Frontispiece. Oblique aerial photograph taken in a south-western direction round km 3 of the truck road; the latter runs through the savanna like a white ribbon (cf. fig. 1). In the foreground regenerating *Dimorphandra conjugata* scrub, which to the left passes into the *Cupania* variant of the dry savanna forest. Where the road turns to the right, a part of area 1 is seen (transect 10–60 to 120). The dark patches here are bushes belonging to the *Ormosia costulata* thicket (cf. fig. 21). In the background the bend in the Suriname River, where the Cassipora Creek discharges into the latter (photograph by J. P. Schulz).

VEGETATION AND SOIL OF A WHITE-SAND SAVANNA IN SURINAME

BY

P. C. HEYLIGERS

VERHANDELINGEN DER KONINKLIJKE NEDERLANDSE
AKADEMIE VAN WETENSCHAPPEN, AFD. NATUURKUNDE

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CHAPTER I

SCOPE OF THE INVESTIGATION; REVIEW OF THE RELEVANT LITERATURE

I 1. Introduction

While ascending the Suriname River we note that this stream winds for about ninety kilometres through flat country, but then at a spot called Jodensavanne we suddenly see on the East bank a 25 m high hill. Jodensavanne, at one time a prosperous settlement of Portuguese Jews who had arrived here some centuries ago from Brazil, is now only a post of the Forest Service used for the shipment of timber. From here a truck road leads to that part in the hinterland where the trees are felled. When following this ascending road we learn that the hill we saw from the steamer is a part of a table land projecting into the valley of the Suriname River, and that it consists of an outcrop of granitic gneiss. The remaining part of the precipitous slopes of this table land is found at a greater distance from the river, and is screened from view by forest. After we have gone a distance of 600 m, the red sandy clay-loam soil changes rather suddenly, i.e. within some ten metres and without a difference in height worth mentioning, into a pure white and rather coarse sand. Here the secondary forest gives way to a poorer forest type, and at this place the first dwellings of the Amerindian village Redidoti are found.

After some 200 m we encounter a totally different landscape; here clumps of shrubs of different extent are surrounded by parts bearing a low vegetation consisting of grass, sedges and suffrutescent plants; this growth is so poor that the white sand is everywhere visible (frontispiece). This landscape type, which is called "sabana" by the Amerindians, has a wide distribution in this region. It is, however, not exactly the same everywhere, but appears in various modifications. Some of the principal ones are seen already along the truck road. In some places groups of shrubs combine into a thicket with a height of about 5 to 8 m, often with one or a few species predominating, and with a litter layer covering the soil. In other parts the height of the shrubs decreases, but here the shrub layer is overtopped by slender spiny palms, and the herbaceous vegetation becomes more dense and more varied. The soil surface is always flat and either horizontal or gently sloping towards one of the creeks. However, the two most important creeks crossed by the truck road, viz. the Aboma Creek and the Blakawatra Creek form an exception, for they are cut 18 m deep into the savanna soil and possess rather steep slopes.

About 15 km to the east the road turns to the south, and the aspect of the landscape changes once more. Only in a few scattered spots the white sand with its scrub vegetation is still met, but elsewhere we are surrounded by a rain forest growing on a red soil. This means that we have entered the mesophytic lowland forest of the Mapane Creek region, which was described in "The Vegetation of Suriname", volume II.

I 2. The nature of the investigation

My purpose was to investigate the savanna vegetation mentioned above from an ecological standpoint. To this end field data were collected from April, 1956 to June, 1957.

The work was carried out at the joint instigation of the Institute of Plant Taxonomy and Geobotany of the State University, Utrecht, director Prof. Dr. J. Lanjouw, and of the Surinam Forest Service, director Ir. I. A. de Hulster, Paramaribo. It was financed by WOSUNA (Foundation for the Advancement of Research in Suriname and the Netherlands Antilles), while personnel and material were made available by the Forest Service.

I 3. The term "savanna"

Areas not covered by rain forest, but varying between more or less open woods and treeless plains, have already for a long time attracted the attention of explorers travelling in the northern part of South America and in the Caribbean Islands. The most widely spread vernacular names for such areas seem to be sabana, sabanna, savanna(h), savanne and savane (vide Lanjouw, 1936). Swamps with a herbaceous vegetation are sometimes included in this conception, but landscapes with scattered scrub found on white sand are in the western part of the Guianas called muri-muri, and in the Amazone region (evergreen) caatinga. From a botanical point of view the term "savanna" is therefore as vague as, for instance, the terms "forest" and "marsh". As this was not always recognized, there is a regrettable confusion in scientific literature concerning the use of the term "savanna". This is especially deplorable when the term is used in combination with other ones as e.g. in the "savanna climate" of Köppen, or when it is included in a formation series like the Marsh Formations, as was done by Beard and Fanshawe.

Beard (1953) considered some definitions of the concept "savanna", but that at which he himself arrived, and according to which "savannas are communities in tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present", is also one of those which cover only a part of the vegetation types to which the name "savanna" has been applied in scientific publications. A vegetation like that of the area near Jodensavanne is in Beard's sense no savanna at all, but as it is in publications dealing with the vegetation of Suriname always indicated as such, it seems practically impossible to avoid the term. For this reason I will use it in this paper in its wider sense, viz. for a tropical vegetation which is neither swamp nor primary or secondary forest.

In his paper: "The savanna vegetation of Northern Tropical America" (1953), BEARD gives an extensive survey of non-forest-vegetations, and RICHARDS, in his "Tropical Rain Forest" (1952), describes the savannas from a circumtropical point of view. More recently the savanna has been a subject of discussion in UNESCO symposia on humid tropics vegetation (UNESCO, 1958, 1961). For general information the reader is referred to these publications.

I 4. THE SAVANNA BELT

The savanna area east of Jodensavanne forms part of the so-called "savanna belt", which comprises that part of northern Suriname in which the savannas are concentrated. Aided by geological and pedological criteria, COHEN and VAN DER EYK (1953) distinguished some types among these savannas, and, by means of the knowledge they had obtained in the field, they were able to trace their distribution by the use of aerial photographs. The savannas near Jodensavanna are classed among the savanna types which they called "Zanderij" and "Cassipora", and which are both found on the white sands of the "Dek" (=cover) landscape. This pedological landscape type occurs on the geological formation called "Zanderij", a series of sediments of unequal and mostly still unknown age. The formation is inserted between the protero- and paleo-zoic formations of the Guiana shield on the one side, and the formations of the coastal plain called "Coropina" and "Demerara", which date from the upper half of the Quaternary Period, on the other side (cf. e.g. BAKKER, 1957; BOYÉ, 1959, 1960; O'HERNE, 1958).

I 5. THE VEGETATION OF THE SAVANNAS BELONGING TO THE TYPES "ZANDERIJ" AND "CASSIPORA"

As the savannas belonging to these types, especially those found at the "type locality" Zanderij, are easily accessible, their flora is comparatively well-known. However, as these savannas were regarded as economically of no importance, a more thorough analysis of the vegetation was not made before 1955. Up to that time the Forest Service confined its attention to the forests by which the savanna is surrounded.

In a report of 1936 on a visit paid at the beginning of the dry season to the Zanderij savanna, LANJOUW distinguished some vegetation types, viz. one dominated by *Trachypogon plumosus*, some other ones dominated by *Rhynchospora barbata* but with different accompanying species, and one on very wet spots with *Utricularia* spp., *Burmannia bicolor*, *Lycopodium meridionale*, *Drosera capillaris*, *Paepalanthus polytrichoides*, *Lagenocarpus tremulus* and *Sauvagesia sprengelii*.

In 1955 the Forest Service required a classification of the savanna

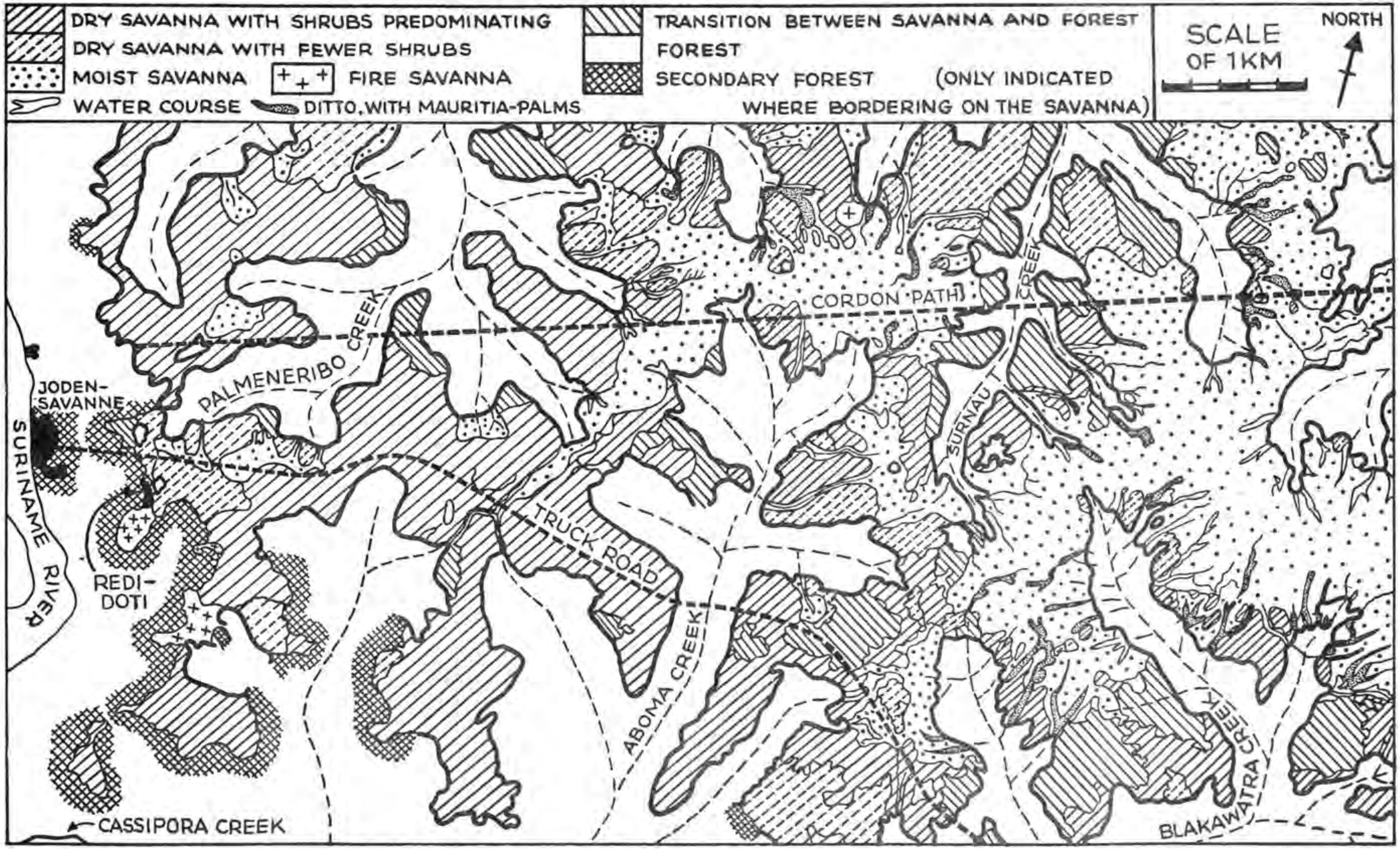

Fig. 1 A. Vegetation map of the Jodensavanne area. *(After Bubberman and Schwellengrebel (1955))*

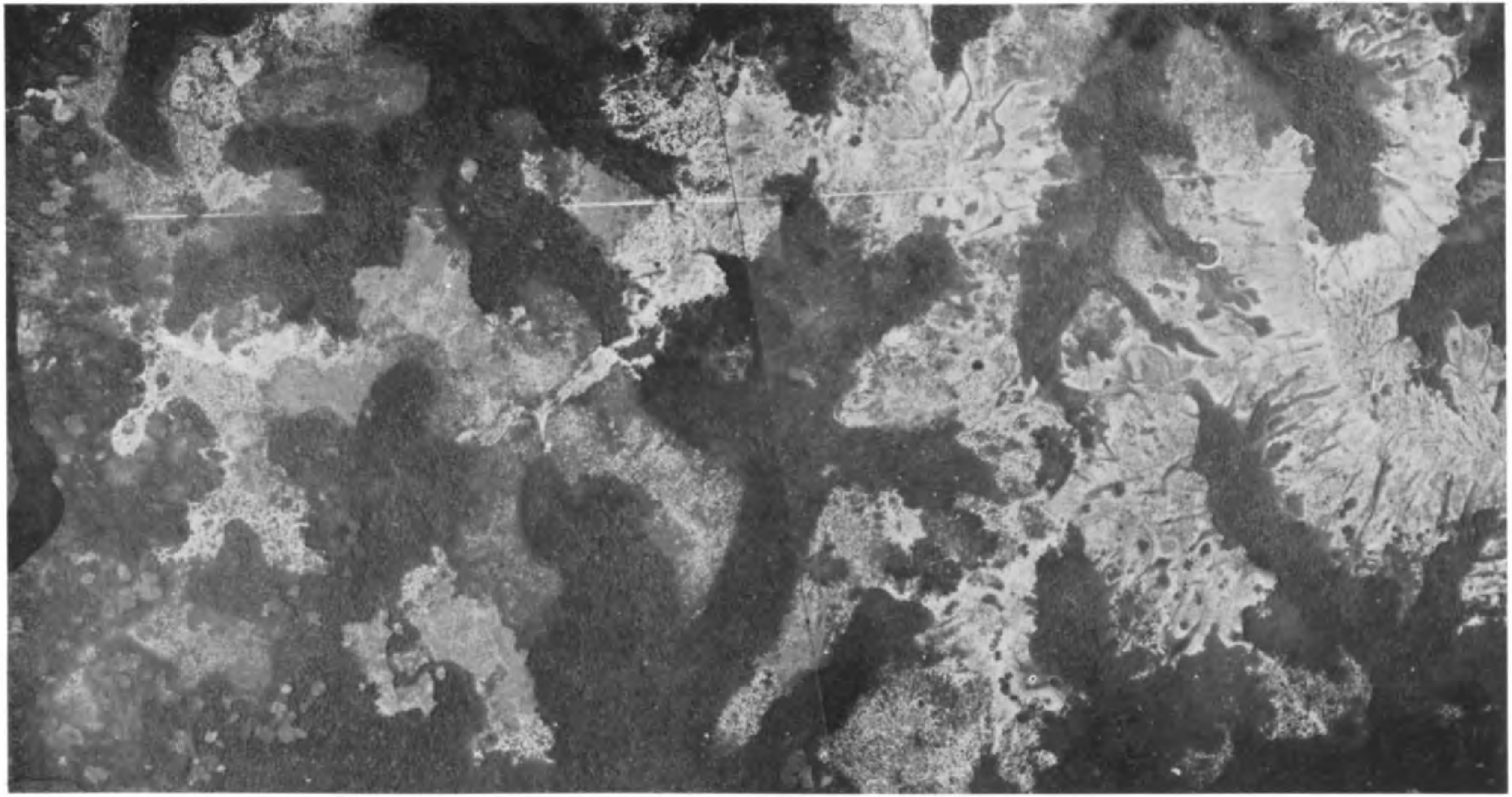

Fig. 1 B. Aerial photograph of the Jodensavanne area, scale 1:40,000.

vegetation, because it hoped to obtain in this way a good base for an intended afforestation with *Pinus caribaea*. To this end the students BUBBERMAN and SWELLENGREBEL then investigated the vegetation of the savannas situated on both sides of the Suriname River. As they wanted a method for identifying the vegetation types shown on aerial photographs (scale 1:40,000), they based their classification of these types on the general aspect of the vegetation and of the soil surface. As their study included the Jodensavanne area, we will summarize their classification here. In addition we will also consider some data obtained from other Forest-Service publications (VAN DILLEWIJN, 1957; LINDEMAN and MOOLENAAR, 1955, 1959). Aerial photographs of the area with the map based on them are reproduced in fig. 1.

1. Tracts along which rain water runs off. These are recognizable on the aerial photographs as narrow dark bands, which together form a more or less dendritic pattern. In the field we find here either a thicket or a vegetation with a large number of grasses. The soil contains peatlike organic matter and shows a hogwallowed structure (so-called "kawfoetoes"). The tract contains a rivulet which only in extremely dry periods ceases flowing. The vegetation on these tracts often shows an emergent layer consisting of about 20 m high *Mauritia flexuosa* palms; these emergent palms are a very characteristic feature of this landscape. The thicket grows higher when the size of the rivulet increases, and it may even pass into a creek forest. A grass vegetation is found more often on the savannas at Zanderij than on those at Jodensavanne. It is very likely dependent on fires for its maintenance.

2. Very wet savanna. On the photographs appearing in the form of spots and bands connected with the tracts mentioned sub 1 or bordering creek valleys, and showing a smooth grey tone. In the field we observe a soggy soil, often with a hogwallowed surface, and densely overgrown by grasses and coarse sedges (e.g. *Lagenocarpus guianensis* and *Becquerelia tuberculata*), *Blechnum indicum*, *Drosera*, etc. and scattered low shrubs. This type is also more common near Zanderij than near Jodensavanne.

3. Wet savanna or wet open savanna. Appearing on the aerial photographs in the form of light grey fields sprinkled with many fine dark specks and some larger dots, occasionally creating a kind of striation. This vegetation type is found on the watersheds and sometimes also where the dry savanna borders on a forest. It consists of scrub varying from knee-deep to a man's height, and may contain e.g. *Licania incana, Clusia fockeana* and *Bactris campestris*, a spiny palm. In the space between them we find a rather thin layer of hygrophilous plants like *Lagenocarpus tremulus* and other Cyperaceae, Eriocaulaceae, *Utricularia* spp., *Drosera* and *Lycopodium*. Grasses play a very subordinate part. Where the rain water stagnates in puddles, the mud sometimes dries up in the form of scales.

The three types dealt with above compose the savannas which COHEN and VAN DER EYK (1953) include in their type "Zanderij".

4. Dry savanna corresponding with the type "Cassipora". This shows on the photographs as a coarser structure than the wet savanna. The sprinkling of dissimilar grey spots on a white underground may become so dense that it is better to speak of a grey underground with many white specks. This means that the dry savanna may be a savanna with few shrubs (dry open savanna) or a savanna in which the shrubs predominate (scrub savanna). The dry savanna is met in areas surrounded by forests as well as in the "axils" between the tracts along which the water runs off. In the field we find all transitions between a savanna with clusters of shrubs reaching more than a man's height and occasionally with a tree among them, separated from each other by sparsely overgrown white sand, at the one end, and at the other end a thicket; in the latter *Dimorphandra conjugata* often predominates. When the *Dimorphandra* scrub recovers after a fire, the pattern shown on the photograph remains the same, but the shade is now light grey (see e.g. the second southern savanna east of the Suriname River in fig. 1). All shrubs show typically xeromorphic features, viz. *Clusia fockeana*, *Licania incana*, *Bombax flaviflorum*, *Swartzia bannia*, *Ocotea schomburgkiana* and *Trattinickia burserifolia*. At the base of the shrubs often epiphytic orchids, mosses and ferns are found, and on bare sand patches *Schizaea incurvata* and *Actinostachys pennula* are seen. On the sand of the dry open savanna only a sparse and poor vegetation of herbs and subshrubs occurs. Here we find e.g. *Lagenocarpus weigelti*, *Bulbostylis conifera* and *B. junciformis*, *Axonopus attenuatus*, *Trachypogon plumosus*, some Eriocaulaceae and *Cassia ramosa*.

5. Fire savanna is a dry and open herbaceous savanna. It appears on the aerial photographs as a light grey stretch representing a grass cover with scattered circular patches indicating scrub surrounded by a border of white sand, the whole being separated from the forest by a sharp boundary line. This type of savanna is found in the vicinity of still inhabited or deserted Amerindian villages. According to VAN DILLEWIJN (1957) the vegetation would consist mainly of Cyperaceae, but this is a mistake, for the predominating species are grasses.

6. "Transition between savanna and forest" or savanna wood. On the photographs one notes almost entirely overgrown areas enclosed by projecting parts of the forest, and gradually reaching almost the same height as the latter. In the field these areas prove to be covered either by a *Dimorphandra* wood recovering after a fire or else by a savanna wood. These woods are not differentiated in stories, 8 to 15 or occasionally up to 20 m high, and consist in their typical form of a dense growth of slender-stemmed trees ("tikitiki-boesi"); the canopy consists of small crowns, and is very regular and closed; on the aerial photographs these woods show a smooth surface. The woody species found in this kind of wood are the same as those occurring in the scrub savanna. These savanna woods are found on dry as well as on marshy soils. On the latter they contain in addition to the other woody species *Clusia nemorosa* and

Humiria balsamifera, and moreover a herb stratum with *Monotagma plurispicatum*, *Rapatea paludosa* and *Ravenala guianensis*.

7. Savanna forest and high savanna forest are found on the slopes towards the creeks and in those places where the white sand occurs in the form of an "island" in a soil of heavier texture. These forests consist of two strata, of which the 25 to 30 m high upper one has many species in common with the adjacent rain forest, whereas in the lower one the typical species of the savanna wood occur; emergents are absent. There is often a tendency to single-species dominance; this enables us to distinguish an *Eperua falcata* forest, a *Dimorphandra conjugata* forest, a *Dimorphandra-Eperua* forest, and a *Dimorphandra-Swartzia bannia* forest. For details on these forests as well as on forests which are not found on the white sands, e.g. creek forest, riverbank forest and high dryland forest (=rain forest), the reader is referred to "The Vegetation of Suriname", vol. I. part 2 and II.

8. Traces of human activity are seen in the photograph reproduced in fig. 1B in the form of houses, trails, a football-field and the "cordonpad" (cordon path); the latter served in the 18th century as a patrol road to protect the plantations in the North against the attacks of maroon leagues. Where this ancient road passes through the savanna, it is still easily recognizable, but where it penetrates into the forest, it is entirely overgrown; however, here too the ditches are still present. In the forest along the Suriname River and along the Cassipora Creek several culture grounds are seen, but the greater part of the latter have been abandoned and are overgrown by secondary forest ("kapoeweri"). Nearly all of them lie outside the white-sand area.

I 6. The soils of the savanna types "Zanderij" and "Cassipora"

At an earlier date the white sands of Zanderij and subsequently also those found elsewhere, e.g. in the Tibiti, the Coesewijne and the Moengo regions, have already been the object of pedological, geomorphological and geological investigations. These studies were often inspired by economical considerations, like plans for afforestation with *Pinus*, for glass manufacture, and for obtaining drinking water. We will insert here a summary of the descriptions of these soils given by Bakker (1951), by Dost and Hooysma (1957), by Van der Eyk (1957), and by Van der Voorde and Hooysma (1956).

The soils on which the savanna vegetations enumerated above are found, belong to the "bleached coarse sand soils". They are moderately to very coarse sands (average particle size 280–1150 μ) with never more than 3 and usually less than 1 % particles with a diameter of less than 16 μ. The coarseness usually increases with the depth, and in deeper layers some gravel is found; on the Tibiti savanna, however, Bakker noted that the sand down to a depth of 2 m was coarse, but that it became medium-grained in the deeper layers.

The colour of these sands is white, which means that the iron has completely been leached out. Estimations made on sand collected at Zanderij II showed

at a depth of 0.9 m 0.14 % iron

at a depth of 2.4 m 0.07 % iron (G.M.D. 1949).

The colour of the top soil varies, according to the nature and the amount of organic matter, from brown to grey. In the subsoil the amount of organic matter decreases, and at a depth of 60 cm the sand is usually perfectly white (content of organic matter 0.06–0.15 %). According to the amount of organic matter in the topsoil four soil types have been distinguished, viz.

1. Slightly humic soils. Topsoil to a depth of 10–15 cm with an average organic matter content of 0.3 % and with a pH varying from 5.0 to 6.0. The uppermost layer with a thickness of a few centimetres is more lightly coloured. This soil type is found on the open savannas.

2. Humic soils. Topsoil to a depth of 40 cm with an average organic matter content of 1.5 % and with a pH varying from 4.2 to 5.0. This type is found under scrub savanna and under savanna wood. The sand is often covered by a 5 cm thick root mat containing a large amount of decaying organic matter. In the *Dimorphandra* wood a mor layer may be present which may reach a thickness of 70 cm or even more.

3. Strongly humic soils. These soils have an average organic matter content of 3.5 % and a pH of 4.0, and they are usually hogwallowed. This type is found on very wet savannas and in the tracts along which the water runs off.

4. Peaty soils. Here the organic matter content may rise to 20 %, and they are provided with an up to 65 cm thick layer of pegasse. This type is found along the creeks. Van der Eyk calls these soils "Creek valley soils", and the less strongly humic soils "bleached dek soils"; together they form what he calls the "Dek" landscape.

The strongly humic and the peaty soils are always poorly drained, but the drainage of the slightly humic and of the humic soils varies from poor to excessive. The drainage is determined largely by the topography of the area; where the watersheds are level and wide, a badly drained "wet" savanna is found, whereas the well-drained parts nearer to the creeks bear a scrub savanna. An estimation with the aid of a level showed that at Zanderij I the top of the watershed lies but 4 m above the creek a kilometre away. In more deeply dissected areas the savanna is better drained, and then the vegetation assumes the form of a dry savanna or of a savanna wood. The degree of drainage is reflected therefore to a large extent in the type of vegetation.

In the vicinity of the creeks the seasonal fluctuations of the phreatic level are comparatively small, viz. about 40 cm. When the groundwater is found at a greater depth, or when the distance to the creek is larger, the fluctuations may exceed 80 cm. This appears from measurements carried out near Zanderij I by VAN DER VOORDE and HOOYSMA.

The bleached coarse-grained sands are usually regarded as extremely poor in plant nutrients. The following micro-chemical analyses are taken from HAMILTON (1945); the organic matter content of this soil was 0.33 %, the pH in water 7.1 and the S-value 0.8 m. aeq. cations/100 g soil.

	K	Ca	Fe[t]	Al	Mn	PO_4	NO_3	Cl	SO_4
Analysis acc. to Morgan	0	< 100	+	1	0	3	< 5	–	–
Analysis acc. to Spurway	0	< 20	–	–	0	< 0.5	< 5	0	0

The opinion that these soils are necessarily poor in plant nutrients is not shared by all investigators. GONGGRIJP and BURGER (1948) are of opinion that the leaching of the white sands can not have been so very strong, as it is possible to grow fruit trees on them, and according to SCHULZ (1960: pp. 122 and 125) the white sands found in the Mapane region under the high savanna forest and even under the rain forest are somewhat poorer in plant nutrients than the heavier textured soils, but by no means so poor as one would be inclined to assume on account of their sterile appearance.

A feature of the white sands which has been mentioned by several authors, but which is still imperfectly understood, is the presence of a dark brown or coffee-coloured hardpan in the subsoil. It may be found at a depth varying between 1 and 5 m, though mostly between 2 and 4 m. VAN DER VOORDE concluded from borings made at Zanderij that this hardpan has a slightly convex shape, i.e. that it lies near the border of the plateau at a greater depth than in its centre and that its thickness varies from 15 to 30 cm, but from the borings carried out by IJZERMAN (1931) we obtain the impression that it may even reach a thickness of 100 cm. Occasionally the hardpan proved to be too hard to penetrate it with the borer. It consists of moderately to very coarse sand cemented by 3.5 to 7 % humus, and occasionally it contains also very fine illuvial material. BAKKER admits that it may be a groundwater laterite, and VAN DER VOORDE (1956) actually regards it as belonging to a groundwater podzol. SCHULZ (1960) observed in the poorly drained white sand under an *Eperua-Dimorphandra* forest in the Wayombo region a humic hardpan in statu nascendi; the latter was found at a depth of 0.5–1 m. BAKKER (1951 et seq.) described the presence of two hardpans in a section made through the soil found under a savanna forest along the Weyne Road near Moengo Tapoe; these pans were about 20 cm thick and were found at a depth of 105 and 225 cm respectively. In the soil near Zanderij Airport several hardpans are said to be present, but exact data with regard to the depth at which they were found, are not available.

The soil underneath the hardpan consists either of clay rich in kaolinite and with or without coarse sand of sedimentary origin (Moengo, Zanderij)

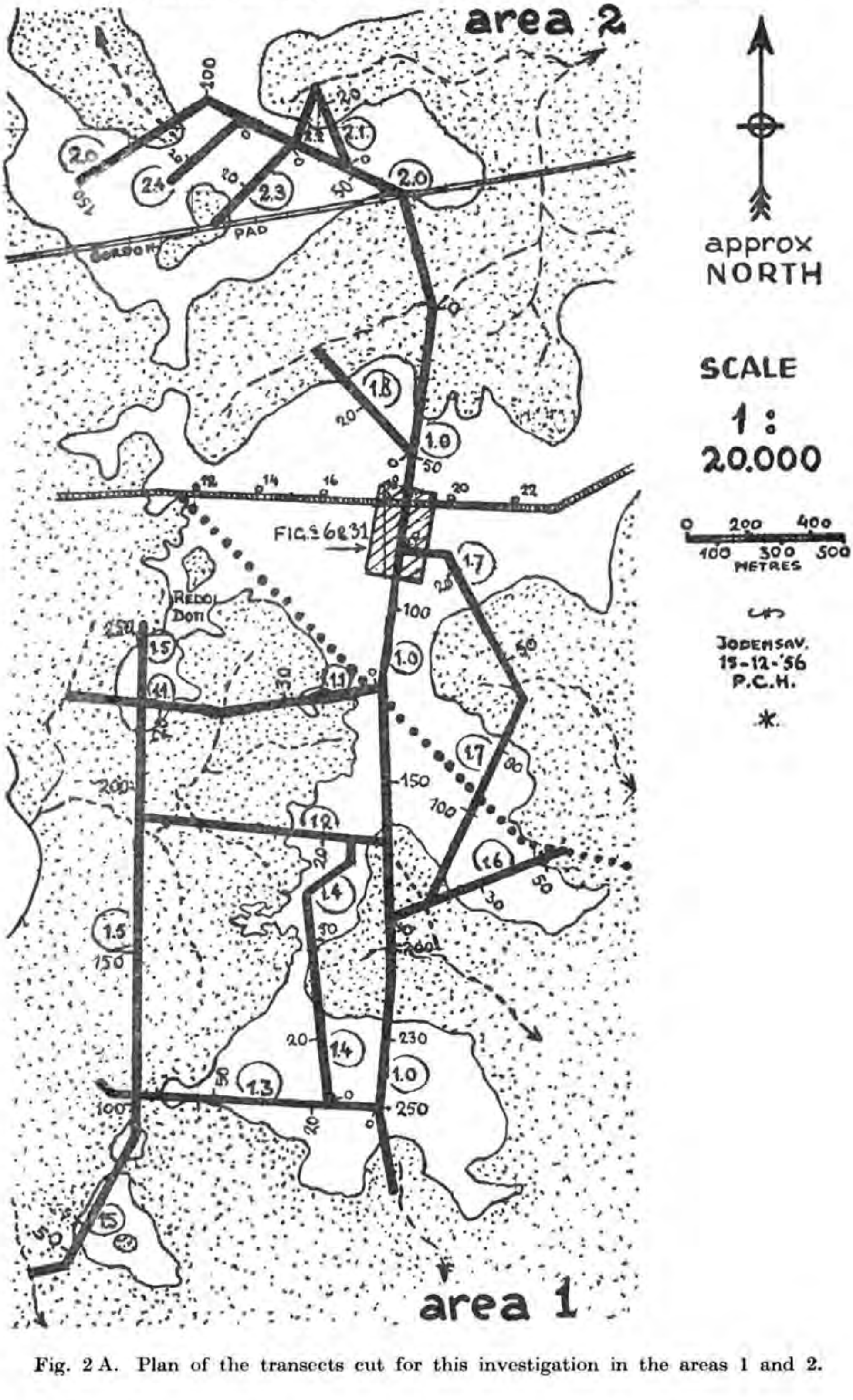

Fig. 2 A. Plan of the transects cut for this investigation in the areas 1 and 2.

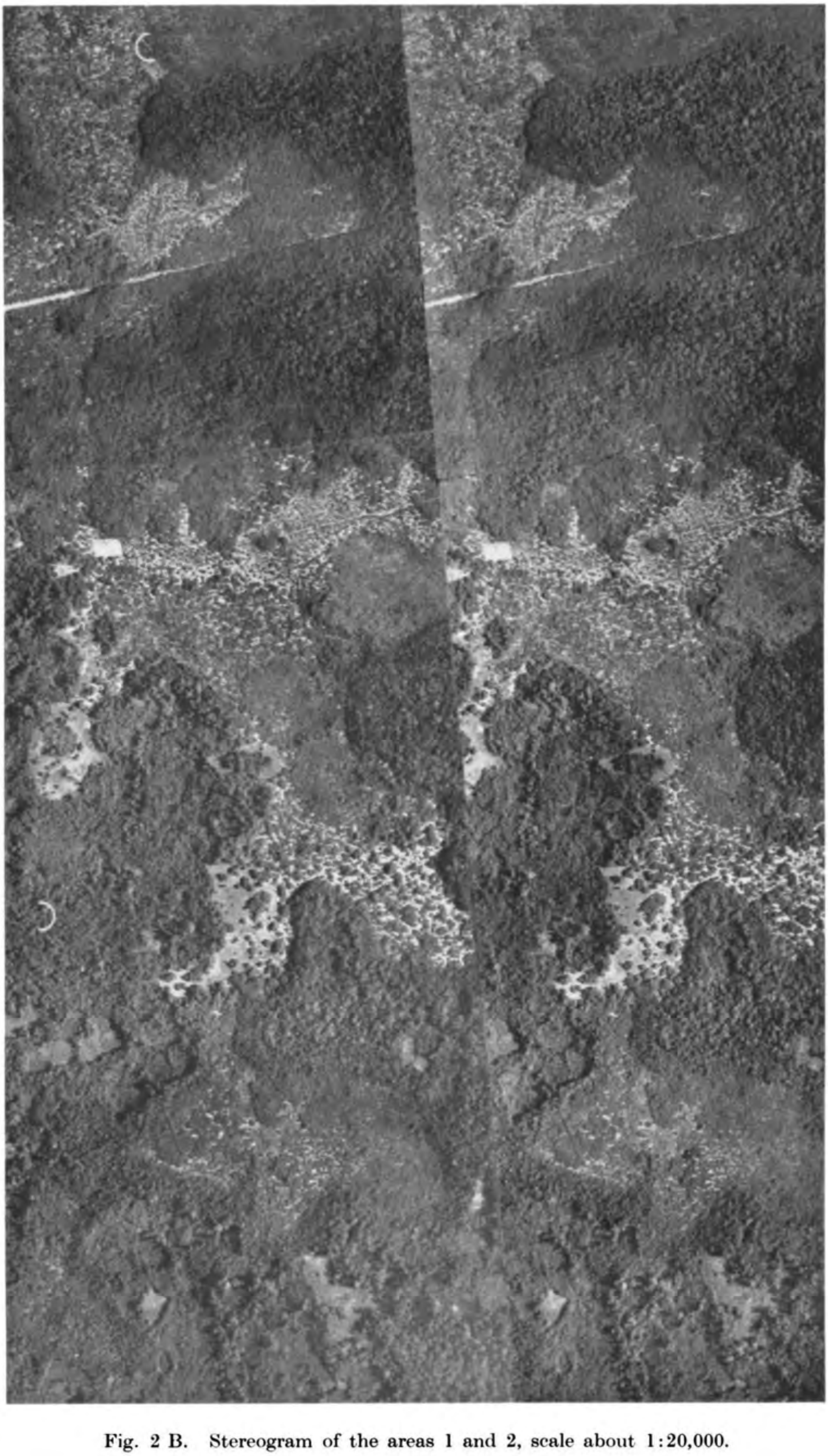

Fig. 2 B. Stereogram of the areas 1 and 2, scale about 1:20,000.

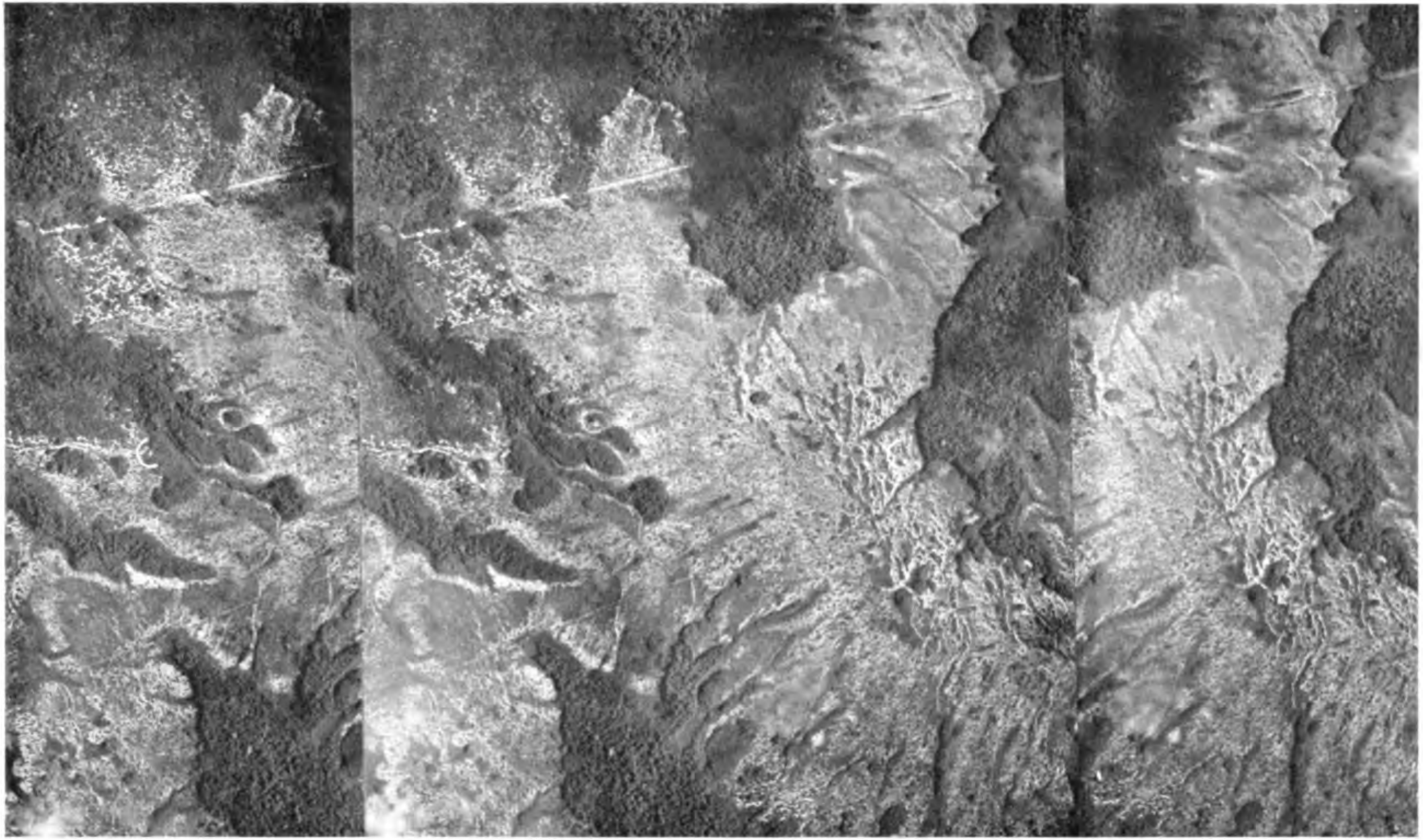

Fig. 2 D. Stereo triplet of area 3, scale about 1:20,000.

