned methods), show from an ecological point of view but little variation for the stations in N Suriname; the marked differences in aspect as well as in floristic composition shown by the forest in this region are, therefore, certainly not due to these climatic differences.

In the following chapters of the first part the methods and the results of the micro-climatic studies are discussed. The measurements give a picture of the daily and seasonal variation observed during two full years and during the very dry season of 1957.

Light intensity (in the range of ca 3500–8500 Å) was measured at different heights in the undergrowth of mesophytic and of xeromorphic forest and in a large clearing by means of a spherical photometer (fig. 12). The advantages and limitations of this method are described in I.3.2. The "daylight factor" (i.e. the ratio between illumination inside and outside the forest) in the undergrowth averaged roughly 2 %; for "vertical illumination" (as measured with a plane-surface photocell, held in a horizontal position) this factor approached a value of 3 %. These figures are considerably higher than those recorded for mesophytic forests elsewhere in the tropics. This is partly due to the fact that other investigators only measured "shadow light" and left patches of bright light out of consideration. The argument that the latter should be left out of the sets of readings because (1) the plants of the undergrowth are adapted to low light intensities and are unable to profit by short bursts of strong light, and (2) above a certain limit the photosynthetic effect of light falls off progressively with increasing intensity, are based mainly on the results of laboratory studies on photosynthesis of individual plant organs or cellsuspensions, which should not be applied unreservedly to whole plants or communities. A few preliminary observations made on the growth of seedlings and saplings of woody species from the Suriname forest gave indications that their growth rate does not approach asymptotically to a limiting value lying below that of full sunlight; all of the species which were investigated showed their maximum growth at full light in large clearings. The method of sampling light intensity in the forest that was used in the present study was discussed in detail in I.3.3; samples were systematically taken along random line transects and, accordingly, included both the enormous spatial as well as temporal variations in light intensity that are encountered under a vegetational cover of complex structure (cf. table II and figs. 14–18). Examples of the results of many series of readings are given in table II and are shown as frequency polygons in figs. 15 and 18. For the computation of the average daily march of mean light intensity at different levels in the forest (figs. 16 and 17) the arithmetic averages of the series of readings have been used (cf. I.3.2). *Total illumination*, as measured with the spherical meter, at 1½ m height in mesophytic forest, averaged 12×10^3 ergs/sec/cm^2 ø between 7 and 17 hr. in the dry season (i.e. during days with the sun unobscured during ca. 85 % of the time). For the plane-surface photometer (*vertical illumination*) a value of 8×10^3 ergs/sec/cm^2 was computed. The average daily amount of luminous energy received during such days by the undergrowth (at 1½ m) was ca. 22×10^7 ergs/cm^2 ø (15×10^7 ergs/cm^2 with a plane-surface meter).

A rough estimate of the *spectral composition* of the illumination in the forest was made by means of measurements made with a plane-surface meter and 3 glass filters (red, green, yellow, cf. fig. 11). The results of the measurements (cf. I.3.5) indicated a considerable increase in the blue and violet end of the visible spectrum (ca. 3500–5000 Å) and also an increase in the transmission of the forest canopy in the red part beyond ca. 6100 Å (fig. 19, table III). The *blue-red shade* found in the undergrowth of the Mapane forest, corresponds in its spectral composition to the shade light found in African forests and in some deciduous forests in temperate regions.

Atmospheric humidity and *evaporation* at various levels in mesophytic forest and in the open were discussed in the sections I.4 and I.5. The variation in these factors closely followed the rather irregular pattern of rainfall distribution. Though humidity reaches its minimum during the long dry season, even during this season dry periods are interrupted regularly by periods consisting of one or more humid and wet days, whereas the 8 wettest months are frequently interrupted by successions of rainless days (figs. 7–9, 30, 35). Accordingly it is difficult to find a general characterization of the march of humidity at various sites, and reference must be made to the graphs which are reproduced in figs. 22–36. The humidity records for the various sites and seasons resemble each other in the presence of a long nightly period in which humidity approaches or reaches saturation; even at the height of a very dry season, during the driest day on record, in the forest undergrowth saturation deficit dropped below 2½ mm (rel. humidity rose above 90 %) during 9 hrs. (fig. 28). In the 8 wettest months of the year saturation deficit in the undergrowth (at 1½ m) only rarely rose above a value of 6 mm (rel. hum. fell below 80 %) for more than one hour per day. During drought periods humidity can drop to rather low values even in the mesophytic forest (figs. 26–29, 33) and a saturation deficit of 15 mm (rel. hum. 55 %) was not seldom recorded.

From readings made simultaneously in an extensive clearing in the forest, it appeared that the humidity, evaporation and temperature prevailing in the two stations resembled each other very closely, and accordingly the records for the clearing are considered to represent also the atmospheric conditions just above the canopy. It appeared that in the dry season(s) saturation deficit in the open could rise to considerable heights (figs. 23–25, 28, 32, 33); during the 8 wettest months it seldom reached a value of 12 mm (rel. hum. 60 %) for longer than ¼ hr./day,but during the 2 driest months the deficit generally rose above 12 mm (rel. hum. below 40 %) during at least 1 hr./day, and values above 20 mm (rel. hum. 45 %) were recorded repeatedly during more than one hour on end. During a very dry season a deficit of 22 mm (rel. hum. 42 %) is reached nearly every day for at least 2 hours, thus approaching values similar to those reported in desert regions. Yet, even during the driest periods there is a long night period of high humidity (fig. 28).

Although the atmospheric humidity of the rain forest in Suriname showed a lower average and reached considerably lower minima than e.g. in Africa, it is uncertain whether these differences are real, because the records from other forests probably did not show the full seasonal range of humidity (I.4.5).

During the present study extensive use was made of a set of *Piche evaporimeters*, although we were fully aware of the limited value of data which are obtained with an instrument that by its nature can never fully integrate the effect of various stimuli to water loss in exactly the same manner in which this is done by plants. Yet the use of a mechanical device that measures the integrated effect of the various factors by which transpiration is promoted may provide data of great ecological value, notably for *comparative* purposes. The advantages and limitations of the values obtained with Piche evaporimeters were discussed in I.5.1 and I.5.2. It appeared that the readings of capillary evaporation, especially when averaged over longer periods, may provide a very convenient measure of the *relative* differences in atmospheric humidity in various habitats (figs. 30, 31, 34, 45).

In the forest the seasonal differences in *air temperature* appeared to be rather small (fig. 31), owing to the small range of the seasonal variations in overall air temperature. The daily maximum in the undergrowth of mesophytic forest generally varied between 25° and 30° C, and the minima between 20° and 22° C. The data on air temperature have been summarized in table V, and are shown graphically in figs. 31, 37–40.

The *soil temperature* under forest cover showed only very small seasonal and daily variations, and at a depth of 2 cm presumably never exceeds a value of 28° C. The data have been summarized in table V and are shown graphically in figs. 41–44. The maximum range of temperature observed at 75 cm depth under closed forest remained below 2°. It may safely be assumed that a single reading at this depth may serve as a close approximation of the long-term average of air temperature in the undergrowth. Although being small, the differences in soil temperature under different types of vegetation appeared to provide a useful, integrating index of environmental factors, as illustrated in fig. 45. In a large clearing, where the bare soil is insolated throughout the day, down to a depth of 75 cm the average temperature is considerably more than 25° C, which is the critical value above which destruction of organic matter in the soil is assumed to proceed at a higher rate than its deposition.