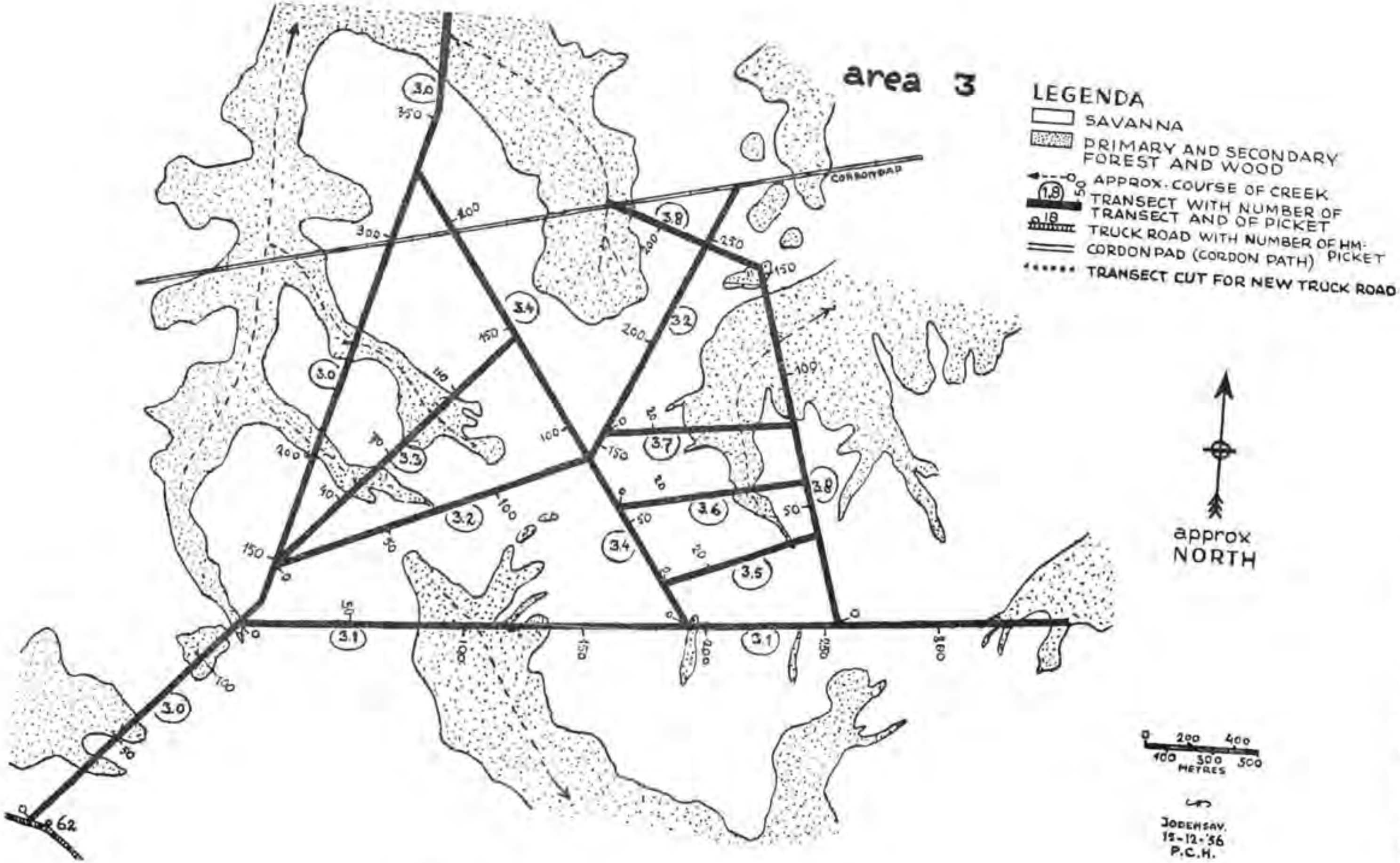

Fig. 2 C. Plan of the transects cut in area 3.

or derived from weathered basement rocks (granite at Zanderij, schists(?) in the Coesewijne region), or else of coarse sands; in the latter case the sands form the upper layer of a series of sandy and clayey sediments, occasionally mixed with vegetal debris and pyrite and extending to a depth of 13 to 21 m, where they rest on the bedrock (Zanderij: d'AUDRETSCH, 1950; IJZERMAN, 1931).

I 7. ORIGIN OF THE SAVANNAS

With regard to the origin of the savannas found on the coarse white sands, opinions differ. From the fact that especially in western Suriname large areas are covered with savanna forest (*Eperua* forest, cf. The Vegetation of Suriname I.2), it is already clear that white sand does not necessarily bear a savanna wood or a lower and more open savanna vegetation.

IJZERMAN (1931) already described parts of the savanna forest, which "seemed destined to give rise to savanna", viz. parts covered with savanna wood or with a dense scrub savanna. He was of opinion that the larger open savannas owed their origin to the fact that the soil had been leached, and that this process had been favoured by the position of these areas (flat watersheds), and perhaps also by erosion or by a rise of the ground-water table. GONGGRIJP and BURGER (1948), on the other hand, are convinced that the savanna owes its origin exclusively to recurrent fires. BAKKER (1951, 1954), COHEN and VAN DER EYK (1953), HAMILTON (1945), LANJOUW (1936, 1954), and LINDEMAN and MOOLENAAR (1955) are of opinion that the condition of the soil is of primary importance. Strong leaching and drainage and large fluctuations in the water content corresponding to the alternation of wet and dry seasons are essential to the development of a xeromorphic vegetation, i.e. of savanna wood and of scrub savanna. The development of a hardpan in the subsoil is by itself not enough to change the forest in a savanna, although it may impede the regeneration of the forest when the latter has been destroyed by fire. Repeated burning too may cause irreversible changes. Because the Amerindians are practising a shifting cultivation, they have within the memory of man been burning down the forests. This is not difficult with the *Dimorphandra* forest, because the thick layer of litter by which the soil is covered, is in the dry period and especially when the latter lasts longer than it usually does, highly inflammable. Under such circumstances even the pegasse layer in the drainage gullies may superficially catch fire!

Therefore, although the climate is in this area not directly responsible for the origin of the savannas, it may favour their development in two different ways. On the one hand the downpours provide the amounts of water by which the soil is leached, whereas, on the other hand, during the rather scarce periods of extreme drought (cf. SCHULZ, 1960) the forest may be devastated by fierce fires (both mentioned by LANJOUW, 1936).

The exposition given above will suffice for the present. Subjects like the distribution of the white-sand savannas outside Suriname and the origin of the white sands themselves have so far been left out of consideration, because they will be discussed in connection with the results of my own studies.

CHAPTER II

PLAN AND METHODS; ACKNOWLEDGEMENTS

II 1. Choice of areas

After a preliminary study of aerial photographs and a reconnaissance in the field, three savanna areas (shown in fig. 2) were selected for more detailed investigation. The first is situated between the source of the Palmeneribo Creek and the lower course of the Cassipora Creek, and comprises the first set of savannas found to the East of the Suriname River. This area contains in the main dry savannas. At the Palmeneribo Creek, however, a small wet savanna is encountered. The second area lies to the North-west of the Palmeneribo Creek; it consists of a wet savanna surrounded by dry open and scrub savanna. The third area is found about 6 km to the East of those previously mentioned and comprises a large set of wet savannas situated on the watershed between the Blakawatra Creek and the Surnau Creek.

These grounds were comparatively easy of access, and it was not very difficult to find one's way on them; they offered, therefore, a suitable opportunity for the study of "typical" vegetations. However, in order to obtain vegetation records of plots that were less arbitrarily chosen, it was deemed desirable to cut some transects through these areas. The position of these transects is shown in fig. 2A and C, which were drawn with the aid of stereograms of aerial photographs on a scale of 1:20,000, and reproduced in fig. 2B and D.

In each area the set of transects were numbered, and each transect was divided in sections of 20 m by means of pickets; the pickets themselves were marked with a figure indicating the distance from the zero point of the transect in multiples of ten metres. So in area 3 a spot on transect 2 situated at a distance of 1,040 m from the starting-point is indicated in this report by means of the symbol 32–104. A stretch of ground is indicated by means of the part of the transect by which it is traversed; 10–228 to 256 means a plot situated in area 1 along transect 0 between the pickets 228 and 256.

II 2. Topographical and pedological aspects

The transects which were cut through the three areas, were levelled by Mr. J. Wekker, at that time attached as geometer to the Forest Service. A low ebb of the Suriname River at Jodensavanne was taken as point zero. Comparison with data found on sheet 22 c of the physical 1:20,000 map, issued by the Central Bureau for Aerial Cartography, shows that our point zero is situated 2 to 4 m above that of the map, i.e. above the average level of the Suriname River near Paramaribo.

Along every transect the composition of the soil was studied with the aid of borings carried out with a so-called Edelman auger provided with large knives; in this way the loose sand was kept together as much as possible. The distance between the successive borings varied from less than 1 m to 100 m, according to the variation that was observed in the composition of the soil. Altogether some 650 borings were made. When the soil was sandy, the boring was continued until an impermeable layer was reached, at least when the presence of ground water or the coarseness of the sand did not prevent this. In the first case the soil below the water-table was "explored" by means of a screw-auger. In this way the presence of a hardpan or of a layer of clay within a distance of 40 cm below the water-table could always be discovered with certainty.

The soil profile was studied also in pits. Five of the latter were dug in white sand, two in red sand, and three in colluvial soil. By supporting the walls of the pits with mats made of palm leaves it was possible to excavate them to a depth of up to 5 m and to prevent their collapse for several months, so that they could be used for a study of the changes in soil-water content. Further information with regard to the deeper layers was obtained in 1960 from borings the results of which were kindly put at our disposal by the Suriname Aluminum Company.

The colour of the soil samples was determined in their original condition as well as after drying; these determinations were carried out by means of Munsell Colour Charts. Analyses were carried out by the soils Laboratory of the Royal Tropical Institute at Amsterdam. The physical fractionation was determined in samples of 20 g, which had been treated with hydrogen peroxide in order to remove the organic constituents. Fractions of a size exceeding 50 μ were obtained by sifting the dried samples; those of a size less than 50 μ were estimated by means of the pipette method. Heavy minerals were estimated in the fraction of 50 to 500 μ after a treatment with concentrated hydrochloric and nitric acid, and after removing the lighter minerals by means of bromoform. Some additional determinations with regard to the morphology of the sand grains were made at the "Laboratoire de Sédimentologie de l'Institut Français d'Amérique Tropicale", at Cayenne. Carbon was estimated by means of the Walkley and Black method, and exchangeable plant nutrients by shaking 10 g soil for two hours with 10 cc of 0.1 n hydrochloric acid, after which Ca, K and Na were determined by spectrophotometry, and Mg, P, NH_4, NO_3, Fe and Mn colorimetrically by the aid of the improved Morgan-Venema method.

The height of the water-table was estimated four to eight times in each bore hole, the estimations being carried out during various parts of the year. In the transects 10–33 to 110, 17–0 to 18 the height of the ground-water level was measured between December, 1956 and the end of June, 1957 three times weekly with the aid of 23 tubes cut from the stems of a *Cecropia* or of bamboo. In the Pinus nursery of the Forest

Service at the Blakawatra Creek during the same period the amount of precipitation and the water level in the creek were measured daily.

II 3. BOTANICAL ASPECTS

Whereas the method of description elaborated by the French-Swiss phyto-sociological school (BRAUN BLANQUET e.a., 1932) can not be applied to the very complex vegetation of the tropical rain forest (cf. SCHULZ, 1960 p. 162 and UNESCO, 1958), it proved quite suitable for the description of the savanna vegetation. It may be summarized as follows. A plot is selected, and in this the number of individuals by which each species is represented and the part of the soil surface that is covered by their projection are estimated, and the way in which they are distributed over the plot is recorded. When the vegetation consists of more than one stratum, each of these strata is surveyed separately. The plot, moreover, must satisfy two conditions: it must not be smaller than the "minimum area" and it must have a homogeneous floristic composition.

In the open parts of the savanna, in which the vegetation consists of a single stratum of herbs, suffrutices and shrublets, it was, as a rule, possible to select a plot which satisfied these conditions. The condition that it must at least possess the minimum area is fulfilled when it appears that in the corresponding vegetation round the plot no new species are found. In opposition to the open parts of the savanna the scrub, especially the *Dimorphandra* scrub, shows a wide range of variability in distribution pattern as well as in stratification (cf. figs. 24 and 25). For this reason whenever selecting plots, the condition that its vegetation must show a homogeneous composition, was considered to be paramount, whereas the requirement that it should not remain below the minimum area, was deemed to be of secondary importance. When the scrub covered an area of limited extent, i.e. in so-called "bushes", the delimitation of the plot was determined by the outline of such a bush. In such cases the canopy, i.e. the part of the vegetation which catches the incident light, is no longer a more or less horizontal stratum, but a dome-shaped one, which along the margin reaches the soil. In such bushes the undergrowth inside the dome represents the shrub stratum. Occasionally the bushes were so small that they contained but a single or a very few individuals, and in such cases it was quite clear that they did not fulfill the "minimum-area" condition. However, as soon as the principal woody species of the savanna were found to be represented in the bush, it was considered to be large enough to be charted according to the precepts of the Franco-Swiss school. When the bushes showed a high degree of similarity, some of them were occasionally united in the same record; this, of course, increased the chance that some of the rarer species would be found.

Finally, the plots of which the records revealed a sufficient degree of similarity in floristic composition, and which, moreover, showed a similar physiognomy and similar dominants, were combined into vegetation types. A survey of the latter is given in the tables 3 and 4. The height of the rectangles that are to be seen behind the species names in the various columns of these tables, indicates a combined estimate of abundance and cover, the base the presence. In case various facies are to be distinguished, the rectangles representing the species which vary in abundance and cover, are divided, the part on the right representing the situation found in the differing facies. The symbol preceding the rectangle indicates whether the plant is able to complete its entire life cycle or only a part of it in the involved vegetation type, and in table 3 also in what stratum of the vegetation it occurs.

The graphs at the head of the columns give information with regard to the the stratigraphy of the vegetation and to the degree of cover, and also to the soil conditions. In the upper graph the range of variability shown by each of the strata is indicated independent from that shown by the other ones. This means that the greatest height of the shrub stratum does not necessarily coincide, as the graph might suggest, with the greatest height of the tree stratum. In the same way the graphs showing the range of variability in the position of the water-table are entirely independent of the data shown in the upper graphs. However, where differences were found which corresponded with differences in facies, the graphs were split up in a similar way as the rectangles which are to be found in the columns themselves and are discussed above.

The forests which border on the savanna were also included in our study, especially in order to obtain some information with regard to the distribution of the species they have in common with the savanna. In plots of 800 sq. metres all tree species were listed to this end by Mr. E. M. HELSTONE, tree-expert of the Forest Service, eventually with the remark "plentiful"; the average and the maximum height of the crowns in the upper storey were also noted. A plot of 800 sq. metres satisfies more or less the demands of the "minimum area" in these forests (cf. LINDEMAN, 1953 p. 85 and LINDEMAN e.a., 1955 p. 25). We know, of course, quite well that such species lists do not give us a fully accurate picture of the composition of the forest, but for our purpose they sufficed. On the base of these species lists various vegetation types were distinguished, of which a survey is given in table 2. The way in which presence and abundance of the various species are recorded in this table is slightly different from that used in tables 3 and 4.

In the vegetations consisting of a single stratum about 150 plots were recorded, in shrub vegetations 125, and in forests 110. The vegetation of the savanna was investigated in area 1 along all the transects, in area 2 along transect 20 between the pickets 50 and 100 and along the transects 21, 22 and 23, and in area 3 along transect 30 up to picket 150, along transect 32 up to picket 250 and along transect 38 between the pickets 180 and 210. Everywhere along the transects species lists were made in the forest. It was not possible to indicate in the tables 2, 3 and 4 all minor variations observed in the vegetation, as this would have been detrimental to the clearness of the graphs. For more detailed information the records on which the tables were based, and which are preserved at the Botanical Museum and Herbarium, Utrecht, should be consulted.

Our study bore a local character. In the absence of detailed plant sociological work on the savannas in other parts of the Guianas (cf. Chapter IV 6) it is impossible to express as yet an opinion on the extent of the areas in which the various vegetation types are found, and on their affinity to vegetation types that are found elsewhere. It would have been desirable to test the value of our classification in the field, for instance by mapping the vegetation. Under the present circumstances nothing can be said with certainty on the rank that is to be assigned to our phyto-sociological units. For this reason we did not consider it advisable to use the terms "association" and "sub-association", or to coin names for our vegetation types according to the nomenclatural schema of the Franco-Swiss school. However, in order to indicate the subdivisions of our "main vegetation types" the use of the terms "variant", "subvariant" and "facies" seemed permissible, as these terms merely indicate a difference in rank, but leave the rank itself undecided. A group of physiognomically as well as floristically related vegetation types is considered to be a "main vegetation type", and the main vegetation types found in the savanna are given names that are derived either from a dominant or from a differential species or, eventually, from a dominant and a differential species, to which is added a term which indicates either its physiognomy or the term "vegetation" when it consists of a single stratum. In naming the vegetation types found in the woods and forests another way was followed, as, on account of the manner in which in these cases the vegetation was recorded, it was not yet possible to use the names of definite species; here, therefore, the names were partly based on the degree of humidity of the soil; this means that in this case we adhered to the use of such long-established names as e.g. "dry savanna wood".

As before my departure to Suriname I had studied (at the Botanical Museum and Herbarium, Utrecht) herbarium material of a large number of savanna plants, I succeeded very soon in recognizing all species of any importance found in the field. Species that were unknown to me, were identified by the staff of the Botanical Museum and Herbarium, Utrecht, with the exception of the Algae, which were identified at the Rijksherbarium, Leiden, by Dr. Josephine Th. Koster. The names used in this publication for the various species are those that were adopted in the "Flora of Suriname", and in some recent revisions. The names adopted by Cuatrecasas in his recent revision of the genus *Humiria* could unfortunately not be used, as I had no satisfactory material for identification; for this reason the specific epithets "*floribunda*" and "*balsamifera*" had to be retained.

II 4. ACKNOWLEDGEMENTS

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During my stay in Suriname the Forest Service placed a house at Jodensavanne at my disposal, lent me a small truck, had the transects through the selected areas levelled for me, and granted me for some weeks the services of a tree-expert. From the Central Bureau for Aerial Cartography also much cooperation was received, whereas the Suriname Aluminum Company sent me the results of some borings which were carried out after I had left the country. To all these Institutions I tender my best thanks.

I must not forget either to remember my amiable relations with the inhabitants of the Amerindian villages Redidoti and Pierre-kondre, of whom several worked for me. Special thanks are due to HARRY and ALFRED DRUIVENTAK for their faithful service and for the devotion with which they performed their task.

The aerial photographs in figures 1 and 2 are reproduced by courtesy of the Central Bureau for Aerial Surveys (C.B.L.) at Paramaribo.

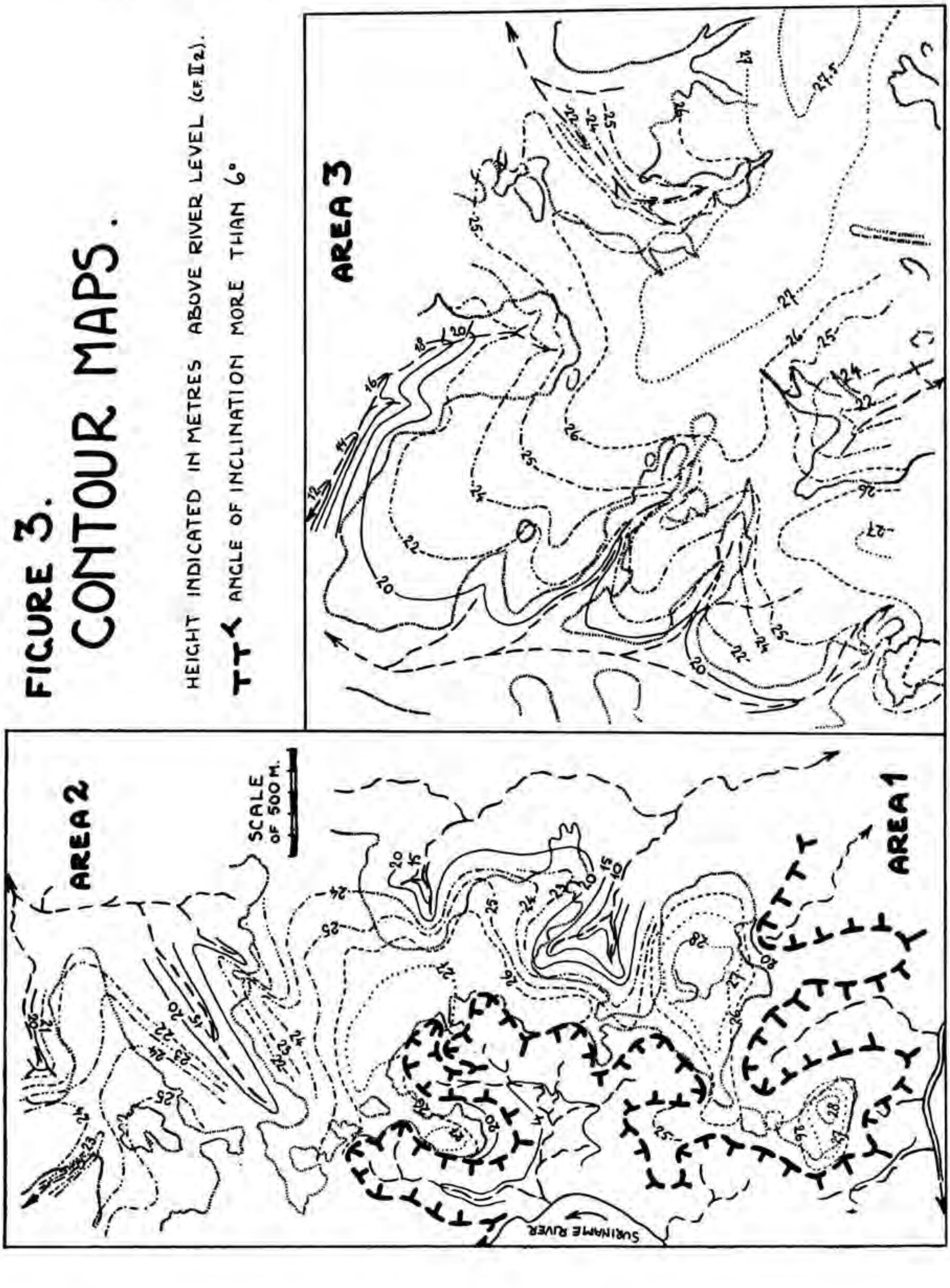


FIGURE 3.
CONTOUR MAPS.

HEIGHT INDICATED IN METRES ABOVE RIVER LEVEL (cf. II 2).
TT ANGLE OF INCLINATION MORE THAN 6°

CHAPTER III

THE SOILS

III 1. Introduction

The contour maps show that the investigated areas possess a level topography, they show a plain shelving from a height of 28 m above river level in the South to 24 m in the North (fig. 3, cf. C.B.L.-map 1:20,000, sheet 22 c and fig. 2). The creeks flowing to the North dissect the terrain but slightly, the creeks running South, e.g. the Blakawatra Creek, cut deeper into the plain. In the western and southern part the savanna plateau descends into the valleys of the Suriname River and of the Cassipora Creek with precipitous slopes.

Medium- to coarse-grained white sands form nearly the whole plain (fig. 4). Their drainage ranges from very excessive to poor. The organic-matter content is low; in the creek valleys, however, a peaty soil may develop. The white sands are to be classed among the "bleached coarse-sandy soils" (I 6).

In area 1 red sands, which sometimes prove to be a little loamy, occur as "islands" in the white sands or as a transition between the white sands and the loamy-sand and sandy-loam soils which are found on the slopes of the Suriname-River valley and on the hills in this valley. They belong to the "coarse-sandy loam soils" (Dost and Hooysma, 1957) or to the "non-bleached cover soils" and "granite-laterite soils" (Van der Eyk, 1957).

Heavier colluvial and alluvial soils occur in the lower parts of the valley. As they are of minor importance for this investigation, I will confine my attention to the soils of the plateau.

In the first sections the features of the white and red sands are described, and attention is paid to local soil formation. In order to explain the general features, in the following sections a theory concerning morphogenesis and related pedogenic processes is developed. The last section of this chapter deals with hydrological features.

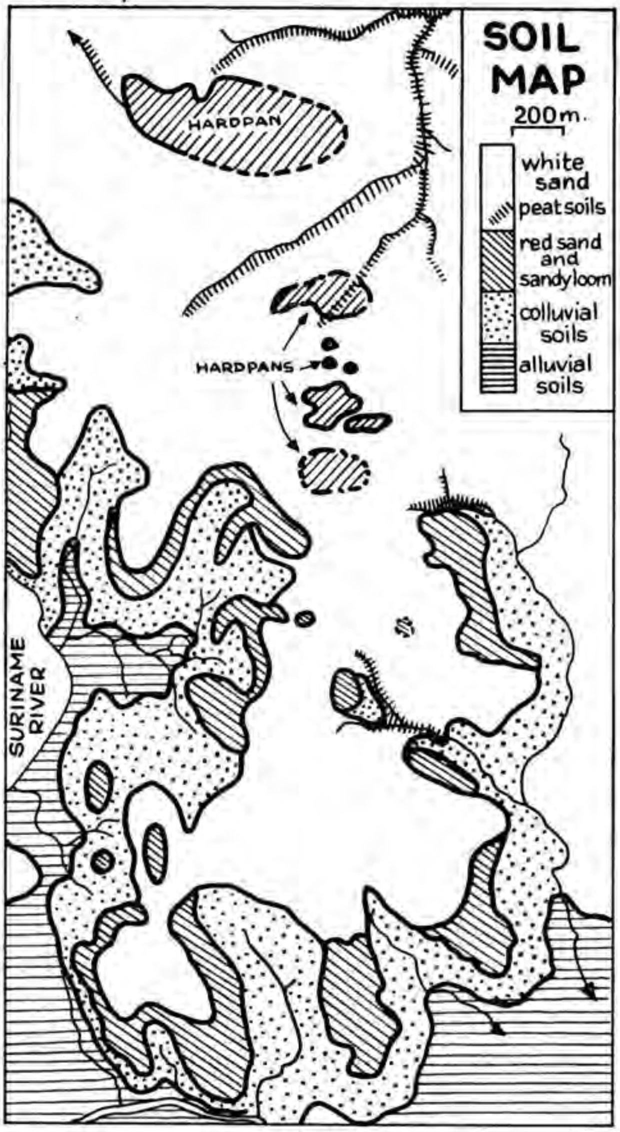
III 2. The white sands

III 2.1. *General character of the white sands and of their subsoil*

The following profile described from a 5.2 m deep pit is representative for the deeply drained soils.

Site: 10-238. Type of vegetation: *Clusia* facies of *Pagamea-Ternstroemia-Matayba* scrub with scattered open spots covered by the typical *Bulbostylis conifera* vegetation. Height above river level 28.09 m, water-table 6.90 m below the surface. Soil samples from a depth below 5.2 m were taken with an auger. Grain-size and heavy-mineral analyses are given in figs. 11, 12 and 13. See photo 24 for upper 70 cm and photo 23 for root development.

FIGURE 4



0–8.5 cm: "micropodzol", viz.

- 0 –1 cm: bleached, light reddish (7½ YR 7/1) sand
- 1 –2.5 cm: darker reddish (7½ YR 7/1–2), somewhat finer sand
- 2.5–8.5 cm: bleached sand.

8.5–40 cm: light to medium, reddish brown (5 YR 7½/1), subangular sand; between 15 and 18 cm an up to 1 cm thick layer of roots (soil sample 4 taken at a depth of 20 cm).

40–75 cm: lighter coloured sand but with spots coloured as the layer above; these spots mainly round roots.

75–210 cm: white, somewhat finer textured sand; about 8 brownish spots round roots per sq.m; these roots are partly living, partly dead (sample 6: 165 cm).

210–deeper than 730 cm: sharp-edged, white sand; its colour is yellowish compared with that of sand which has been exposed some days to the air; sand becoming coarse and more densely packed at about 300 cm (sample 8: 355 cm); between 450 and 550 cm up to 3 cm big quartz pebbles and some dark quartz fragments up to 0.8 cm (sample 10: 510 cm); below 550 cm sand somewhat less coarse (sample 12: 680 cm); down to a depth of 270 cm with some dead roots. Below the sand a kaolinitic clay.

The following description is of an auger-boring made about 400 m W S W of the above-described pit.

Site: 13–34; vegetation: *Clusia* facies of *Humiria-Ternstroemia-Matayba* scrub; height 27.15 m

0–555 cm: comparable with profile of 10–238

555–570 cm: white, coarse-sandy kaolinitic clay with greyish brown (10 YR 7½/3) spots and light orange brown (10 YR 7/5) streaks (sample 1, see for analysis figs. 11 and 12).

570–590 cm: ditto without streaks.

590–600 cm: cream white, coarse-sandy clay with somewhat darker spots.

600–615 cm: ditto with light purplish-red and some dark greyish-green spots, with small mica flakes.

This kaolinitic clay subsoil was found in many places South of transect 11. From the Suralco borings it appeared that these light-coloured, mostly sandy, kaolinitic clays fade after some metres into darker coloured clays which are weathered granitic and gneissic rocks (Granite 3; O'Herne, 1958). Sometimes the surface of this subsoil is more or less congruent with the surface topography. Mainly in the southern part, however, the clay subsoil lies in the form of "hills" under the sand, with the tops nearly at the same level, viz. +20 m above riverlevel. To the North the clay layer dips to a level of +3 to +11 m. In area 3 the results from borings suggest an undulating subsoil topography.

So, a 4 to 22 m thick layer of quartz sands covers this subsoil. The texture of these mostly more or less stratified sands varies between fine and very coarse. Only in the south-eastern part of area 3 some thin clay layers were encountered, sometimes to 2 m below the surface. Except in the humic topsoil the colour of the sands is in the upper metres always white, and at greater depth white, light yellow, brown, yellowish grey or dark grey.

III 2.2. *Hardpans*

Hardpans were encountered in the northern part of area 1, in area 2 and in a few parts of area 3.

From the following profile the hardpan could be studied and sampled, owing to its favourable situation with regard to the groundwater.

Site: 10–80; open spot in scrub savanna (*Clusia* facies of *Licania-Ternstroemia-Matayba* scrub); height above river level 26.10 m; water-table during sampling just below the pan (for analyses see table pag. 31 and figs. 11, 12 and 13.)

0– 3 cm: reddish (5 YR 7/1) sand on top of a thin grey layer of charcoal.

3–25 cm: light reddish brown (5 YR 6/1) sand, grey-spotted, with many roots and rootlets; some of the roots thicker and running horizontally (sample 2: 10 cm).

25–75 cm: light reddish brown (5 YR 8/1) sand with some greyish spots; many rootlets (sample 3: 40 cm).

75–hardpan (170 to 220 cm): nearly white sand with some darker spots round rootlet concentrations; thin rootlets down to the hardpan; sand becoming coarser with increasing depth (sample 4: 90 cm; 5: 170 cm; 5a: 220 cm); on the hardpan a very thin layer of beige-grey (7½ YR 5/2) silty sand.

Hardpan: Surface of the pan irregular: apart from a microrelief, the central part of the plot of 2 square metres that was laid bare, proved to be flat, but to the sides there were slopes in two directions perpendicular to each other (about 0.5 m over a distance of 1 m, see photo 25); the stratification within the hardpan runs parallel with its surface.

170–180 cm: blackish brown (5 YR 3½/1), not coarse sand, moderately strong cemented (sample 6), fading into dark brown.

180–190 cm: dark and coffee-brown (5 YR 3½/3) sand, here more, there less strongly cemented (sample 7); in both layers rootlets and roots to 8 mm in diametre. Sometimes (preformed?) fractures in which rootlets here penetrated; also dead roots causing black spots.

190–220 cm: light rusty brown (7½ YR 6/5), strongly cemented, coarser sand (sample 8), darker in places with dead rootlets, fading into light brown.

220–240 cm: light brown (10 YR 6½/4), cemented sand (sample 9).

240–255 cm: still lighter brown (10 YR 8/2) (sample 10), with some darker spots.

255–263 cm: fairly abrupt transition into dark brown (5 YR 3½/3), coarse, less strongly cemented sand (sample 11).

263–270 cm: blackish brown (5 YR 2/2), but slightly cemented, coarse sand with dead roots and other organic detritus (sample 12).

Subsoil: 270–280 cm: loose, grey (7½ YR 5/1), coarse sand (sample 13).

280–deeper than 460 cm: loose, glistening white, very coarse sand (sample 14: 285; 15: 325 cm).

The features of the hardpan found at the sites 10–110 and 17–18 and investigated by augering, are similar to those found at 10–80. The depth at which it was found, was respectively 447 cm and 220 cm below the surface.

The colour is determined to a high degree by the amount of organic matter (see fig. 5). Strongly cemented layers contain more than 0.7 % aluminum. The iron content is relatively low. The high calcium and the low magnesium contents are striking. The potassium content is high in layers with a high organic-matter content and also in places where a layer is in contact with the ground-water (samples 6, 7, 12, and 5, 5a, 13 respectively).

As the surface of the hardpan at 10–80 was irregular, a detailed survey was made (fig. 6 and 15). The hardpan looked like strayed wreckage

ANALYSIS OF THE SAMPLES MENTIONED ABOVE

Number of sample	Median grain size in μ	Spec. surface	Fraction $< 50\ \mu$ (% of weight)	Organic matter content (% C in dry soil)	Composition of the extract obtained with 0.1 n. HCl (mg per 100 g dry soil)								
					Al	Fe	Ca	Mg	K	Na	P	NH_4	NO_3
2	300	44	1	0.3	18	2	3	7	24	3	1	2	1
3	270	45	4	0.1	5	1	1	4	9	1	tr	2	1
4	290	49	2	0.1	2	$< \frac{1}{2}$	< 1	9	7	1	tr	< 1	1
5	280	56	4	0.1	2	1	< 1	10	12	1	tr	< 1	1
5a	340	53	4	0.0	2	1	< 1	9	20	2	tr	< 1	1
6	290	68	9	1.2	640	3	1	2	39	10	1	2	2
7	—	—	—	1.1	920	9	6	3	39	4	2	2	1
8	310	53	4	0.5	810	2	13	$< \frac{1}{2}$	4	2	tr	4	1
9	—	—	—	0.2	720	2	12	$< \frac{1}{2}$	4	2	2	4	1
10	330	67	9	0.1	910	8	24	$< \frac{1}{2}$	8	3	tr	3	1
11	—	—	—	0.7	830	9	8	$< \frac{1}{2}$	5	3	5	4	1
12	420	44	4	1.0	490	2	4	$< \frac{1}{2}$	11	3	2	4	1
13	440	28	tr	0.2	160	2	3	$< \frac{1}{2}$	12	3	1	4	2
14	—	—	—	0.1	5	2	2	6	4	1	1	6	1
15	1230	12	tr	0.1	7	1	4	3	2	1	1	3	1

tr = trace. In none of the samples Mn was detected.

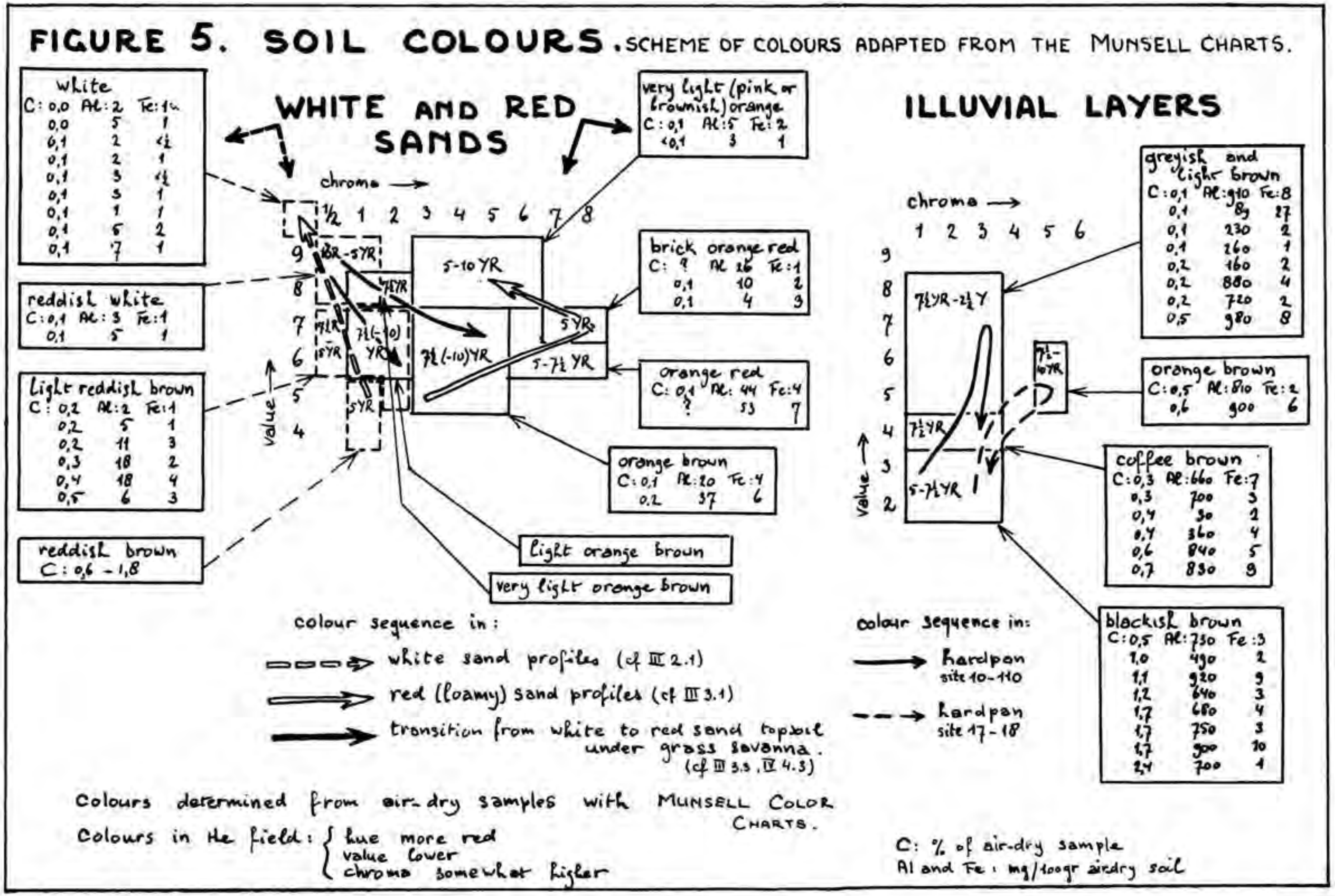


FIGURE 5. SOIL COLOURS. SCHEME OF COLOURS ADAPTED FROM THE MUNSELL CHARTS.
WHITE AND RED SANDS
ILLUVIAL LAYERS
white C: 0,0 Al: 2 Fe: 1½; 0,0 5 1; 0,1 2 ‹½; 0,1 2 1; 0,1 3 ‹½; 0,1 3 1; 0,1 1 1; 0,1 5 2; 0,1 7 1
reddish white C: 0,1 Al: 3 Fe: 1; 0,1 5 1
light reddish brown C: 0,2 Al: 2 Fe: 1; 0,2 5 1; 0,2 11 3; 0,3 18 2; 0,4 18 4; 0,5 6 3
reddish brown C: 0,6 - 1,8
very light (pink or brownish) orange C: 0,1 Al: 5 Fe: 2; ‹0,1 3 1
brick orange red C: ? Al: 26 Fe: 1; 0,1 10 2; 0,1 4 3
orange red C: 0,1 Al: 44 Fe: 4; ? 53 7
orange brown C: 0,1 Al: 20 Fe: 4; 0,2 37 6
light orange brown
very light orange brown
chroma →
value →
5-10 YR
5 YR
5-7½ YR
7½ (-10) YR
10R-5YR
7½YR
7½(-10) YR
5YR
greyish and light brown C: 0,1 Al: 910 Fe: 8; 0,1 89 27; 0,1 230 2; 0,1 260 1; 0,2 160 2; 0,2 880 4; 0,2 720 2; 0,5 980 8
orange brown C: 0,5 Al: 810 Fe: 2; 0,6 900 6
coffee brown C: 0,3 Al: 660 Fe: 7; 0,3 700 3; 0,4 30 2; 0,4 360 4; 0,6 840 5; 0,7 830 8
blackish brown C: 0,5 Al: 730 Fe: 3; 1,0 490 2; 1,1 920 9; 1,2 640 3; 1,7 680 4; 1,7 750 3; 1,7 900 10; 2,4 700 1
7½YR-2½Y
7½-10YR
7½YR
5-7½YR
colour sequence in:
white sand profiles (cf III 2.1)
red (loamy) sand profiles (cf III 3.1)
transition from white to red sand topsoil under grass savanna. (cf III 3.3, IV 4.3)
colour sequence in:
hardpan site 10-110
hardpan site 17-18
Colours determined from air-dry samples with MUNSELL COLOR CHARTS.
Colours in the field: hue more red; value lower; chroma somewhat higher
C: % of air-dry sample
Al and Fe: mg/100gr airdry soil

buried in the sand; its topography is irregular and in general somewhat convex.

Elsewhere in the northern part of area 1 the hardpans appear to occur as small fragments. Between them no hardpan is present, as was demonstrated by a Suralco boring at location 10–64.

In a large part of area 2 too a hardpan was encountered. A sharp boundary was found in the northern part; the boundary at the southern side could not be established with certainty (fig. 4 and 10).

In area 3 the sites where a hardpan was found, center round the water-courses and the upper reaches of the creeks in the SE of the area. Here the pans were found at depths of 1 to 1.5 m.

We did not find therefore a continuous hardpan under the savanna as was mentioned for Zanderij I by VAN DER VOORDE and HOOYSMA (1956) (cf. I 6).

Because of the strong cementation it was impossible to determine the thickness of the hardpans. At 10–110 it was more than 1.5 m, at 17–18 more than 1.1 m and 40 m East of 10–83 even more than 2.5 m. According to the Suralco borings the thickness of the hardpan South of 20–50 is about 4 m, whereas that in area 3 varied from 1 to 2 m. The hardpan that was laid bare during the construction of the truck road on the eastern slope to the Aboma Creek, is 1 m thick. Below the hardpan sandy clay was found here (BAKKER, 1955), elsewhere always fine to coarse, badly sorted sand (Suralco).

III 2.3. *Texture and pore space*

III 2.3.1. Texture (figs. 7 and 10)

The sand is of a rather homogeneous texture and moderately coarse (average size of the particles between 230 and 400 μ) in the upper part, but becomes much coarser (700–1350 μ) in the deeper strata. Although the transition to this coarser sand is gradual, the transition zone is usually small, from some decimetres to half a metre.

The surface relief of the coarser sand is more strongly flattened than that of the uppermost layer. So, on the slopes the coarse sand may be found at a depth of 1 m, while it lies on the plateau at a depth of 3 to 4 m.

In deeper strata often quartz gravel, sharp-edged, but friable between the fingers, was found. The greatest diameter of the pebbles was 3 cm, but it varied mostly between 0.5 and 1 cm. Usually this gravel occurred in a well-defined zone in the coarse sand which began at 1 to 2 m, mostly at 1.5 m below the transition zone. The thickness of the zone varied between some decimetres and one metre. Sometimes some thinner zones occurred above each other.

This stratification is well developed in the southern savannas (10–200 to 260; 13–0 to 80; 15–44 to 100) and on the savanna south of Rediloti (11–60 to 95; 15–215 to 250). In the savannas with clay subsoil, on the other hand, only locally quartz gravel is found, which in this case rests on the subsoil. In some parts gravel is totally wanting (16–32 to 42; 17–72 to 104). Along the creeks very coarse sand and gravel is sometimes concentrated on the clay subsoil (10–264 to 268; 12–0 to 2; 17–52 to 57).

In some spots in the part of area 1 which is provided with a hardpan in the subsoil, this pan is immediately overlaid with finer sand. The survey showed that the coarse sand lies here in a ridged relief below the finer sand. North from the crown of the hardpan the layer of coarse sand wedges out.

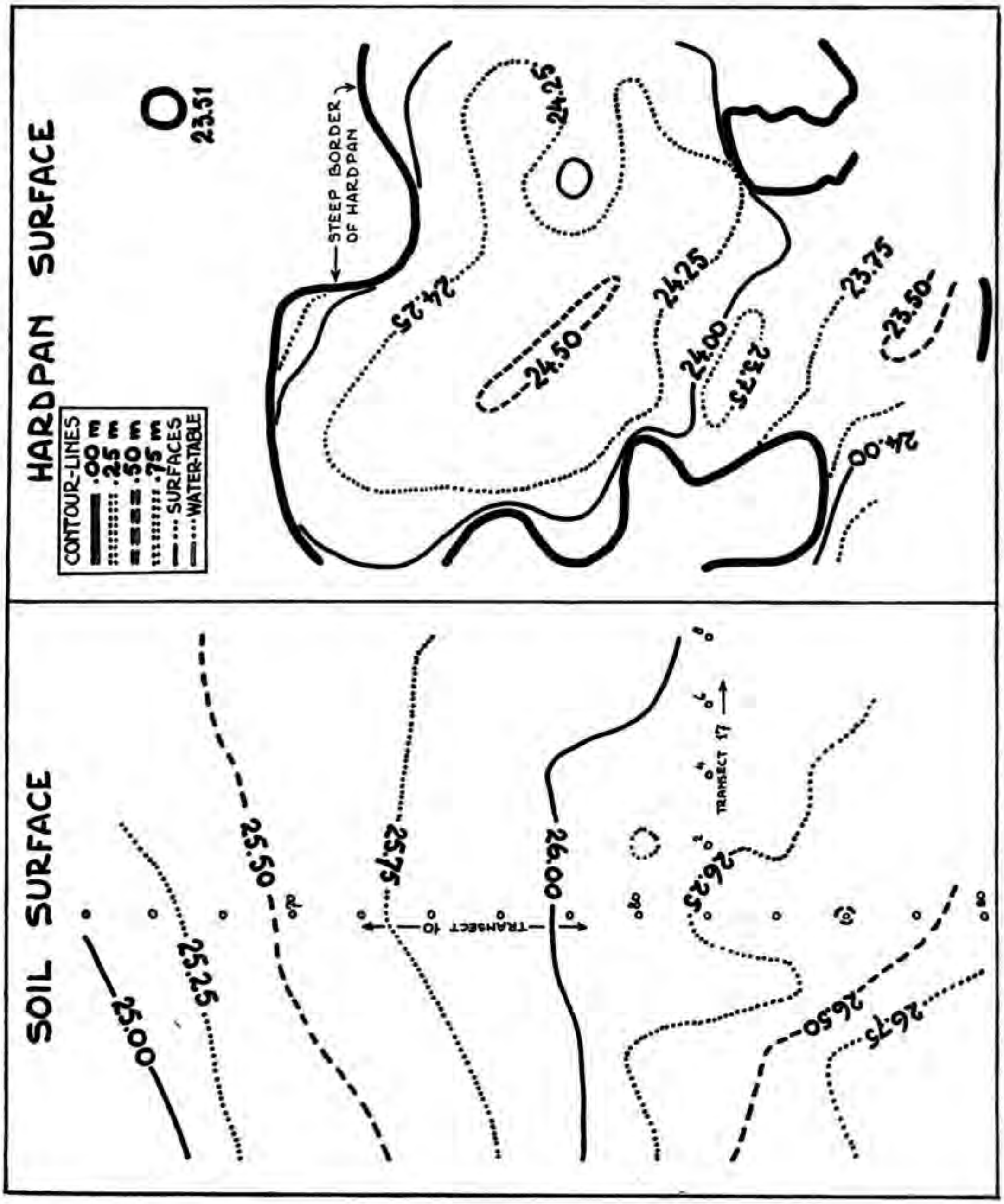
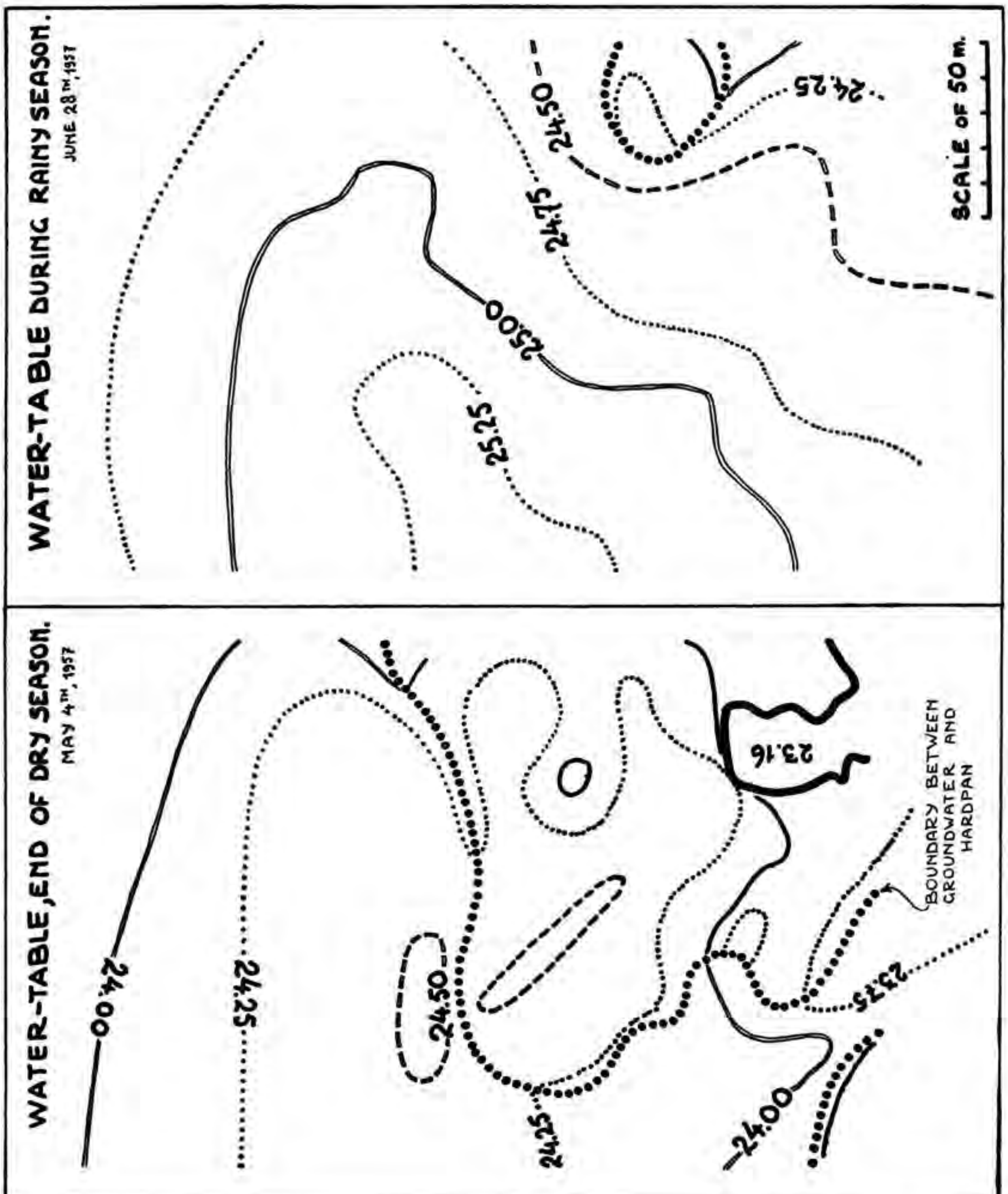


FIGURE 6. CONTOUR MAPS OF THE 4 HA.- INVESTIGATION PLOT

400 m to the North, at a level 4 m deeper, a coarse sandy layer is found wedging out to the South over the hardpan, if the latter is present.

The hardpan of area 2 is bedded in a coarse sandy layer found at the same level. In the northern part no coarse sand is found on this pan, while it occurs in the adjacent zone as a but one decimetre thick layer. North of the hardpan border coarse sand was encountered once more in deeper strata.

In area 3 too the finer sand is underlain by coarser sand. Owing to the high water-table in this area it was mostly impossible to bore deeper than



ROUND SITE 10-80. (CF PROFILES OF FIG. 10 AND 15 AND MAPS OF FIG 31.)

1 m. When it was possible to bore deep, the coarse sand appeared to be underlain by a layer about half a metre thick of finer sand, merging into coarse sand with gravel. Where this situation was encountered, the hardpan was mostly overlain by coarse sand.

III. 2.3.2. Pore space

I am much indebted to Dr. J. P. SCHULZ for making determinations of the pore space in the topsoil found at the sites 10–55 and 10–85. The table shows that the pore space in the topsoil of the dry savanna at site 10–85 has a fairly constant value of about 47 %. In the wet savanna at site 10–55, however, the pore space is smaller, viz. about 40 %, and it shows a greater variation. Two of the three series of samples taken at this place agree with our idea that the sand at greater depths is somewhat more densely packed.

Site	Depth of water-table in cm	Depth of sampling	Average grain-size in μ	Specific surface (U-figure)	Total pore space in % of soil volume	Air content in % of pore space
		3	290	46	44	39
	55	22	295	42	44	38
		50	360	33	32	18
	30	3	275	49	45	36
10–55		30	305	41	39	23
		3	290	44	33	21
	30	20	315	39	41	28
		50	300	42	41	26
	deeper than	5	300	41	47	44
	150	22	310	41	45	41
10–85	deeper than	3	380	28	48½	46
		20	360	33	46	43
	150	50	370	36	48	44

In the Mapane region SCHULZ (1960, p. 152) found the pore space in a loose, coarse, bleached sand overgrown by rain forest to be 44 %, a figure which agrees very well with that found at Jodensavanne.

III 2.4. *Translocation of fine fractions*

In the sand the finest fractions are apparently translocated, since we often find on the hardpan a one or more centimetres thick, beige-coloured (7½ YR 4–6/2) layer, containing about 15 % silt (2–20 μ) and only traces of clay ($< 2\ \mu$). Its organic-matter content varies between 0.1 and 0.4 % C.

Where the clay subsoil was within reach of the auger, it appeared to be overlain by a 1 to 2 dm thick layer of sandy loam. This represents the lowest white-sand layer; it is mixed with the subsoil and with fine illuvial material. The colour of this layer, and sometimes that of the upper layer of the kaolinitic clay too, varies from greyish- or yellowish-white, with or without light brown or orange spots, to dark brown. From the data collected by us it may be concluded that the dark-brown colour caused by humus compounds occurs in sites, where the groundwater rises 30 cm or more above this layer, and that the lighter colours occur in sites with a lower water-table, i.e. where this layer during a great part of the year lies above the groundwater. It is also worth noting that these dark layers appear to occur mainly in those sands which are found in the vicinity of red sands and of loamy sands. It is difficult, however, to obtain a complete picture of the circumstances, as the great depth at which this sandy loam layer is found hinders its exploration.

In the bare savanna patches the very fine sand fraction (20–75 μ) is eluviated from the uppermost soil stratum to the underlying sand. In these thin layers too colour differences appear. We may call such a small profile a "micropodzol" (see also SCHULZ, 1960 p. 117). It has already been described from profile 10–238. The following description and granulometric analysis represents a typical profile. For a chemical analysis see table 1.

Site: 10–30; vegetation: a very sparse cover of grasses and sedges, representing the *Axonopus pulcher* variant of the *Bulbostylis conifera* vegetation; no litter; see photo 26.

0–0.7 to 1 cm: reddish (7½ R 7/2), moderately coarse sand (sample 1).

0.7 to 1 – 2 to 3 cm: reddish brown (2½ YR 5/2), fine sand (sample 2).

deeper than 2 to 3 cm: "white" (about 10 R 9/1), fine to moderately coarse sand with some humic spots round roots. Many rootlets (sample 3).

Number of sample	Weight in % of fractions obtained by sieving										
	> 2 mm	2000	1000	600	300	150	105	75	50	20	< 20 μ
1	trace		9	10	37	39	4	1	traces		
2	trace		2	2	16	40	12	5	2	21	traces
3	trace		4	4	23	49	12	5	2	1	traces

The separation into the microhorizons is mainly brought about by the impact of rain drops. The coarse uppermost layer, however, is too thin to provide the large quantity of fine illuviated material. I presume that the sand produces fine material because the grains grind against each other during downpours. Perhaps some coarse sand is eroded away by saltation transport (cf. 2.8).

On the dry savannas micropodzols are better developed than on the wet ones.

III 2.5. *Organic matter in the topsoil*

A series of samples taken under various vegetations between sites 10–38 and 10–87 from the upper two decimetres of soil and from the pits, gave with regard to the organic-matter content the following results:

Vegetation	Organic-matter content in % C of air-dry sample	Colour in the field	Colour of air-dry sample
open savanna	0.0	white, N 10	white, N 10
	0.1	5–7½ YR 5½–7/1–2	5–7½ YR 7½–8½/0–1
	0.2–0.5	5 YR 3–6½/1	5 YR 6–7/1
bushes on dry savanna; soil hogwallowed	0.7–0.9	5–7½ YR 2–3/1	5 YR 4–5/1
bushes on wet savanna	1.3–1.8	2½ YR 2–3/1	5 YR 5/1

(The organic-matter content may approximately be obtained by multiplying the value for % C with a factor 2.24; compare also fig. 5 and table 1).

These values correspond with those found by VAN DER VOORDE and HOOYSMA (1956) respectively for the slightly humic, the humic, and the strongly humic soils of the Zanderij I savannas (cf. I 6).

The thickness of the humus-coloured soil depends on the vegetation and drainage conditions. On the well-drained savannas it amounts to 70 to 100 cm under open savanna, and sometimes even to 250 cm under scrub and savanna wood. On the wet savannas white sand is often already encountered at a depth of 40 to 60 cm, but there is much variation. On the whole the analyses (table 1) show very low percentages of organic matter below the first foot of soil.

As a rule the humic sand fades very gradually into the white sand; sometimes, however, I observed a sharp boundary, but I could not discover the cause of this phenomenon.

The soils with the highest organic-matter content are found in the tracts along which the water runs off and along the creeks. Owing to their topography these soils are therefore poorly drained. This explains that in the deeper valleys peat formation is possible. Peat is found in tracts up to 50 m wide and 20 to 225 cm thick, underlain by dark-coloured sand or, in places where the kaolinitic clay subsoil lies at 70 to 100 cm below the surface, by very coarse sand containing up to 3 cm big pebbles.

"Kawfoetoes", small hummocks and depressions which together offer an image somewhat reminiscent of the soil surface in a hog wallow, occur in the tracts along which the water runs off and sometimes likewise in the adjacent tracts of marshy land and along scrub patches. DOST and HOOYSMA (1957) and VAN DER VOORDE (1957) ascribe their origin to the activity of earth-worms. However, for the Jodensavanne areas I could not confirm their observations, as no earthworms were found! I

TABLE 1. CHEMICAL DATA OF THE SAVANNA SOILS.

a = open savanna and scrubsavanna
b = savannawood and -forest on white sand
c = grass savanna on red sand

(Methods of determination: cf II 2) tr = trace.

EXCHANGEABLE PLANT NUTRIENTS IN MILLIGRAMS/100 GRAMS OF SOIL (0.1 N HCL EXTRACTION)

	ORGANIC MATTER CONTENT % C			Al			Fe			Ca		
	a	b	c	a	b	c	a	b	c	a	b	c
UPPER SOIL: micropodzol (locality 10-30) resp. first 5 cm of topsoil	0.5 0.2 0.1	0.8	0.2	6 11 3		37	3 3 1		6	1 <1 <1		<1
sand at a depth of 10 cm	0.2	0.4		13			2			3	36	
sand at a depth of 30 cm	0.1	0.2	0.1	5			1			<1	14	
sand deeper than 100 cm	0.0 - 0.1			2	3	53 ↓ 10	<½ - 1		7 ↓ 2	<1	5 ↓ 2	<1
sand above hardpan or clay subsoil	0.0 - 0.1			1		4	<½ - 1		2	<1	6	<1
HARD-PAN: brownish sand upon hardpan	0.3			30 - 89			2 - 27			3		
little to moderately cemented brown-black upper part	1.1 - 2.4			640 - 700			3 - 4			7		
strongly cemented, dark to light brown center part	0.1 - 0.7			700 - 920			3 - 10			20		
little or not cemented brown-black underside	1.0 - 1.7			230 - 490			2 - 4			8		
not cemented brown-grey to white, waterlogged sand below pan	0.1			260 - 6			2			3		
CLAY SUBSOIL	0.1			12 - 320			3			<1		
CLAYEY COLLUVIAL SOIL	0.3			30 - 270			3			<1		
Sandy, well drained soils without lime (data Soils Lab., Royal Tropical Institute)				0 - 1			0 - 2			10 - 20		
Excessively drained sands → loamy sands of the Mapane-region (Schulz 1960, table VII).				17.1			6			<5		

	Mg			K			Na			P		
	a	b	c	a	b	c	a	b	c	a	b	c
UPPER SOIL: micropodzol (locality 10-30) resp. first 5 cm of topsoil	11 11 9		4	19 15 6		9	3 2 2		2	1 tr tr		2
sand at a depth of 10 cm	7	14		24	7		3	6		1		
sand at a depth of 30 cm	4	8		9	5		1	2		tr		
sand deeper than 100 cm	9	4	3 ↓ 5	7	2	8	<1 - 1		½	tr		1
sand above hardpan or clay subsoil	9	6	4	20	3	5	2	3	½	tr		1
HARD-PAN: brownish sand upon hardpan	3			6			3			1		
little to moderately cemented brown-black upper part				20								
strongly cemented, dark to light brown center part	<½			6			3			tr - 2		
little or not cemented brown-black underside				15								
not cemented brown-grey to white, waterlogged sand below pan	5			3			1			1		
CLAY SUBSOIL	2½			19			2½			1		
CLAYEY COLLUVIAL SOIL	3			17			3			2		
Sandy, well drained soils without lime (data Soils Lab., Royal Tropical Institute)	2 - 5			1 - 5			0 - 2			0.1 - 2		
Excessively drained sands → loamy sands of the Mapane-region (Schulz 1960, table VII).	0.15			3.4						tr		

	NH_4			NO_3			MOISTURE CONTENT OF AIR-DRY SOIL % H_2O			NUMBER OF ANALYSES
	a	b	c	a	b	c	a	b	c	
UPPER SOIL: micropodzol (locality 10-30) resp. first 5 cm of topsoil	4 2 2		6	1 1 1		1	0,2 0,1 0,1	0.6	0.1	
sand at a depth of 10 cm	2	12		1	7		0.2	0.4		27
sand at a depth of 30 cm	2	8		1	2		0.1			
sand deeper than 100 cm	<1	4	4	1	2	2	0.0 - 0.1			
sand above hardpan or clay subsoil	<1	4	4	3	5	3	0.0			
HARD-PAN: brownish sand upon hardpan	5			2			0.2			2
little to moderately cemented brown-black upper part							1.3 - 2.5			
strongly cemented, dark to light brown center part	5			2			0.2 - 2.3			25
little or not cemented brown-black underside							1.0 - 2.2			
not cemented brown-grey to white, waterlogged sand below pan	4			1			0.0			
CLAY SUBSOIL	6			2			0.4			9
CLAYEY COLLUVIAL SOIL	6			2			0.4			4
Sandy, well drained soils without lime (data Soils Lab., Royal Tropical Institute)	0.1 - 2			0 - 2						
Excessively drained sands → loamy sands of the Mapane-region (Schulz 1960, table VII).	3.3			1.4						13

presume that they are in these areas caused by peculiar microtopografical differences in combination with influences exercised by the vegetation (cf. IV 5.1.1.).

III 2.6. *Organic matter in the subsoil*

In those parts of the savannas where even in the rainy season the groundwater does not reach the surface, we encountered under forest, thicket and high scrub and near the wet savanna likewise under a more open scrub vegetation in the white subsoil a light reddish-brown zone. The colour of this 5 to 100 cm thick zone points to an accumulation of humus (and iron?) compounds. It lies within the zone of fluctuation of the groundwater, mostly in the lower part. Where on the slopes in area 1 the white sand merges into colluvial soil, the accumulation zone is darker brown, but neither coffee-brown colours nor cementation occur (unfortunately we did not take samples of such layers).

The following phenomena were observed only once. In transect 11–28 to 30, a white sandy soil is inserted between a red sandy soil and the colluvial soils on the slope (fig. 7). At site 11–28 a 40 cm thick, dark brown (5 YR 3/1 to 7½ YR 4/3), locally cemented layer is found in the sand at a depth of 315 cm; at site 11–29 its thickness is 55 cm, at site 11–29.5 100 cm and at site 11–30 120 cm. At the latter site it passes into the colluvial soil, and here the layer is stratified, locally containing clay and cemented. Here it reaches the clay subsoil. Some metres down the slope only locally a coffee-brown streak fading in the greyish-brown clayey sand is observable.

The chemical analyses of the accumulation zone gave results analogous to those of the hardpans. They are combined in table 1.

III 2.7. *Plant nutrients*

In table 1 the results of the extraction with 0.1 normal hydrochloric acid are summarized. If we compare these with the norm given by the Soils Laboratory of the Royal Tropical Institute for sandy, well-drained soils without lime, than the values of the white sand soils are generally somewhat higher, except for calcium which in the topsoil under forest is present in moderate quantities, but gives very low values for the rest. The rather high amounts of iron and especially of aluminum are striking. All quantities of plant nutrients other than potassium are smaller under lower and more open vegetation than under wood and forest.

When these values are compared with those of the excessively drained bleached sands and loamy sands of the Mapane region (Schulz, 1960 p. 122 seq.), they appear to be rather high. This is probably caused by the use of an other liquid for the extraction; for the Mapane soils sodium acetate in acetic acid was used. In our opinion Schulz's conclusion: "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" is applicable to our soils too, and for this reason I believe that his supposition that "probably the leached sands carrying xeromorphous savanna forest are considerably poorer" is not right.

In the savanna too the physical soil factors will be more important for the vegetation than the chemical factors (cf. SCHULZ, 1960 p. 101).

III 2.8. *Erosion relief*

Traces of erosion occur mainly on the wet savanna. Generally speaking, they are of little importance, and mainly noticeable in the paths worn out by the Amerindians, where sometimes gullies of one decimetre deep have been eroded.

On the dry savanna too sand displacement may take place. The displacing agent is not the running down of rain water, for there is no run-off on these savannas, but the flagellating action of the rain drops. The effect of this factor appears from the sand which accumulates against fallen branches. A casual observation at site 10–70 showed ½ to 2 cm in one year. The thinness of the toplayer of the micropodzol (III 2.4) may also be due to this kind of transport.

As already mentioned in III 1 the topography is rather flat, and especially the headwater creeks in the wet savanna are only slightly cut in. In area 3 and adjacent parts these creeks are running in a distinct direction, viz. NE–SW, NW–SE and N–S. Dr. M. BOYÉ and Dr. H. CRUYS drew my attention to the fact that these directions, especially NW–SE, are also the prevailing ones in the region of the Caribbean granites and gneisses in French Guiana (cf. CHOUBERT, 1957). The bedrock of the Jodensavanne area consists of granites and gneisses, originated in the same period as the Caribbean granite (Granite 3; O'HERNE, 1958). I suppose that here too the direction of the creeks is determined at least partly by the nature of the bedrock. In the southern savannas where the bedrock lies nearer to the surface, its influence on topography is still more predominating.

Along the transects, however, in the sections 10–33 to 63, 18–0 to 7, 20–56 to 82 and 30–72 to 83, depressions in the terrain occur which can not satisfactorily be explained by this kind of valley formation. Their boundary with the adjacent "ridge" is formed by a brief steep slope (fig. 10). These depressions are remnants of a former erosion relief that will be discussed in III 5.4.

III 3. THE RED SANDS AND THE SOILS WITH A HEAVIER TEXTURE

III 3.1. *Profile descriptions*

Where white sand, red sand and sandy loam succeed each other regularly (cf. III 1 and soil map fig. 4), the variations in texture point to an analogous origin. The transition between red-sand soil and sandy-loam soil is always gradual. Sometimes the red-sand soil is developed only as a

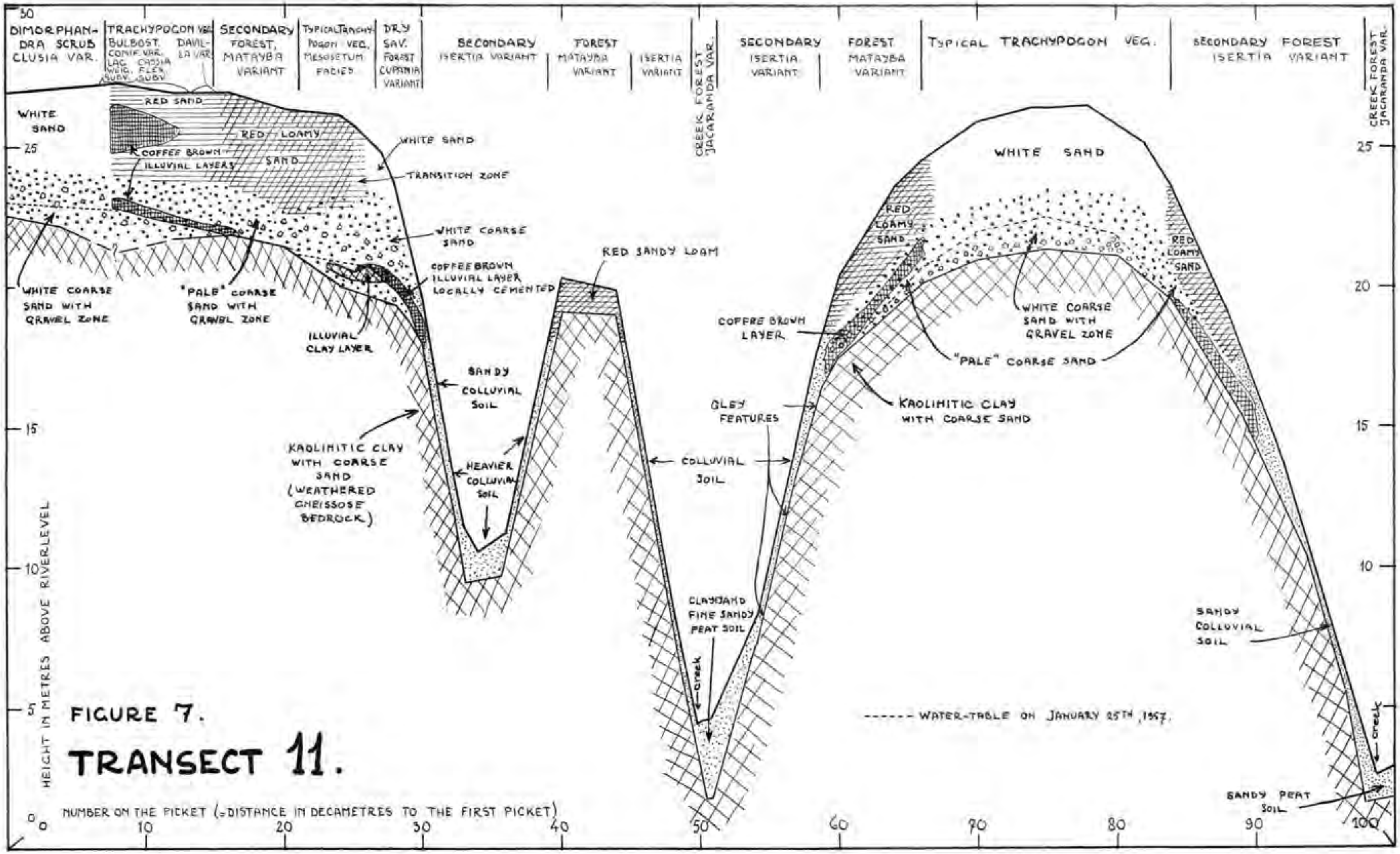


FIGURE 7.

TRANSECT 11.

narrow transition zone between the white sand and the sandy-loam soil. Between the white sand and the red sand there is always a very sharp vertical boundary line.

Profile description of a red-sand soil made in a 5.3 m deep pit:

Site: 11–24 (fig. 7); vegetation: grass savanna: *Mesosetum* facies of typical *Trachypogon* vegetation; height above river level 26.17 m; highest water-table 530 cm; chemical analysis: table 1; grain-size analysis: fig. 13

0–25 cm: fairly light reddish-brown (7½ YR 5/4) sand with many rootlets (sample 1: 5 cm), fading in the next zone.

25–75 cm: light brown (7½ YR 6/6) sand with yellowish orange spots.

75–140 cm: yellowish orange (5–7½ YR 6/7) sand with light brown spots.

140–185 cm: brown colour disappears, and orange-pink hue increases (sample 5: 165 cm).

185–323 cm: orange-pink (5 YR 7/8) sand, below 270 cm with brown spots, one of them round an old root channel; sand somewhat cemented, downwards slightly increasing in coarseness; below 290 cm coarse and loose sand (sample 8: 310 cm), after a clear transition zone of about 20 cm; rootlets under the topsoil not frequent, found up to 210 cm; charcoal is met frequently, often in thin horizontal layers, sometimes continuous all over the pit walls; such layers occurred at the following depths: 20, 45, 65, 78, 112, 148, 240 and 255 cm.

323–333 cm: transition zone coarse sand, changing from orange pink to very light orange.

333–370 cm: very light orange (5 YR 9/4), coarse sand with pinkish orange spots.

370–380 cm: pinkish orange (7½ YR 8/6) layer.

380–425 cm: light orange (7½ YR 8½/6), coarse sand with pinkish orange spots (sample 11: 405 cm).

425–525 cm: coarse sand with a very irregular colour stratification; these colours are: orange-red (5 YR 6½/8), brownish orange (7½ YR 8½/8), pink-orange (7½ YR 8/6), very light orange (5 YR 9/4), pink-orange with brown spots (7½ YR 8/5), and ochreous (10 YR 8/5) (sample 17: 520 cm).

525–570 cm: layer of compact coarsely sandy clay, light grey to 560 cm (sample 18: 540 cm), then brownish grey (7½ YR 7½/2); the surface of this layer is inclined or undulating.

570–610 cm: light greyish-brown (about 10 YR 8/5) sand with orange-brown (7½ YR 7/8) spots (sample 20: 600 cm).

deeper than 610 cm: brownish (10 YR 6½/3) sand with clay; impossible to bore deeper because of groundwater, but the kaolinitic clay of the weathered bedrock will certainly lie at a depth of about 7 m.

The following description, made from an auger boring, is an example of a sandy loam soil.

Site 12–34; vegetation: *Matayba* secondary forest; height 25.12 m; highest water-table interpolated at 415 cm; some litter and roots at the surface.

0–85 cm: dark brown, somewhat loamy sand.

85–110 cm: lighter brown, fading into the colour of the next zone.

110–170 cm: light reddish-brown loamy sand.

170–320 cm: orange-red, fine sandy loam, below 300 cm more yellow-orange with orange-red spots.

320–360 cm: sand ochreous yellow, coarser, below 340 cm with darker spots.

360–410 cm: lighter coloured coarse sand, less loamy.

410–430 cm: coffee-brown coloured zone; 410–425 cm: less coarse, more loamy sand; 425–430 cm: layer of quartz gravel; impossible to bore deeper.

The increase in intensity of the orange-red colour with increasing depth in the upper 3 to 4.5 m is a general feature of these red soils (fig. 5). It is probably caused by the decreasing amount of organic matter as well as by the change of the iron compounds that are present as a coating on the quartz grains, in a less hydrated form; this follows from the fact that the amount of exchangeable iron decreases with increasing depth. Between the orange-red zone and the clay subsoil a 1 to 2 m thick "pale zone" is always encountered. Here all colours between orange and white may occur, as is shown by the profile descriptions and by fig. 5. This pale zone is practically always found in coarse sand. In pit 11–24 the transition to the pale zone is found in that part of the profile where the sand is already coarse, but in pit 11–16 the boundary coincides exactly with the sharp limit to coarse sand at a depth of 345 cm, and the red colour changes through irregularly distributed orange colours into white (photo 27).

A 10 to 80 cm thick coffee-brown, non-cemented layer is often seen in the pale zone. This layer is perhaps correlated with the upper part of the zone in which the water-table fluctuates, but it is not always present. Just as with the white sands, it was difficult to ascertain the features exactly because of the great depth at which this layer occurs.

On the slopes towards the Suriname River valley the sandy loam soils merge into colluvial soils which have a higher clay content, and below which the kaolinitic clay is found already at a depth of about 1 m. The coffee-brown layer of the sandy loam passes on steep slopes into the colluvial soil, and rests immediately on the clay subsoil, just as described for site 11–28 to 30 (III 2.6).

III 3.2. *Plant nutrients*

Only samples of red sand found under grass savanna (site 11–24) were analysed for exchangeable ions (table 1). The phosphorus and ammonium values are higher than those of the comparable white sands, the magnesium value is somewhat lower. The amount of aluminum and that of iron, however, differ conspicuously from those found in the white sand.

III 3.3. *Translocation of humus compounds and sesquioxides in transitional profiles* (fig. 7)

On the border line with the white sands, no matter whether this is found in grass savannas or in forests, the red sands show features which point to a translocation of humic and sesquioxidic substances. A darker coloured, sometimes even coffee-brown zone occurs below the humic topsoil at a depth of 50 to 120 cm. This zone is up to 1.5 m thick, and may consist of several smaller zones, one above the other. Below this zone, and eventually between the thinner zones, the sand shows the normal red colour.

Besides a slightly increased organic-matter content the layers which show the darkest colour, show a considerable increase in aluminum content.

The immediately adjoining white sand shows locally brownish and greyish shades or brown and orange spots. Some metres away from the boundary line with the red sand, however, there is nothing to be seen in the white sand that might point to the proximity of red sand.

An explanation of this sharp boundary line will be given in III 6.

III. 4. Roots and traces of animal and human activity encountered in the profiles

III 4.1. *Roots*

Most data were obtained from the pits, for by means of borings we gain only a very incomplete idea into the root development in the profile.

The descriptions of the profiles 10–80 and 10–238 show the characteristic picture of the division of the roots occurring below the open patches of the dry scrub savanna. Note especially the occurrence of a layer of up to 1 cm thick roots at a depth of 15 to 20 cm. These roots belong to the scrubs growing along the border of the open space. The factor which is responsible for the development of this wide-spread rootsystem, is probably the competition for water (cf. Schulz, 1960 p. 126). In these soils with a deep water-table it is necessary to collect as much as possible from the percolating rain water. How far the overlying micropodzol with its layer of accumulated fine material plays a part in retaining rain or even dew water, has not been investigated (see for the influence of fine-grained layers on the capillary behaviour of water: Pfalz, 1951; Versluys, 1916). That competition for water is at least one of the factors, is illustrated by the fact that roots often grow through decayed trunks and branches or dead roots, obviously preferring the moisture and the organic matter which undoubtedly retains plant nutrients, to sand. This may also be a factor in the development of the rootmat.

Such a rootmat consists of roots, rootlets, decaying litter and some sand, rests on the sandy soil and is covered by some litter. It is found in the center of bushes as well as below savanna wood and forest and below secondary forest on red sand. Its thickness varies considerably, viz. from a layer of single roots to a mat several decimetres thick. In *Dimorphandra* vegetation still thicker rootmats with much organic material are encountered. There the mean thickness is 50 cm; below old scrubs even 110 cm was measured (cf. IV 2.1.2.).

Except in the *Dimorphandra* woods there is no development of a rootmat in the wet savanna. Likewise no rootmat occurs on heavier soils. In these cases the thicker roots grow in the topsoil. The soil-water conditions will probably be the most important factor in the development of the rootmat (cf. MINDERMAN, 1960).

So, the major part of the thicker roots is found just below or on the surface. Some of them, however, penetrate vertically into the soil; with the auger we encountered up to 1 cm thick roots under savanna and savanne forest to a depth of 3 m.

From the rootmat thin roots and rootlets enter the topsoil. The sand under the scrubs on the wet savanna too is densely packed with roots. These roots are concentrated in the upper decimetre of the profile, but they can penetrate the white sand even to a depth of 1 to 2 m, under forest to 2.6 m and they often have a small humic zone around them.

On the grass savanna and in the open spots of the wet and dry savanna the roots are limited to a one decimetre thick upper layer.

In deeper layers of the profile, viz. down to 3 m, in or mostly above the zone in which the ground-water fluctuates rootlets were sometimes also met with. Their occurrence coincided in some cases with the transition from finer into coarser sand. Sometimes I also found roots in the layer resting on the hardpan and in the upper layer of the pan.

The root systems of the savanna plants were investigated by Mrs. W. A. E. VAN DONSELAAR–TEN BOKKEL HUININK. Her results will be published in the "Vegetation of Suriname".

III 4.2. *Traces of animal and human activity*

In the white sandy soils, especially in those of the open savanna and of the savanna scrub, animal activity is very restricted. Only termites (M. A. KNOPPE, 196.) and some burrowing mammals may affect the upper soil strata.