In *savanna forest* (xeromorphous forest) intensity of illumination, air temperature, evaporation, saturation deficit and soil temperature were on the average higher than in mesophytic (rain) forest, and showed somewhat greater daily and seasonal amplitudes. During the greater part of the year the differences were very small, but they became larger during the dry season (figs. 22, 27, 31, 36, 37, 39, 44, 45).

The second part deals with the *soils* of the regions where our ecological studies were carried out. Two main geomorphological units are recognizable in this area (II.2.1, II.3): (1) the Old cristalline Basement which is of Pre-cambrian age and which in the area under consideration consists mainly of acidic, highly metamorphous rocks with igneous intrusions; (2) the Zanderij formation which forms the nearly flat "cover landscape" between the Basement and the Coastal Sediment series. The soil studies were chiefly carried out in the transitional zone between the two formation(-series): Mapane- and Upper-Coesewijne-region, and were described in sections II.2 and II.3 (cf. figs. 1–3, 46, 48, 53, 54). In this region the surface of the Basement Complex, which is the remnant of a very old peneplain, is undulating to fairly flat, dissected by numerous creeks and gullies; the soils vary from sandy clays to loamy coarse sands, and for the greater part are covered with (sub-) mesophytic lowland forest. Farther inland, ferrallitic soils – with abundant pisolithic ironstone gravel in the upper horizons – may predominate (II.4) and, locally on plateaus, very shallow soils may cover a sheet of lateritic ironstone (ferrite/ferro-bauxite); the forest (III.4) is sub-mesophytic or (sub-)xeromorphous hill-forest. The "Zanderij sands" which form the oldest non-consolidated sediments, vary from bleached coarse sands (with open savanna/savanna forest) to red sandy clay-loams (with sub-mesophytic forest).

Although it was not our intention to develop a classification of the forest soils found in the lowlands of central Suriname, behind the coastal belt, the soil profiles were divided into 4 groups, depending on the degree of drainage, viz.: impeded, partially impeded, free, or excessive; the ferrallitic soils were kept apart. The distribution of the main types of vegetation on the nutritionally poor soils behind the coastal belt (figs. 46 and 53), presumably is mainly controlled by physical features on which the moisture relations in the soil depend; mesophytic forest is found on mesic sites, viz. on well-aerated soils where water-supply is sufficient throughout the greater part of the year.

The results of the laboratory analyses (tables VI–XI) show that the majority of the soils in the sites studied, though varying in some of their characteristics (structure, texture, topography, parent materials) share many qualities which may be regarded as being typical for the majority of the soils of the rain-forest belt: in texture they are loamy to clayey, but invariably sandy, especially in the upper horizons; they are invariably acid, and are highly deficient in exchangeable bases (particularly in calcium and phosphorus), the kaolinitic clay-kolloid being strongly degraded; their organic-matter content is rather low, and the narrow C/N ratio – which is noted even in the upper horizons – indicates that humification is nearly complete and must take place very rapidly. The soils are practically devoid of weatherable minerals. The parent rock is weathered down to considerable depth and practically is split up in quartz (gravel, sand, silt), kaolin and iron (in the ferro-form in the soil solution and as ferri in coatings on the quartz grains and occasionally in the form of iron concretions). The base exchange capacity of kaolinite being very low, the humus colloids form the only adsorption complex of any importance.

In the Mapane area the soil was sampled systematically in a 50-ha complex with the principal object to ascertain how much the soil varied over a small area, and to what extend variations in soil factors might account for the striking irregularities of the distributional pattern of the trees. As a matter of fact individuals of many species in stands of mesophytic forest show a *non-random distribution* (II.2.3, IV.5, figs. 47, 50, 52, 69); for the majority of the species studied no correlation could be found between their distribution and definite soil properties (II.2.3). Only for two species such a correlation could be ascertained (II.2.3, figs. 50, 52). The peculiar distribution of *Vouacapoua americana* (fig. 46) was discussed in detail in II.2.3. By means of distributional maps for two important tree species in small areas in the Upper-Coesewijne region (figs. 55–57) the very wide ecological amplitude of many tree species of the mesophytic forest is demonstrated.

Combined data on *pore space* and *soil moisture*, being of paramount ecological interest, were determined (by means of constant-volume rings) at different depths of the soil profile for a range of soil types. Methods and results are discussed in section II.6. The porosity figures given in table XII show that the total pore volume in the upper horizons of soils under forest cover is within wide limits independent of the mechanical composition of the soil, and varies between 39–47 % in the main zone of biological activity in the profile. As might have been expected, soil moisture appeared to be strongly correlated with the mechanical composition of the soil (fig. 59, tables XII–XIV). It was made plausible that the occurrence of mottling in the soil profile is connected with an interference in aeration during at least part of the year.

The third part deals with a number of *botanical surveys* carried out in various types of mesophytic forest. Here too it was not the intention to arrive at a sociological classification, but we merely wished to obtain an impression of the order of magnitude of the differences found in these types of forest. To this end sample plots of 0.3–1 ha were divided into squares of 10 × 10 m; in each of these quadrats all trees of 5 cm d.b.h. and over were identified and measured. In 10 % of the quadrats also the undergrowth of 2–4½ cm d.b.h. was enumerated. The method of *quadrating* is described in III.1, in which section also emphasize was laid on the fact that both the size of the sample plots and of the quadrats was arbitrarily chosen; the present investigations are only meant to give a first insight in the order of magnitude of the variability existing in the composition of the forest in a small area (Mapane region) as well as over larger distances.

The studies were carried out in stands of mesophytic forest belonging to the same "floristic" or "natural" area, which means that every species that was encountered in the sample plots has a natural range which is greater than the region under consideration. Yet, as was clearly demonstrated, the floristic composition of the forests which were sampled showed marked differences (tables XVII and XVIII). The heterogeneity of what is supposed to be a single stand on homogeneous (?) soil appears from the tables in which the results of enumerations in neighbouring plots are given (e.g. tables XIX–XXI).

The forest on mesic sites in Suriname is typical mixed forest in that it shows the same pecularities in the distribution of the constituent species as have been described for other equatorial countries: the forest seldom shows any tendency towards single-species dominance; the composition shows distinct variations from place to place; each of the sample plots shows a different assemblage of relatively abundant, "leading" species. The latter do not exceed 20 in number, although in the whole of Suriname there are in the mesophytic forest at least some 200 species of large trees, the majority of which never become codominant. The preliminary study of the forest in Suriname indicates that it might be possible to distinguish geographic regions, within which the forest on mesic sites shows approximately the same group of "leading" species (although within such a region the relative numerical importance of each of the "leading" species shows considerable fluctuations from one place to another). Notwithstanding these heterogeneities the average floristic composition remains more or less the same in such a geographic region.