In savanna wood and in savanna forest sometimes low broad sandheaps are found round the entrances of the nests of leaf-cutting ants, *Atta* spec. div. These ants, however, are more often met in forest on red sandy loam. Some features, viz. old organic matter from fungus beds, some coarse grains in the finer sand, and the occurrence of charcoal in the first 2 m, sometimes in a distinct zone of 0.5 m, may be caused by the activity of these ants in places that are now no longer inhabited by them.

In the pits in the white sand the charcoal, when present, appeared to occur in the form of local lumps, but in the red sand it was spread throughout the first 2 or 2.5 m and often concentrated in distinct thin layers (cf. profile description of pit 11–24; III 3.1).

The charcoal is formed when the forest is burnt down by the Amerindians in order to obtain fields for their cultures, or, in the case of *Dimorphandra* forest, for obtaining firewood. For their fields they burn mainly forest growing on red loamy sands and heavier soils, rarely on white sand, on which they preferably build their houses. In accordance with these facts I found charcoal on the ground or in the topsoil as well as in the above mentioned deeper strata in nearly all heavier soils and in white sand soils under savanna forest with much *Dimorphandra* or under *Dimorphandra* wood. On the savanna it seems to take 50 years before the charcoal is decomposed, under forest conditions perhaps shorter. SCHULZ (1960, p. 126) estimated the age of the charcoal under the Mapane forests to be at least two centuries. Differences in aeration and in the water conditions will be important determining factors, and will cause much variation in the time the disintegration requires in variously textured soils.

III 5. MORPHOGENESIS OF THE AREA

III 5.1. *Short outline of the geology of the Guiana lowlands*

The soils that have been studied developed from sediments which lie as a fringe along the Guiana Shield.

The rocks that are at present outcropping from the Shield in Dutch and French Guiana, are mainly of Palaeo- and Proterozoic age. For the minor part they are igneous rocks (granite, dolerite), but the bulk is formed by metamorphosed igneous and clastic rocks (gneisses and, for instance, schists, grauwackes and conglomerates of the Orapu Formation).

In front of this Shield the lowland sediments spread out as a fan with its axis between the Courantyne and Berbice Rivers. The deposits have been provided mainly by the Shield and, regarding the clays, for a part also by the Amazon. These sediments form the Courantyne Series, subdivided into the Berbice or Zanderij, the Coropina and the Demerara Formation. The most landinward sediments occur at about 150 km from the present-day coastline between the Kabalebo and Mazaruni Rivers at a height of 125 to 135 m above sea-level. From the present shore-line the continental shelf dips gently down to its edge, which lies at about 100 km offshore and at a depth of 60 to 110 m under sea-level.

By means of drillings for water, oil and bauxite many data with regard to the stratigraphy of the sediments in the coastal plain became available, while deposits on the floor of the Guiana Shelf between the mouth of the Orinoco and that of the Essequibo were investigated by a hydrographical-sedimentological expedition (D'AUDRETSCH, 1953; BLEACKLEY, 1956, 1957; BOYÉ, 1960; VAN LOON, 1958; NOTA, 1958).

Formerly fossils (Molluscs) were observed only in the youngest sediments. Recently, however, at greater depths sediments rich in microfossils of Palaeocene age (Foraminifera, Ostracoda, pollen grains) were discovered, first in French Guiana in the region of Mana at a depth of 20–80 m, lately also in British Guiana under bauxite and in Suriname (CRUYS, 1959; DROOGER, 1960; resp. VAN DER HAMMEN e.a., 1961; and VAN VOORTHUYSEN, 1960).

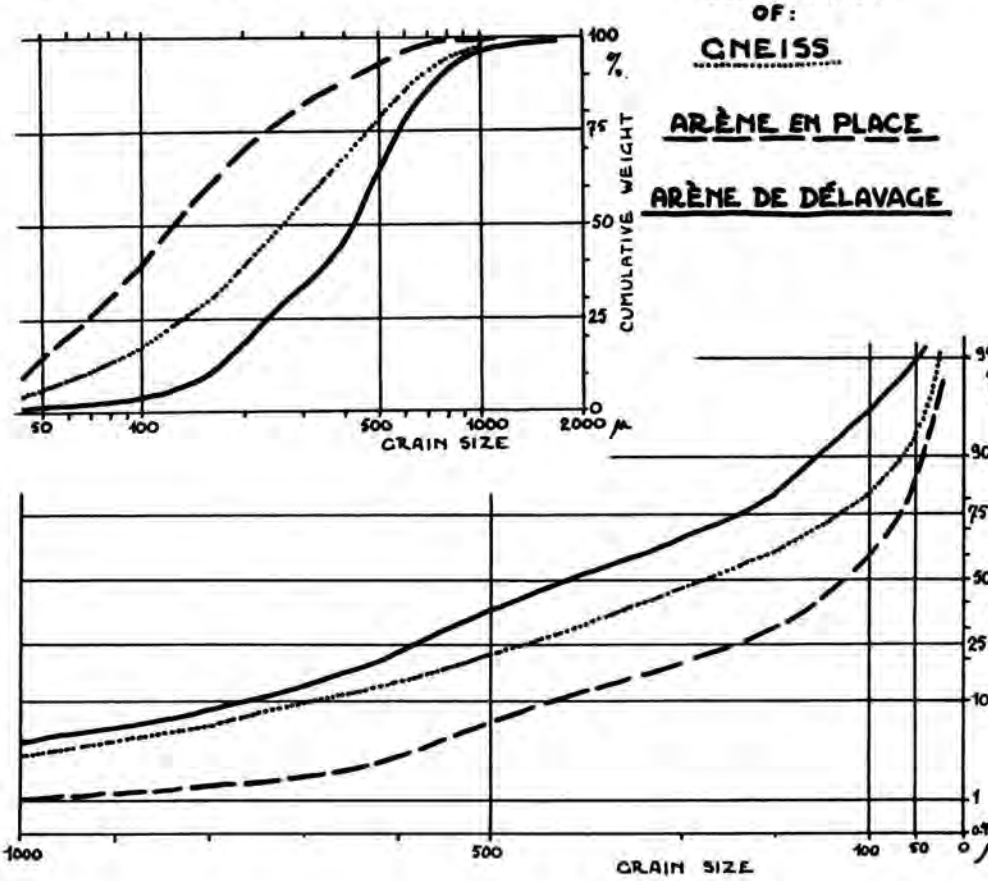
It is difficult to date the intermediate strata. In the upper ones, however, oscillations of the ocean level caused by glacial periods have clearly been demonstrated. These glacial periods presented themselves in the tropics as pluvial periods with a decrease in temperature of some 7° C (VAN DER HAMMEN e.a., 1960). To the sediments of Pleistocene and Holocene age belong those of the Coropina and Demarara Formation and some sedimentary petrological provinces on the Guiana Shelf. The age of the Berbice Formation is still uncertain, but for a part at least older than Quaternary. We will return to this point at the end of the following section.

III 5.2. *Washed-out detritic sands*

A peculiar phenomenon was discovered by BOYÉ (1960), viz. the occurrence of a kind of sand formerly known only from the Zanderij Formation, at several stratigraphic levels. He called this sand "arène de délavage", in english: "washed-out detritic sand" or "pluvial washed-out sand". It is directly related to the weathering bedrock.

In the sites investigated by BOYÉ (1960) this bedrock is often biotite-gneiss. We may summarize his descriptions of its weathering as follows (fig. 8). During the initial period of weathering first the feldspath and biotite crystals become affected. In the upper strata of the weathering gneiss they still occupy their original position, but they are fully decomposed. During the progression of the chemical weathering, by which the more aggressive character of several palaeo-climatic periods must be

FIGURE 8.



taken into account, the texture of the gneiss is lost, and fine fractions arise; the result is an "arène en place" ("eluvium from crystalline rocks" or "continental detritals from rocks weathered in situ") with an orange colour. Leaching and reworking affected by heavy rainfall during pluvial periods cause a bleaching of the sand grains and the washing away of the finer fractions; so greyish white, coarser "arène de délavage" is formed, which still is a sediment in the initial stage of its evolution. The quartz grains forming the main constituent of these detritic sands are sharp-edged and often show the former planes of contact with the other minerals.

Data about granite weathering in Suriname (BAKKER, 1957, 1958a, b, 1960; BAKKER and MÜLLER, 1957) correspond very well with those obtained in French Guiana, and the granulometric analyses of the sand fractions give fairly analogous results.

Schists of the Orapu Formation by weathering sometimes supply a sand fraction which granulometrically resembles that of the granitic sands, but the detritic sand is mostly coarser and contains gravel. Granites and pegmatites too supply sometimes coarser sand (G.M.D., 1950; WIGGERS, 1956).

Because granitic and schistose rocks are important constituents of the bedrock, pluvial washed-out sands can be expected in all parts of the lowlands. Some curves representing sands from the Montgomery Mine and from the Kamakabra boring in British Guiana (BLEACKLEY, 1956) for instance agree with the curves of fig. 8, while the granulometric analyses of the "bleached cover soils" (VAN DER EYK, 1957) are also very similar.

BOYÉ (1960) encountered washed-out detritic sands on several stratigraphic levels, for example at the base of the Zanderij Formation, but also in younger and older deposits, even in strata below the Palaeocene sediments. For this reason, we can no longer use this kind of sand as a guide layer for the Zanderij Formation, and it even becomes doubtful whether the outcropping Zanderij Formation and its equivalents in French and British Guiana may be regarded as a facies of the same age.

Although unfit for age determination, the washed-out detritic sands are important for stratigraphical classification, because they give an indication with regard to environment and climate in the period of their deposition.

III 5.3. *Sedimentological interpretation of the granulometric analyses*

The purpose of this section is to give a short explanation of the terms used in the following section.

At first it was tried to fix the grain-size distribution by means of some parameters such as the median value, sorting coefficient and skewness (KRUMBEIN and PETTYJOHN, 1938; INMAN, 1952; CAILLEUX, 1956). Later on, stress was laid on the possibility of interpretating the graphically plotted grain-size frequency, for it became clear that several of the distribution patterns could not be expressed by simple mathematical formulae (DOEGLAS, 1952; RIVIÈRE, 1952).

DOEGLAS (1952, 1955) plotted the frequency curve of the cumulative weight beginning with the coarsest fraction on arithmetic probability paper (grain-size on abscis with arithmetic scale). He demonstrated that from material with a grain-size distribution indicated by him as "C", when suspended in running water, three types of sediment may be obtained by two sudden decreases in the velocity of the current (fig. 9), viz.

1. an R-sediment, which owes its origin to the settlement of the coarsest grains of the suspended material; these grains possess a sharply defined smallest size (R means "rolling", because these grains are usually transported rolling along the bottom).
2. an S-sediment, originating by the settlement of the coarser part of the remaining suspended matter, thus with a sharply defined largest as well as smallest size

(S means "saltatory", the transport of these sediments is by "saltation" of the grains).

3. a T-sediment, originating when the rest of the suspended material settles; this happens when the velocity of the current falls to zero (T means "transient", for these sediments remain suspended during a long time and pass long distances without settling).

So, each of these sediment types apparently reflects different environmental conditions prevailing at the time at which they were deposited. Their limits are not correlated to pre-determined dimensions, but the recognition is exclusively based on the shape of the curves on arithmetic probability paper.

With other current velocities and another composition of the supplied material, as a rule, transitions between the three types will result.

Doeglas mainly based his system on analyses of Dutch sediments, but his methods appeared to give satisfactory results for other sediments too, for instance for those of the Guiana Shelf (VAN ANDEL e.a., 1954; NOTA, 1958).

For our purpose the C, R and S types of sediment are important.

R-sediments: gravels and coarse sands, reworked older deposits and deposits due to a sudden decrease in current velocity; they can exist only so long as the current remains continuous, so that the material at the bottom is always moving and erosion often goes on, i.e. in streambeds of rivers and in places with strong marine currents.

S-sediments: deposited owing to a down-stream decrease in the velocity of the current or by a sorting effect they occur, for instance, on beaches and at the lee side of sandbanks and in other protected places. In running water with varying velocities mixtures of R and S types will appear.

Sediments of the C type originate during a sudden strong decrease of the current velocity, in which case the whole suspended material settles, or by deposition of unsorted material close to its source, which may be, for example, rock outcrops (cf. Soldado Platform near Trinidad, VAN ANDEL e.a., 1954), in which case it is a washed-out detritic sand.

RIVIÈRE (1952, 1954, 1957) plots the cumulative frequency curves starting from the finest fraction on semilogarithmic paper with the grain-size on the logarithmic abscis. He ascertained that the grain-size distributions of many fine-grained sediments can be expressed by means of a simple algebraic formula. In that case each distribution can be fixed by two indices, viz.

1. sorting index g, which is the ^{10}log of the diameter ratio biggest grain/smallest grain;

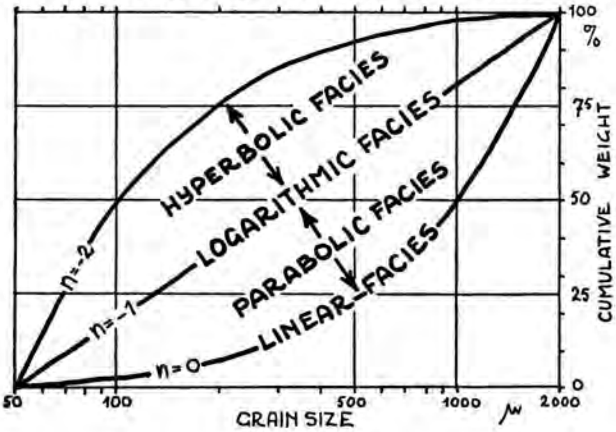
2. development index n, which is determined in the following way: on the abscis the ^{10}log of the ratios of the grain-size limits of the fractions down to the lower limit of the finest fraction are plotted; on the ordinate the cumulative amounts of the fractions according to an arithmetic scale, so that the 100 units of percentage on the ordinate have the same length as the unit for g on the abscis. The obtained curve is compared with a number of norm curves, so called "courbes canoniques", calculated for various possibilities for the value $(n + 1)$ g, so that one can estimate the value for n. Rivière distinguished a number of four granulometric facies according to the values of the development index n, viz.

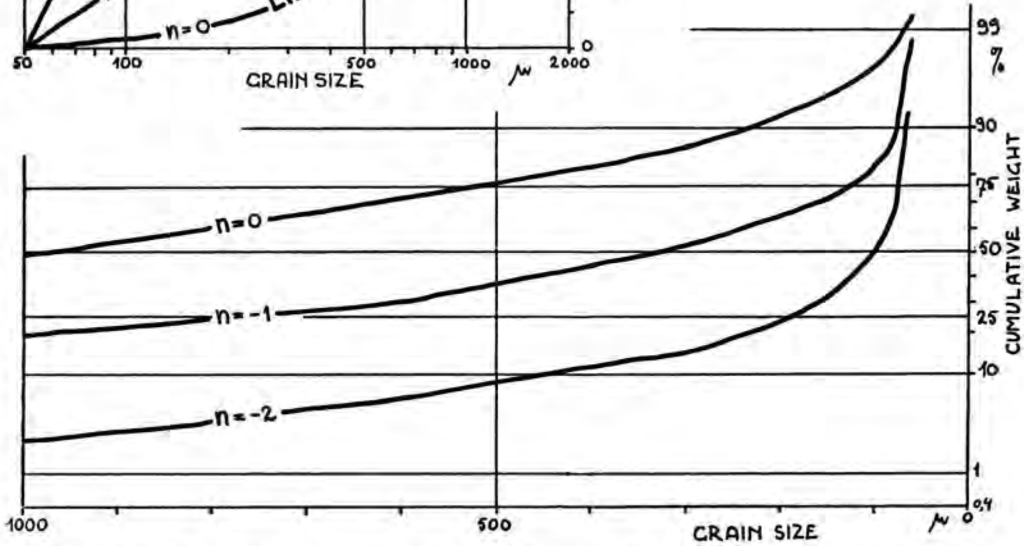
   I. linear facies ($n = 0$); this is found in not-developed deposits like non-sorted, reworked and desintegrated sediments, glacial sands and sheet-flood deposits; the cumulative distribution curve is straight when plotted on paper with arithmetic coordinates;

FIGURE 9. TYPES OF SEDIMENTS.

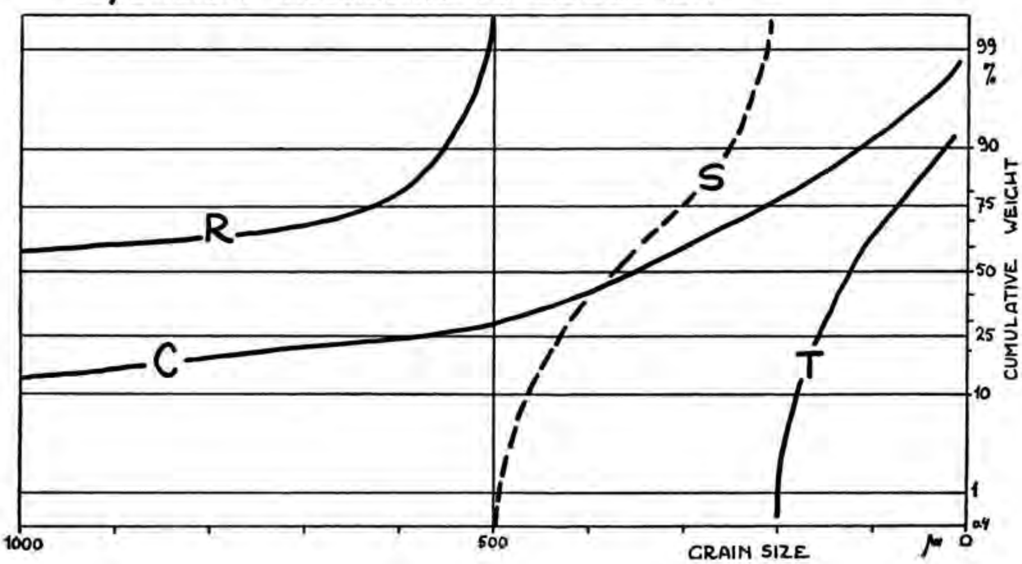
GRANULOMETRIC FACIES ACCORDING TO RIVIÈRE PLOTTED IN RIVIÈRE'S AS WELL AS DOEGLAS'S WAY FOR SEDIMENTS WITH A MINIMUM GRAIN-SIZE OF 50 μ AND A MAXIMUM ONE OF 2000 μ.

(COMPARE THE TEXT AT III 5.3)





DIFFERENTIATION OF SUSPENDED MATERIAL C IN THE DEPOSITS R, S AND T ACCORDING TO DOEGLAS.



II. parabolic facies (n between 0 and − 1); this comprises sediments developed to a certain degree by transport: river and beach deposits, also lagoon deposits washed out by wave action; the semilogarithmic cumulative frequency curve is concave in the upper direction;

III. logarithmic facies (n = − 1); this comprises sediments developed to a high degree by transport: river sands and mainly river, estuary and seashore muds (laguno-marine environment); the semilogarithmic frequency curve becomes a straight line;

IV. hyperbolic facies (n between − 1 and − 2); comprises sediments developed to a high degree by eluviation: clays in the large sedimentation basins; oceanic and laguno-marine environments; the semilogarithmic frequency curve is convex in the upper direction.

When a distribution can be fixed by the above-mentioned algebraic formula, the value of the development index is independent of the part of the distribution chosen for the calculation. So, if we consider mixed sediments with bimodal or plurimodal curves, it is possible to determine the development index for each component separately.

A peculiar example of mixed sediments are the deposits showing "courbes bimodales redressées" (fig. 11, upper curves). Boyé gave them this name because the steepest part of the bimodal curve is more or less straight, around the medium size. In fact, such curves have three equations:

- a parabolic facies for the smallest grain sizes,
- a more or less logarithmic facies for the grain sizes between the first and third quartile,
- a great dispersion due to hazard for the largest grain sizes.

Originally used in France and Algeria (cf. RIVIÈRE, 1954), Rivière's method gave also striking results when applied to the lowland of French Guiana (BOYÉ, 1959, 1960).

III 5.4. *Explanation of the stratigraphy* (fig. 10–13)

From the data obtained by granulometric analyses and by heavy-mineral counts combined with those obtained by the investigation in the field, the following picture of the geological history can be drawn, at least when we suppose that the original grain-size distribution is not substantially altered by pedological processes and biological activities. I think that this supposition is justified, as it could be shown that transport of fine material and animal influences are of restricted and local importance only (III 2.4 and 4.2). I have to admit that I used only a few sedimentological methods, fully neglecting others, so that the picture must be of restricted value.

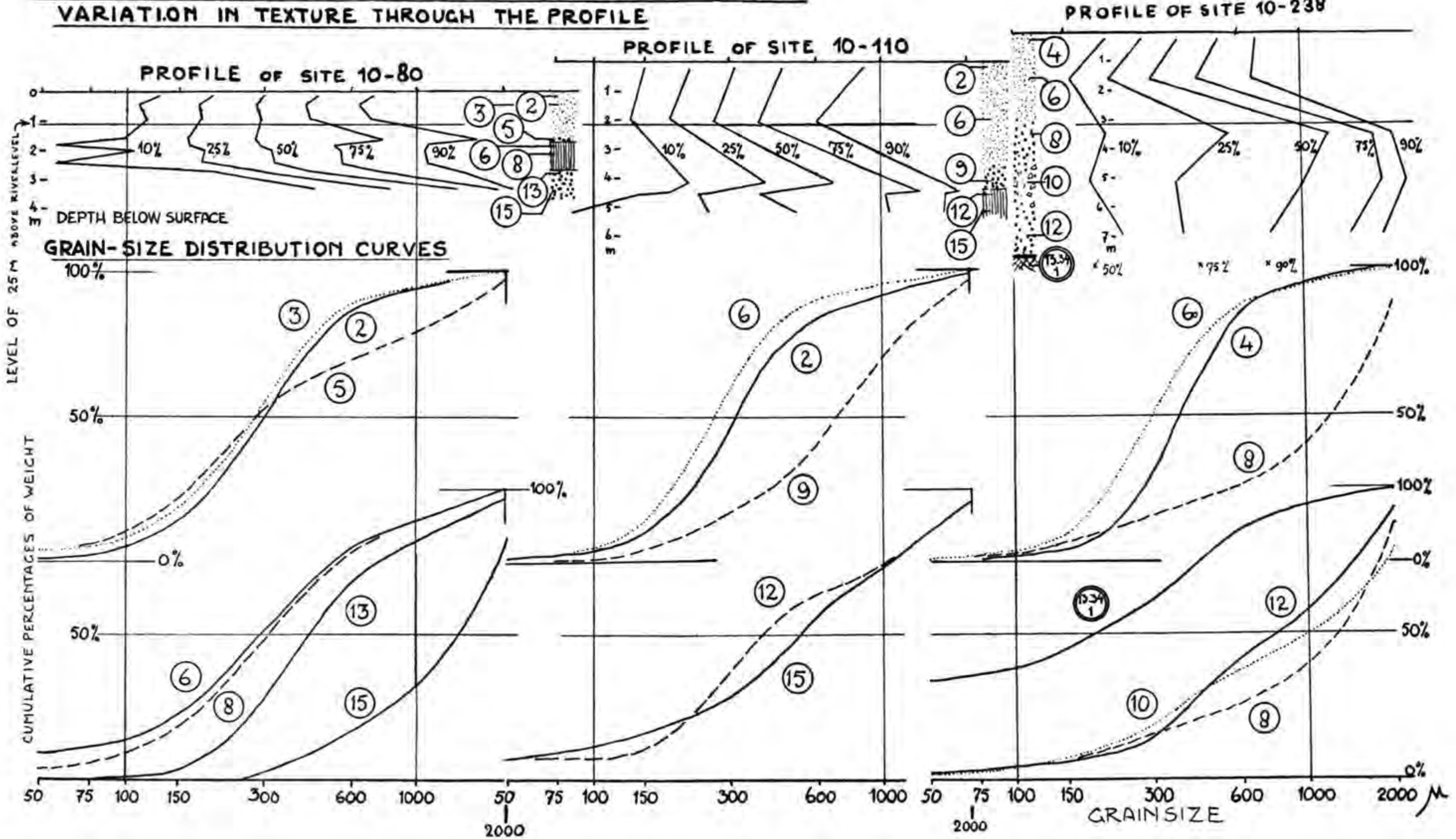
The surface of the bedrock obviously owes its topography to an old erosion. The upper strata are now strongly weathered. Three samples were investigated for heavy-mineral composition. In 13–34/1 and 15–248/2 the characteristic components are epidote, fibrolite (fibrous variety of sillimanite) and minor quantities of anatase, titanite and spinel, while in 15–248/2 much tourmaline occurs. Neither zircon nor staurolite predominate, and rutile as well as kyanite occur in small quantities only (fig. 12). The whole association points to a gneissic rock, more or less influenced by contact metamorphism (cf. the "Granite 3", mentioned by O'HERNE (1958) for Jodensavanne: granitic gneiss with newly formed biotite and with the conversion minerals chlorite and epidote, in which well-developed vein quartz, sometimes with tourmaline, occurs). In sample 10–210/1 garnet is strongly predominating, viz. with 93 %. This, too, points to contact metamorphism at the time when it intruded into the schists of the Orapu Formation. The granulometric composition of 13–34/1 (fig. 11) resembles that of other granitic rocks (cf. III 5.2.).

The deposits resting on the bedrock, are of a coarse C-type and show a plurimodal or linear facies (samples 10–80/15; 10–110/12, 15; 10–238/10, 12; 11–24/11, 17, 18, and 20). They are washed-out detritic sands: non-developed deposits which stayed in their place of origin or were transported over short distances after the rocks had been eroded by strong pluvial currents. The heavy-mineral content affirms their local origin. Sample 10–80/15 is obviously related with the gneissic bedrock, as zircon and staurolite occur both in about 40 %, and as there is very little rutile and kyanite, rather much tourmaline and even some grains of titanite and spinel. Samples 10–238/12, 11–24/17 and 18 are of another association: 14–25 % zircon, 3–6 % rutile, 60–70 % staurolite, 4–13 % kyanite and 1–2 % sillimanite. These deposits are so rich in staurolite that the coarser crystal fragments, measuring up to 5.5×2.5 mm are easily seen between the quartz grains. The source of the large amount of staurolite and kyanite is to be sought in the Taffra Group of the Orapu Formation, the contact-metamorphic zone between the schists and the granite intrusions. At present the Taffra Group is outcropping some 15 km South of area 1. O'HERNE (1958) found there the ground in some places strewn with beautiful idiomorphic crystals of staurolite. The occurrence of coarse fragments of staurolite in the sands, too, points to a source in the near vicinity, for "staurolite is rather fragile and in no case can stand several sedimentary cycles" (BOYÉ, 1960 p. 97). It is noteworthy that DOEGLAS (1952) mentions the staurolite-kyanite-association as principally occurring round old continental blocks. The Guiana Shield is one of these blocks!

Heavy minerals were not counted in the coarse sandy deposits with quartz gravel (10–238/10; 11–24/11; cf. III 2.3.1.). This gravel and very coarse sand may have been produced by the quartz veins in the granites as well as by the weathered schists of the Orapu Formation (III 5.2.). At any rate they give evidence of the torrential character of the rain in the pluvial climate.

The sediments overlying these deposits are still coarse-grained. The grain-size distribution of the lower ones is of the C-type: they are pluvial washed-out sands. Gradually the deposits become less coarse, and the upper ones even contain some silt. The curve changes from an R-type to a mixed R-S-type. In their bimodal facies the parabolic part becomes predominating in the upper deposits. These facts point to a gradual

FIGURE 11. GRAIN-SIZE DISTRIBUTIONS OF 3 PROFILES.
VARIATION IN TEXTURE THROUGH THE PROFILE

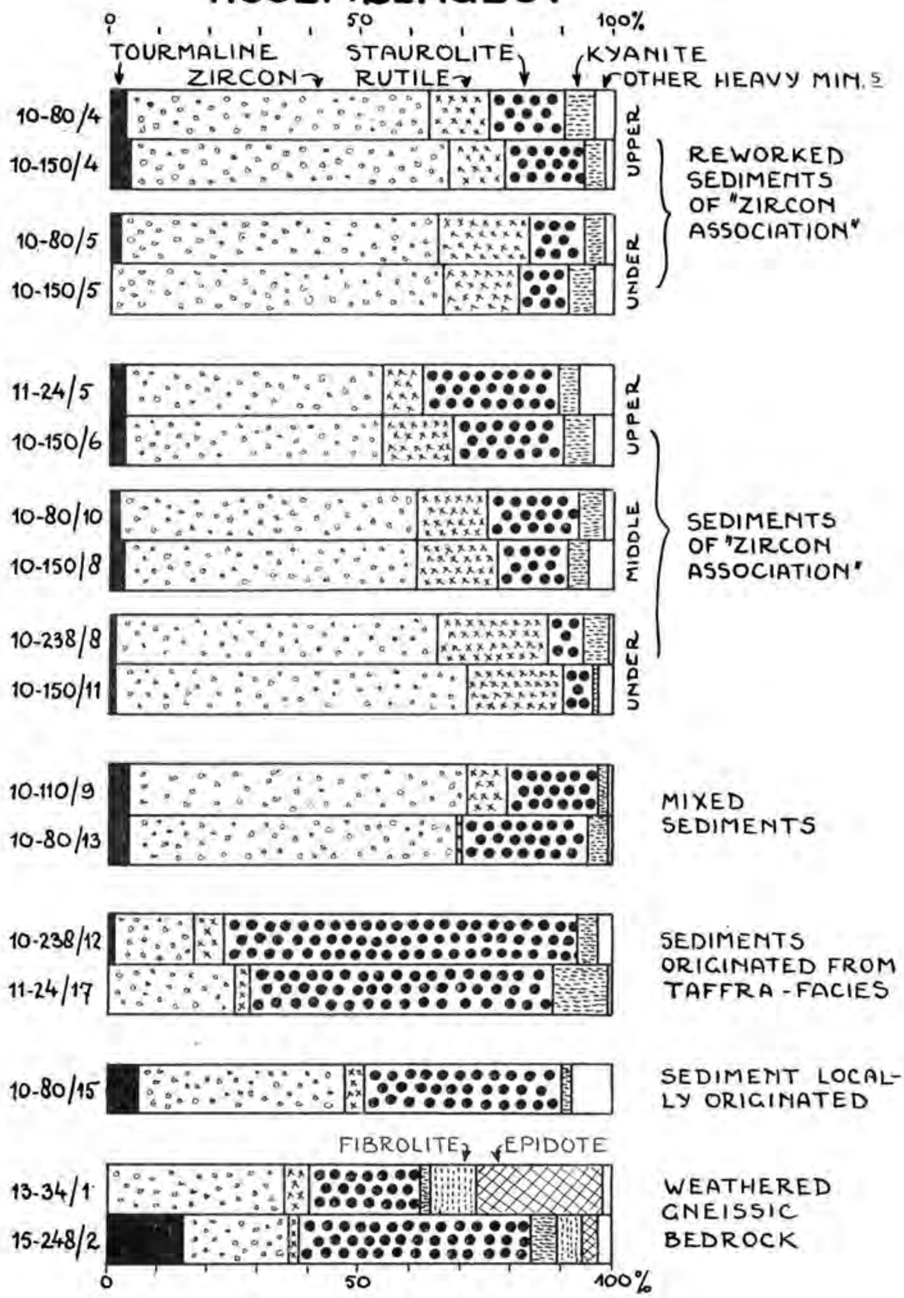


change in environment, the pluvial activity diminishing and the climate becoming drier. The parabolic facies, however, indicates that transport, most likely a fluvial one, was going on. The altered deposition conditions are also demonstrated by a marked change in the heavy-mineral assemblage. Greater quantities of zircon and rutile are supplied, but in the higher strata the amount of staurolite increases at the expense of both zircon and rutile ("zircon-association"). Thus, the lowest sediments (10–238/8; 10–150/10, 11) contain about 66 % zircon, 20 % rutile, 8 % staurolite, 3 % kyanite and some tourmaline, andalusite and garnet grains, but this association passes via that of the middle sediments (10–150/9, 8, 7; 10–80/10; 11–24/8) into the association found in the upper ones (10–150/6; 11–24/5), which contains 51 % zircon, 11 % rutile, 25 % staurolite, and kyanite, garnet and tourmaline in almost the same quantities as in the lower sediments, no andalusite, but some grains of sillimanite. These washed-out detritic sands have very likely been produced by a less strongly metamorphosed facies of the Orapu Formation (Bonidoro Series), for mineralogically they are closely related to the lower deposits of the sedimentary soils of the Mapane region, which were developed in eluvium from crystalline rocks weathered in the immediate vicinity (cf. SCHULZ, 1960, profile D/0).

At the sites 10–238 and 11–24 the sediments of the "zircon-association" overlie the deposits with gravel, but in the northern part of area 1 the latter are wanting. There the sediments of the zircon-association settled on the bedrock (site 10–150) or on detritic sands without gravel (site 10–80). The curves of the grain-size distribution in the layers at site 10–80 pictured in fig. 11 demonstrate a change in the conditions under which the deposition took place, for they pass from the linear facies of sample 15 to the mainly parabolic facies of sample 6, with a major discontinuity between the layer of the washed-out detritic sand (sample 15) and the detritic sands rich in zircon (samples 13 to 6). The change in transport, indicated by the 30 % parabolic curve of sample 13, is confirmed by the "mixed" heavy-mineral assemblage, which occurs in sample 10–110/9 too. They share the rutile content of 1–8 % with sample 10–80/15, the 65–67 % of zircon, however, with the overlying strata.

During the driest period, which perhaps resembled the present one, but may have been even drier, pedogenic processes affected the deposits. Leaching brought about eluviation of organic matter and of aluminum and iron compounds; and probably fine fractions were transported too. They precipitated in the zone of the groundwater fluctuation and indurated the silt-containing deposits in this zone to a hardpan. In other instances these precipitates merely coated the grains, but did not cement them. The general drainage conditions were probably much like the present-day ones, i.e. determined by the structural lines in the bedrock (cf. III 2.8). So, in the region North of the dipping bedrock on site 10–120, owing to the favourable combination of silty deposits and groundwater

FIGURE 12. COMPOSITION OF THE NON-OPAQUE HEAVY MINERAL ASSEMBLAGES.



fluctuations, a hardpan was formed, while South of this site only the coarse sediments or the upper layer of the bedrock were affected. For this reason strata of different age and origin show the signs of this palaeo-climatic leaching process, viz. in the form of a hardpan at the sites 10–80 and 10–110, and of dark coated grains at several places between picket 120 and 160 of transect 10 (cf. III 2.2, 2.4 and 2.5).

A new, but not very strong, pluvial erosion period attacked this soil, partly reworking the upper strata, partly removing them, especially in the northern part. In this way the hardpan too was eroded. Locally, perhaps where it was less strongly indurated, the pan disappeared entirely, and in this way its present-day occurrence "like strayed wreckage" will have arisen.

The granulometric curves of the reworked deposits are all "courbes bimodales redressées" with a striking similarity in shape (figs. 11 and 13). The lower sediments are the coarsest ones (10–150/5), and when they have been mixed with some of the coarse sand underneath they sometimes even show a plurimodal facies (10–80/5). The middle deposits are of somewhat finer texture than the upper ones (10–80/3 resp. 2; 10–110/6 and 2; 10–238/6 and 4). The shape of the Doeglas curve, which is of a coarse S-type, and the more or less predominating parabolic facies, with a hyperbolic facies for the greater sizes, points to a rather constant fluvial or pluvial transport. The origin of the strata by the reworking of older sediments is demonstrated by the close resemblance between their heavy-mineral assemblages. The samples 10–80/4 and 5, and 10–150/4 and 5 belong to the zircon-association: 60–66 % zircon, 11–18 % rutile and 10–16 % staurolite, the samples 5 are more nearly related to the deeper strata, and the samples 4 to the upper ones, while sample 10–238/4 with 22 % rutile and 26 % staurolite showed the influence of even deeper layers (10–238/8).

This new period of erosion is for a large part responsible for the present topography, e.g. for the peculiar features which obviously are dried talwegs, i.e. depressions in the terrain bordered by ridges with low steep slopes described in III 2.8.

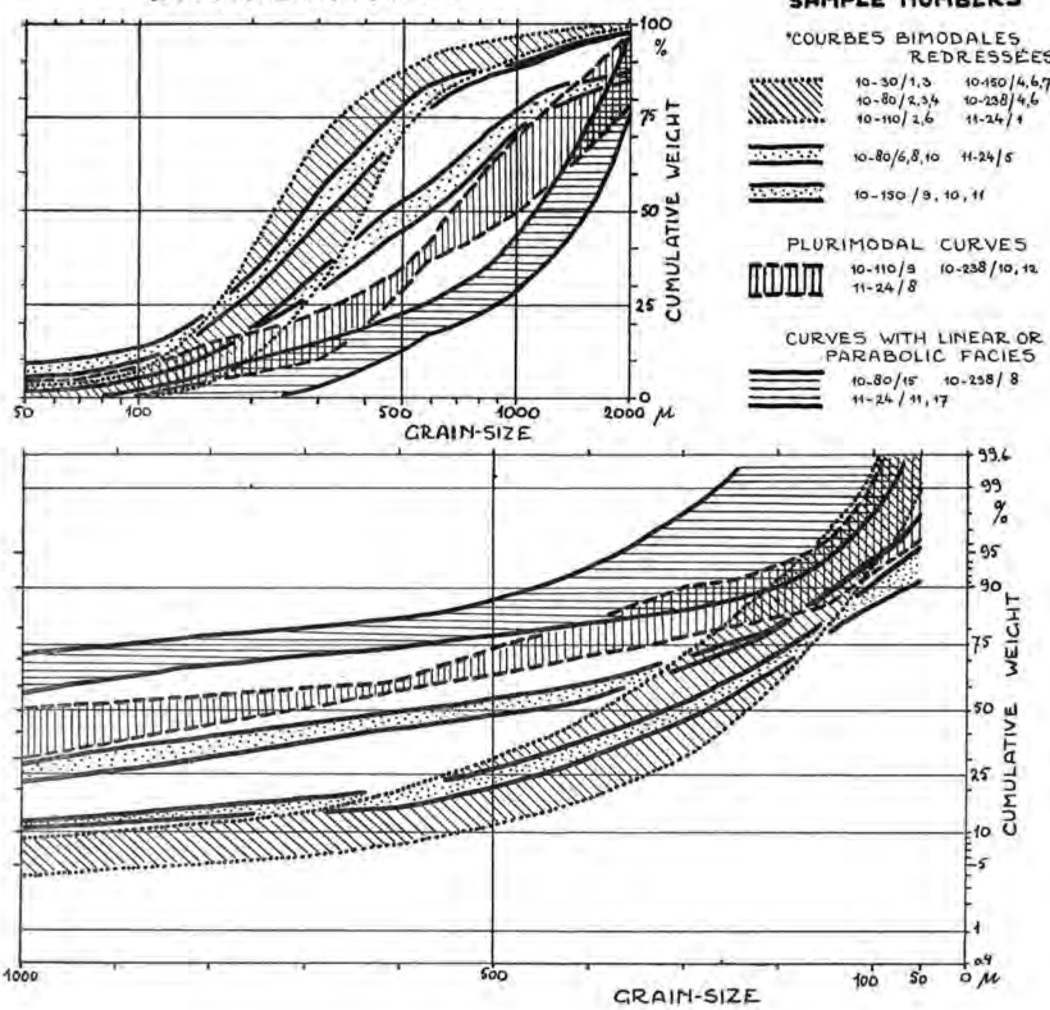
Summarizing our exposition we may say that in the upper 6 m of the sediments at least two sedimentation phases are recognizable. The older phase is the more important one, ending with soil-forming processes. The younger phase eroded the upper soil strata, deposited about 1 to 1.5 m of sediments over the older deposits and shaped the present-day topography.

The period of pedogenesis and the dried-up water-system are the only more or less reliable marks available for dating. The hardpan was probably formed in the Eemian, the Riss-Würm Interglacial Period; the latter is the first quaternary transgression which in many places of the Guiana lowlands is clearly noticeable. Consequently the older phase is at least of Rissian Pleistocene age, but it may even be much older, for it cannot be dated exactly. It is also very likely that several periods were involved in this phase; this seems to follow from the different heavy-mineral associations. The younger phase represents one or more pluvial periods of the Würmian Pleistocene, of which the latest, the Preflandrian Pluvial, is responsible for the development of the erosive water-system; an analogous extinct topography is known from French Guiana and could be exactly dated (BOYÉ, 1959).