Although it is admitted that some sort of phytosociological classification of the types of mesophytic forests found in Suriname is necessary, and also that it will be possible after much more data have been collected, the vegetational continuity will render any classification highly arbitrary (III.7). The hylaean forests probably form the best illustration of the principles of species individuality and community continuity, which ideas are familiar as GLEASON's "*individualistic concept of the plant association*".

The preliminary sociological studies in the mesophytic forest in N Suriname scarcely brought us nearer to the methodology upon which some sort of classification – artificial as though it may be – should be based. There seem to be serious difficulties attached to an application of the standard methodology and the concepts of the Zürich-Montpellier school (III.7). Although classifications based on *dominance* have often been regarded as unsatisfactory, for a first, rough characterization of the composition of mesophytic forest in Suriname *abundance* (relative number of individuals above a certain diameter per unit area, i.e. "*density*" according to N-American ecologists) might prove to be the best single expression indicating the relative importance for each species. As was shown, each of the investigated stands was characterized by such a group of "leading" (i.e. numerically preponderant) tree species (table XVII); however, further study certainly will reveal that among this group of "leading" species there are many indifferents of small diagnostic value. For reasons which were discussed in section III.1, the characterization of the relative importance of a species – at least at the present state of the investigations – should be based upon a simple analytical character like the number of established individuals, which should be given preference over some complex "importance index". As a matter of fact, abundance should be calculated using different lower diameter limits for the various socions; for instance, for the species of the upper storeys a lower limit of 25 cm d.b.h. was used.

At the present it is impossible to define exactly what should be understood by an "adequate sample" ("*minimal area*") for sociological purposes; any discussion on the problem of adequate sampling will have to wait till at least the broad principles of a classification of the forests have been defined and till the criteria are determined upon which the distinction of the vegetation units is to be based. If, for instance, a classification is to be based on the composition of the assemblage of the 10 most abundant ("leading") tree species, the present study shows that in certain cases a small sample area of one hectare – provided that it is laid out adequately – in which all individuals over 10 cm are counted (and which is subsampled at 10 % for the undergrowth species over 2 cm d.b.h.) may be sufficient to establish whether a given stand belongs to a certain community or not.

The use of a constant quadrat-size enabled the computation of (quadrat-) *frequency* data (cf. III.1 and table XV).

In section III.2.1 a short description was given of mesophytic forest in the Mapane area as an example of this formation in the northern lowland regions. As was expounded in this section, to my opinion *no well-marked tree strata* are distinguishable in this forest; the woody species were divided into 4 size groups only for the sake of convenience.

In section III.5 a comparison is made between the floristic composition of mesophytic lowland forest in Suriname and that of sample plots in analogous communities in neighbouring countries. The close resemblance between the first and an Amazonian "terra-firme" forest plot becomes particularly striking when the leading species are arranged by families.

During the preliminary *regeneration* studies in the Suriname forest in the first place attention was paid to the diameter-class representations of the trees, especially of the main-storey species (IV.2). As was shown in section IV.2 (table XXIII, figs. 63 and 65), the *diameter-class distributions* of the leading canopy species differ from that of many of the principal species in African rain forests in so far that for the majority of the tree species in mesophytic forest in Suriname the number of individuals decreases logarithmically as the diameter increases. This kind of curve is typical of mixed stands of primary-forest species which are (comparatively!) shade-tolerant during their juvenile stage and which are regenerating rather continuously in climax forest (IV.I, IV.3). Only a few, strongly light-demanding species may show a marked deficiency in the middle and/or lowest diameter-classes (fig. 64).

For the majority of the main-storey species germination is the critical stage in the establishment of regeneration (IV.3); under natural conditions, i.e. on the forest floor, a very large proportion of the tree seeds decays or is destroyed before germination. Only very few main-storey species of primary forest need illumination for the germination of their seeds ("cicatricielles durables", e.g. *Goupia glabra*: IV.2, IV.3). The vast majority of the species of mesophytic forest are shade-tolerant, although this is true only in a relative sense: they need no light for the germination of their seeds and their growth in seedling and sapling stage may be much slower than that of the typical light-demanders, but for all species which were investigated it appeared that their growth in all age-classes is (strongly) stimulated by extra illumination, up to full sunlight (IV.3).

For a number of important economic species measurements of girth-increment were made in various stands of mesophytic forest, using DAWKINS' 10-ring method (IV.4). The results of the measurements show that very large differences in increment between the species and even between individuals of one species (fig. 66) exist, further they demonstrate the seasonal and daily variations in girth (fig. 67) and the fact that rate of growth and local abundance of a species are not necessarily correlated.

Making use of the preliminary results of the ecological investigations, a 50-ha forest-refining experiment was undertaken in unexploited forest in the Mapane region. Here 10 replications in 5 degrees of removal of non-commercial tree species were carried out by killing the trees with arboricides (IV.7).

SUMARIO ESPAÑOL

En la obra presente se exponen los resultados de una parte de las observaciones ecológicas, realizadas durante los años 1955–'57 en algunos tipos del llamado "selva de tierra firme" de la parte central del norte de Surinam, o sea en la selva mesofítica que, fisiognómica y florísticamente corresponde más o menos al tipo de vegetación que en otra parte de la América tropical ha sido clasificado como formación de "selva tropical de lluvia".

Estas observaciones han sido realizadas sobre: 1°. una investigación dirigida hacia los factores constitutivos de dicha formación; 2°. la variedad en la composición floral de algunos complejos forestales pertenecientes a la mencionada formación; y 3°. el modo de rejuvenecimiento de algunos especies de árboles dados bajo diversas circunstancias tanto naturales como artificiales.

En el capítulo primero se resumen algunos factores macro-climatológicos, importantes para la vegetación. En primer lugar se atiende al modo de distribución mensual y anual de la lluvia. El clima del norte de Surinam demuestra una división evidente en estaciones (véase figs. 4–9). La marcha anual cuantitativa de la lluvia recogida se relaciona estrechamente con la de la temperatura y humedad atmosféricas y el número de horas diarias de sol (véase figs. 4 y 31). Por consiguiente la florescencia, el crecimiento y el cambio de hojas en ciertos tipos de árboles muestran una periodicidad manifiesta (fig. 68).

Desde el punto de vista ecológico la duración y la intensidad de la(s) *sequedad(es) anual(es)* son de una importancia máxima. Para un análisis provisional de las cifras pluviales obtenidas en las estaciones meteorológicas se usó un método de cálculo, aconsejado ya por MOHR y aplicado por SCHMIDT y FERGUSON en Indonesia. Este método con el que se calcula el número de meses secos por año tomando el promedio de los mismos que están determinados separadamente cada año (fig. 8, tabla I), representa mejor el verdadero número de tales meses por año que cuando tomamos como base el promedio mensual durante varios años (como indica el sistema de Köppen). En este cálculo provisional de las cifras pluviales se considera como „seco" un mes en que la caída pluvial era menos de 60 milímetros, y como "húmedo" cuando ésta ascendía a más de 100 mm. Estos valores liminares están basados en cifras obtenidas en otras partes de los trópicos, relativas al uso global de agua de la vegetación, y encuentran también algún apoyo en las mediciones de la caída pluvial realizadas en Surinam, y los débitos de la parte superior del Río Surinam. En la parte septentrional de Surinam (exceptuada una estrecha franja costera mucho más seca) el promedio, calculado en la manera susodicha, de los meses secos por año oscila, para la mayoría de las estaciones, entre 1.5 y

1.8. De este promedio, un 0.3–0.5 coincide con el período seco corto y un 0.9–1.8 con el largo.

De este análisis de las cifras mensuales, sin embargo, no se evidencia la gran variedad anual de duración e intensidad de el (los) período(s) igualmente anual(es) de sequedad, ni tampoco la variedad de la caída íntegra también anual, pudiendo ser ambas muy notables (fig. 6). Pero los años extremadamente secos, aunque sólo se dan con grandes intervalos, pueden tener una influencia enorme sobre el desarrollo de la vegetación, sobre todo cuando – como pasa p.e. en Surinam – tales períodos de sequedad acarrean incendios antropógenos. Por lo tanto se aplicó, para una caracterización mejor de los períodos secos, un método, mediante el cual se calcula para cada uno de los 30 días anteriores la cantidad total de la lluvia que ha caído. Estos *totales corrientes de* 30 *días* están dibujados gráficamente en las figs. 7, 8 y 9. Para la comparación de las estaciones en la llanura costera se tomaron también, con este método, una medidas de 60 y 100 mm. como valores liminares.

Tanto la caída pluvial entera durante el año (fig. 5 y 10) como los máximos y mínimos absolutos del total anual, y la duración e intensidad de los períodos anuales de sequedad (véase la tabla I), sólo muestran, para las diferentes estaciones del Norte de Surinam (con excepción de la susodicha franja estrecha costera), desde el punto de vista ecológico unas diferencias relativamente pequeñas. Además, estas diferencias, que en parte son debidas a los distintos períodos de observación, seguramente no podrán ser consideradas responsables de las enormes diferencias fisiognómicas y florísticas en la vegetación del norte de Surinam.

En el resto del primer capítulo se discuten la metodología y los resultados obtenidos de la medición de algunos factores microclimatológicos en distintas alturas en la selva mesofítica de tierra firme y en abras artificiales de la misma.

Las *mediciones de luz* se efectuaron, principalmente, con células fotoeléctricas, montadas en un fotómetro esférico (I.3.2. y fig. 12). La marcha cotidiana de la intensidad de la luz (en onda con un alcance aproximado de 3500–8500 Å) fue medida en distintas alturas de la selva y en un claro grande (figs. 13–18, tabla II). El "factor luz" (es decir la relación entre la intensidad de luz dentro y fuera de la selva) fue, por término medio, en una altura de un metro y medio en días de sol (con 8 horas de sol aproximadamente) de 2 %, empleando el fotómetro. Para la irradiación de los rayos luminosos verticales (medida con una célula plána) dio un factor de 3 %. El hecho de que este valor de aquel "factor luz" sea más alto de lo que generalmente se indica para una selva tropical lluviosa, se explica en parte por el que otros investigadores, en general, sólo solían medir la "luz de la sombra", mientras que en la selva de Surinam se tomaron "muestras" a lo largo de líneas de medida de la intensidad de luz, en cuya ocasión las mediciones realizadas en maculas de luz fueron incluídas en el cálculo del promedio aritmético de una serie de mediciones.

Los resultados de tal serie se pueden dibujar gráficamente en la forma de una fracción de frecuencia (figs. 15 y 18). En el cap. I.3.3 se expone por qué se dio la preferencia al método aquí usado antes que a una medición que evite medir, intencionadamente, la luz intensa que entra por aberturas en el dosel de copas. Entre otras cosas se llama la atención hacia el hecho de que pareció existir una correlación casi rectilínea entre el crecimiento y la intensidad de luz, sin que pareciera manifestarse una saturación de la misma antes de llegar al alumbrado máximo dado, (es decir: luz normal del día).

Una impresión global de la *composición espectral* de la luz de la selva se consiguió midiendo con una célula fotográfica plana y 3 filtros (véase fig. 11). Resultó que la luz de sombra de la selva era relativamente más rica en rayos rojos (> 6100 Å) y, sobre todo, azules (< 5000 Å) que la luz de un claro (fig. 19, tabla III). La mutua relación de las intensidades en las varias regiones espectrales depende principalmente de la parte que tiene la luz difusa del firmamento en la irradiación total (fig. 20).

La humedad del aire, *la evaporación* y la *temperatura* fueron medidas, durante casi dos años y medio, en distintos lugares tanto de la selva pluvial como de la de sabana y en una gran abra de aquélla. Aunque resultó que durante el día pueden darse grandes diferencias en la *humedad del aire*, sin embargo, se evidenció que todos los lugares dentro y fuera del bosque se caracterizan, durante todo el año, por un largo período de noche en que el aire está casi o completamente saturado de vapor de agua (figs. 22–29). Resultó también que la humedad del aire, medida en distintas alturas de la selva mesofítica, puede descender hasta valores notablemente más bajos que los que constan en la literatura para la selva tropical lluviosa de África (fig. 33). Sin embargo, el resultado de varias de las mediciones que se efectuaron en otras partes – y muchas veces sólo durante breves períodos – no da un valor seguro para considerarlas como representativas respecto a la amplitud. Se puso en claro que, en la selva de Surinam, el déficit de saturación en la subvegetación, no pocas veces, puede subir hasta 13 mm. (humedad relativa 60 %) durante más de media hora. En tiempos extremadamente secos (1957 p.e.) fueron alcanzados, repetidas veces, valores de más de 15 mm. (figs. 28, 30, y 32). Inmediatamente encima del dosel y en claros grandes el déficit subió, durante por lo menos 5 horas diarias, en muchos días de la época de lluvia (estación lluviosa), hasta más de cinco mm. (es decir: bajaba hasta 80 % de la humedad relativa), mientras en ese mismo sitio se registraron, muchas veces, en períodos secos, más de 15 mm. (humedad relativa 55 %), durante más de 5 horas diarias. En la época extraordinariamente seca del año 1957 se hallaron a menudo valores de 30 mm. (humedad relativa 30 %).

La *temperatura atmosférica* demuestra, bajo el dosel de copas cerrado, sólo una amplitud diaria poco importante y una anual muy insignificante (figs. 37–40 y tabla V). En la selva cerrada eran muy raros los máximos superiores a 30°, y mínimos bajo 20°.

De la medición de la *temperatura del suelo* (figs. 41–44, tabla V) se concluye, entre otras cosas, que las diferencias de ésta están en estrecha relación con el carácter de la vegetación y que son independientes, dentro de límites amplios, del del suelo. Aunque son pequeñas estas diferencias entre las temperaturas del suelo en los varios tipos de selva y, probablemente, de poca importancia, indirectamente no dejan de tenerla, puesto que resultaron estar en estrecha relación con otros factores micro-climatológicos, los cuales tienen interés desde el punto de vista ecológico (fig. 44). En aquellas abras de la selva através de las cuales el sol puede alcanzar el suelo, la temperatura del mismo puede subir hasta más de 25° durante gran parte del año. Se considera esta temperatura como crítica para la aparición del equilibrio entre formación y destrucción de la materia orgánica. Bajo una selva cerrada la amplitud es tan pequeña que una sola medición a 75 cm., en cualquier momento, da la temperatura media anual (24° aproximadamente) tanto en esta profundidad de 75 cm. como a una altura de metro y medio sobre el suelo con 1° de exactitud.