In this exposition in broad outline an explanation is given of the stratigraphy of the some metres thick upper part of the soil; it focussed its attention on area 1, but, allowing for local differences, the interpretation

FIGURE 13.

PRINCIPAL GROUPS OF GRAIN-SIZE DISTRIBUTIONS.



also holds for the other areas. From a pedogenic point of view the recognition that the hardpan and at least some of the dark coffee-brown layers represent fossilized soil features, which consequently are not due to leaching of the present overlying soils, is to be regarded as an important result.

Finally I wish to state that I am greatly indebted to Dr. M. Boyé. In giving this section its final form, I advantageously made use of the remarks he made on my preliminary report. His additional morphoscopical analyses of the quartz grains of several samples, too, gave fully conformable results.

III 6. Leaching and podzolization

In connection with the fossil hardpans the question arises whether under present-day conditions too "podzolization" occurs.

Very fine sandy soils containing layers illuviated with organic matter and resting on a clay subsoil (Palissade-Soil Series) as well as slightly to strongly cemented strata found in the zone of the water-table fluctuation in the fine sandy ridge soils (Rijsdijk Series), occur in the ridges of the Old Coastal Plain (Bakker, 1954; unpublished data of the Scientific Expedition 1948–1949; Van der Eyk, 1957; Van der Eyk en Hendriks, 1953; Van der Voorde, 1956, 1957). The surface of these hardpans lies at a depth of 40 to 150 cm and their thickness is 5 to 80 cm. The pan consists of dark brown sand cemented by organic matter and showing a varying degree of accumulation of iron in the lower zone; its colour is mottled yellow, brown and/or yellowish red. Leaching bleaches the overlying, primarily yellowish-brown sand. In none of the profiles a litter layer is developed, but the topsoil contains a more or less considerable amount of organic material. Van der Eyk (1957) mentioned in some instances the occurrence of a second, iron, hardpan in the sand below the first pan. This second pan rests on the subsoil.

Eluviation of iron is also observed in the ridges of the Young Coastal Plain. In the fine-sandy Vredenburg Series a not cemented 90 cm thick illuvial zone lies at a depth of 50 cm; in the coarse-sandy ridge soils a 20 cm thick layer of slightly friable sand occurs at a depth of 85 cm.

In III 5.4. I stated that the Jodensavanne hardpans were formed in the zone of the groundwater fluctuation in somewhat silty deposits. Unfortunately chemical analyses are wanting, so that the degree of illuviation of organic matter and sesquioxides in the hardpans of the ridges can not be compared with that in the pans that were investigated.

Consequently these podzol-like features in the lowlands of Suriname always originated under the influence of groundwater, which may stagnate upon a sedimentary clay layer. Podzols described from other tropical lowlands are also in most, if not in all, instances "groundwater podzols", and there too they often occur in Pleistocene sandy deposits (Browne, 1958; Mohr and Van Baren, 1954, chapter XIII; Richards, 1952). In the literature I have found no examples of true podzol profiles which originated independently of groundwater. In the investigated areas I found only in the transition zone of red to white sand, a situation which reminded me of a "true podzolization"; I will consider this below. Even under *Dimorphandra* wood with its thick litter layer and rootmat no indications of true podzolization were observed, though recent illuviation zones caused by the influence of the groundwater were certainly met with.

So in III 2.6 the fact was mentioned that under scrub and woods in the groundwater fluctuation zone a slight stagnation in the leaching of organic matter occurs. This illuviation zone will immediately disappear when the organic matter supply decreases; this follows from the fact that such zones do not occur under more open vegetations. The removal of considerable amounts of humus compounds from the white sand areas appears already from the deep tea-colour of the water in the creeks (cf. the name "Blakawatra", meaning: "Black Water").

Very dark coloured layers were sometimes encountered on the kaolinitic subsoil under white as well as under red sand and at the upper side of the slope at 11–28 even a more or less strongly cemented pan was found. Because these features may be related to the bleaching of the red sand, I will first discuss this bleaching.

The bleached soils described from the Mapane region by SCHULZ (1960), which are related to the sand under consideration, are only for a minor part completely bleached: most of the grains still have an orange or red colour owing to the coating with iron. The sediments in the Jodensavanne region too, can not have been deposited as white sands, but at least in a major part as coated grains of the kind that is still encountered in the deeper borings of area 3 and in the coastal plain. Otherwise the formation of the illuvial layers described in the previous section would not have been possible, as this process presupposes a supply of iron and aluminum compounds.

BLEACKLEY and KAHN (1959, cf. also JONES, 1959) studied the process of bleaching in bauxite mines at Mackenzie and Ituni. Here white sand with the same grain-size distribution as 10–238/6 extends sidewards as well as downwards at the cost of the red loamy sand and sandy loam, and this is accompanied by a practically complete dissolution of the iron and aluminum compounds, visible as dark rims round the red patches in the profile, and by eluvation of a part of the clay fraction. Iron, aluminum and humus substances may be precipitated at a depth of 6 to 12 m, forming a more than 30 cm thick cemented pan resting on the heavier, red, sandy sediments. The chemical substances governing the bleaching processes will be supplied in the main by the decomposing organic matter in the topsoil. For this reason the kind of vegetation is an important factor, BLOOMFIELD (1955) clearly demonstrated this by the differences in dissolving capacity of leachates produced by various kinds of litter.

The sharp boundary line between the white and the red sand in area 1 may be explained as follows. SCHULZ (1960, p. 121) describes in what way a forest type that is typical for heavier soils may transgress the boundary between the latter and the lighter, bleaching soils. When such a forest type maintains itself on the one part of the bleaching sand, while on the other part a vegetation type develops that causes a somewhat stronger bleaching by a more open stand of the vegetation or by producing another kind of litter, then this sharp boundary line in the vegetation, perhaps favoured by single-species dominance, will cause also a sharp boundary line in the lighter soil. Fire may also play a role, in the first place as a factor in the succession of the vegetation, and possibly also owing to an exaggerated leaching of compounds from the ashes (oral communication, 1960, by Prof. Dr. R. TÜXEN on the dissolution of illuvial horizons in podzols under heath in northwestern Germany). In this way an equilibrium is established between the few places where, owing to a slightly heavier texture, the red soils remained covered by a vegetation of the mesophytic type, and the rest of the area where the soil was carrying a xeromorphic vegetation and was bleached and converted into white sand.

At site 17–110 I found over a small area a light orange-brown layer as a remnant of the red sand. It was 30 cm thick and lay at a depth of 75 cm. At 20 m North of site 12–21 in the grass savanna a patch of red sand occurred with a diametre of about 10 m, totally surrounded by white sand.

During recent disturbances of the forest on the red-sandy soils it appeared that leaching became more intensive in places where a grass cover developed. Under a bleaching topsoil (0.1 % C, 20 p.p.m. Al, 4 p.p.m. Fe) an illuvial horizon (0.3 % C, 660 p.p.m. Al, 7 p.p.m. Fe) is formed 3 to 4 m above the water-table. This should therefore be regarded as a real podzolization.

The higher degree of bleaching observed in the coarse facies of the red-sandy soils may be due either to a different iron content or a different iron compound, or to its coarseness or, as mentioned in the previous section, to a former groundwater regime. The blackish brown zone in this coarse sand is obviously an old illuvial layer (0.5 % C, 730 p.p.m. Al and 3(!) p.p.m. Fe) that resisted the bleaching by the inertia of the aluminum and humus compounds, while the iron compounds were mobilized by the conditions prevailing below the water-table which favoured their reduction, and were drained away (cf. RUSSELL, 1950 p. 533) (see, for instance, fig. 7; transect 11–8 to 16). I consider the occurrence of such dark illuvial layers in white sand profiles (III 2.6), whether they may be a palaeopedogenic feature or not, as an indication that the bleaching process is nearing its end. This kind of layer occurs also below bleached sand in the Mapane region (profile D/0), and is mentioned by VAN DER EYK (1957) as a "hardpan" in his profile description of the "bleached cover soils".

After percolating the red soil the water follows a lateral course and

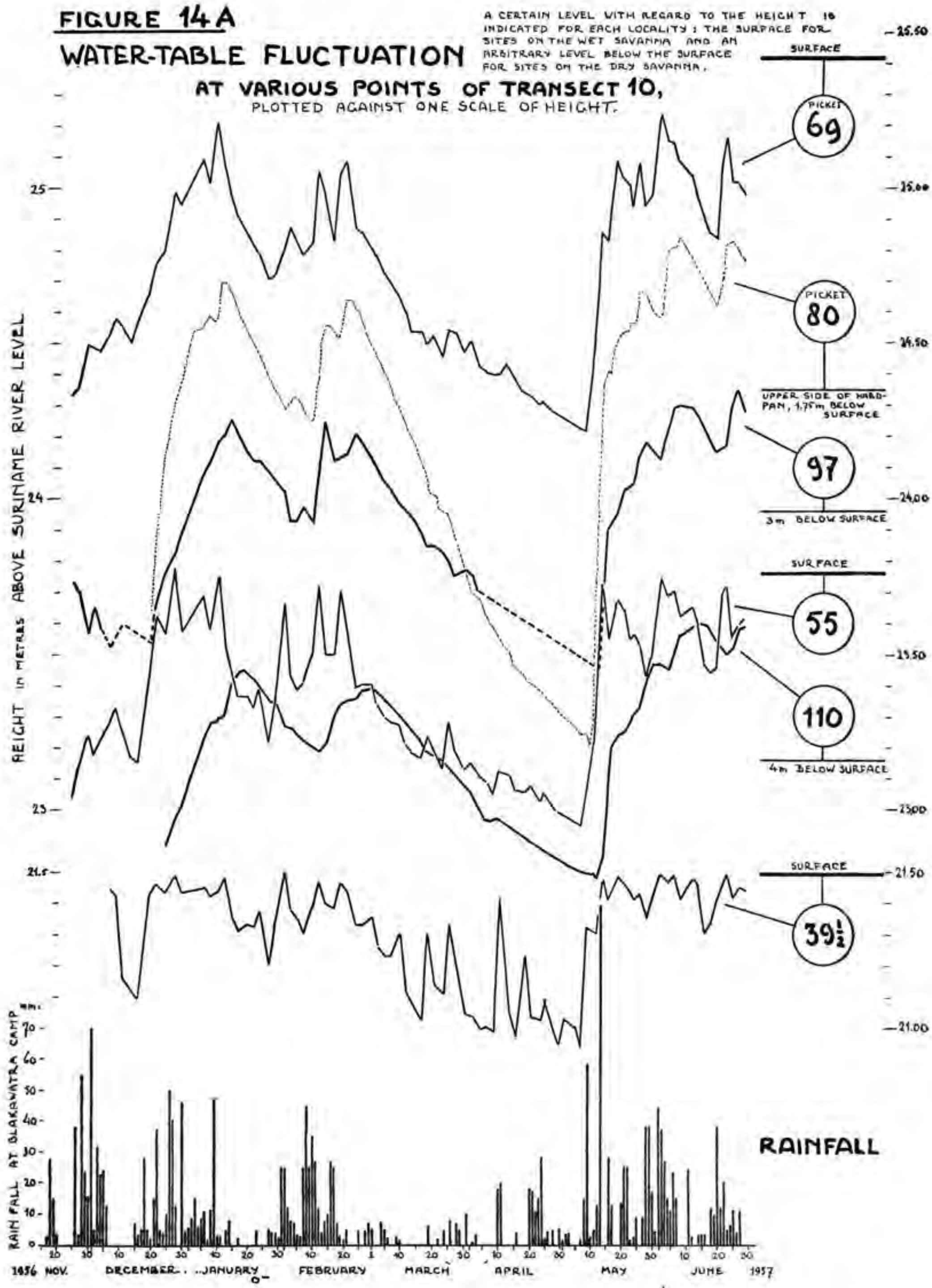


FIGURE 14 A
WATER-TABLE FLUCTUATION
AT VARIOUS POINTS OF TRANSECT 10,
PLOTTED AGAINST ONE SCALE OF HEIGHT.
A CERTAIN LEVEL WITH REGARD TO THE HEIGHT IS INDICATED FOR EACH LOCALITY: THE SURFACE FOR SITES ON THE WET SAVANNA AND AN ARBITRARY LEVEL BELOW THE SURFACE FOR SITES ON THE DRY SAVANNA.
SURFACE
PICKET 69
PICKET 80
UPPER SIDE OF HARD-PAN, 1.75 m BELOW SURFACE
97
3 m BELOW SURFACE
SURFACE
55
110
4 m BELOW SURFACE
SURFACE
39½
HEIGHT in METRES ABOVE SURINAME RIVER LEVEL
RAIN FALL AT BLAKAWATRA CAMP mm.
RAINFALL
1956 NOV.
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
1957

FIG. 14 B


* BRIDGE SURFACE = 10.29 m ABOVE SURINAME RIVER LEVEL.
HEIGHT OF THE WATER-LEVEL IN CM BELOW THE BRIDGE-SURFACE *
WATER-LEVEL OF BLAKAWATRA CREEK

becomes responsible for the development of illuvial layers below the red loamy sand as well as in the adjoining heavier colluvial soil on the upper part of the slopes (fig. 7: 11–60 to 66, and 82 to 90). In the latter the clayey layers are often cemented. On slopes where white sands merge into a colluvial soil hardpan-like features are absent, unless the white sand lies between red loamy sand and colluvial soil (fig. 7: 11–26 to 30). In that case the leachates to which the illuvial horizon owes its origin, are not derived from the white sand but from the red soil.

Summarizing, I conclude from my results that under present-day conditions the bleaching of the sandy deposits in the Jodensavanne region does not give rise to permanent illuvial horizons. Consequently, the white sandy soils are neither podzols sensu stricto nor groundwater podzols, but merely leached sands.

III 7. The groundwater

III 7.1. *Observations made between pickets* 33 *and* 110 *of transect* 10

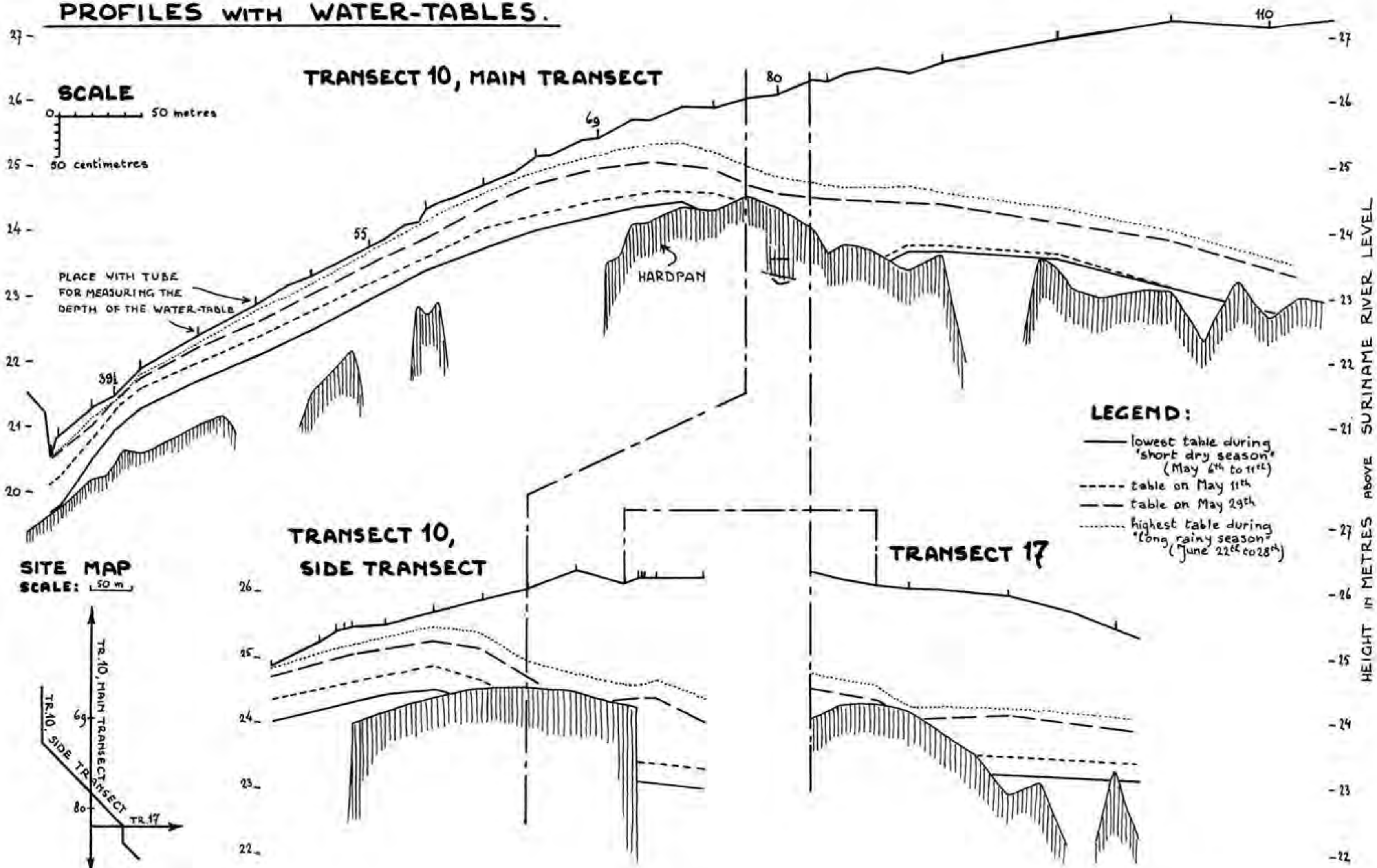
The results of the observations on the water-table made between the end of November, 1956 and the end of June, 1957 between the pickets 33 and 110 of transect 10 are shown in the figures 6, 14 and 15. For the construction of fig. 14A six series of readings were selected and the position of the water-table is indicated with regard to the level of the Suriname River. From this figure a remarkable difference in the fluctuation of the watertable appears to exist between sites where the groundwater does reach the surface (wet savannas), and sites where it does not (dry savannas). In the wet savanna a rise appears to be the immediate result of a rain-shower; especially when after a period of dryness (March to April) the first rains come down the rise is very rapid. When the water-table is found at a lower level, the effect of irregular supply appears to be markedly smoothed, and in such sites the rise and fall are more gradual.

A distinct rise of the water-table at site 10–69, which lies just on the actual watershed, appears later and is less marked at sites that are situated at increasing distance from the watershed; thus at site 10–110 at a distance of 410 m from the watershed, where the water-table lies about 3 m deeper, the rise is observed 6 days later. The disappearance of some of the peaks indicates that the rain water is retained for some time in the upper layers of the soil (i.e. in the root-mat and in the finer sand), and that only gradually part of it percolates to the groundwater in the deeper layers. Concurrently the amplitude of the water-table fluctuation decreases with increasing depth of the groundwater: at 10–69, where the water-table may rise to 18 cm below the surface, the amplitude amounted to 102 cm, whereas at 10–110, where the highest measured water-table was at 357 cm below the surface, the amplitude was 81 cm.

Between 10–69 and 10–33 the amplitude of the fluctuations in the water-table also shows a decrease (at 10–55 it was 82 cm, at 10–39 only 55 cm),

FIGURE 15.

PROFILES WITH WATER-TABLES.



but this is due to a particular combination of general drainage condition and local topography, which will be discussed in III 7.2. Moreover, in sites like these, where the soil has a single-grain structure and where the groundwater is so high that it reaches the surface by capillarity, some special events have to be taken into consideration. One of these is the so-called "Wieringermeer effect" (HOOGHOUDT, 1952): when the menisci of the capillaries in the groundsurface layer do not have their maximal tension a minute evaporation will result in a strong increase of this tension and so of the capillary forces, causing a fall in the water-table as measured in the bores, till at last a depth is attained equal to the maximum capillary rise for that particular soil. A very small amount of precipitation is sufficient to minimize the surface tension of the menisci, so that the capillary forces are neutralised and, consequently, the water-table rises to the surface. This rise, called "reversed Wieringermeer effect" is thus much stronger than the same amount of precipitation would bring about in case of a deeper water-table.

Increasing soil temperature causes decrease of the surface tension in the menisci and, consequently, the capillary rise diminishes, resulting in a rise of the water-table as measured in the bore holes (KRUL, 1952). Evaporation and increase in temperature, therefore, have an opposite effect. At any rate, it should be realized that so long as the water-table does not sink below a depth of about 0.5 m, measurements in the bore holes may show changes which do not correspond to actual changes in the water content of the soil, because these changes may entirely be due to changes in the capillary forces.

Fig. 6 and fig. 15 show that in the dry season the watershed is found in the same position as in the wet season. The facts that the creeks in the southern part of area 1 are deeply incised and at rather close mutual distances cause that the watershed is not found at the highest point. In the dry season the greater part of the hardpan falls dry. At site 10–80, where the hardpan had been hacked through, and at site 10–83, the water-table showed a stronger fall (160 cm) than at the other sites where measurements were made. This points perhaps to a local increase in drainage. Local effects like the flooding of the hardpan, e.g. by a lateral supply, the hardpan's capacity to absorb water, and the precipitation storing effect of the forest, in our opinion play but a subordinate part.

At site 10–80 I studied the permeability of the hardpan by measuring the rate at which water was absorbed at the surface as well as in bores of different depth. For the elaboration of my data I am greatly indebted to Mr. A. HEYLIGERS, dipl. phys. engineer. While the hardpan was above the water-table measurements made in 40, 60 and 75 cm deep bores showed that at first the water was rapidly absorbed, especially down to a depth of 20 cm, where the size of the sand grains is smaller and where they are less strongly cemented than in the deeper layers. In the upper 20 cm the absorption rate was on the average 0.4 cm/min., in the deeper layers on the average 0.05 cm/min. The absorption capacity, however, appeared to decrease as the moisture content of the hardpan material increased. This decrease was more

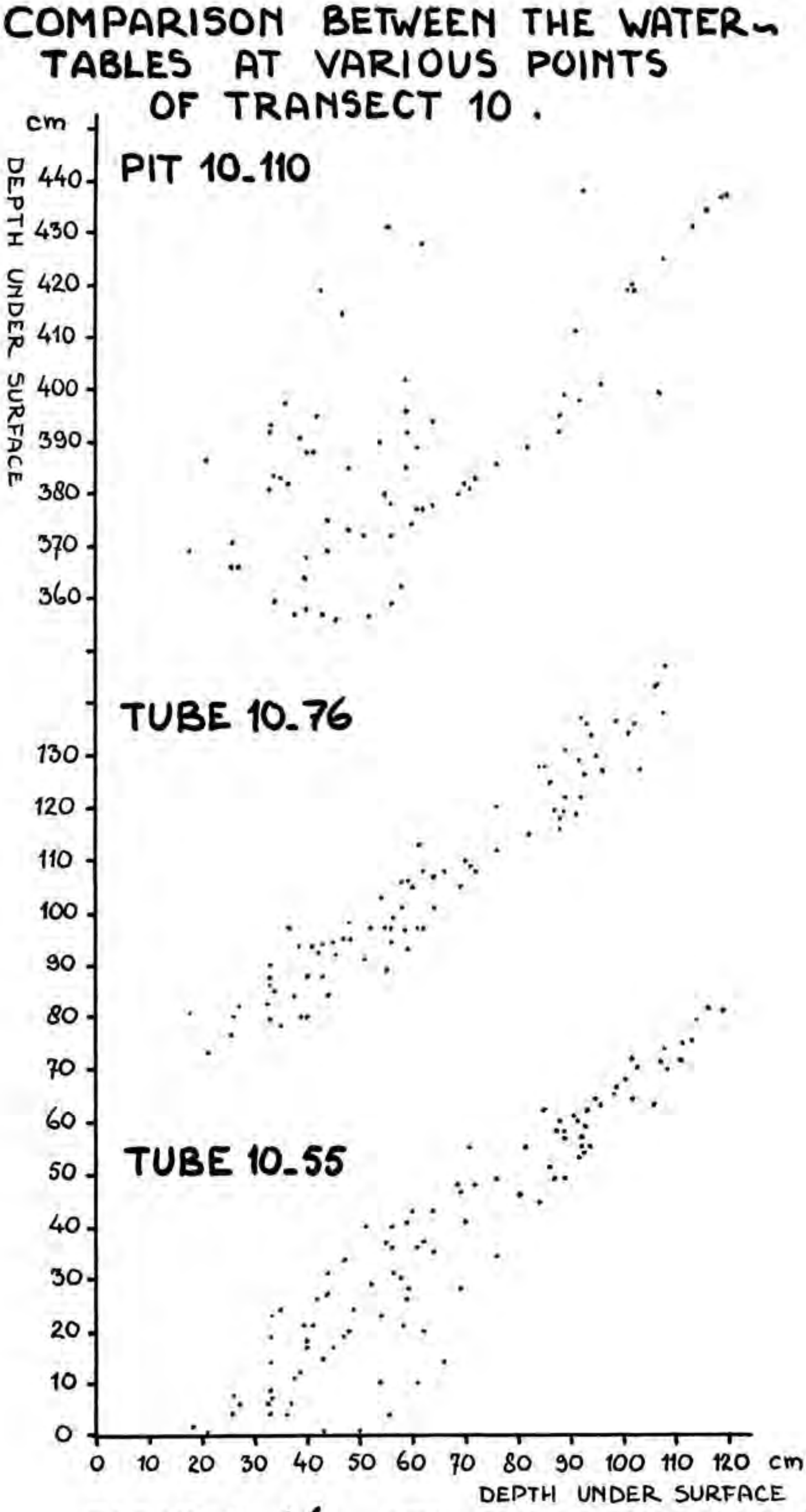


FIGURE 16. STANDARD TUBE 10_69

rapid in the layers with the highest absorption capacity. The power factor found for the retardation amounted in the first case to 0.1, in the second to 0.01. During the period in which the hardpan is submerged in the groundwater, the latter does not penetrate more than 0.0004 cm per minute (= 0.6 cm per day); when the water-table remains below the surface of the pan, this value may rise to 1.0 cm per day. Possibly it is on account of the absorption that the central part of the hardpan and not its highest one remains dry for the longest period. The permeability of the hardpan, however, is so small in comparison to that of the overlying sand, where it reaches a value of 40 m per day, that it would certainly retard the drainage if it formed a closed layer. Now, due to its scattered occurrence, it can at the most exercise only some local effects. The general pattern of the drainage is not affected by it.

III 7.2. *Hydrology of the savanna region*

In the course of the year the position of the water-table was determined 4 to 8 times in each of the auger holes situated in the savanna parts of the transects. A method by the aid of which the observations made in different parts of the same area or in areas that are more or less widely separated from each other, may be compared, has been indicated by VISSER (1952). A site at which the water-table never reaches the surface is taken as standard. The observations at the site which is to be compared with the standard are plotted as ordinates of a graph with the standard as absciss. When the area in which the two sites are situated is homogeneous or when the two sites are situated in similar areas, the collection of points obtained in this way will form a swarm which is scattered round a straight line. The tangent of the angle which this line includes with the absciss, is a measure of the amplitude of the water-table fluctuation.

When the observations mentioned in the preceding section were tested by means of this criterion, some not entirely unexpected deviations were encountered. The set of observations made at site 10–69 was chosen as standard. In the graph (fig. 16) in which the observations made at site 10–55 are compared with this standard, the points in the lower part, i.e. in the part where the highest water-tables have been plotted, show a very wide scattering in the swarm, what has been caused by the "Wieringermeer effect". In the case of the observations made at site 10–76, which lies close to the standard one, the agreement with the latter appears to be quite satisfactory, but in the case of site 10–110, where the water-table is found at a much greater depth, the variability appears to be even larger than at site 10–55. This is doubtless due to a more gradual supply of water caused by the buffer-effect of the overlying layers.

Thus, strictly speaking, the part traversed by transect 10 cannot be regarded as homogeneous from the hydrological point of view, and in order to compare the observations made at other sites with those made along this transect, we will have to use different standards. From what has been said above, it will be clear that the latter must be chosen in accordance with the depth at which the water-table is found. Some of the results obtained with standards that have been chosen according to this principle, are shown in fig. 17.

COMPARISON OF THE WATER-TABLES IN SOME AUGERBORES WITH THOSE IN TUBES OF TRANSECT 10.

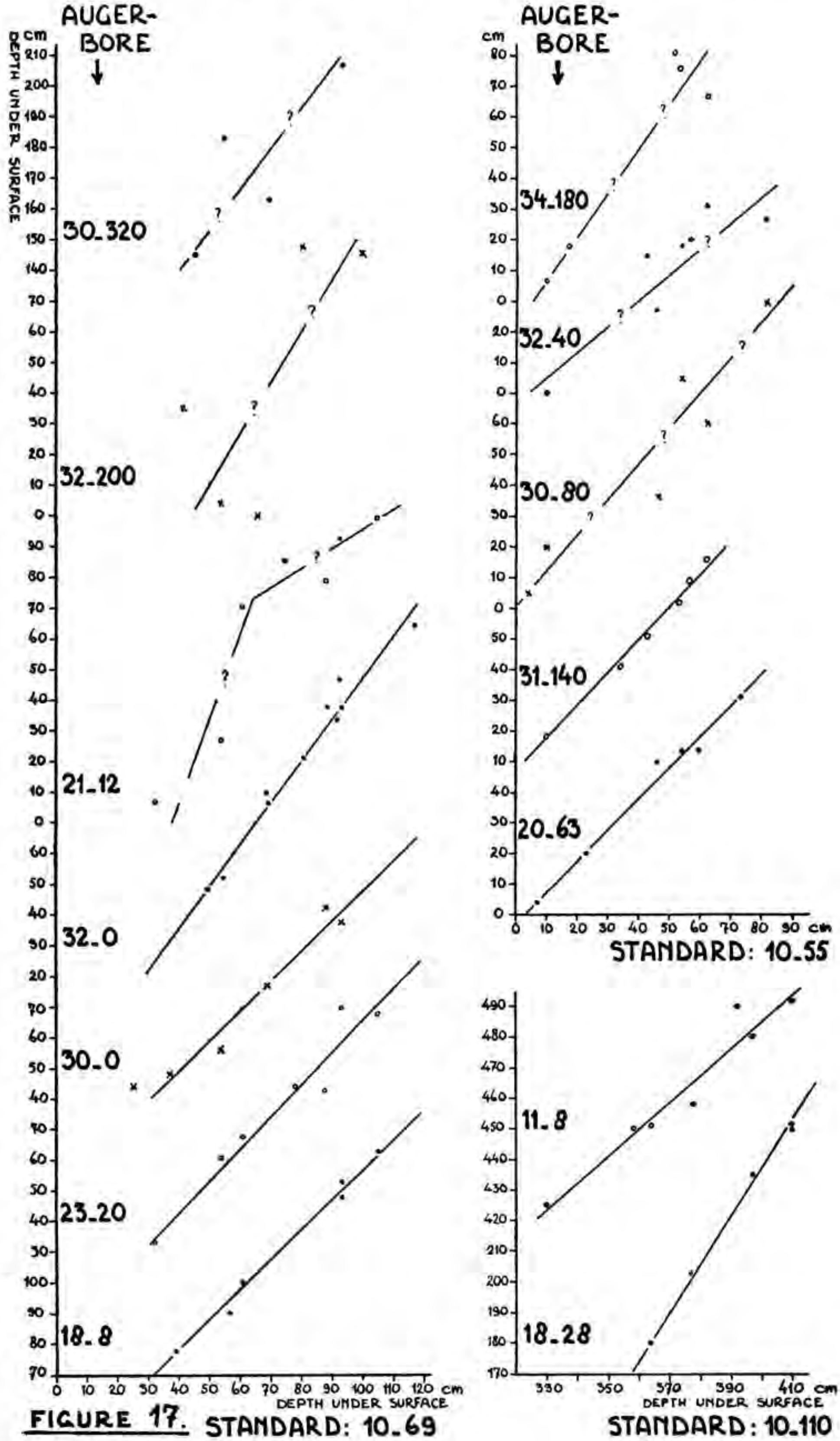


FIGURE 17.

For sites where the water-table is found at a greater depth, the agreement is, on the whole, quite good. Where the water-table was found nearer to the surface, the agreement with the standard site 10–69 was also quite satisfactory when the sites had a similar topographic situation, viz. in the vicinity of a watershed. But when the sites were situated in the near vicinity of a creek, the correlation was much less satisfactory, probably because in such situations the position of the water-table will be influenced by a lateral supply of groundwater and eventually by rain water which has ran off along the slopes.

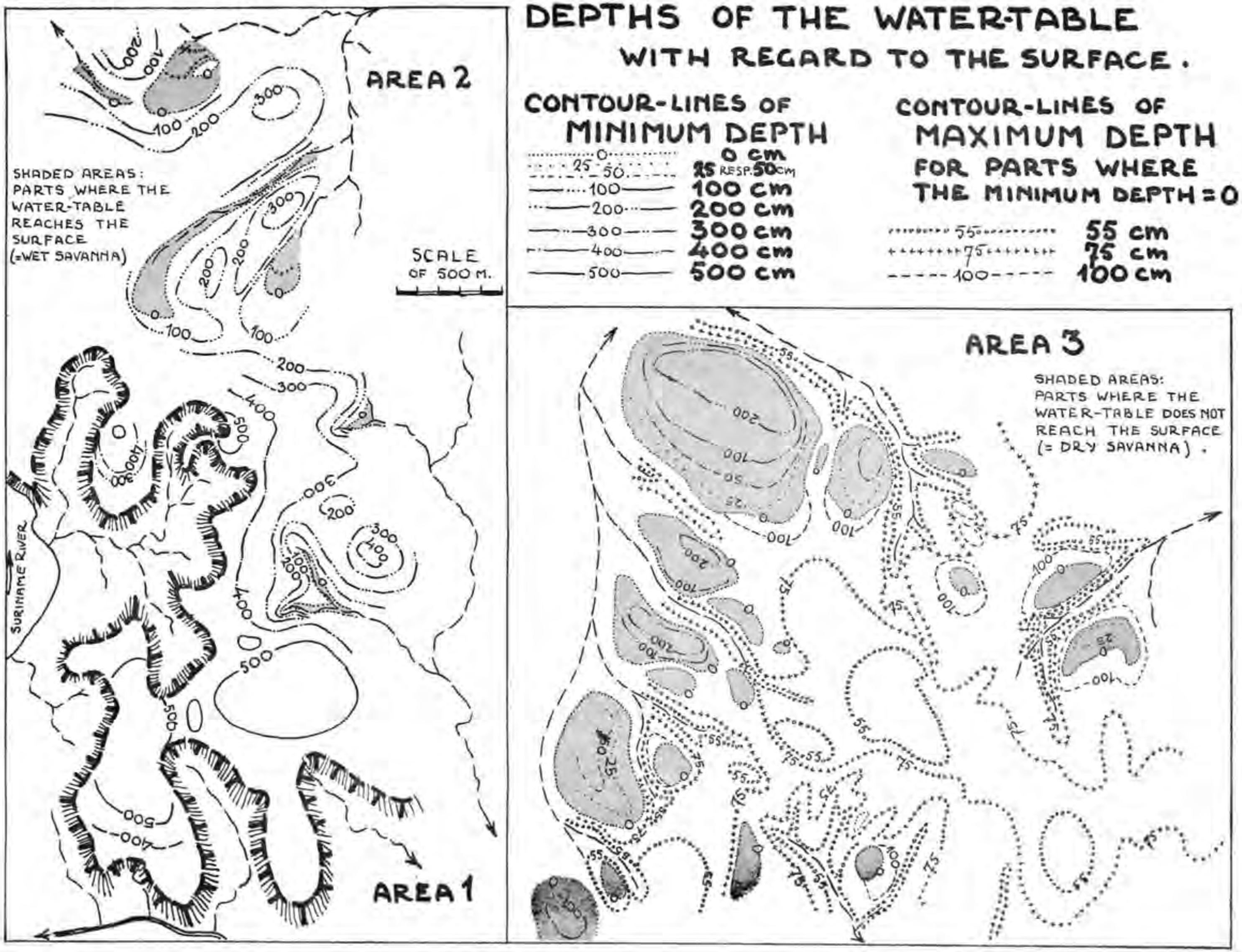
The groundwater levels in the wet savanna of area 1 appear to correlate very well with those in the wet savanna of area 2, but with those in the wet savanna of area 3 the correlation is, as a rule, less satisfactory. Two reasons may be adduced for this; in the first place the circumstance that the wet savannas of the areas 1 and 2 are not, like those of area 3, found on a watershed, but on slopes, and in the second place the fact that the areas 1 and 2 are separated from area 3 by a distance of 6 km, which means that there may be considerable differences in the amount of precipitation. That such differences really occur, appeared when we compared our own field notes on the rainfall in area 1 with the amounts registered at the Blakawatra camp with a rain-gauge. For this reason the influence of factors like the "Wieringermeer effect" will not be the same in these two areas.

Where good agreement was found, the amplitude of the fluctuations in the water-table appeared to lie, as a rule, between 0.8 and 1.5 times of that found at the standard site.

From a hydrological point of view, therefore, the areas 1, 2 and 3 may be regarded as very similar. On account of this similarity the highest and the lowest position of the water-table in each bore has been calculated, if possible by means of Visser's method, otherwise by estimation. The data obtained in this way were used to compile the hydrological maps reproduced in fig. 18. As the depth of the water-table below the surface is to be regarded as an important ecological factor the minimum depth is used for compilation. Although the observations have been made during a rather short period, it is not to be expected that an extension of the observations over several years would have led to a significant change in the general aspect of the map. This applies also to those parts of the map in which the lowest position of the water-table has been indicated, viz. in the wet savanna, where the highest position is found in or above the surface.

In that part of the savanna which is nearest to the slopes descending towards the valleys of the Suriname River and the Cassipora Creek, the water-table is found at a depth of more than 4 m; on the higher parts of the isolated savannas in the south even at a depth of more than 7 m. The clayey toplayer on the crests of the bedrock, underlying the sandy deposits, falls dry in the course of the dry season. The Palmeneribo Creek

FIGURE 18.


DEPTHS OF THE WATER-TABLE
WITH REGARD TO THE SURFACE.
CONTOUR-LINES OF
MINIMUM DEPTH
0 cm
25 RESP. 50 CM
100 cm
200 cm
300 cm
400 cm
500 cm
CONTOUR-LINES OF
MAXIMUM DEPTH
FOR PARTS WHERE
THE MINIMUM DEPTH = 0
55 cm
75 cm
100 cm
AREA 2
SHADED AREAS:
PARTS WHERE THE
WATER-TABLE
REACHES THE
SURFACE
(=WET SAVANNA)
SCALE
OF 500 M.
SURINAME RIVER
AREA 1
AREA 3
SHADED AREAS:
PARTS WHERE THE
WATER-TABLE DOES NOT
REACH THE SURFACE
(= DRY SAVANNA).

and the tributaries of the Cassipora Creek are sufficient deeply incised, to keep the water-table in the remaining part of the areas 1 and 2 at a depth of more than 1 m. Where in some parts of these areas the water-table reaches a higher level, this is always due to the presence of local depressions (cf. III 2.8) which are just deep enough to bring the surface under the influence of the water-table (fig. 19).

In area 3 the creeks are not so deeply incised and over large stretches the groundwater reaches the surface. However, one finds dry savanna where the slope of the surface exceeds the grade of the groundwater, as for instance in the areas near to confluent, somewhat incised creeks.

When it rains, the wet savanna is flooded in a short time, so that most of the precipitation runs off along the surface. Even where the water-table is found at a depth of 50 cm, the layer which is not saturated with capillary water, is only about 10 cm thick. During a shower with a capacity of 0.5 mm/min, assuming that the total amount of air has to be dislodged, this upper layer would be soaked completely within a quarter of an hour. The rain water that comes down after that time runs off entirely. As long as the capillary zone of the groundwater reaches the surface, practically the full amount of precipitation will run off. For this reason each shower causes a considerable rise of the level in the main creeks, sometimes as much as 0.5 m within a few hours, which, however, is followed by a fall of the same order of magnitude when the run-off water is drained off (fig. 14B; as the water level in the Blakawatra Creek was measured but once a day, the maximum rises after showers are not accurately known). On the dry savanna, on the other hand, there is no run-off at all, not even after the heaviest showers.

III 7.3. *Explanation of the drainage pattern observed in the wet savanna*

It has often been assumed that the wet savannas owe their origin, at least to some extent, to the presence of a hardpan. My own observations are, in my opinion, not in accordance with this assumption. It seems therefore worthwhile to discuss the drainage conditions prevailing in area 3 in some detail. I will base my considerations on the drainage formula drawn up by Hooghoudt (1940), viz.

$$s = \frac{2kdh + kh^2}{e^2}, \text{ in which}$$

s = the amount of precipitation (in m/24 hours) required for the maintenance of a constant level in the creek

k = the permeability factor, i.e. the horizontal displacement (in m/24 hours) of a water particle in the soil

h = maximum height (in m) of the convex groundwater table above the water level in the creek

e = distance (in m) between the position of h and the creek

d = height (in m) of the 'equivalent layer"; this factor is dependent upon e, upon the width of the creek, and upon the thickness of the soil layer in which the degree of permeability remains the same, in other words upon the depth at which an impermeable layer is found eventually.

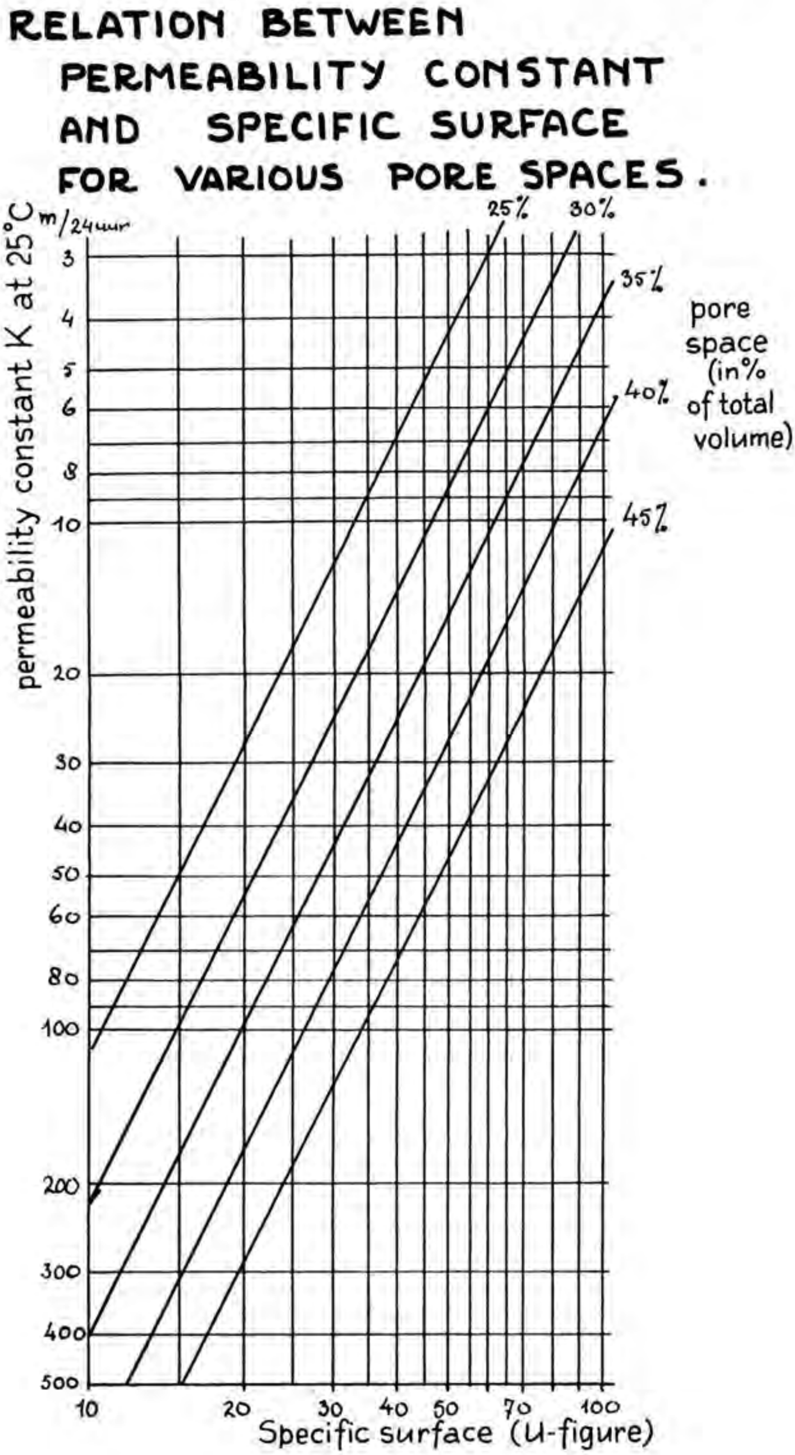
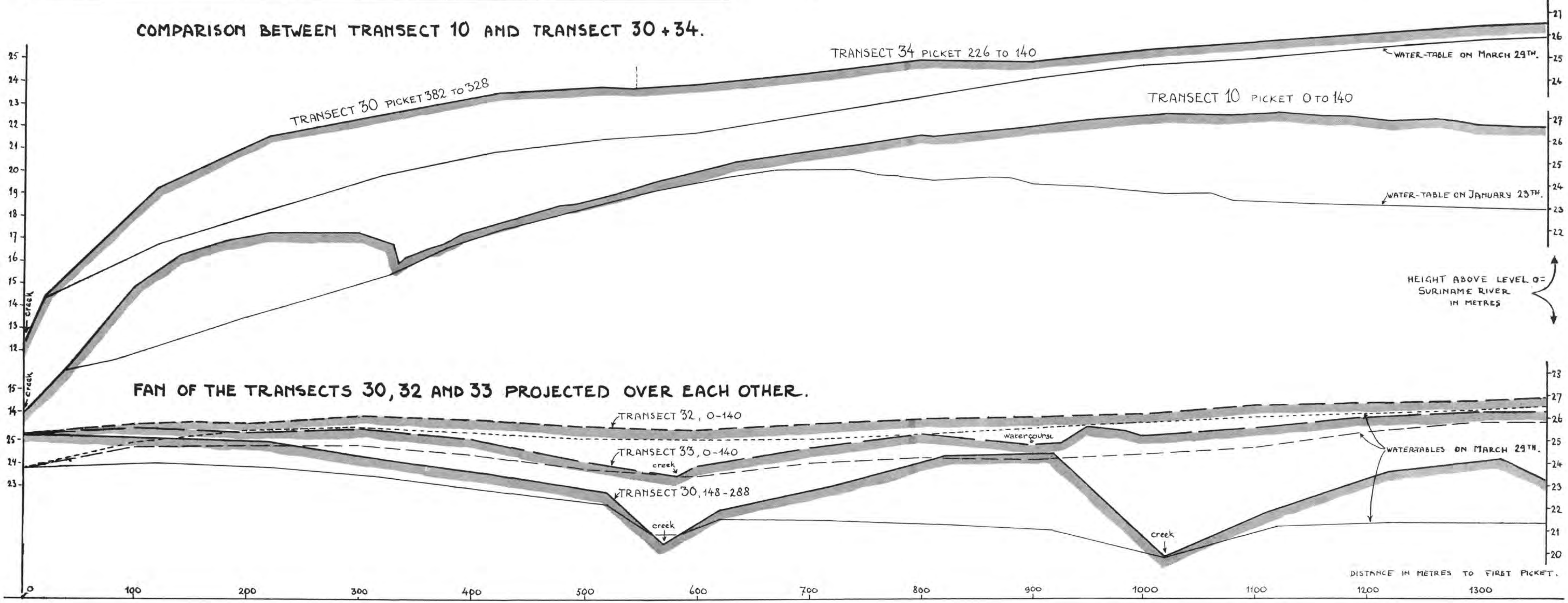

RELATION BETWEEN PERMEABILITY CONSTANT AND SPECIFIC SURFACE FOR VARIOUS PORE SPACES.
permeability constant K at 25°C
m/24uur
3
4
5
6
8
10
20
30
40
50
60
80
100
200
300
400
500
25%
30%
35%
40%
45%
pore space (in% of total volume)
10
20
30
40
50
70
100
Specific surface (U-figure)

FIGURE 20

FIGURE 19.

DRAINAGE CONDITION IN RELATION TO TOPOGRAPHY.

(COMPARE FIGURE 2 ABOUT THE SITUATION OF THE TRANSECTS.)



This equation was drawn up for a situation in which the supply of water is equalled by the loss of water. In a "saturated" wet savanna this condition is more or less fulfilled, for when groundwater lies at the surface, it feeds the parts where the groundwater-level lies deeper. Other conditions, like a sufficiently large distance between the draining channels and the absence of impermeable layers above the drainage plane, are also fulfilled. Unfortunately, the various operative factors were not directly measured, but had to be found in an indirect way.

An approximate value for s may be obtained in two ways. In the first place from measurements of the water level in the Blakawatra Creek, which in rainless periods shows a fall of up to 1 cm per day, and in the second place from the measurements of the water-table along transect 10, where the fall in rainless periods is due partly to discharge and partly to evaporation, and where the gross loss of water was calculated at 1.0 cm on the average per day. The loss by evapotranspiration amounts to about 0.3 cm per day (VAN WIJK and DE VRIES, 1954; OSTENDORF, 1957). In this way we find $s = 1.0 - 0.3 = 0.7$ cm per day.

The permeability factor k depends on the temperature, of which we will assume that it has a constant value of 25° C, and on the grain size and the pore space of the sand.

$$k = \frac{394200}{U^2} \cdot \frac{p^3}{(1-p)^2}, \text{ in which}$$

U = the specific surface of the sand fraction, i.e. the ratio, for equal weights, between the total surface of the grains in the sand fraction, and the total surface of spherical sandgrains with a diameter of 1 cm (cf. HOOGHOUDT, 1934, and DE VRIES and DECHERING, 1948)

p = the pore space expressed as a percentage of the total soil volume.

The figure 394200 is a constant, calculated from data given by HOOGHOUDT (1940) for sandy soils which are poor in humus and in silt.

The relation between the permeability factor k and the specific surface U in sands with different pore spaces p is shown in fig. 20, which appears to agree with a graph given by VAN ITERSON (1926) for the permeability of sands. This relation applies only to sands in which the joint content of humus and clay does not exceed 3 %. The pore space is on the average 40 %, and the specific surface 42 (III 2.3.2), the permeability factor k is therefore 40 m/24 hours. VAN DER VOORDE and HOOYSMA (1956), who determined the permeability factor experimentally in the sands at Zanderij, found values which varied between 2.5 and 6 m/24 hours, with an average of 4.5 m (75 estimations). Mrs. W. A. E. VAN DONSELAAR–TEN BOKKEL HUININK told me that the sands at Zanderij are somewhat finer-grained, and this might explain, at least to some extent, this much lower value.

It has already been mentioned (III 2.1) that in area 3, apart from the layer of clay which rests immediately on the bedrock, no continuous layers of clay or hardpans are found. When we estimate the height above the river level at which the clay layer on the bedrock is found, at 10 m, and that of the level of the draining creek at 23 m, then the height of the "equivalent layer" d, which can be calculated by the aid of the equations given by HOOGHOUDT (1940), will amount to about 12.5 m.

Assuming the ground surface at a height of 26.5 to 27 m above river level and the level of the draining creeks still at 23 m the maximum value for h, without being the water-table too near to the surface, is 3 m.

Now that the values that are to be substituted for k, d and h are estimated, the value of e can be calculated.

$$e = \sqrt{\frac{2kdh + kh^2}{s}} = \sqrt{\frac{2 \times 40 \times 12.5 \times 3 + 40 \times 3^2}{0.007}} = 693 \text{ m}.$$

Thus, up to a distance of about 700 m from the creek the drainage will be "normal". When the distance between two creeks is less than twice this value, the convex water-table will not reach its maximum height, which means that the area will be better drained. This is what we observe in the "axils" formed by confluent creeks. When the distance between the two creeks is more than 1,400 m the convexity of the water-table reaches such a height that in the watershed the surface becomes waterlogged.

The conclusions which have been arrived here by means of a calculation show a satisfactory agreement with what was actually observed in area 3. This means primarily that the occurrence of wet savannas in this area is a result of its topography, and secondly that an impermeable layer at a depth of a few meters is no need for achieving wet savanna condition.

CHAPTER IV

THE VEGETATION

IV 1. Introduction

If we confine our attention to the Vascular Plants, the number of species occurring in the savannas found in the areas 1–3 amounts to about 250, and if we leave the species that are confined to the savanna forests out of consideration, about one fifth of them are trees or shrubs. A large part of these species, and especially the leading ones, are found in vegetations of rather different aspect. For this reason it was not possible to arrive at a satisfactory delimitation of the various vegetation types on the base of their floristic composition alone, dominance and physiognomic features had also to be considered. A survey of the vegetation types derived in this way is given in the tables 2 to 5. The method to obtain the tables 2 to 4 has already been described in chapter II, section 3, and there the meaning of the various symbols, in so far as they are not explained in the legends of the tables themselves, has been expounded also. The choice of the names by which the vegetation types are indicated was also discussed there. A schematic survey of the various vegetation types distinguished by us is given in table 5.

Where the vegetation consists of more than one stratum, the following physiognomic units were recognized:

forest, a vegetation consisting of trees, with a stratified canopy, with a height which usually exceeds 15 m, and with a considerable number of trees provided with a distinct bole.

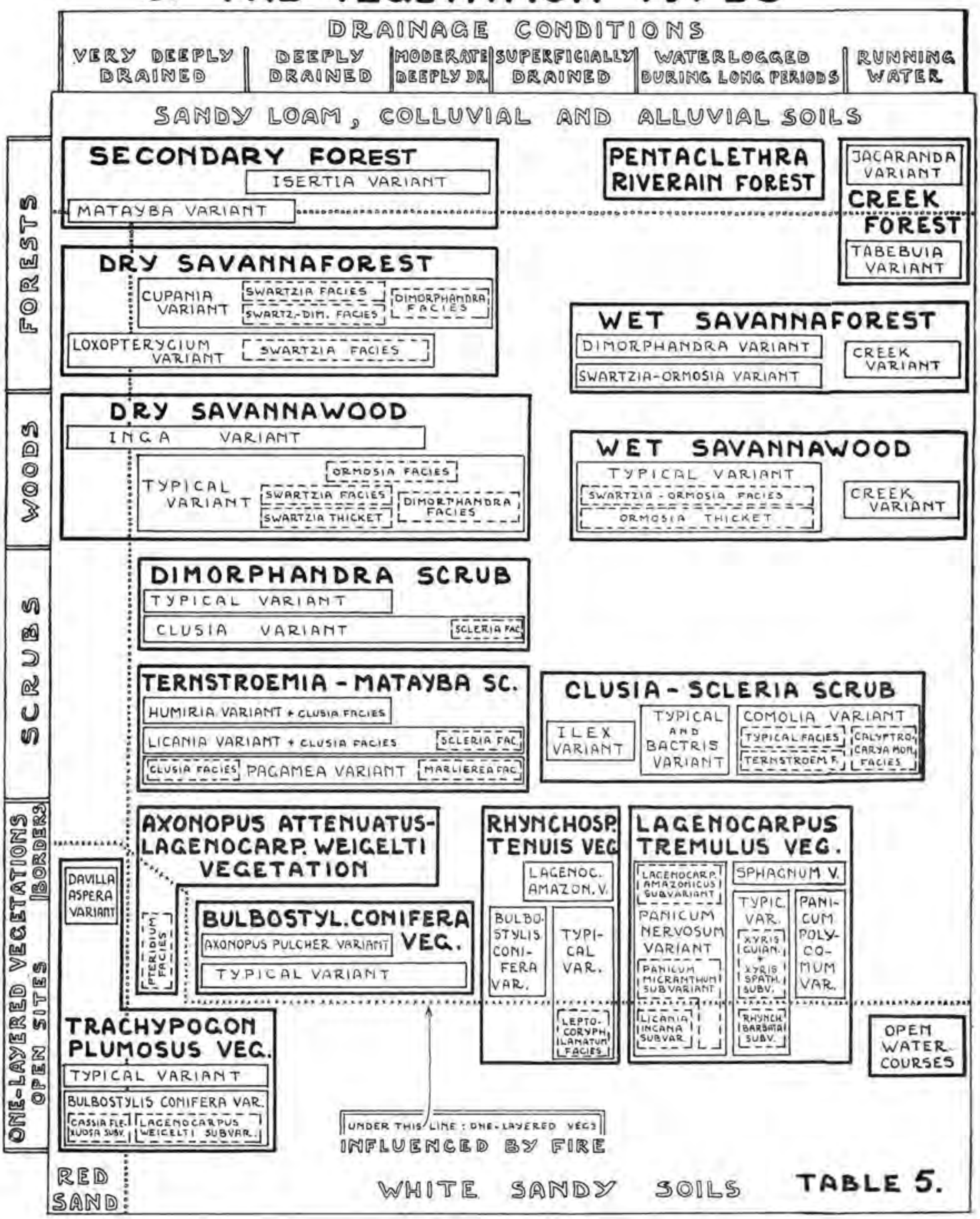
wood, a vegetation consisting of trees of which the canopy forms but a single stratum, with a height not exceeding 15 m, and often formed by a large number of small trees with thin stems.

scrub, a vegetation consisting of shrubs and small trees, showing a fairly regular canopy, occasionally with a few projecting branches or crowns, rarely exceeding 6 m in height, and containing several species which show a distorted growth.

thicket, a vegetation consisting of a dense shrub stratum and an open tree stratum of which the height does not exceed 12 m.

Where these physiognomic units cover a large and uninterrupted stretch of ground, the name indicates not only a special physiognomy, but also the position which the vegetation occupies in our system of classification. Where the savanna consists in the main of a single stratum, not rarely small patches are met which are covered by one of the abovementioned physiognomic types; in such cases we will refer to "*bushes*".

SCHEMATIZED ECOLOGICAL RANGE OF THE VEGETATION TYPES



In the sections 2, 3 and 4 of this chapter a survey is given of the forests and woods which surround the open savanna, of the scrub and the bushes that are found on the open savanna, and of the vegetation of the latter itself. They are not confined to a description of the vegetation types, but discuss also their distribution and the kind of soil on which they are found. In section 5 the problem of the ecological significance of the groundwater and that of the influence of field fires is considered. Section 6, finally, deals with the distribution of the savanna on white sands.

IV 2. FORESTS AND WOODS (table 2)

IV 2.1. *Savanna forests and savanna woods*

The savanna forests and savanna woods that are found in the three areas which were studied by us, agree with those described by LINDEMAN (1953, p. 89 et seq.) and by LINDEMAN e.a. (1959, p. 21 et seq.).

The savanna forests and woods are characterized by the presence of the following species: *Clusia fockeana* and *Cl. nemorosa*, *Licania incana*, *Conomorpha magnoliifolia*, *Bombax flaviflorum*, *Pagamea guianensis*, *Matayba opaca*, *Ocotea schomburgkiana* and *Humiria floribunda*.

All these species are found in the open savanna too. This fact and the circumstance that these arboreal vegetations are less luxuriously developed than the rain forest, are reasons that the former in Suriname have received long ago the name "savanna forest" which is in current use there and was employed in botanical literature e.g. by LANJOUW (1936). The distinction between savanna forest and savanna wood was introduced by LINDEMAN (1953, 1959) following BEARD's restricted meaning of the words forest and wood to express in a short way physiognomic differences.

Throughout the manuscript I have retained therefore the terms "savanna forest" and "savanna wood" though in fact savanna, and forest or wood are contradictory terms.

Note: Afterwards, however, I realised in how different a meaning these terms are used in other parts of the world and I wished to have replaced them by the terms "xeromorphic forest" and "xeromorphic wood".

The savanna forests and woods are almost entirely confined to white sands. As shown in table 2, it is possible to distinguish among them various types differing in the composition of the list of accompanying species. The classification at which we arrived in this way agrees very well with differences in the structure of the vegetation and with differences in the hydrological condition of the soil on which it is found. These kinds of differences find their expression in the names we have chosen for the various types.

IV 2.1.1. Dry savanna forest

The dry savanna forest is on the average 25 m high, and is found on well-drained soils. It appears in two variants, the "*Cupania scrobiculata* variant" (photo 22) with a somewhat larger number of species and on the average somewhat higher, and the "*Loxopterygium sagotii* variant" with a somewhat smaller number of species. In both variants *Swartzia bannia* may be present in large numbers, and is in that case accompanied by *Ocotea glomerata* and *Ormosia* spp., in the *Cupania* variant also by *Dimorphandra conjugata*; moreover, in the latter *Licania incana* is better represented. In the *Cupania* variant *Dimorphandra* may become very abundant, and, as in that case *Swartzia* disappears, there is good reason here to distinguish two facies, a "*Swartzia* facies" and a "*Dimorphandra* facies", but this distinction has not been carried through in table 2.

IV 2.1.2. Dry savanna wood

The dry savanna wood reaches on the average a height of 10 to 12 m and differs from the dry savanna forest in the higher presence and sometimes also in the greater abundance of *Ternstroemia punctata, Pagamea capitata, Retiniphyllum schomburgkii, Humiria floribunda* and *Ormosia costulata,* whereas several species from the savanna forest, especially from the *Cupania* variant, are lacking. The dry savanna wood too occurs in two variants, the "typical" one and the "*Inga lateriflora* variant"; in the latter a somewhat greater number of species from the savanna forest are found, among which *Inga lateriflora* and *Licania divaricata* occupy the most important position.

In the typical variant *Swartzia bannia, Ormosia costulata* or *Dimorphandra conjugata* may be present in large numbers. The presence of *Swartzia* and that of *Ormosia* do not influence the floristic composition of this variant so strongly as the presence of *Dimorphandra* does; the latter causes a considerable reduction of the number of accompanying species. This is due to the amount of litter which it produces, and which forms a springy mattress at least 0.5 m and sometimes more than 1 m thick. This litter consists of a loose upper layer formed by the recently shed leaves, a slightly compressed central layer formed by partly decayed leaves, and a lower compost layer which forms one half or more of the whole packet and which is traversed by a large number of roots; towards the base the latter, moreover, is mixed with some sand. In habit *Dimorphandra* varies from a tree with a more or less gnarled stem (photo 21) to a large shrub whose branches may reach a diameter of 30 cm. In the latter case the wood apparently developed out of a scrub. As *Dimorphandra* grows in groups, the canopy of the wood is in these cases locally interrupted. The gaps in the canopy are not completely filled up by other species, as the latter, although they may penetrate into the crowns of the *Dimorphandra* shrubs, are unable to reach the same height as these. The water-table in the *Dimorphandra* facies rises to a higher level than it does in the typical dry savanna wood; this explains the abundance of *Marlierea montana* in the undergrowth. The *Dimorphandra* facies may in fact be regarded as a transition between the dry savanna wood and the wet savanna wood (on the possible cause of its dominant position in some parts of the dry savanna cf. IV 5.2.3).

The dry savanna wood does not always form a closed vegetation, but occurs also in the form of bushes in the open savanna; these bushes will be dealt with in IV 3.1.6.

IV 2.1.3. Wet savanna forest

The wet savanna forest, of which the height is about 25 m, occurs on white sands in which the water-table is found periodically or permanently at the surface. Three variants are to be distinguished, viz. the "Creek variant", the "*Dimorphandra conjugata* variant" and the "*Swartzia bannia–Ormosia costulata* variant".

Apart from *Clusia, Licania, Conomorpha* and *Ocotea glomerata* we find in the tree stratum of the creek variant (photos 14 and 17) numerous specimens of *Symphonia globulifera, Caryocar microcarpum* and *Diospyros guianensis,* and in the undergrowth *Elaeis melanococca* and *Rapatea paludosa.* The soil contains a large amount of humus (cf. III 2.5 and I 6; "creek-valley soils"). The surface water and the groundwater of the savanna runs off through it, often without forming a distinct brook, but through a wide tract where the surface shows a hogwallowed relief, and is covered by a tangle of looped *Symphonia* pneumatophores.

The *Dimorphandra conjugata* variant and the *Swartzia bannia–Ormosia costulata* variant are differentiated by the great abundance of the species after which they are named. They may therefore be regarded as different facies of a "typical variant" in which these species are not so prevalent, but a vegetation of that kind was not observed. In the soil on which the *Swartzia–Ormosia* variant occurs, the drainage is insufficient in the rainy seasons, so that in depressions large pools are formed which may persist for a long time. The *Dimorphandra* variant also grows on a soaked soil, but not on one with stagnant pools. The layer of litter is sometimes of normal thickness and sometimes of more than normal thickness, but it is never as thick as in the *Dimorphandra* facies of the dry savanna wood.

IV 2.1.4. Wet savanna wood

Here we distinguish a "*creek variant*" and a "*typical variant*", the latter occurring in two facies.

In the creek variant the height of the trees is on the average 14 m, but the variability is rather large. Several of the species which are found in the creek variant of the wet savanna forest are lacking, and are replaced by species like *Retiniphyllum schomburgkii* and *Miconia ciliata*. It owes its particular aspect in a large measure to the presence of *Mauritia flexuosa*, a palm which may raise its crown up to 10 m above the canopy (photo 13). In this respect it differs markedly from the creek variant of the wet savanna forest, where the crowns of the *Mauritia* palms do not project beyond the canopy. The broken line in the graph shown in table 2 indicates the height of these palms, which are absent only in those parts where this vegetation penetrates farthest into the open savanna. The soil conditions here are the same as in the creek variant of the wet savanna forest. The hogwallowed surface is often densely covered with herbs like *Abolboda grandis*, *Calyptrocarya glomerulata* and *Scleria pyramidalis*.

The typical variant as such was found but once, viz. at site 10–42 in the form of a bush covering an area of 500 square metres. The height was 8 m and the canopy fairly continuous. *Clusia*, *Licania* and *Marlierea* were well represented, whereas it differed from the dry savanna wood especially in the presence of *Bactris campestris* and *Miconia ciliata*. The two most important species of the creek variant, *Mauritia* and *Symphonia*, were each represented by a single juvenile specimen only.

Of the *Swartzia–Ormosia* facies of the typical variant too but a single record was made, viz. at site 22–8; in table 2 this record is combined with that of the typical facies. It differs from the *Swartzia–Ormosia* variant of the wet savanna forest, which grows on a similar kind of soil, because it is lower and contains fewer species.

IV 2.2. *Other forest types*

IV 2.2.1. Creek forest

The creek forest is found on the waterlogged tracts along the creeks. It has on the average a height of 30 m and is therefore the highest forest found in this region. The highest trees, e.g. *Symphonia globulifera* and *Chaunochiton kappleri*, reach a height of more than 42 m.

Two variants of the creek forest are here distinguished, viz. the "*Tabebuia insignis* variant", which has several species in common with the creek variant of the wet savanna forest, and occurs on colluvial white sands with a clayey subsoil at a small depth (cf. III 2.5), and the "*Jacaranda copaia* variant", which contains a larger number of species from the evergreen seasonal forest and occurs on the heavier colluvial and alluvial soils. The last-mentioned variant shows a strong resemblance to the *Symphonia* marsh forest, although *Euterpe oleracea* is less well represented in it, and also with some records from the typical evergreen forest (nos. 71, 81 and 85), another type of forest described by LINDEMAN (1953). Especially in the *Tabebuia* variant the upper stratum is not very compact, and the lower strata too are rather open; this type of forest is therefore very light.

In the upper stratum of the forest found on the lower alluvial soils along the

Suriname River and the Cassipora Creek, *Pentaclethra macroloba* is the dominant species, in the floristic composition too this forest differs markedly from the creek forest described above. It may be distinguished as the "*Pentaclethra riverain forest*", but is not included in table 2.

IV 2.2.2. Secondary forest

This kind of forest, very rich in species, is found in those places where the original forest was felled by the Amerindians in order to obtain grounds for the primitive form of agriculture practised by them. In the valley of the Suriname River this shifting cultivation required so much ground that here almost nothing is left of the original forest.

In this secondary forest, which represents various stages in the regeneration of the climax vegetation, two variants may be distinguished, viz. the "*Isertia coccinea* variant" and the "*Matayba opaca* variant".

The *Isertia* variant occurs on heavy soils, and has many species in common with the *Jacaranda* variant of the creek forest. It is found in the immediate vicinity of the latter, and as the creek forest too is not rarely felled, it may have replaced it.

The *Matayba* variant, found on the lighter soils in the upper part of the slopes descending towards the valleys of the Suriname River and of the Cassipora Creek, contains species like *Clusia fockeana*, *Matayba opaca* and *Ocotea schomburgkiana*, which indicate its affinity with the dry savanna forest.

IV 2.3. *The spatial distribution of the savanna forests and woods in our area* (figs. 2, 7, 10 B, 21 and 22)

The greatest variety in forest and wood types is found in area 1, because in this part the topographic contrasts and the soil conditions are more diversified than in the two other areas. In the wide valley of the Suriname River the wet soils are covered with the *Jacaranda* variant of the creek forest, and in those parts where the soil is still more marshy and is flooded periodically, with the *Pentaclethra* riverain forest. The remaining part of the valley is occupied by secondary forest in all stages of regeneration, as here the Amerindians are still adhering to their primitive agricultural methods. The *Matayba* variant of this forest type grows on the lighter colluvial soils along the margin of the plateau, on the red sands of the latter and on the isolated hills in the valley; the other soils are of a heavier type, and bear the *Isertia* variant (figs. 7 and 10B). At various places (transects 11 and 12; transect 15–220 and 250; photo 7) the *Matayba* variant ends abruptly in the open savanna, which in that case bears a *Trachypogon plumosus* vegetation. In the southern part of the area, on the other hand, the open savanna is always separated from the *Matayba* variant of the secondary forest by a more or less wide stretch of dry savanna wood, which occasionally passes into dry savanna forest. In these woods and forests too often indications of former reclaimings are found, but here the regeneration did not lead to the development of a secondary forest of the kind described above, but to a vegetation which is clearly recognizable as savanna forest or wood. This must doubtless be ascribed to the soil conditions.

The *Tabebuia* variant of the creek forest grows along the creeks having their source in the white sands (10–0, 170 and 200; 16–12; 17–55). Where the soil does not consist of white sand, this variant is replaced by the *Jacaranda* variant (compare the vegetation at site 16–10 with that at the other side of the creek). The width of the zone covered by the *Tabebuia* variant amounts but rarely to more than a hundred metres, and this zone receives a constant supply of ground water from the rather steep slopes. Where, on account of the presence of a clayey subsoil, a wider part of the slope is permanently soaked, the *Tabebuia* variant ascends also some way up the latter (site 17–54, cf. figs. 10A and B).

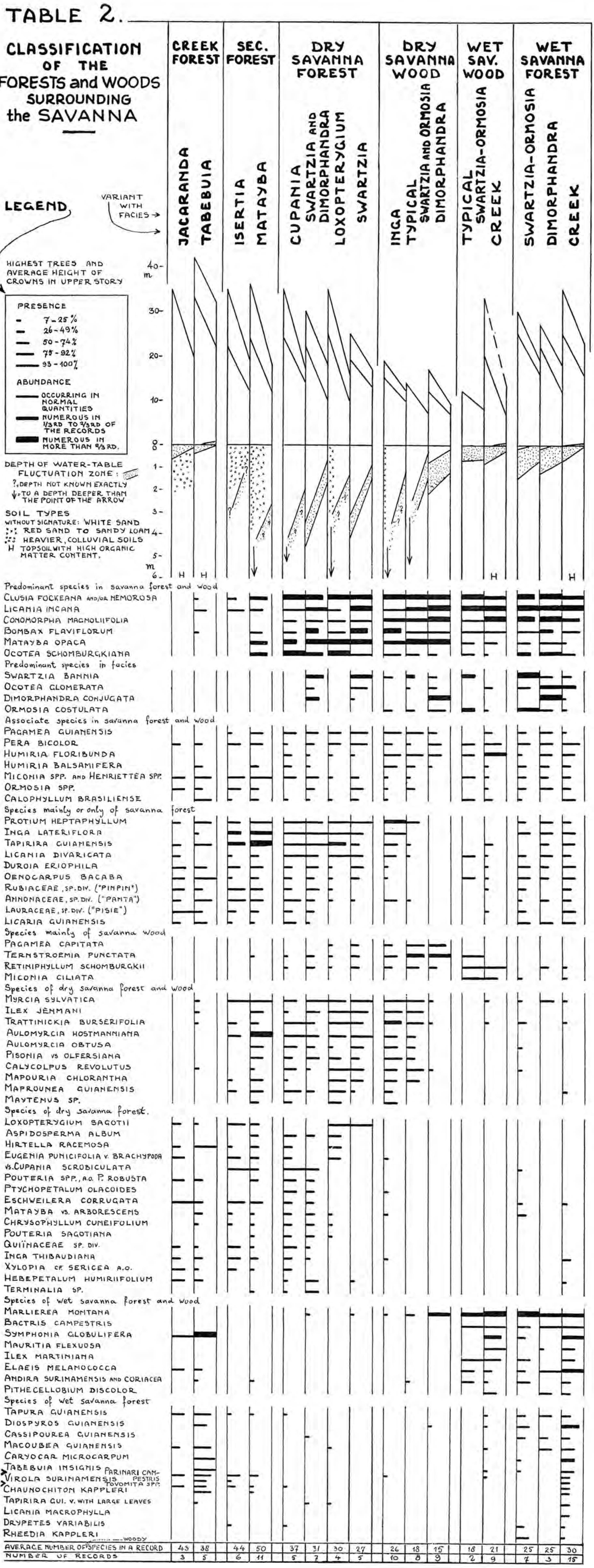


TABLE 2.
CLASSIFICATION OF THE FORESTS and WOODS SURROUNDING the SAVANNA
CREEK FOREST
SEC. FOREST
DRY SAVANNA FOREST
DRY SAVANNA WOOD
WET SAV. WOOD
WET SAVANNA FOREST
JACARANDA
TABEBUIA
ISERTIA
MATAYBA
CUPANIA
SWARTZIA AND DIMORPHANDRA
LOXOPTERYGIUM
SWARTZIA
INGA
TYPICAL
SWARTZIA AND ORMOSIA
DIMORPHANDRA
TYPICAL
SWARTZIA-ORMOSIA
CREEK
SWARTZIA-ORMOSIA
DIMORPHANDRA
CREEK
LEGEND
VARIANT WITH FACIES
HIGHEST TREES AND AVERAGE HEIGHT OF CROWNS IN UPPER STORY
PRESENCE
7-25%
26-49%
50-74%
75-92%
93-100%
ABUNDANCE
OCCURRING IN NORMAL QUANTITIES
NUMEROUS IN 1/3RD TO 2/3RD OF THE RECORDS
NUMEROUS IN MORE THAN 2/3 RD.
DEPTH OF WATER-TABLE FLUCTUATION ZONE:
?: DEPTH NOT KNOWN EXACTLY
↓: TO A DEPTH DEEPER THAN THE POINT OF THE ARROW
SOIL TYPES
WITHOUT SIGNATURE: WHITE SAND
RED SAND TO SANDY LOAM
HEAVIER, COLLUVIAL SOILS
H TOPSOIL WITH HIGH ORGANIC MATTER CONTENT.
40 m
30
20
10
0
1
2
3
4
5
6 m
Predominant species in savanna forest and wood
CLUSIA FOCKEANA AND/OR NEMOROSA
LICANIA INCANA
CONOMORPHA MAGNOLIIFOLIA
BOMBAX FLAVIFLORUM
MATAYBA OPACA
OCOTEA SCHOMBURGKIANA
Predominant species in facies
SWARTZIA BANNIA
OCOTEA GLOMERATA
DIMORPHANDRA CONJUGATA
ORMOSIA COSTULATA
Associate species in savanna forest and wood
PAGAMEA GUIANENSIS
PERA BICOLOR
HUMIRIA FLORIBUNDA
HUMIRIA BALSAMIFERA
MICONIA SPP. AND HENRIETTEA SPP.
ORMOSIA SPP.
CALOPHYLLUM BRASILIENSE
Species mainly or only of savanna forest
PROTIUM HEPTAPHYLLUM
INGA LATERIFLORA
TAPIRIRA GUIANENSIS
LICANIA DIVARICATA
DUROIA ERIOPHILA
OENOCARPUS BACABA
RUBIACEAE, SP. DIV. ("PINPIN")
ANNONACEAE, SP. DIV. ("PANTA")
LAURACEAE, SP. DIV. ("PISIE")
LICARIA GUIANENSIS
Species mainly of savanna wood
PAGAMEA CAPITATA
TERNSTROEMIA PUNCTATA
RETINIPHYLLUM SCHOMBURGKII
MICONIA CILIATA
Species of dry savanna forest and wood
MYRCIA SYLVATICA
ILEX JENMANI
TRATTINICKIA BURSERIFOLIA
AULOMYRCIA HOSTMANNIANA
AULOMYRCIA OBTUSA
PISONIA VS OLFERSIANA
CALYCOLPUS REVOLUTUS
MAPOURIA CHLORANTHA
MAPROUNEA GUIANENSIS
MAYTENUS SP.
Species of dry savanna forest.
LOXOPTERYGIUM SAGOTII
ASPIDOSPERMA ALBUM
HIRTELLA RACEMOSA
EUGENIA PUNICIFOLIA V. BRACHYPODA
VS. CUPANIA SCROBICULATA
POUTERIA SPP., A.O. P. ROBUSTA
PTYCHOPETALUM OLACOIDES
ESCHWEILERA CORRUGATA
MATAYBA VS. ARBORESCENS
CHRYSOPHYLLUM CUNEIFOLIUM
POUTERIA SAGOTIANA
QUIÏNACEAE SP. DIV.
INGA THIBAUDIANA
XYLOPIA CF. SERICEA A.O.
HEBEPETALUM HUMIRIIFOLIUM
TERMINALIA SP.
Species of wet savanna forest and wood
MARLIEREA MONTANA
BACTRIS CAMPESTRIS
SYMPHONIA GLOBULIFERA
MAURITIA FLEXUOSA
ILEX MARTINIANA
ELAEIS MELANOCOCCA
ANDIRA SURINAMENSIS AND CORIACEA
PITHECELLOBIUM DISCOLOR
Species of wet savanna forest
TAPURA GUIANENSIS
DIOSPYROS GUIANENSIS
CASSIPOUREA GUIANENSIS
MACOUBEA GUIANENSIS
CARYOCAR MICROCARPUM
TABEBUIA INSIGNIS
PARINARI CAMPESTRIS
VIROLA SURINAMENSIS
TOVOMITA SPP.
CHAUNOCHITON KAPPLERI
TAPIRIRA GUI. V. WITH LARGE LEAVES
LICANIA MACROPHYLLA
DRYPETES VARIABILIS
RHEEDIA KAPPLERI
WOODY
AVERAGE NUMBER OF SPECIES IN A RECORD 43 38 44 50 37 31 30 27 26 18 15 18 21 25 25 30
NUMBER OF RECORDS 3 5 6 11 5 7 4 5 10 8 9 2 9 7 3 15

The higher parts of the slopes are covered by dry savanna forest, which passes sometimes via dry savanna wood into savanna scrub, but which may also abut immediately on the open savanna, in which case it surrounds the latter in the form of a high fence (10–160; 16–16). The dry savanna forest along transect 17 between the pickets 30 and 80 appears to belong entirely to the *Swartzia* facies, that along the transects 10–5 to 20 and 20–0 to 30 belongs either to a transition between the *Swartzia* and the *Dimorphandra* facies or to the latter itself. It does not look improbable, but needs further investigation, to prove that the greater frequency of *Swartzia* and *Dimorphandra* is due to the position of the water-table, lying higher in these facies than in the typical variant of the dry savanna forest.

The creek savanna forest is found in the wide, permanently wet tracts which border the less deeply incised creeks. We find this in the northern part of area 2, but it is much better represented along the creeks in the wet savannas of area 3. The difference between this forest type and the *Tabebuia* variant of the creek forest is perhaps to be sought in the fact that in the creek savanna forest, on account of the slight degree of erosion, the roots are unable to reach the clayey subsoil.

In area 3 the gallery forests belong partly to the creek savanna forest and partly to the *Swartzia–Ormosia* variant of the wet savanna forest. Where the slopes towards the creeks are somewhat steeper, i.e. at those places where two creeks are about to join, the *Swartzia–Ormosia* variant of the wet savanna forest is replaced by the *Dimorphandra* variant of the same, which requires a soil which is less wet and on which no stagnant pools are found. Where the soil is drained still better, we find either the *Dimorphandra* facies of the *Cupania* variant of the dry savanna forest or else the *Dimorphandra* facies of the dry savanna wood, in some parts accompanied by *Ternstroemia–Matayba* scrub.