Se midió la *evaporación* con ayuda de algunos *evaporí-metros de Piche.* Del examen efectuado en cada uno de los lugares correspondientes a los distintos tipos surinameños de vegetación resultó existir una relación constante y sencilla entre cierta cantidad de agua evaporada y el promedio de la humedad del aire en el mismo período (fig. 34). Una vez establecida la relación, el metro de Piche puede muy bien substituir al higrógrafo. El gran valor de los resultados de mediciones de la evaporación capilar en una investigación ecológica introductora estriba, sobre todo, en la posibilidad que ofrecen para la mutua comparación de los diferentes medios ambientes, de la influencia común de los factores ecológicos importantes, de los cuales depende la evaporación (humedad del aire, temperatura, irradiación y movimiento del aire), sin que haga falta analizar separadamente estos factores (figs. 30, 31 y 44).

En el capítulo segundo se describe el *suelo,* encontrado en las regiones donde tuvo lugar la investigación florístico-ecológica. Dentro de esta región hay 2 unidades geomorfológicas posibles, a saber:

1°. el conjunto básico, o sea la montaña precambriana que, principalmente, consiste en esquistos empujados y antiguas batolitas graníticas y diques de dolerita más jovenes, mientras está allanada la montaña a causa de varios ciclos erosivos. Esta montaña, aquí y allí, puede estar cortada notablemente por el sistema de drenaje de hoy;

2°. el suelo que cubre el conjunto básico y que tiene cimas sumamente planas, está constituído por los sedimentos más viejos sin consolidación, indicados geológicamente con el nombre de "formación Zanderij". La capa situada sobre el complejo básico varía desde arcillas hasta limos con arena gruesa, y por la mayor parte lleva selva mesofítica de tierra firme. En terrenos ferro-sialíticos muy drenados (p.e. lateritos con muchas piedras ferruginosas) que se encuentran en las divisorias de agua, se hallan desde bosques sub-mesofíticos hasta sub-xeromórficos (sobre colinas). Los terrenos de la capa que cubre el conjunto básico están formados muchas veces por limos rojos hasta blancas arenas gruesas y lavadas. Éstas son muy permeables y cubiertas por una vegetación xeromórfica; es de suponer que la selva xeromórfica (selva de sabana) constituye el clímax edáfico de este procedimiento. Se cree en la posibilidad de que las variedades de textura no sólo sean causadas por diferencias de la roca madre, sino que, en parte, puedan ser la consecuencia del lavado de arcilla y hierro, cuyo proceso se hubiera acelerado por influencias antropógenas.

No era la intención de llegar a una clasificación de los terrenos forestales en la región examinada, sino solamente tener una primera impresión de la medida en que varíen los distintos factores edáficos. Aunque entre sí difieren bastante en las condiciones físicas (como textura, estructura, capacidad retentiva de agua, porosidad, etc., véase tablas VI–XIV), resultó que todos los terrenos forestales examinados, al sur de la joven llanura costera, se parecían en su gran carencia de materias nutritivas de plantas, la degradación fuerte del conjunto de arcilla y por lo tanto una pH baja, y el porcentaje elevado o muy alto de arena. La roca madre está siempre erosionada hasta una profundidad muy grande y prácticamente descompuesta en sus componentes: cuarzo, (guijas, arena y limo), hierro (en forma de ferro en cuanto a la solución del suelo y en forma de ferri como epidermis, en cuanto a los granos de cuarzo y, a veces agrumado hasta concreciones) y caolines (como arcilla coloidal). La capacidad de adsorción de los caolines es mínima y como complejo de adsorción casi sólo entra en cuenta el humus. La relación C/N resultó ser baja en todos los terrenos debajo de una selva mesofítica (casi siempre 10–15, tabla VII), lo que indica una mineralización rápida y completa de la materia orgánica. Los minerales fáciles de descomponerse se encuentran en estos terrenos muy viejos en cantidades mínimas.

De un cuadro de 50 hectáreas se sacaron, sistemáticamente, muestras para averiguar el orden de variedad en breves distancias, de algunos factores del suelo y correlaciones eventuales con el modelo de difusión de ciertos tipos de terreno de la selva mesofítica. Para 2 de estos tipos se hizó probable tal relación (figs. 50 y 52). A base de algunos otros mapas de difusión (figs. 55–57) se ilustra cómo para otras especies ésta puede ser independiente, dentro de límites muy amplios, de las variedades de un factor edáfico determinado.

Se expresa en cifras el *volumen de los poros* y la *marcha de la humedad* durante períodos secos y húmedos de algunos perfiles de tipos de suelo, notablemente diferentes entre sí. Resultó que, bajo una selva primaria, el volumen de poros en aquella parte del terreno donde hay actividad biológica, es independiente de la textura, dentro de límites amplios (tabla XII).

El tercer capítulo estudia los resultados e algunos *exámenes florísticos* realizados en varios tipos de la selva mesofítica de tierra firme del norte de Surinam. Esta investigación tampoco se efectuó para llegar a una clasificación de las unidades sociológicas, eventualmente presentes, dentro de esta formación, sino solamente para obtener una impresión del carácter de la variedad de la composición florística dentro de este tipo de selva en una parte del norte de Surinam. Con este objeto se dividieron los cuadros de experimentación de una superficie de 0.3–1 hectárea en cuadritos de 10 por 10 metros en los cuales fueron clasificados y medidos todos los árboles de 5 cm. de diámetro y más. La mayoría de las veces se incluyó también en un 10 % de los cuadritos, la subvegetación de un diámetro de 2 hasta 4½ cm. Del resultado de un examen de especies sobre una superficie de 5 hectáreas y media se da la lista entera (tablas XV y XVI), mientras para las demás, las tablas (XVII–XXII) sólo suministran los números de las especies más abundantes. Aunque no predomine una especie determinada en la selva pluvial tropical mixta, sin embargo se caracteriza un tipo de selva por un grupo relativamente reducido de especies pertenecientes a varios estratos, que, en conjunto, forma más de la mitad del número total de los árboles. Este grupo de especies "directivas" resultó muy diferente, en cuanto a composición, para cada uno de los terrenos forestales examinados, aunque éstos pertenecen a una sola "área florística".

Todavía no se puede esperar una contestación a la pregunta de si, y en caso afirmativo, cómo, se puede hacer una clasificación sociológica de la selva mesofítica de Surinam, a causa del número reducido de conjuntos forestales analizados. Solamente se comprobó que, en efecto, hay grandes diferencias florísticas dentro de dicha formación y que parece probable que estas diferencias existan entre otras cosas a consecuencia de factores edáficos. A un análisis sociológico pone trabas el gran número de especies y la heterogeneidad notable en todos los estratos dentro de una sola parcela. Esta heterogeneidad que ofrece a la selva un aspecto calidoscópico, es debida, probablemente, en primer lugar a circunstancias fortuitas, p.e., al modo de diseminación, formación de claros etc. A pesar de la composición sumamente heterogénea resultó posible obtener una valoración razonable de la composición de un complejo forestal calculando los distintos factores en cuadros de experimentación de una hectárea solamente. Bien es verdad que no se encuentra en tal superficie pequeña todas las especies que se dan en la superficie entera, pero semejante inventario ofrece una característica del complejo en cuestión en el sentido de que la composición del grupo de especies representativas pueda resultar de él con bastante exactitud.