Especially in the northern and western parts of area 3 the aspect of the forests and woods has undergone marked changes under the influence of field fires. Several *Dimorphandra* vegetations were burnt down recently ,and the skeletons of the *Dimorphandra* trees are easily recognizable even on aerial photographs (fig. 2). The margins of the creek variant of the wet savanna forest too are attacked by the fires, with the result that forests of this type, without a fringing belt of shrubs, may border abruptly on the open savanna (site 38–216; photo 14). The open tracts with *Mauritia flexuosa* found along water-courses, are also due to fires; *Mauritia* itself is fire-resistant and as a rule suffers no other damage than that its dead leaves and leaf-sheaths are destroyed, but when the fires succeed each other with short intervals the regeneration of the accompanying trees is prevented.

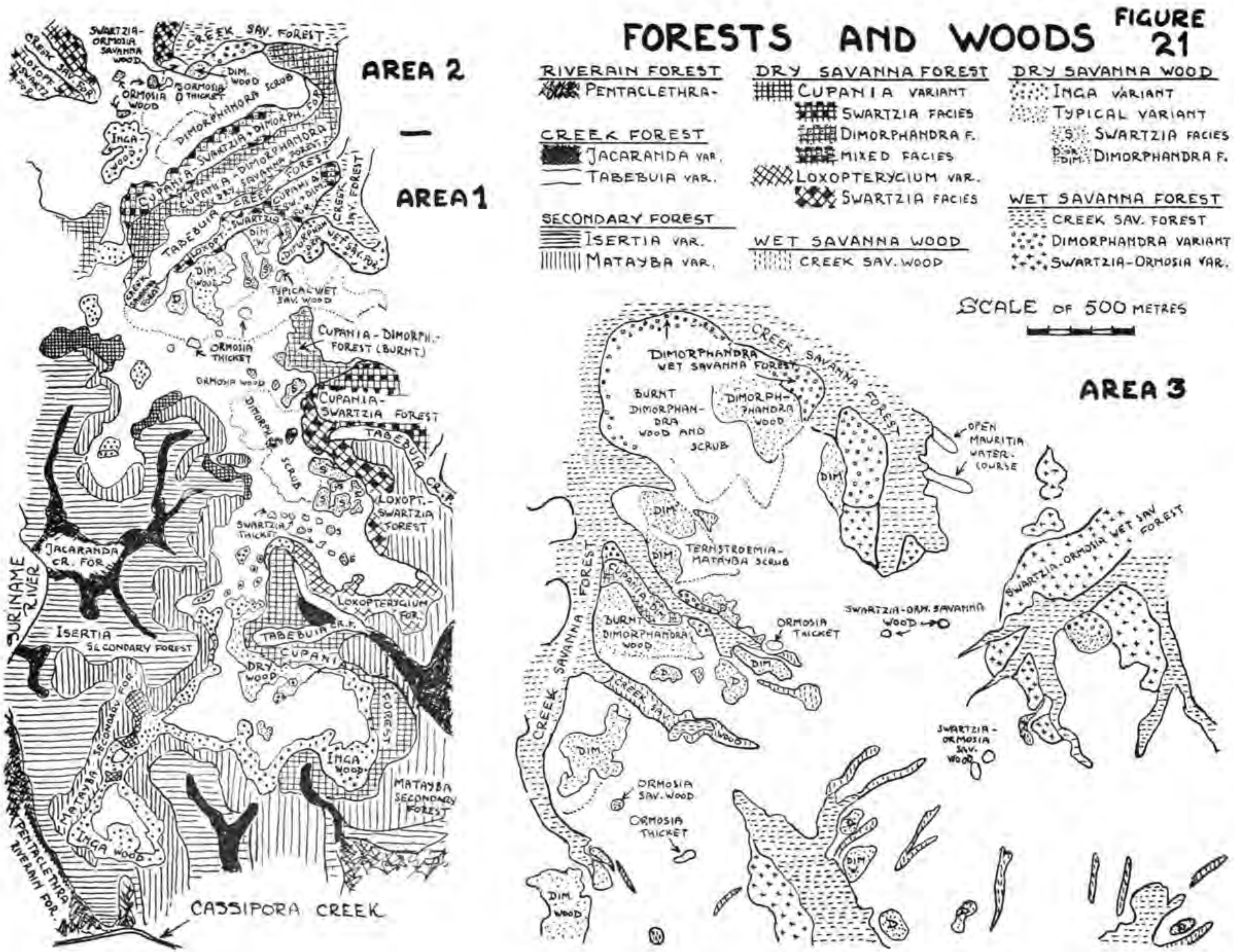
The creek variant of the wet savanna wood with its emergent stratum of *Mauritia* crowns is, at least in many cases, a regeneration stage of the creek variant of the wet savanna forest. It is found, therefore, in company of the latter along the creeks, but it may also be present in the form of more or less isolated patches in the open savanna, viz. in the tracts along which the rain water runs off towards the creeks.

IV 3. Scrub and bushes (table 3)

IV 3.1. *Isolated patches of savanna wood in the open savanna*

IV 3.1.1. The Inga lateriflora variant of the dry savanna wood

This type of vegetation occurs in some parts of the open savanna in the form of bushes covering a surface of about 1000 sq. metres (sites 10–228; 12–10, 16; 14–64, photo 9; 15–232). The canopy has a cover-percentage of 70 to 80 %, and reaches, according to the size of the bush,


FORESTS AND WOODS
FIGURE 21
RIVERAIN FOREST
PENTACLETHRA-
CREEK FOREST
JACARANDA VAR.
TABEBUIA VAR.
SECONDARY FOREST
ISERTIA VAR.
MATAYBA VAR.
DRY SAVANNA FOREST
CUPANIA VARIANT
SWARTZIA FACIES
DIMORPHANDRA F.
MIXED FACIES
LOXOPTERYGIUM VAR.
SWARTZIA FACIES
WET SAVANNA WOOD
CREEK SAV. WOOD
DRY SAVANNA WOOD
INGA VARIANT
TYPICAL VARIANT
SWARTZIA FACIES
DIMORPHANDRA F.
WET SAVANNA FOREST
CREEK SAV. FOREST
DIMORPHANDRA VARIANT
SWARTZIA-ORMOSIA VAR.
SCALE OF 500 METRES
AREA 2
AREA 1
AREA 3
CREEK SAV. FOREST
SWARTZIA-ORMOSIA SAVANNA WOOD
ORMOSIA WOOD
ORMOSIA THICKET
DIM. WOOD
DIMORPHANDRA SCRUB
INGA WOOD
TYPICAL WET SAV. WOOD
CUPANIA-DIMORPH.-FOREST (BURNT)
ORMOSIA THICKET
ORMOSIA WOOD
CUPANIA-SWARTZIA FOREST
TABEBUIA
LOXOPT.-SWARTZIA FOREST
SWARTZIA THICKET
JACARANDA CR. FOR.
SURINAME RIVER
ISERTIA
SECONDARY FOREST
LOXOPTERYGIUM FOR.
TABEBUIA CR. F.
CUPANIA
DRY WOOD
INGA WOOD
MATAYBA SECONDARY FOREST
MATAYBA SECONDARY FOR.
INGA WOOD
PENTACLETHRA RIVERAIN FOR.
CASSIPORA CREEK
DIMORPHANDRA WET SAVANNA FOREST
BURNT DIMORPHANDRA WOOD AND SCRUB
DIMORPH-PHANDRA WOOD
CREEK SAVANNA FOREST
OPEN MAURITIA WATER-COURSE
SWARTZIA-ORMOSIA WET SAV. FOREST
TERNSTROEMIA-MATAYBA SCRUB
BURNT DIMORPHANDRA WOOD
ORMOSIA THICKET
SWARTZIA-ORM. SAVANNA WOOD
CREEK SAV. WOOD
SWARTZIA-ORMOSIA SAV. WOOD
ORMOSIA SAV. WOOD
ORMOSIA THICKET
DIM. WOOD

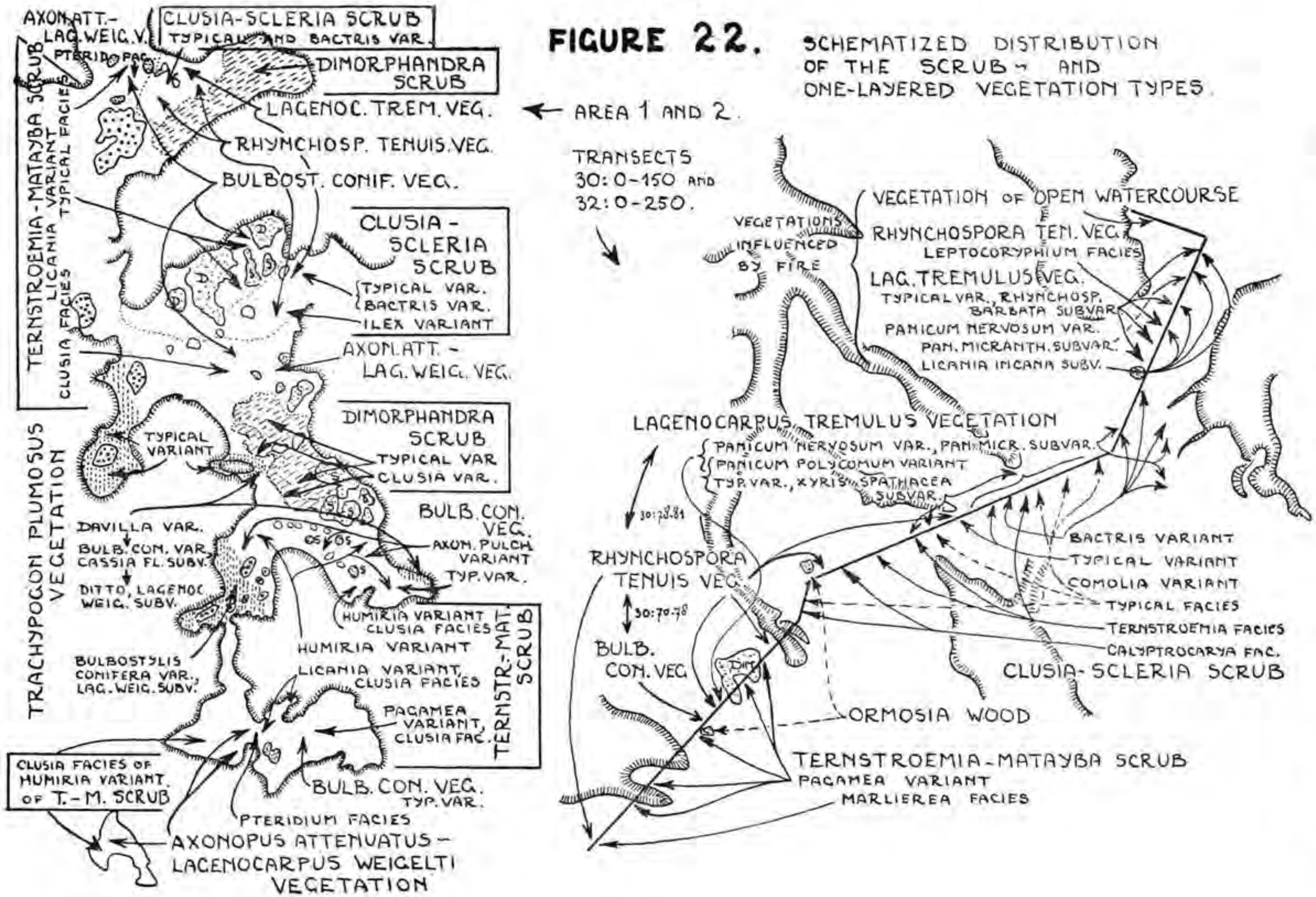


FIGURE 22. SCHEMATIZED DISTRIBUTION OF THE SCRUB- AND ONE-LAYERED VEGETATION TYPES.

a height varying from 6 to 15 m. The dominant species are *Clusia fockeana*, *Conomorpha magnoliifolia*, *Matayba opaca* and usually also *Humiria floribunda*. The *Humirias* often possess thick slanting stems which offer an ideal substrate for the development of epiphytic orchids, Araceae, Polypodiaceae and Hymenophyllaceae. The species which distinguishes this variant from the typical one is *Inga lateriflora*, which is sometimes accompanied by *I. thibaudiana* and *I. stipularis*, *Licania divaricata* and *Tapirira guianensis*. In the undergrowth, which is rather scanty, the most prominent species are *Myrcia sylvatica*, *Calycolpus revolutus* and *Maytenus* sp., occasionally also *Retiniphyllum schomburgkii*. The herb stratum is practically absent, but sporadically *Actinostachys pennula*, *Schizaea elegans* and a small terrestrial orchid (no. 207), which may be either *Encyclis oncidioides* or else a *Catasetum* species, are met. Of the many epiphytes found on the lower part of the stems and often also on mouldering wood, some also occur on the ground, e.g. the orchids *Bifrenaria aurantiaca* and some species of *Maxillaria*, and the Aracea *Philodendron insigne*. Occasionally also a small cushion of *Cladonia sandstedei* or of the moss *Octoblepharum cylindricum* is encountered. The litter layer is thin, and the layer of roots varies in thickness up to 25 cm (cf. III 4.1.).

IV 3.1.2. The typical variant of the dry savanna wood

This type of vegetation also occurs in the open savanna in the form of more or less isolated bushes (sites 13–12; 14–26). The small trees and shrubs are either lean or gnarled. In the canopy, which reaches a height of 6 to 10 m, *Clusia fockeana* predominates, but *Ternstroemia punctata*, *Conomorpha magnoliifolia*, *Matayba opaca* and *Ilex jenmani* are also well represented. *Licania incana*, *Humiria floribunda*, *Pagamea capitata* and *P. guianensis*, *Bombax flaviflorum*, *Pisonia* sp., *Protium heptaphyllum*, *Trattinickia burserifolia*, *Mapouria chlorantha* and *Ocotea schomburgkiana* are also found. The total cover amounts to about 70 %. The undergrowth consists of young plants of these trees and shrubs and further in the main of *Myrcia sylvatica*, *Calycolpus revolutus* and *Aulomyrcia obtusa*. On thick gnarled stems a large number of epiphytes are seen, but the orchids are less well represented than in the *Inga* variant. The herb stratum is mainly the same as in the *Inga* variant, but *Schizaea elegans* and the abovementioned terrestrial orchid (no. 207) were not found. The layer of litter is thin, and the network of roots has at the most a thickness of 15 cm.

In some parts of these bushes the vitality of the trees and shrubs is markedly reduced, and in that case they are draped with the liverwort *Frullania nodulosa*. There appear gaps in the canopy, with the result that the herb stratum shows a better development; *Schizaea incurvata* and *Lagenocarpus weigelti*, the Bryophytes *Frullania nodulosa* and *Campylopus surinamensis*, and Lichens belonging to the section *Clausae* of *Cladonia* become plentiful.

At site 14–20 to the West of the dry savanna wood, a scrub vegetation was found consisting of groups of shrubs which showed another habit and another floristic composition than the savanna scrub which we will describe hereafter. These groups of shrubs appeared to represent a regeneration stage of the dry savanna wood, which originally must have been present at this place, but which had been destroyed by fire. We arrived at this conclusion because the vegetation of the open spaces between the groups of shrubs represented the *Pteridium* facies of the *Axonopus attenuatus – Lagenocarpus weigelti* vegetation, which is characteristic for parts where the original vegetation has been destroyed by fire. Records of the vegetation types mentioned in this and in the preceding paragraph are not included in table 3.

IV 3.1.3. The Swartzia bannia facies of the typical dry savanna wood

This vegetation may occur in the form of a closed stand, but it occurs also in the form of bushes covering a surface of up to 500 sq. metres (sites 17–75 to 95 and 18–10). According to their age the aspect of these bushes varies from a dense agglomeration of thin stems to a more open stand, in which the *Swartzia* stems may reach a diameter of 30 cm or more. *Swartzia* is always strongly dominant, while *Licania incana* and *Clusia fockeana* are abundant, and this applies occasionally also to *Ternstroemia*, *Conomorpha* and *Humiria*.

When the bushes formed by the *Swartzia* facies are smaller, they show a characteristic aspect, for in this case we find in the centre a nucleus of say 50 sq. metres formed by the *Swartzia* facies which is surrounded by a belt of lower height belonging to the *Humiria* variant of the *Ternstroemia – Matayba* scrub (fig. 23A). In the central part it are especially *Swartzia* and *Humiria*, occasionally with *Ormosia costulata* present in a few specimens with stems of 12 to 45 cm in diameter, which determine the aspect, whereas *Clusia* remains confined to the lower part of the canopy, where it is dominant. Just as for the bushes of larger size, the undergrowth is rather open and epiphytes are scarce or absent.

IV 3.1.4. The Swartzia thicket

Sometimes the centre of the bushes described above merges entirely in the surrounding scrub; in that case we speak of a *Swartzia* thicket (fig. 23B). These thickets form a transition between the dry savanna wood and the savanna scrub, and may also be regarded as a subvariant of the *Humiria* variant of the *Ternstroemia – Matayba* scrub (cf. IV 3.2.4.). In several of these thickets the dead stems proved to be covered by a large number of epiphytes.

In the *Swartzia* thicket as well as in the *Swartzia* variant of the dry savanna wood the layer formed by the network of roots is often rather thick, viz. 10–30 cm, locally even up to 40 cm.

Fig. 23 A. Bush of *Swartzia bannia* facies with belt of *Humiria – Ternstroemia – Matayba* scrub.

Fig. 23 B. *Swartzia* thicket.

IV 3.1.5. The Ormosia costulata facies of the typical dry savanna wood

In some other bushes *Ormosia costulata* plays an important part. The surface covered by these bushes varies between 75 and 200 sq. metres and they reach a height of 7 to 8 m. The degree of cover of the canopy varies between 60 and 75 %. *Ormosia* is accompanied here by *Licania incana*, *Humiria floribunda* or *H. balsamifera* and *Clusia fockeana*; the latter occupies an important position in the lower part of the canopy when the *Ormosia* crowns leave gaps between them. In the undergrowth an important part is played by *Retiniphyllum schomburgkii*, and sometimes also by *Myrcia sylvatica*. The more the size of these bushes decreases, the more prominent the influence of the species belonging to the savanna scrub becomes. *Pagamea capitata* then becomes an important constituent, *Humiria floribunda* becomes more abundant, whereas the importance of *Licania* decreases. A herb stratum is practically absent and epiphytes are scarce or lacking. The litter layer as well as the root layer are thin.

IV 3.1.6. The Dimorphandra conjugata facies of the typical dry savanna wood

This facies covers, as a rule, large stretches; but rarely it is found in the form of isolated bushes. In that case habit and composition are the same as in the larger stretches (cf. IV 2.1.2.), and for this reason these bushes are not included in table 3.

IV 3.1.7. The Swartzia – Ormosia facies of the typical wet savanna wood

This facies was represented in the wet savanna by a single bush which covered a surface of 150 sq. metres (site 32–184). The canopy reached a height of 7 m and showed a degree of cover of 75 %. *Swartzia*, *Ormosia*, *Conomorpha*, *Bactris*, *Clusia* and *Ternstroemia* proved to be the dominant species in the canopy, and the open undergrowth consisted mainly of young plants belonging to the species of the tree stratum. In the herb stratum, which was also rather open, *Hypolythrum pulchrum* appeared to be fairly abundant; the saprophytes *Leiphaimos aphylla* and *Apteria aphylla* var. *hymenanthera* were also present and *Encyclia oncidioides* was represented by a single tuft. Epiphytes were not numerous; we noted the presence of *Epidendrum nocturnum* and of the orchid no. 276, whose rhizomes were covered with a felt of thin roots. The litter layer had a thickness of a few cm, and the root layer one of about 10 cm, and just as in the *Swartzia* – *Ormosia* wet savanna forest (cf. IV 2.1.3.) holes in the ground were present.

IV 3.1.8. The Ormosia thicket

These bushes are on the one hand related to the *Ormosia* facies of the typical dry savanna wood, and on the other hand to the *Swartzia* – *Ormosia* facies of the wet savanna wood. On account of the rather open canopy (degree of cover 10 to 35 %), the undergrowth becomes rather dense (degree of cover 65 %) and forms a closed stratum in which *Licania*, *Clusia*, *Retiniphyllum* and *Scleria pyramidalis* play a dominant part (photo 18). In the canopy the dominant species are *Ormosia* and *Licania*, but *Conomorpha* and *Bactris* may also occupy an important position. In the undergrowth *Marlierea montana*, *Tibouchina aspera*, *Miconia ciliata* and *Lisianthus uliginosus* are found. In the herb stratum *Encyclia oncidioides* and *Epidendrum nocturnum* occur, which are also present as epiphytes. Round the stems of *Ormosia* the root layer may reach a thickness of 40 cm, but elsewhere it is sometimes practically absent.

IV 3.1.9. The position of the bushes in the savanna

The position of the bushes in the open savanna is in the main in accordance with the distribution of the vegetation types in which they are included by us. They are bound to the same types of soil and to the same hydrological conditions. The situation of the most important bushes is indicated in fig. 21.

The typical variant of the dry savanna wood grows on soils in which the water-table, when present, is found at a great depth (southern savanna of area 1). The *Inga* variant of this vegetation is usually found on similar soils, and in places where in the rainy season the water-table was reached at 3 m below the surface (site 12–10), in the dry season the clayey subsoil fell entirely dry, just as in those places where in the rainy season the water-table remained at a greater depth.

Below the *Swartzia* facies of the typical dry savanna wood and below the *Swartzia* thicket on the south-eastern savanna of area 1 the water-table is found at a depth of 2 to 4 m, but here too the groundwater disappears entirely in the dry season. This is not so in the soil below the *Swartzia* facies of the *Loxopterygium* variant of the dry savanna forest on transect 18, where the water-table is found at a depth from 150 to 250 cm.

In the *Ormosia* facies of the typical dry savanna wood the water-table is found at less than 3.5 m below the surface, and may rise to 0.5 m below the latter. The *Dimorphandra* facies of this vegetation type is confined to soils in which the water-table reaches its highest position at a depth which varies between a few decimetres and one metre.

The *Swartzia* – *Ormosia* facies of the typical wet savanna wood and the *Ormosia* thicket are found on the wet savanna, where the water-table during the dry season does not sink below a depth of 1 m.

The influence of the groundwater-regime was well illustrated by what we saw along transect 20. Near picket 80 two bushes were found which could be identified as *Ormosia* thickets; each of them occupied an area of about 100 sq. metres. Some metres further on, after the surface had risen about 30 cm, a bush belonging to the *Ormosia* facies of the typical dry savanna wood was found, which covered an area of 300 sq. metres; in contrast to the thickets at picket 80, this bush contained neither *Bactris* nor *Scleria* nor *Miconia*, but on the contrary *Matayba*, *Calycolpus* and *Myrcia*.

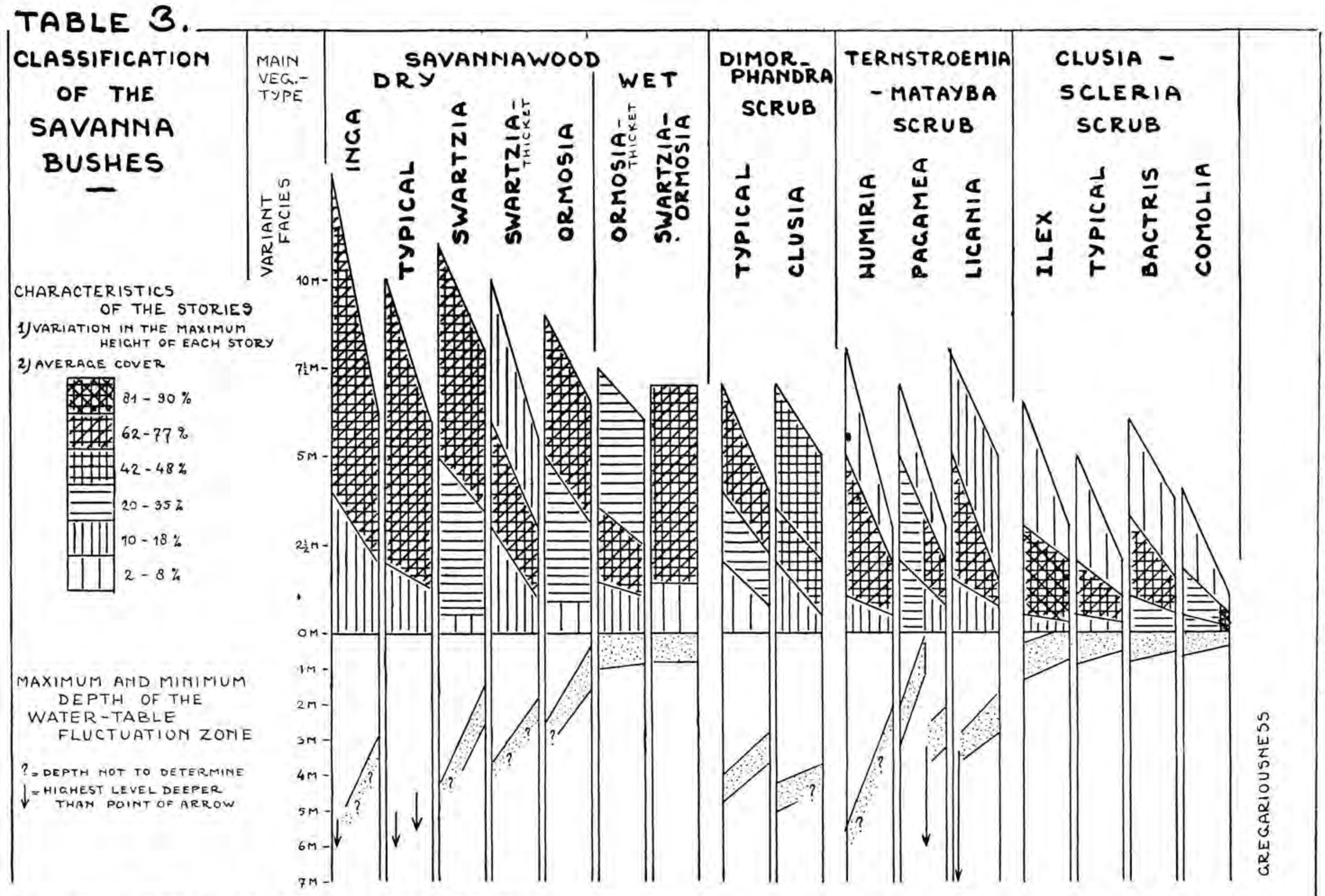
IV 3.2. *Savanna scrub*

IV 3.2.1. Physiognomy

Between the savanna scrub and the savanna wood there is in the first place a physiognomic difference (photos 1 and 2). The scrub is not only lower (it rarely rises above a height of 5 m), but the habit of several species, which in the savanna wood still grow as trees, is different. *Clusia*

TABLE 3.

CLASSIFICATION OF THE SAVANNA BUSHES



	Gregariousness
PREDOMINANT SPECIES OF UPPER AND MIDDLE STRATA	
Ternstroemia punctata	1,2
Humiria floribunda	1,2,3
Pagamea capitata	1
Licania incana	1,(2)
Clusia fockeana	1,2,2,3,4,5
Conomorpha magnoliifolia	1,(2),(2)
Retiniphyllum schomburgkii	1,(2)
Swartzia bannia	1
Ormosia costulata	1
Dimorphandra conjugata	1,2,2
Bactris campestris	1,2,2
Scleria pyramidalis	(1),2,3,4
ASSOCIATE SPECIES, PRINCIPALLY OF UPPER STRATA	
Bombax flaviflorum	1,(2)
Ilex jenmani	1
Matayba opaca	1,(2)
Pisonia sp.	1
Mapouria chlorantha	1
Pagamea guianensis	1,(2)
Trattinickia burserifolia	1
Protium heptaphyllum	1
Clusia nemorosa	1
Ocotea schomburgkiana	1,(2)
ASSOCIATE SPECIES OF LOWER STRATA	
Maytenus sp.	1,(2)
Calycolpus revolutus	1,2,3
Myrcia sylvatica	1
Aulomyrcia obtusa	1,2
Eugenia punicifolia	1,2
Aulomyrcia hostmanniana	1,2
Byrsonima crassifolia	1
Marlierea montana	1,(2)
Tibouchina aspera	1
Miconia ciliata	1
Lisianthus uliginosus	1
Comolia vernicosa	1,(5)
Lagenocarpus tremulus	1,2
Panicum nervosum	1
Miconia sp. with brown hairs	1
Croton hostmanni	1
CLIMBERS	
Bredemeyera densifl. v. glabra	1
Tetracera asperula	1,(2)
Doliocarpus calinea	1
Cassytha filiformis	1
PRINCIPAL SPECIES OF THE HERB- AND MOSS STRATUM	
Actinostachys pennula	2
Encyclia oncidioides	2,2,3
Cladonia sandstedei	2,3
Catasetum spp.	1,(2)
Epidendrum nocturnum	2
Leiphaimos aphylla	1
Pteridium aquilinum	1
Trachypogon plumosus	1,2
Axonopus attenuatus	1,2,2
Lagenocarpus weigelti	1,(2)
Schizaea incurvata	2
Borreria suaveolens	1
Apteria aphylla v. hymenanthera	1
Lagenocarpus amazonicus	2,3
Sphagnum antillarum	2,3,5
Hypolythrum pulchrum	1,2,3
Raddiella nana	2
Lindsaea stricta v. parvula	1,2

NUMBER OF RECORDS	Inga	Typical	Swartzia	Swartzia-thicket	Ormosia	Ormosia-thicket	Swartzia-Ormosia	Typical	Clusia	Humiria	Pagamea	Licania	Ilex	Typical	Bactris	Comolia
	6	3	6	4	5	4	1	5+2+2	5	7+5	6+5	2+9	7	10	7	6+3+2

LEGEND FOR SYMBOLS (COMPARE SECTION II 3)

● ◎ ○ MAINLY OCCURRING IN THE DENSEST STORY
▲ ◬ △ " " ABOVE " " "
♦ ◈ ◇ OCCURRING IN AND ABOVE " " "
▼ ⊽ ▽ MAINLY OCCURRING UNDER " " "
♦ ◈ ◇ OCCURRING IN AND UNDER " " "
→ ONLY SPECIMENS OF REDUCED VITALITY OR SEEDLINGS PRESENT
→ VEGETATIVE PARTS FULLY DEVELOPED, ALSO JUVENILE STAGES PRESENT
→ ALL DEVELOPMENT PHASES REPRESENTED WITHIN THE VEGETATION TYPE

▭ → COMBINED ESTIMATE OF ABUNDANCE AND COVER:
→ PRESENCE

- x ___ VERY SPARCELY PRESENT
- x–1 ▬ SPARCELY PRESENT, COVER VERY SMALL
- 1 ▬ RATHER PLENTIFUL, SMALL COVER VALUE
- 1–2 ▭ PLENTIFUL, " " "
- 2 ▭ VERY NUMEROUS OR COVERING 1/20 TO 1/4
- 3 ▭ ANY NUMBER, COVERING 1/4 TO 1/2
- 4 ▭ " " " 1/2 " 3/4

* FOR COMPLETE RECORD OF UNDERGROWTH: SEE SPHAGNUM VARIANT OF TABLE 4.

fockeana remains here a shrub which sometimes begins to branch already in that part of the stem from which the prop-roots spring (photo 5). *Licania incana* too remains a shrub. *Humiria floribunda* develops thick, often slanting stems, but occurs also in the shape of a decumbent shrub, and as such it often forms an encircling belt round bushes or round single large shrubs in the open savanna (photos 3, 9 and 20). Whether these differences in habit may be correlated with differences of a genetic character, remains undecided (see my remarks on the identification of the specimens at the end of section 3 of chapter II). *Dimorphandra conjugata* too remains more or less shrub-like, for the stems often form groups, and they are, moreover, already ramified once or more before they have reached a height of 1 m (photo 6, fig. 24). *Marlierea montana* is seen in two forms, viz. as an erect and as a decumbent shrub; in the dry savanna it is mostly a decumbent shrub. *Ternstroemia* is always a shrub, even where it occurs in very old scrub (photos 2 and 19). On the wet savanna it does not become higher than 2 m and develops but very few branches; the leaves, moreover, are almost entirely confined to the end of the branches, which gives these shrubs a peculiar, impoverished aspect (photo 13). However, some species, like *Pagamea capitata* (fig. 23), *P. guianensis*, *Conomorpha magnoliifolia* (photos 12 and 18), *Mapouria chlorantha*, *Bombax flaviflorum* (photo 16), *Trattinickia burserifolia* and *Matayba opaca*, retain their tree-like aspect, even when very small. The crown, however, may be reduced to a few branches or even to a single tuft of leaves. *Bactris campestris* always remains a typical "crown palm" (photos 12 and 15).

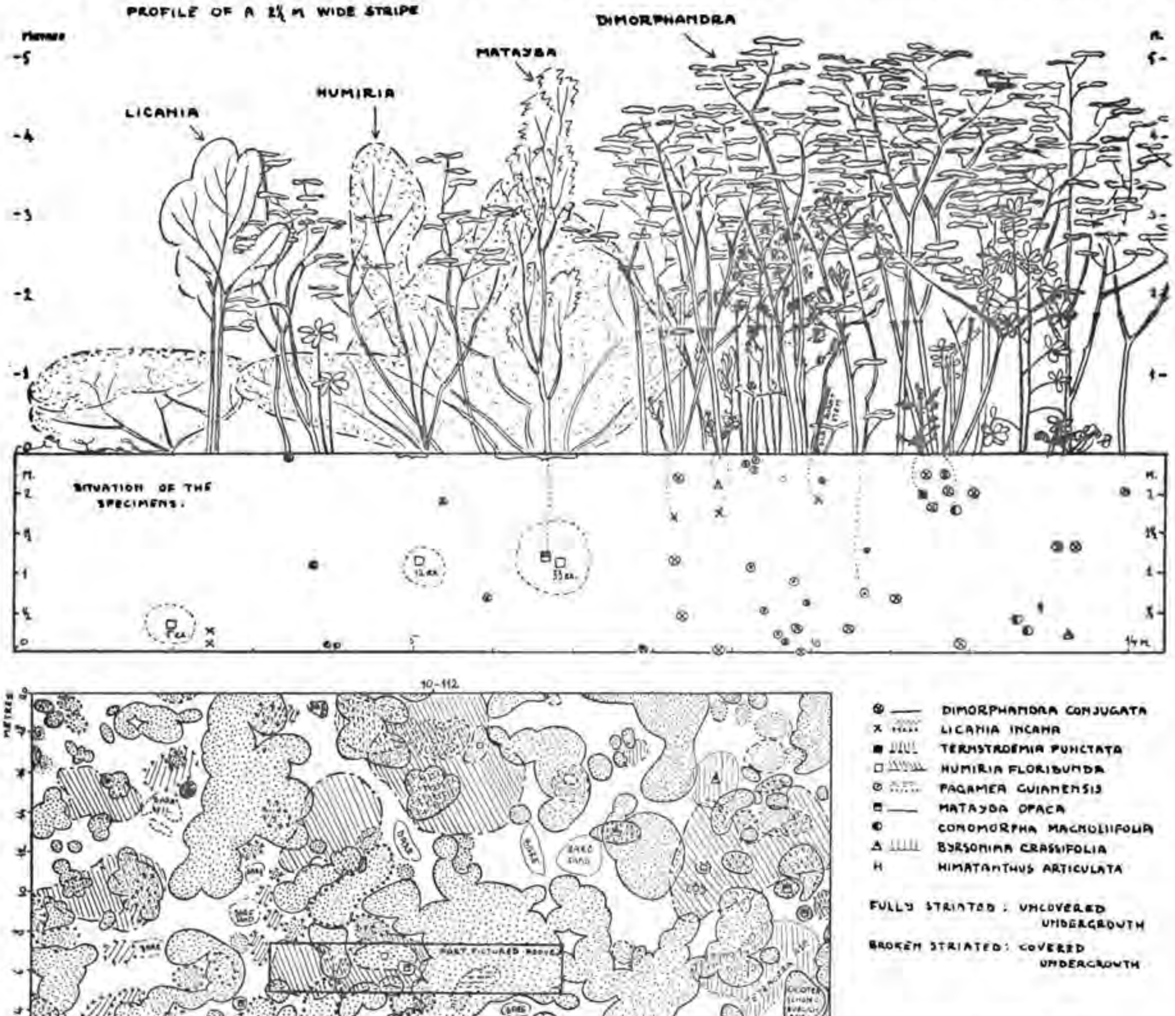
IV 3.2.2. The main types of savanna scrub

Just as among the savanna woods and savanna forests, we may distinguish two kinds of savanna scrub, a "dry" one and a "wet" one. As in this case the floristic composition of the two kinds was more thoroughly investigated, we prefer to use names for these two kinds of savanna scrub in which the floristic composition is reflected. For the dry savanna scrub we will use therefore the name "*Ternstroemia punctata* – *Matayba opaca* scrub", and for the wet savanna scrub the name "*Clusia fockeana* – *Scleria pyramidalis* scrub".

The records obtained from some of the plots covered by variants of the savanna scrub are from a floristic as well as from an ecological point of view intermediary between the *Ternstroemia* – *Matayba* scrub and the *Clusia* – *Scleria* scrub. These deviating records are rather rare, usually not more than a single one per variant; this is due to the fact that the transitional zone between the wet and the dry savanna is, as a rule, only narrow, so that the chance to meet such a plot is small. In table 3 these deviating records are omitted.

Which of the species are to be regarded as the characteristic species of the two main types of scrub, is seen at once when we look at table 3.

FIGURE 24. TYPICAL VARIANT OF DIMORPHANDRA SCRUB.



However, where *Dimorphandra* is present in the *Ternstroemia – Matayba* scrub, it usually appears to be present in such a large number that it may become the only dominant species, and even a very strongly dominant one. The habit of this kind of scrub differs therefore very strongly from the other forms of *Ternstroemia – Matayba* scrub. For this reason we have separated this *Dimorphandra* facies from the rest of the *Ternstroemia – Matayba* scrub, and given it a higher status; we call it the "*Dimorphandra conjugata* scrub".

IV 3.2.3. The Dimorphandra conjugata scrub (figs. 2, 21, 24–26)

A special study of the *Dimorphandra* scrub was made in area 1 (transects 10 and 11). Notwithstanding the strongly dominant position of *Dimorphandra*, the composition of the scrub remains heterogeneous. In patches of varying extent the undergrowth and the litter layer may be lacking, with the result that the white sand is exposed, but even when the undergrowth is present there is a good deal of variation. 1°. The *Dimorphandra* shrubs may stand close together, in which case the canopy is nearly continuous with a degree of cover of 80 %, but contains very few shrubs of other species (typical aspect of the typical variant). 2°. Round open spots some *Dimorphandra* shrubs are found, but there is no increase in the frequency of the other species, occasionally with the exception of *Ternstroemia* (depauperated facies). 3°. The *Dimorphandra* shrubs are not very close together, but in the undergrowth *Humiria* is abundant (*Humiria floribunda* facies). 4°. The canopy formed by *Dimorphandra* shows gaps which are filled by *Licania*, occasionally with the assistence of *Ternstroemia* (*Licania incana* facies). 5°. The dominance of *Dimorphandra* is less marked and the accompanying species are better represented; *Licania*, *Ternstroemia*, *Clusia* and *Matayba* may become codominant or subdominant; the undergrowth is dense (*Clusia fockeana* variant).

IV 3.2.3.1. *The typical variant* (fig. 24)

The ramification of the *Dimorphandra* stems begins at a height of 2 to 3 m above the ground, and the canopy reaches a height of 4 to 7 m. The degree of cover varies from 70 to 85 %. The largest girth of the stems measured immediately above the ground amounted to 25 cm. *Dimorphandra* is strongly dominant, but it is nevertheless always accompanied by *Licania*, *Ternstroemia*, *Conomorpha* and *Matayba*, often by *Pagamea guianensis*, and occasionally by *Clusia* and *Pagamea capitata*. In the *Licania* facies *Licania* is subdominant.