Es posible que, precisamente entre aquellas especies que nunca adquieren un grado alto de abundancia, se encuentren algunas que más tarde resultarán tener un gran valor diagnóstico. Por de pronto parece ser más lógico tratar de basar una clasificación de la selva mesofítica del norte de Surinam en la composición de las especies más abundantes del grupo. Una clasificación basada, en primer lugar, en el predominio, fue aplicada ya, y con algún éxito, en la Guyana inglesa. Para la valoración del "éxito ecológico" de una especie determinada de selva, se propone usar la abundancia de aquellos ejemplares de una especie que han pervivido por unidad de superficie. Para las especies de los varios estratos hay que tomar diámetros minimos de tronco, fijados arbitrariamente. Para las especies del estrato superior se propone p.e. un diámetro de tronco de 25 cm., por el hecho de que éste es el promedio de aquellos árboles cuya copa ha llegado al dosel, probando con esto que han ganado la lucha de concurrencia con ejemplares de otras especies.

Se discute por qué se prefiere el uso de una sola cualidad como p.e. abundancia a "índices de importancia", compuestos, e.o.c. por una combinación de abundancia, masa y frecuencia cuadrada.

Probablemente será imposible clasificar la selva mesofítica del norte de Surinam siguiendo el método de la escuela antigua franco-suiza. En lugar de estar compuesto de unidades discretas fitosociológicas, comparables con asociaciones, parece que la selva pluvial tropical de Suramérica es más bien un "continuum" grande en el cual las especies se extienden más o menos independientes entre sí. En este aspecto sería comparable la selva con la frondosa mesofítica, rica en especies, de los estados del noreste de América del Norte, que, ahora, se considera también como un "continuum" en el que las especies demuestran una difusión independiente entre sí.

En el capítulo cuarto siguen los resultados de la investigación que tenía relación directa con el rejuvenecimiento de la selva en su conjunto, y particularmente, el de algunos tipos de madera. Se discute también las divisiones de clases de diámetros de ciertos complejos de selva. Resultó que la "pirámide de población" de la mayoría de los tipos de árboles de la selva de Surinam tiene una forma que es característica para populaciones que se están rejuveniciendo continuamente, como se encuentran p.e. en una selva-climax con una composición medial, estable de especies (tabla XVIII, fig. 63). En este aspecto esta selva (como también la pluvial tropical de otras partes de Suramérica) difiere fundamentalmente de semejantes selvas en Ásia o África donde, para muchos especies del estrato superior, las clases de edad más jóvenes y medias o una de ambas, son relativamente escasas c.q. faltan. En Surinam tal situación solamente se encuentra en algunos especies que obligatoriamente necesitan luz para poder rejuvenecerse, así que nada más que en grandes claros de la selva (fig. 64). De unos 10 especies de árboles se fijó, durante 2 años, el aumento mensual del perímetro en las distintas clases de grueso (figs. 66, 67), con ayuda de un método sencillo mediante el cual es posible medir el perímetro hasta en 0.5 milímetro de exactitud. Con los resultados de las mediciones de crecimiento se puede reducir aproximadamente, entre otras cosas, las clases diamétricas a las de edad. Algunos tipos demuestran una periodicidad evidente en el crecimiento del grueso, que se relaciona con la de la caída pluvial (fig. 68).

Se tratan también algunos resultados provisionales de un experimento de mejoración de la selva (que DAWKINS llama "refinamiento"), a base de la forma de divisiones de clases diamétricas y los resultados de la investigación de germinación y crecimiento. Se estudia aquí la influencia de varios grados de posición de luz (obtenida, destruyendo selectivamente los tipos indesables con ayuda de una arborícida de contacto) en el aumento de masa de algunos tipos de madera valiosos para el mercado.

REFERENCES

ALLEE, W. C. (1926) Measurement of environmental factors in the tropical rain-forest of Panama. Ecology 7: 273–302.

ASHTON, P. S. (1958) Light intensity measurements in rain forest near Santarem, Brazil. J. Ecol. 58: 65–70.

AUBRÉVILLE, A. (1938) La forêt coloniale; les forêts d'Afrique équatoriale. Bois & For. trop. 2: 24–35.

——— (1949) Climats, forêts et désertification de l'Afrique tropicale. Paris.

——— (1950–'51) Le concept d'association dans la forêt dense équatoriale de la basse Côte d'Ivoire. Bull. Soc. Bot. Fr. 97: 145–58.

ATKINS, W. R. G. (1932) The measurement of daylight in relation to plant growth. Emp. For. J. 11: 42–52.

ATKINS, W. R. G., H. H. POOLE & F. A. STANBURY (1937) The measurement of the intensity and the colour of the light in woods by means of emission and rectifier photo-electric cells. Proc. Roy. Soc. London Ser. B. 121: 427–50.

BACON, E. M. (1939) The use of photoelectric cells for sampling light in forest stands. J. Forestry 37: 55–60.

BAKER, J. R. & T. H. HARRISSON (1936) The seasons in a tropical rain-forest. Meteorology. J. Linn. Soc. (Zool.) 39: 443–63.

BAKKER, J. P. (1954) Über den Einflusz von Klima, jüngerer Sedimentation und Bodenprofilentwicklung auf die Savannen Nord-Surinams (Mittelguyana). Erdkunde (Bonn), B: 89–112.

——— (1957) Quelques aspects du problème des sédiments corrélatifs en climat tropical humide. Ztschr. f. Geomorph. 1: 1–43.

——— (1957) Zur Entstehung von Pingen, Oriçangas und Dellen in den feuchten Tropen, mit besonderer Berücksichtigung des Voltzberggebietes (Surinam). Abh. Geogr. Inst. d. Fr. Univ. Berlin, 5: 7–20.

BEARD, J. S. (1944) Climax vegetation in tropical America. Ecology 25: 127–58.

——— (1946) The natural vegetation of Trinidad. Oxf. For. Mem. 20.

BEIRNAERT, A. (1941) La technique culturale sous l'équateur. I. Publ. I.N.E.A.C., sér. techn. 26.

BARNARD, R. C. (1950) The elements of Malayan silviculture. Mal. For. 13: 122–9.

——— (1955) Silviculture in the tropical rain-forest of Western Nigeria compared with Malayan methods. Mal. For. 18: 173–90.

BLACK, G. A., TH. DOBZHANSKI & C. PAVAN (1950) Some attempts to estimate the species diversity and population density of trees in Amazonian forests. Bot. Gaz. 111: 413–25.

BRAAK, C. (1928–'29) Het klimaat van Nederlands Indië. Verh. Kon. Magn. & Meteor. Observ. Batavia.

——— (1935) Het klimaat van Nederlands West Indië. Med. & Verh. Kon. Ned. Meteor. Inst. 36.

BROWN, W. H. (1919) Vegetation of Philippine mountains. Manilla.

BÜNNING, E. (1947) In den Wäldern Nord-Sumatras. Bonn.

CAIN, S. A. (1947) Characteristics of natural areas and factors in their development. Ecol. Monogr. 17: 185–200.

CAIN, S. A., G. M. DE OLIVEIRA CASTRO, J. MURÇA PIRES & N. T. DA SILVA (1956) Application of some phytosociological techniques to Brazilian rain-forest. Am. J. Bot. 43: 911–41.

CARTER, G. S. (1934) Reports of the Cambridge Expedition to British Guiana, 1933. J. Linn. Soc. (Zool.) 38: 579–89.

CARTON, P. (1930) Température du sol à Phu-Lien (Tonkin). Bull. Econ. de l'Indochine. C. R. d. Trav. 1928–'29: 688^B–707^B.

CHEVALIER, A. (1953) Ce qu'il faut penser des associations végétales du systhème Braun–Blanquet. Rev. Int. Bot. Appl. Agr. Trop. 33: 323–4.

COHEN, A. & J. J. VAN DER EYK (1953) Klassificatie en ontstaan van savannen in Suriname. Publ. no. 11, Centr. Bur. Luchtkaart. Paramaribo.

COOMBE, D. E. (1957) The spectral composition of shade light in woodlands. J. Ecol. 45: 823–30.

CORBET, A. S. (1935) Biological processes in tropical soils, with special reference to Malaya. Cambridge.

CURTIS, J. T. & R. P. MCINTOSH (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476–97.

DAVIS, T. A. W. (1941) On the island origin of the endemic trees of the British Guiana peneplain. J. Ecol. 29: 1–13.

——— & P. W. RICHARDS (1933–'34) The vegetation of Moraballi Creek, British Guiana. J. Ecol. 21: 350–84; 22: 106–55.

DAWKINS, H. C. (1953) Trials of non-toxic arboricides in tropical forest. Emp. For. Rev. 32: 253.

——— (1955) The refining of mixed forest: a new objective for tropical silviculture. Emp. For. Rev. 34: 188–191.

——— (1956) Rapid detection of aberrant girth increment of rain-forest trees. Emp. For. Rev. 36: 449–54.

DONIS, C. & R. MAUDOUX (1951) Sur l'uniformisation par le haut. Publ. I.N.E.A.C., Sér. Scient. 51.

DOST, H. & J. HOOIJSMA (1957) Overzichtskartering Sara-Zanderij. Versl. & Rapp. Dept. Landb. & Visserij, Surin. 19.

EMBERGER, L. (1950) Observations phytosociologiques dans la forêt dense équatoriale. Arch. Inst. Grandducal Luxemb. 19: 119–123.

——— (1954) Observation sur la fréquence en forêt dense équatoriale (Côte d'Ivoire). Vegetatio 5/6: 169–76.

———, G. MANGENOT & J. MIÈGE (1950a) Existence d'associations végétales typiques dans la forêt dense équatoriale. C. R. Séan. Acad. Sci., Paris, 231 (14): 640–2.

———, ——— & ——— (1950b) Caractères analytiques et synthétiques des associations de la forêt équatoriale de la Côte d'Ivoire. C. Rend. Séan. Acad. Sci., Paris, 231 (7): 812–4.

EVANS, G. C. (1939) Ecological studies on the rain forest of Southern Nigeria. II. J. Ecol. 27: 436–82.

——— (1956) An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks, including an analysis of data from rain forest in Southern Nigeria. J. Ecol. 44: 391–428.

EYK, J. J. VAN DER (1957) Reconnaissance soil survey in northern Surinam. Thesis, Wageningen.

FANSHAWE, D. B. (1952) The vegetation of British Guiana, a preliminary review. Imp. For. Inst., Oxf., Inst. Pap. 29.

——— (1954) Forest types of British Guiana. Carib. For. 15: 73–111.

GERMAIN, R. & C. EVRARD (1956) Étude écologique et phytosociologique de la forêt a Brachystegia laurentii. Publ. I.N.E.A.C., Sér. Scient. 67.

GLEASON, H. A. (1926) The individualistic concept of the plant association. Bull. Torrey Bot. Club. 53: 7–26.

HADDOW, A. J., J. D. GILLET & R. B. HIGHTON (1947) The mosquitoes of Bwana County, Uganda. V. Bull. Ent. Res. 37: 301–30.

HARDY, F. (1936) Some aspects of tropical soils. Trans. 3rd. Int. Congr. Soil Sci. (Oxf.), 2: 150–63.

———— (1945) The soils of South America. In "Plants and plant Science in Latin America" (ed. F. Verdoorn), Waltham, Mass.

———— (1946) Seasonal fluctuations of soil moisture and nitrate in a humid tropical climate. Trop. Agr. Trin. 23: 40–9.

———— & R. R. FOLLETT–SMITH (1931) Studies in tropical soils II. J. Agr. Sci. 21: 739–61.

———— & L. F. DERRAUGH (1947) The water and air relations of some Trinidad sugar-cane soils I. Trop. Agr. Trin. 24: 76–87.

HARRISON, J. B. (1934) The katamorphism of igneous rocks under humid tropical conditions. Imp. Bur. Soil Sci., Harpenden.

HEINSDIJK, D. (1953) Begroeiing en luchtfotografie in Suriname. Publ. Centr. Bur. Luchtkaart., Paramaribo, 13.

HEIM, R. (1950) Sur la forêt de Basse Côte d'Ivoire. Bull. Soc. Bot. Fr. 97: 162–7.

JENNY, H. (1930) A study of the influence of climate upon the amount of nitrogen and organic matter content of soils. Miss. Agr. Expt. Stat. Bull. 152.

JONES, E. W. (1950) Some aspects of natural regeneration in the Benin rain forest. Emp. For. J. 29: 108–24.

———— (1955–'56) Ecological studies on the rain forest of Southern Nigeria. IV. The plateau forest of the Okomu forest reserve. J. Ecol. 43: 564–94 and 44: 83–117.

KARSTEN, G. (1924–'26) Das licht im tropischen Regenwalde. Vegetationsbilder, Reihe 16, Hft. 3.

KRAMER, F. (1933) De natuurlijke verjonging in het Goenoeng-Gedeh-complex. Tectona, 26: 156–85.

KRAMER, C., J. J. POST & J. P. M. WOUDENBERG (1954) Nauwkeurigheid en betrouwbaarheid van temperatuur en vochtigheidsbepalingen in de buitenlucht met behulp van kwikthermometers (with Eng. summ.). Med. & Verh. Kon. Ned. Meteor. Inst. 60.

LANDON, F. H. (1955) Malayan tropical rain-forest. Mal. For. 13: 30–38.

LEATHER, J. W. (1915) Soil temperatures. Mem. Dept. Agr. Ind., Chem. Ser. 4: 19–84.

LINDEMAN, J. C. (1953) The vegetation of the coastal region of Suriname. The veget. of Surin. I, part 1. Utrecht.

———— & S. P. MOOLENAAR (1959) Preliminary survey of the vegetation types of northern Suriname. The veget. of Surin. I, part. 2 Utrecht.

LOUIS, J. (1939) Rapport de la Divis. de Bot., in: Rapp. ann. pour l'excerc. 1938, p. 17–36. Publ. I.N.E.A.C., hors sér.

McLEAN, R. C. (1919) Studies in the ecology of tropical rain-forest: with special reference to the forests of South Brazil. J. Ecol. 7: 15–54, 121–72.

MANGENOT, G. (1950a) Les forêts de la Côte d'Ivoire. Bull. Soc. Bot. France, 97: 156–7.

———— (1950b) Essai sur les forêts denses de la Côte d'Ivoire. Bull. Soc. Bot. France, 97: 159–62.

MARBUT, C. F. (1932) Morphology of laterites. Proc. & Papers 2nd Int. Congr. Soil Sci., Moscow: 72–80.

MARTONNE, E. DE (1926) Une nouvelle fonction climatique: l'indice d'aridité. La Météor. 19: 449–58.

MAUDOUX, E. (1953) Notes sur les variations de quelques facteurs microclimatiques en forêt dense équatoriale. C.R. XIe Congr. Union Int. Inst. Rech. Forest., Rome: 235–7.

Mijer Drees, E. (1954) The minimum area in tropical rain-forest with special reference to some types in Banka (Indonesia). Vegetatio 5/6: 517–23.

Mildbraed, J. (1930) Probeflächen–Aufnahmen aus dem Kameruner Regenwald. Notizbl. d. Bot. Gart. u. Mus. Berl.–Dahlem 10: 951–76.

Mohr, E. C. J. (1933) De bodem der tropen in het algemeen en die van Nederlandsch-Indië in het bijzonder. Med. Kon. Inst. Trop., Amsterdam, 31, vol. 1.

——— & F. A. van Baren (1954) Tropical soils. Amsterdam.

Murça Pires, J., Th. Dobzhanski & G. A. Black (1953) An estimate of the number of species of trees in an Amazonian forest community. Bot. Gaz. 114: 467–77.

Naegeli, W. (1939) Lichtmessungen in Freiland und in geschlossenen Altholzbestanden. Mitt. Schweiz. Anst. f. d. Forstl. Vers. w. 21: 250–306.

Orth, R. (1939) Zur Kenntnis des Lichtklimas der Tropen und Subtropen sowie des tropischen Urwaldes. Gerl. Beitr. z. Geophys. 55: 52–102.

Ostendorf, F. W. (1956a) Ons klimaat, 6. Over zware regen (On heavy rainfall). Surin. Landb. (Paramaribo) 4: 27–33.

——— (1956b) Ons klimaat, 7 Zonneschijn (Sunshine). Surin. Landb. 4: 96–102.

——— (1957) Ons klimaat, 8. Natte en droge perioden (Wet and dry periods). Sur. Landb. 5: 168–78.

Pendleton, R. L. (1936) Amer. Soil Survey Assoc. 17: 102–38.

Prescott, J. A. & G. B. Stirk (1951) Studies on the Piche evaporimeter. Austr. J. Appl. Sci. 2: 243–56.

Puri, G. S. (1950) Soil pH and forest communities in the Sal (Shorea robusta) forests of the Dehra Dun Valley, U.P., India. Ind. For. 76: 292–309.

Rabinowitch, E. I. (1956) Photosynthesis, vol. II, part 2, chapt. 33.

Raup, H. M. (1947) Some natural floristic areas in boreal America. Ecol. monogr. 17: 221–34.

Richards, P. W. (1939) Ecological studies on the rain forest of Southern Nigeria, I. J. Ecol. 27: 1–61.

——— (1941) Lowland tropical podsols and their vegetation. Nature, Lond. 148: 129–31.

——— (1952) The tropical rain forest. Cambridge.

Scaëtta, H. (1935) Terminologie climatique, bioclimatique et micro-climatique. La Météról. 30.

Schmidt, F. H. & J. H. A. Ferguson (1952) Rainfall types based on wet and dry period ratios for Indonesia and Western New Guinea. Verh. Kement. Perhub. Djaw. Meteor. & Geofisik (Djakarta), 42.

Schols, A. & H. Cohen (1953) De ontwikkeling van de geologische kaart van Suriname. Geol. & Mijnb., Nw. Ser. 15: 142–151.

Schulz, J. P. (1954) Vergelijkend literatuuronderzoek inzake de ecologische consequenties van het "Combinatie-plan Suriname Rivier". Foundat. for Scient. Res. in Sur. & Neth. Ant., Utrecht. (Mimeogr.)

Senstius, M. W. (1930–'31) Agro-geological studies in the tropics. Soil Res. 2: 10–56.

Seth, S. K. (1955) Applied ecology in forestry. Ind. For 81: 456–64.

Seybold, A. (1936) Über den Lichtfaktor photophysiologischer Prozesse. Jahrb. f. Wiss. Bot. 82: 741–95.

Shanks, R. E. (1956) Altitudinal and microclimatic relationships of soiltemperature under natural vegetation. Ecology 37: 1–7.

Shirley, H. L. (1935) Light as an ecological factor and its measurement. Bot. Rev. 1: 355–81.

Smith, J. S. (1936a) Light and the forest canopy. Mal. For. 5: 7–12.

——— (1936b) Measurements of light intensity (corresp.) Mal. For. 5: 206–7.

Steenis, C. G. G. J. van (1941) Oecologische eigenschappen van pionierplanten. Versl. 28ste Verg. Ver. Proefst. Pers. (Ned. Ind.): 195–205.

——— (1958a) Basic principles of rain forest sociology. Proc. Kandy Symposium UNESCO: 159–65.

——— (1958b) Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. Proc. Kandy Symposium UNESCO: 212–8.

STEPHENS, C. G. (1946) Austr. Counc. Sci. Industr. Res. Bull. **206**: 1–21.

VETH, B. M. (1940) Over de lichtbehoefte van planten in de tropen. Bull. Agr. Congo Belge. **31**: 75–81.

VOORDE, P. K. J. VAN DER (1957) De bodemgesteldheid van het ritsenlandschap en van de oude kustvlakte in Suriname. Thesis, Wageningen.

DE VRIES, D. A. & H. J. VENEMA (1954) Some physical considerations on the behaviour of the Piche evaporimeter. Vegetatio **5/6**: 225–34.

WALTON, A. B. (1936a) More investigations on light intensity. Mal. For. **5**: 111–4.

——— (1936b) Measurement of light intensity (corresp.) Mal. For. **5**: 208–9.

——— (1954) The regeneration of Dipterocarp forests after high lead logging. Emp. For. Rev. **33**: 338–44.

WASSINK, E. C. & C. VAN DER SCHEER (1951) A spherical radiation meter. Meded. Landb. Hsch. Wageningen **51**: 175–83.

WIESNER, J. (1895) Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die Vegetations von Wien, Kairo und Buitenzorg (Java). S. B. Akad. Wiss. Wien, Mathem.-Naturw. Cl. **104**: 605–711.

IJZERMAN, R. (1931) Outline of the geology and petrology of Surinam (Dutch Guiana). Thesis, Utrecht.

ZONNEVELD, J. I. S. (1950) Opmerkingen naar aanleiding van analyses van enkele Surinaamse sedimenten. Jaarversl. Geol. Mijnb. D. Surin. 1950.