The undergrowth, i.e. the vegetation which does not reach the canopy, is not dense at all, the degree of cover varying between 3 and 20 %. It consists of *Myrcia sylvatica*, *Calycolpus revolutus*, *Humiria floribunda*, *Byrsonima crassifolia* and *Tetracera asperula*; occasionally *Pisonia* sp., *Aulomyrcia obtusa* and *Eugenia punicifolia* are also represented, as well as young plants of *Bredemeyera densiflora* var. *glabra* and *Doliocarpus calinea;* seedlings of species from the upper stratum may also be found. When the canopy is somewhat less dense, *Humiria* begins to dominate in the undergrowth (*Humiria* facies). The *Humiria* shrubs show a peculiar habit; a number of branches arise from the rooting centre and grow out to a tuft; afterwards part of them continue their growth in a horizontal direction, whereas other branches turn downwards and after they have reached the soil, begin to creep through the litter, all the while sending out leafy side-branches. Another part of the branches in the tuft grow out in the original direction, and may reach the canopy. Where *Humiria* grows at the margin of an open space, its branches, including those turned downwards, are densely covered with leaves and in that case it forms a nicely rounded whole. Where it grows inside the scrub, it usually offers a less dense aspect.

The soil is densely covered with litter, especially round the base of the *Dimorphandra* stems and round the *Humiria* shrubs. Here the litter layer reaches in combination with the layer of roots a thickness of 30 cm. The only herbs which are thriving in such a thick layer of litter, are *Actinostachys pennula* and *Leiphaimos aphylla*. Where the litter layer is less thick and where there are gaps in the scrub vegetation (depauperated facies), *Schizaea incurvata* and *Lagenocarpus weigelti* are developing well. In the last-mentioned habitats we often find also *Axonopus attenuatus* and some blades of *Trachypogon plumosus*.

The highest position of the water-table is found at a depth varying from 3 to 4 m (along transect 20 between the pickets 32 and 52, however, at a depth varying from 0.5 to 3 m. No records were made of the scrub along this transect, but it looked very much like that studied in area 1, the only difference being the somewhat greater frequency of *Ternstroemia*).

Sporadically charred stumps of *Dimorphandra* stems were found, and in the open spaces a thin layer of charcoal appeared to be hidden in the sand. These are indications of a fire which according to the tree-expert HELSTONE must have ravaged this area about 30 years ago. The uniformity in size observed among the shrubs is therefore due to a similar age. That *Dimorphandra* and similarly *Ocotea schomburgkiana*, which was found a few times in this kind of scrub, sometimes grow in clumps, is another indication of such a fire; for these stems must have arisen from the surviving underground stump of a tree that was burnt down to the base. In several spots outside area 1 I noticed *Dimorphandra* scrub which had been attacked by fires at a more recent date (photo 6). It was rather open and contained large spaces in which shrubs were entirely lacking, and where the vegetation consisted exclusively of large tufts of *Axonopus attenuatus*. The depauperated facies of the *Dimorphandra* scrub which we found at some places along transect 10, is therefore to be regarded as representing various stages in the regeneration of the scrub, where the individual shrubs were still too small to form a closed vegetation.

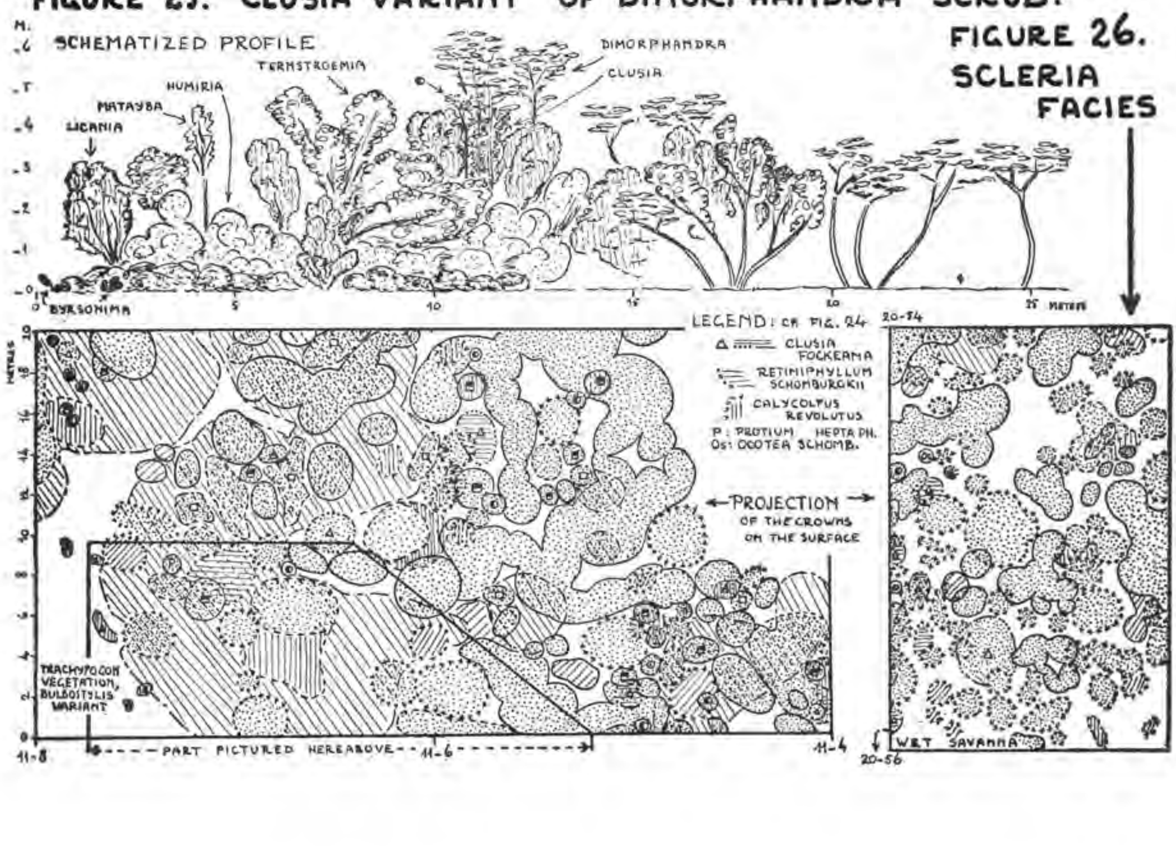
Such open vegetations may apparently persist for a long time; the small size of the *Dimorphandra* shrubs doubtless points to growth conditions that were even for this species extremely poor.

IV 3.2.3.2. *The Clusia fockeana variant* (fig. 25)

The *Clusia fockeana* variant is found in the zone where the *Dimorphandra* scrub borders on the shrub savanna. The degree of cover in the canopy varies between 30 and 70 %. The denser canopies consist of an upper, rather open stratum of *Dimorphandra* crowns and a denser lower stratum formed by *Licania*, *Ternstroemia* and other species. Because of this stratification the height of the canopy is rather variable, viz. from 3.5 to 7 m. *Dimorphandra* reaches here a greater height than in the adjoining typical variant. Apart from this species *Licania*, *Clusia*, *Ternstroemia*, *Humiria* and *Matayba* are abundant and occasionally dominant, and they are accompanied by *Conomorpha*, *Pagamea capitata* and *P. guianensis*, and *Pisonia*, and less often by *Trattinickia*, *Protium*, *Ilex* and *Byrsonima crassifolia*.

The undergrowth is dense, with a degree of cover varying from 50 to 70 % when the canopy is discontinuous, and more open, with a degree of cover of about 20 % when the canopy is closed. *Humiria* is dominant

FIGURE 25. CLUSIA VARIANT OF DIMORPHANDRA SCRUB.



in this stratum, and *Clusia* or *Calycolpus* may also be dominant, whereas *Aulomyrcia obtusa* may be abundant. Accompanying species are *Tetracera, Doliocarpus, Myrcia, Eugenia punicifolia* var. *dipoda* and var. *brachypoda, Aulomyrcia hostmanniana, Maytenus* sp. and *Psychotria farameoides.*

In the herb stratum *Actinostachys* is more numerous than in the typical variant. Seedlings are also numerous, not only those of species belonging to this variant, but also of species belonging the other vegetation types, e.g. of *Mapouria chlorantha, Tapirira guianensis, Erythroxylum citrifolium, Humiria balsamifera* and *Rapanea guianensis*. Epiphytes are rare; *Rodriguezia secunda* was found a few times. The litter layer and the root layer together have a thickness varying more or less between 5 and 15 cm. The water-table is found below 3.5 m.

This variant was found along transect 11 between the pickets 0 and 6 and between the pickets 10 and 130. The *Ternstroemia – Matayba* scrub on which it bordered, belonged to the *Humiria* variant.

At picket 55 of transect 20 the same variant bordered on wet savanna with bushes of the *Clusia – Scleria* scrub, and was developed as a *Scleria* facies (fig. 26, beside 25). The record of this facies is not included in table 3. *Dimorphandra* and *Licania* were here the dominant species, with *Clusia* and *Ternstroemia* as subdominants, and the total degree of cover amounted to 45 %. The degree of cover in the undergrowth was 25 %; here much *Retiniphyllum* and some tufts of *Scleria pyramidalis* were met with. The herb stratum had a degree of cover of 3 %, and here we found e.g. *Lisianthus uliginosus, Miconia ciliata, Tibouchina aspera, Hypolythrum pulchrum* and *Lagenocarpus amazonicus,* all of them species that are characteristic for the wet savanna. As on account of the presence of these plants was to be expected, the water-table rose here in the rainy season to a level of 10 to 20 cm below the surface. The soil was covered everywhere by litter, although the layer was in some places not more than one leaf thick. A root layer was lacking.

IV 3.2.4. The Ternstroemia punctata – Matayba opaca scrub

This kind of scrub is characterized by the great frequency of *Ternstroemia punctata, Pagamea capitata, Humiria floribunda, Licania incana* and *Clusia fockeana.* According to the degree of dominance shown by these species, various variants could be distinguished. Of the accompanying species *Matayba opaca, Calycolpus revolutus, Pisonia* sp. and *Bredemeyera densiflora* are almost always present, and together with *Pagamea guianensis, Protium heptaphyllum, Trattinickia burserifolia, Mapouria chlorantha, Myrcia sylvatica* and *Aulomyrcia obtusa* the presence of these species distinguishes this scrub from the *Clusia – Scleria* scrub.

The herb stratum is poorly developed, and apart from seedlings and young plants of the species from the upper strata only few species are found here. Most often met is *Actinostachys pennula,* then *Lagenocarpus weigelti, Schizaea incurvata* and, especially in the *Pagamea* and *Licania* variants, *Axonopus attenuatus*. When *Actinostachys* as well as *Schizaea* are present, *Actinostachys* is always more abundant. Three orchids are not rare either, viz. *Catasetum* sp., a true terrestrial plant, *Encyclia oncidioides* and *Epidendrum nocturnum*, the latter two occurring more often as epiphytes. *Borreria suaveolens*, *Stylosanthes viscosa* and an unidentified Bromeliacea may also be present.

IV 3.2.4.1. *The Humiria floribunda variant* (photo 20; fig. 23)

This vegetation appears in the form of bushes covering a surface of 100 to 600 sq. metres, and reaching a height of 2.5 to 5 m, in which besides *Ternstroemia* we find *Humiria* as dominant species in the canopy. *Humiria* is usually provided with a slanting stem which reaches a diameter of some decimetres, and with thick, gnarled branches which stand out in various directions, some of them even bending downwards. The branches of *Ternstroemia* may reach a diameter of more than 10 cm.

As a rule, the canopy is, at least in the lower part, well-closed, with a degree of cover of about 70 %. Apart from *Ternstroemia* and *Humiria* *Pagamea capitata* may be abundant, occasionally even codominant. In about half the records *Clusia* appears to be codominant, and in this case we distinguish the vegetation as a "*Clusia* facies". Another feature of this facies is that *Conomorpha* is abundant, whereas *Licania* may be entirely absent and *Pagamea* rather rare. For the rest, however, the composition does not differ from that of the typical aspect.

Above the general level of the canopy project, as a rule, some rather meagre crowns of *Trattinickia*, *Matayba*, *Conomorpha*, *Bombax*, *Pagamea guianensis* or *Mapouria* and a few branches of *Licania* and *Ternstroemia*.

A characteristic accompanying species of the *Humiria* variant is *Clusia nemorosa*.

Where this kind of scrub borders on the open savanna, the space between the canopy and the ground is screened by a dense belt of *Humiria* or of the latter and *Ternstroemia*. *Humiria* appears here in the form of a low, densely leafy shrub with its branches decumbent or hanging down to the ground, whereas *Ternstroemia* may be present either in the form of small, up to 2 m high shrubs with pendulous, densely leafy branches or merely in the form of branches springing from the higher shrubs that are growing somewhat deeper in the scrub. The enclosure, however, is not always so perfect, and may consist also of more or less isolated and low shrubs of *Pagamea*, *Clusia*, *Licania* and *Humiria*.

The degree of cover of the undergrowth, i.e. of the shrubs which do not reach the canopy and which do not belong to the marginal belt, varies from a few per cent to about 75 %; this depends mainly on the abundance of *Retiniphyllum*.

The soil is covered by a thin layer of litter, and below the latter the network of roots forms a layer usually less than 10 cm thick, but which may reach a thickness of 25 cm. The surface is often uneven with up to

30 cm high ridges caused by the presence of decaying stems under the litter.

Epiphytes are on the whole rare, although somewhat less rare in scrub belonging to the *Clusia* facies, where, apart from a few thick living stems, the decaying ones that are resting on the soil serve as substrate. It are the same species as are found in the *Inga* variant of the dry savanna wood.

The water-table is found at a depth of at least 2 m, and in the dry season groundwater is, as a rule, entirely absent.

This variant, also called *Humiria – Ternstroemia – Matayba* scrub, was seen only in the southern part of area 1, where practically all the bushes found on the south-eastern savanna belonged to the typical variant; the *Clusia* facies of this variant, however, is found also on the south-eastern savanna. In the typical aspect it forms the belts round the *Swartzia* bushes and occasionally also round the *Inga* bushes of the dry savanna wood (cf. IV 3.1.3. and 3.1.1.). The *Swartzia* thickets described in IV 3.1.4. may also be regarded as a subvariant of the *Humiria – Ternstroemia – Matayba* scrub (cf. IV 3.1.4.).

IV 3.2.4.2. *The Pagamea capitata variant* (photo 19)

This kind of scrub does not reach a height of more than 3 to 4 m, though occasionally a branch projecting above the canopy may reach a height of 5 m. *Ternstroemia* and *Pagamea* play the most important part in the canopy, though *Pagamea* is subdominant with regard to *Ternstroemia*. *Licania*, *Clusia* and *Humiria* are usually also represented, but play a subordinate part only. As the leaves of *Ternstroemia* are congested at the top of the branches, and as the ramification of the old *Ternstroemia* shrubs is but meagre, the degree of cover of the canopy is on the average but 35 %; for this reason this kind of scrub looks rather open. The degree of cover of the undergrowth varies between 15 and 40 %. The special form of *Humiria* characterized by the decumbent branches here plays an important part, and this applies also to dwarf shrubs of *Pagamea capitata*, especially when the scrub reaches a great age. Occasionally *Psychotria farameoides* is found.

The greater part of the accompanying species are but rarely met with. *Matayba* is mostly present, but disappears where the water-table approaches the surface. Such sites are recognizable by the presence of *Tibouchina aspera* or *Scleria pyramidalis* in the undergrowth.

In the "*Clusia* facies" of this variant *Clusia* is codominant, with the result that the canopy shows fewer gaps (average degree of cover 65 %), and that the undergrowth is poorly developed (average degree of cover 10 %). The most important shrub in the undergrowth is *Humiria*.

In the "*Marlierea* facies", which is not included in table 3, *Marlierea montana* appeared to be codominant in the canopy as well as in the undergrowth. In the canopy *Scleria* was well represented, as in the undergrowth

Lagenocarpus amazonicus and *Axonopus pulcher*; this means that in the wet season the water-table will rise to nearly to the surface.

The litter layer as well as the layer formed by the network of roots are thin. Only when *Dimorphandra* is present, the litter may locally reach a thickness of 10 cm.

On the ground we often find some isolated cushions of *Cladonia sandstedei*. Epiphytes are not numerous, and may be entirely absent. *Epidendrum nocturnum*, however, was noted in more than half the records. *Phthirusa squamulosa* was found occasionally on *Licania*, and a species of *Oryctanthus* on *Ternstroemia*.

The typical aspect of this variant forms, as a rule, extensive vegetations in which locally small open spaces occur; occasionally, however, it is found in the form of bushes covering a surface of about 100 sq. metres and surrounded by a *Humiria* belt. The *Clusia* facies appears in the form of bushes which may be connected with each other by a growth of *Ternstroemia* or by a *Humiria* belt in which much *Retiniphyllum* may be present. Occasionally the bushes are united into a more extensive scrub vegetation.

Between the pickets 30 and 120 of transect 30 some beautifully developed examples of the typical aspect were seen; they alternated with old *Dimorphandra* scrub. The typical aspect was found also on the dry savanna in the northern part of area 1 (site 10–30). The water-table reached heights varying between 10 and 210 cm below the surface. The *Clusia* facies was found on the southern savanna of area 1 (transect 10–236 to 256 and site 13–6) where the water-table was found at a depth of more than 6 m, and at site 18–10 where the water-table lay at a depth of more than 210 cm. The *Marlierea* facies was noted only once, viz. at site 30–4, where it formed a bush springing from the border of a *Dimorphandra* scrub.

IV 3.2.4.3. *The Licania incana variant*

The typical aspect of this variant appears in the form of groups of high shrubs and isolated trees united into a scrub by the intermediary of lower, sometimes not more than 1.5 m high shrubs; this scrub alternates with rather large open spaces. In the canopy the degree of cover is about 65 %. *Licania* and *Ternstroemia* are dominant, and *Matayba*, *Bombax* and *Pagamea capitata* may be abundant; in the lower parts *Humiria* and *Retiniphyllum*, occasionally also *Calycolpus* and *Tetracera*, are well represented. Remarkable was the presence of *Rapanea guianensis*.

The high frequency of *Licania* and the presence of such species as *Ormosia costulata*, *Ocotea schomburgkiana*, *Inga lateriflora* and *Humiria balsamifera* indicate an affinity with the dry savanna wood.

We have made but two records of the typical aspect of this variant, viz. at the sites 18–14 and 20–88. At the first-mentioned site there had obviously been a fire; some charred stems were still present. In the undergrowth *Axonopus attenuatus* was very abundant, and *Tibouchina aspera* and *Coccocypselum guianense* were also found. It is not impossible that this is a regeneration stage; this would account for the large differences in height which we noted here.

In the undergrowth the most abundant species proved to be *Retiniphyllum* and *Humiria*, and apart from these species a large number of young plants of the species that formed the canopy, were present. Epiphytes were absent.

The highest position reached by the water-table was at a depth of about 2 m. In a bush situated at 18–7, i.e. near the decline towards the wet savanna, where e.g. *Scleria pyramidalis* and a single specimen of *Bactris* were noted, but where *Calycolpus*, *Myrcia* and similar species were lacking, the water-table was found at a depth of 40 cm below the surface.

The "*Clusia* facies" of this variant is a scrub of which the canopy reaches a height of 1 to 5 m with a degree of cover of 65 %. Besides *Licania* and *Ternstroemia* we find here *Clusia* as a dominant species, and *Humiria*, *Conomorpha* and *Matayba* are often abundant. *Pagamea capitata* may also be numerous, but this happens less often, and occasionally this species is even absent in the upper stratum. At some sites (18–20, 10–224) *Licania*, *Ternstroemia*, *Matayba* and *Conomorpha* project rather conspicuously above the canopy, which consists mainly of *Clusia* or sometimes of the latter and *Retiniphyllum*.

In the undergrowth the degree of cover varies from 5 to 10 %. *Myrcia sylvatica* and *Aulomyrcia obtusa* are most often met with, and further especially young plants of the species which form the canopy.

The *Clusia* facies is not only found in the form of a more or less extensive scrub, but occurs also in the form of bushes which often are confined to plots varying in size between 25 and 75 sq. metres. With regard to the abundance of the dominant species, there is not always much difference with the larger stretches, but sometimes either *Ternstroemia* or *Licania* is less well represented. This is due to the small size of the bushes, which remains below that of a bush in which we may expect the average representation of the whole set of species (fig. 27).

Occasionally a rich development of epiphytes is noted, but in other bushes the latter are entirely lacking. *Phthirusa squamulosa* was sometimes present on *Licania*. The litter layer and the network of roots have at the most a thickness of a few centimetres.

Bushes representing the *Clusia* facies as well as larger stretches covered by the latter were found mainly along transect 10, viz. between the pickets 78 and 100, and between 18 and 20. The highest level reached by the water-table varies here between 125 and 250 cm below the surface. At site 10–76 it rose to 40 cm below the surface, and here *Scleria pyramidalis* was plentiful, whereas *Matayba* and similar species were lacking. In habit, however, this bush, which covered a surface of 225 sq. metres, looked quite normal.

At site 10–80 this kind of vegetation bordered on typical dry savanna

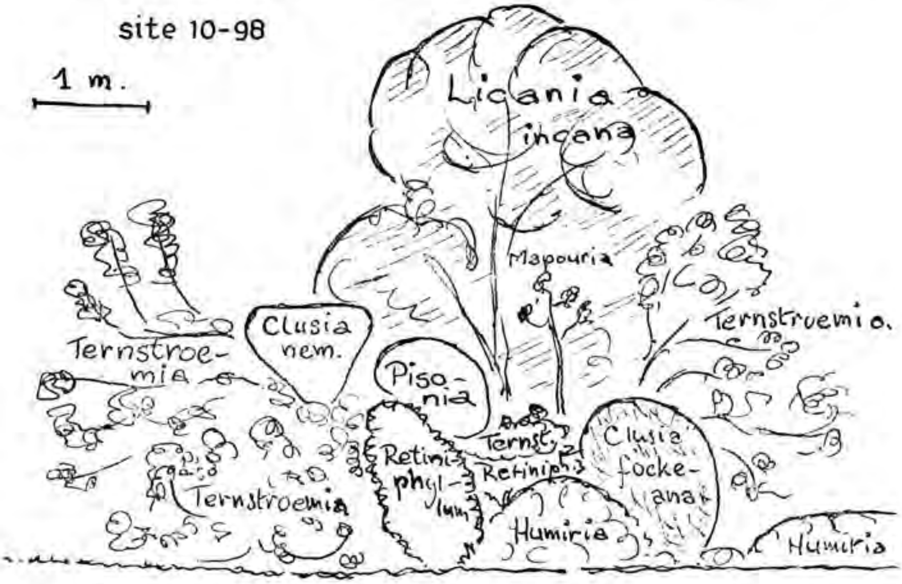


Fig. 27. *Licania* variant of the *Ternstroemia – Matayba* scrub, *Clusia* facies.

wood. At this site a centimetre below the surface a layer of charcoal was found (III 2.2.). Distinct indications of a fire were present at site 14–7, where the scrub was not yet closed and consisted of solitary shrubs, small groups, and small bushes.

Whether in the course of the succession the dominant species remain the same, is uncertain (cf. IV 3.1.2. and IV 4.2.). At site 10–224 where, just as at site 14–7, the water-table was found at a great depth, the *Clusia* facies occurred at the margin of a typical dry savanna wood. Here we saw decaying stems on the ground which were perhaps left there by a fire which devastated the area a long time ago. They were covered by a rich flora of epiphytic orchids of a kind similar to that which we saw in the *Clusia* facies of the *Humiria* variant of the *Ternstroemia – Matayba* scrub and in bushes belonging to the *Inga* variant of the dry savanna wood. The presence of a few cushions of the moss *Octoblepharum cylindricum* was another indication pointing in the direction of the dry savanna wood. At site 17–108 finally a bush was surveyed which covered a surface of about 150 sq. metres. Here some thick and slanting stems of dead trees were seen which might have been *Humirias*, and further a *Ternstroemia* whose stem had a diameter of 20 cm. In view of the fact that the other bushes in this part of the savanna belonged to the *Humiria* variant of the *Ternstroemia – Matayba* scrub, it seems plausible to assume that here too the vegetation belonged originally to this variant, and that it owes its present composition to the decline and death of the old *Humirias*.

IV 3.2.4.4. *Fragments of the Ternstroemia – Matayba scrub* (photographs 2, 3 and 5)

The small groups of shrubs and the shrubs that occur singly in the open parts of the dry savanna are regarded by us as fragments of the *Ternstroemia – Matayba* scrub.

Of nearly all the shrubs and of most of the trees of the *Ternstroemia – Matayba* scrub occasionally an isolated specimen is seen on the open savanna, especially on those parts where we find indications of devastations caused by a fire. However, the number of species of which more often solitary specimens are seen, is but small; it are in the main *Licania*, *Ternstroemia* and *Clusia*. The single *Ternstroemia* trees are sometimes surrounded by *Humiria* shrubs, but where the latter are lacking, *Ternstroemia* itself produces branches that hang down to the ground, and mimics in this way a bush which may cover an area of 3 to 30 sq. metres. Especially under *Ternstroemia* often young plants of *Clusia*, *Retiniphyllum*, *Pagamea capitata*, *Conomorpha*, *Tetracera* and/or *Doliocarpus* are found, as also *Calycolpus* and *Byrsonima crassifolia*.

The term "group" is used by us if different species, each represented by a single or a very few specimens, are growing close together. In such groups the following combinations were observed: *Ternstroemia – Licania*, *Ternstroemia – Licania – Matayba*, *Ternstroemia – Clusia – Matayba*, *Humiria – Trattinickia*, *Humiria – Matayba*, *Ilex – Conomorpha – Pagamea capitata*, *Ternstroemia – Humiria – Clusia – Conomorpha*. Combinations of a larger number of species were also noted, sometimes in the form of an undergrowth below an up to 6 m high tree, which may be either a *Humiria*, an *Ilex*, a *Matayba* or an *Ormosia*, or below a group of trees, which in that case proved to belong to *Bombax flaviflorum*. The surface covered by such groups does not exceed a hundred sq. metres. On a larger surface the number of species becomes sufficiently large to allow the identification of the vegetation with one of the kinds of scrub described above.

IV 3.2.5. The Clusia fockeana – Scleria pyramidalis scrub

In this kind of scrub the dominant species are *Clusia* and *Scleria*, and the latter is at the same time the species which distinguishes this type from the *Ternstroemia – Matayba* scrub. Associate species which are characteristic for this type are in the first place *Bactris campestris* and the undershrubs *Tibouchina aspera*, *Miconia ciliata* and *Comolia vernicosa*, further the herbs *Lagenocarpus tremulus*, *Lisianthus uliginosus* and *Cassytha filiformis*. *Marlierea montana* is here more often present than in the *Ternstroemia – Matayba* scrub. *Ternstroemia*, *Humiria* and *Pagamea capitata* are found only as poorly developed specimens, and they never reach the same dimensions as in the *Ternstroemia – Matayba* scrub. *Ternstroemia* and *Pagamea* often consist of a single shoot with some leaves at the top.

In contrast to the *Ternstroemia* – *Matayba* scrub, which may cover areas of considerable extent, the *Clusia* – *Scleria* scrub occurs usually in the form of bushes which may vary in size, but which, as a rule, cover less than 100 sq. metres.

IV 3.2.5.1. *The Ilex jenmani variant* (fig. 28)

This vegetation forms the transition between the *Clusia* facies of the *Licania* variant of the *Ternstroemia* – *Matayba* scrub and the typical variant of the *Clusia* – *Scleria* scrub.

The *Clusia* shrubs are only 1.5 to 3 m high, and are interspersed with *Scleria pyramidalis*. Above this *Clusia* stratum, which has a degree of cover of 70 to 95 %, the crowns or sometimes single branches of *Licania*, *Conomorpha*, *Ternstroemia* and *Ilex*, occasionally also of *Mapouria* and *Pisonia* are projecting up to a height of 6.5 m; together these projecting crowns and branches may reach a degree of cover of 25 %. A similar closed canopy with projecting crowns and branches was found in some bushes occurring on the dry savanna, especially in bushes which represented the *Clusia* facies of the *Licania* variant of the *Ternstroemia* – *Matayba* scrub (IV 3.2.4.3.), but in the *Ilex jenmani* variant of the *Clusia* – *Scleria* scrub it is more pronounced.

The floristic composition is intermediate between that of the *Clusia* facies of the *Licania* variant of the *Ternstroemia* – *Matayba* scrub and the typical variant of the *Clusia* – *Scleria* scrub. Species which it has in common with the first-mentioned vegetation type, but which are absent in the other one, are *Ilex*, *Bredemeyera*, *Pisonia*, *Mapouria* and *Matayba*. *Ilex* and *Bredemeyera* are fairly regularly present, but the three other ones are less common. Of the species which are not found in the first-mentioned vegetation, but which occur in the second, *Scleria* and *Mar-*

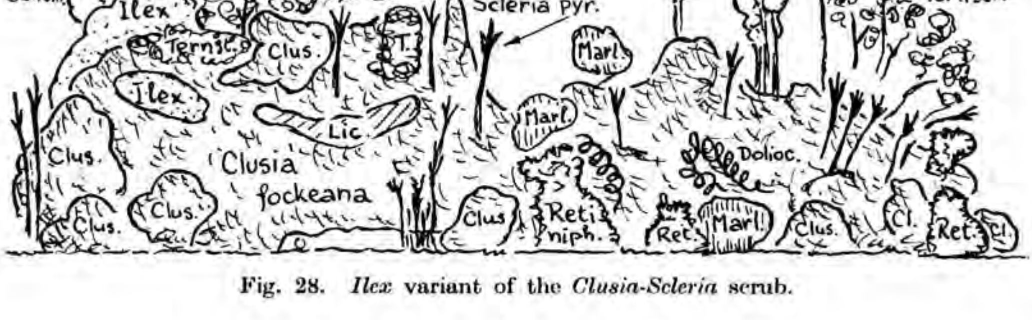


Fig. 28. *Ilex* variant of the *Clusia-Scleria* scrub.

lierea are always present, and *Tibouchina* and *Cassytha* are also fairly common. These points of resemblance and the fact that the dominance relations in the vegetation under consideration and the typical *Clusia* – *Scleria* scrub are similar and different from those in the first-mentioned type, seem to justify our conclusion that this type of vegetation is to be regarded as a variant of the *Clusia* – *Scleria* scrub.

The *Ilex* variant is found only in the form of bushes covering a surface of some tens of square metres. As the crowns of the *Clusia* shrubs extend downwards to a few decimetres from the ground, the undergrowth is poorly developed and consists mainly of seedlings, especially of *Clusia* itself. Occasionally a few vigorous clumps of *Encyclia oncidioides* are seen. The litter layer has a thickness of a few centimetres and covers a thin layer of roots. The margin of the bush is formed exclusively by *Clusia* shrubs.

The *Ilex* variant was found along transect 10 between the pickets 57 and 73 and at site 18–7; it formed a belt along a vegetation belonging to the *Licania* variant of the *Ternstroemia* – *Matayba* scrub. The water-table may rise in these sites to a few centimetres below the surface. Two bushes in which the groundwater reached the surface and in which *Ilex* and *Bredemeyera* accordingly were lacking, were nevertheless included in this vegetation type because *Bactris*, *Miconia*, *Lisianthus* and some other species were lacking, which means that they could not be included in one of the other variants of the *Clusia* – *Scleria* scrub.

In a narrow zone round these bushes where the soil of the savanna is covered by some litter, the vegetation shows a composition which deviates from that of the vegetation found at a somewhat greater distance (photo 11). This margin consists of the *Lagenocarpus amazonicus* variant of the *Rhynchospora tenuis* vegetation (cf. IV 4.4.).

IV 3.2.5.2. *The typical variant*

The typical variant of the *Clusia* – *Scleria* scrub forms bushes covering a surface of 8 to 20 sq. metres. The *Clusia* stratum has a degree of cover of 50 to 80 %, and a height of 1 to 2 m, but the crowns and branches which project above this stratum may reach a height of 3.5 m. The highest ones often belong to *Licania*, but sometimes to *Conomorpha* or to *Bactris*. However, in about half the records *Bactris* occurs only in the form of young plants.

In the *Clusia* stratum *Clusia* is dominant and *Scleria* codominant, whereas *Licania* and *Retiniphyllum* are often sobdominant. Associates with a high presence are *Marlierea*, *Conomorpha*, *Pagamea capitata*, *Humiria*, the lianas *Tetracera*, *Doliocarpus* and *Cassytha*, and the herbs *Lisianthus uliginosus*, *Lagenocarpus tremulus* and *Panicum nervosum*. Less frequent are *Ternstroemia*, *Tibouchina*, *Miconia* and *Comolia*. Epiphytes are almost entirely absent, though *Phthirusa squamulosa* is not rarely met on *Licania*.

A layer consisting of a network of roots is not developed, but especially below the *Clusia* shrubs the soil is densely covered with loose litter, and where this is so, there is practically no undergrowth. Apart from seedlings of the woody species, sporadically a small tuft of *Actinostachys pennula* or a blade of *Lagenocarpus amazonicus* are seen. Where at the border of the bush the foliage of the *Clusia* shrubs does not reach the ground, and also in spots where the *Clusia* stratum is more open, an undergrowth is found in which *Sphagnum antillarum* predominates; this will be discussed in IV 4.5. Immediately around the bushes with a dense *Clusia* stratum once more a zone is found with a vegetation of which the composition deviates from that found somewhat further away. Here this margin is the *Lagenocarpus amazonicus* subvariant of the *Panicum nervosum* variant of the *Lagenocarpus tremulus* vegetation. This vegetation will also be dealt with in IV 4.5.

At site 21–8 a record was made of a bush which covered a surface of 25 sq. metres, and in which the degree of cover of the *Clusia* stratum was but 15 %. In this case there was no difference between the undergrowth and the vegetation of the marginal zone. It agreed in the main with the typical variant, though *Clusia* and *Scleria* were less strongly dominant, and we regard it therefore as a depauperated aspect of the typical variant (It is not included in table 3).

At site 10–40 a bush (fig. 22) representing the typical variant was found on a stretch of ground over which the rain water runs off towards a creek. The hogwallowed soil was here densely overgrown by *Abolboda grandis* (cf. IV 4.5.), and this species was also dominant in the undergrowth of these small bushlets which covered about 10 sq. metres, together with *Lindsaea stricta* var. *parvula*.

In the rainy season the water-table reaches the surface, while in the dry season it sinks to a depth of 70 to 90 cm.

The typical variant was found at the following sites: 10–40, 10–47 to 51, 20–71, 21–2 to 6, 32–70, 32–90, and 35–4.

IV 3.2.5.3. *The Bactris campestris variant*

In this variant (photo 15) the *Clusia* stratum is about one metre higher and less dense than in the typical variant. The degree of cover varies between 50 and 65 % in this stratum itself, and from 3 to 15 % in the stratum formed by the projecting crowns and branches.

Bactris is the dominant species in the layer of the projecting crowns. *Conomorpha* is herein also well represented, whereas *Licania*, *Ternstroemia* and some other species project less often above the canopy.

Here too *Clusia* and *Scleria* are the dominant species in the *Clusia* stratum, but several of the associates are also abundant and occasionally even subdominant. This applies to *Bactris*, *Conomorpha*, *Pagamea*, *Ternstroemia*, *Licania*, *Marlierea*, *Retiniphyllum*, *Tetracera* and *Doliocarpus*.

The amount of litter is but small. The soil itself contains a rather large amount of organic matter. Occasionally shallow depressions are present or the surface is more or less hogwallowed. The herb and moss stratum is, as a rule, fairly dense, the degree of cover being some 25 %; about half of it is formed by thick cushions of *Sphagnum antillarum*, and there are usually also some cushions of *Octoblepharum cocuiense*. Characteristic species of this variant are the herbs *Perama dichotoma*, *Apteria aphylla* and *Calyptrocarya glomerulata*; the last-mentioned herb is often plentiful. The predominating Cyperacea in the undergrowth is *Hypolythrum pulchrum*. Occasionally a tuft of *Lagenocarpus amazonicus* is seen, but this species is here of no importance. *Siphanthera hostmannii* and *Raddiella nana* were occasionally also met with. *Humiria* is found mainly in the undergrowth, together with *Marlierea*.

Epiphytes were present in about half the records. They are mainly orchids, viz. *Encyclia oncidioides*, *Polystachya luteola*, *Epidendrum nocturnum* and an as yet unidentified species (no. 230) with white flowers and long roots which creep along the thin stems, e.g. those of *Bactris*. This species was seen also in the wet savanna wood.

The bushes formed by the *Bactris* variant cover on the average an area of 100 sq. metres, and are often drawn out in one direction. A distinct marginal zone is absent or only locally developed (cf. IV 5.1.1.). The water-table sinks in the dry season to a depth of 55 to 80 cm.

These *Bactris* bushes are especially common in area 3, but they are found also in area 1 and in area 2. We studied them at the sites 32–95, 156 and 178; 36–14; 37–20; 10–38, and 20–63.

The high abundance of *Bactris* and *Hypolythrum* and the presence of *Apteria* indicate affinity with the *Swartzia* – *Ormosia* variant of the wet savanna wood. The soil on which it is found, is also similar.

IV 3.2.5.4. *The Comolia vernicosa variant*

This variant appears in the form of small bushes, covering a surface of at the most 20 sq. metres, but often not exceeding 1 sq. metre (photo 12). Occasionally, however, these bushes are found so close together that they seem to form an extensive scrub vegetation. They are always low and rather open. The height varies between 0.5 to 1.5 m, but some of the crowns, in the main those of *Bactris* and *Conomorpha*, project above the canopy and reach a height of up to 3 m. The degree of cover of the canopy varies between 15 and 40 %. Although in this kind of scrub *Clusia* is dominant also, it is not as strongly dominant here as in the other variants, and for this reason it is not possible to speak here of a "*Clusia* stratum". The proportion in which the various dominants are represented, varies moreover from bush to bush. *Comolia vernicosa* is sub- to codominant, and *Licania* as well as *Lagenocarpus* are usually present in large numbers. *Ternstroemia* may be entirely absent, but it may also be abundant and even dominant, in which case it forms a special "*Ternstroemia* facies" (photo 13). *Scleria* is less frequent and may even be absent. *Retiniphyllum*, *Tibouchina* and *Miconia* are absent or rare. Restricted to the "*Calyptrocarya monocephala* facies", which occurs on the tracts along which the rain water runs off to the creeks, are *Bombax* and *Panicum nervosum*. The soil is in this facies strongly hogwallowed, and the holes between and under the *Clusia* and *Comolia* shrubs are filled with *Calyptrocarya monocephala*.

Because the soil is never completely and often only sporadically covered with litter, and because the canopy is never continuous, the undergrowth may develop very richly. *Sphagnum* plays here an important part and *Cladonia sandstedei* may be present in varying amounts. As this undergrowth shows a strong resemblance to the vegetation found in some open stretches, it is treated as a *Sphagnum* variant of the *Lagenocarpus tremulus* vegetation, which will be considered in IV 4.5.

The ground in the bushes lies, as a rule, somewhat higher than that of the surrounding savanna, so that the relief of the area, at least when the bushes are close together, is distinctly rugged. On the sloping parts the herbaceous vegetation covers but a few per cent of the surface, but on the flat parts it may cover up to 15 %. These "white borders" round the bushes lend the whole complex a characteristic aspect when seen from an aeroplane (fig. 30; cf. IV 5.1.1.). The water-table which in the rainy season reaches the surface, sinks in the dry period to a depth of 40 to 70 cm.

The typical form as well as the *Ternstroemia* facies of this variant were found at various places along transect 32 between the pickets 30 and 150, the *Calyptrocarya* facies at the sites 30–132 and 32–16.

IV 3.2.5.5. *Fragments of the Clusia – Scleria scrub*

The only species which occur on the wet savanna as solitary shrubs are *Licania*, *Humiria*, *Byrsonima* and *Ternstroemia*; in the vicinity of the typical variant of the *Clusia – Scleria* scrub the first three are found, and in the vicinity of the *Ilex* variant moreover *Ternstroemia*. These species may also occur in small groups, and in that case a stratum of *Sphagnum* and *Cladonia* may develop at their base, it also happens that *Axonopus pulcher* or *Tetracera* form a rather dense vegetation there.

In area 3, *Licania* grows in the form of a low shrub in the wet savanna; these shrubs may be scattered or combined into small groups which (in IV 4.5.) will be described as the *Licania* subvariant of the *Panicum nervosum* variant of the *Lagenocarpus tremulus* vegetation.

IV 4. Vegetations consisting of a single stratum (table 4)

Among this kind of vegetations we will distinguish five main types, viz. the "*Bulbostylis conifera* vegetation", the "*Axonopus attenuatus – Lagenocarpus weigelti* vegetation", the "*Trachypogon plumosus* vegetation", the "*Rhynchospora tenuis* vegetation" and the "*Lagenocarpus tremulus* vegetation".

IV 4.1. *The Bulbostylis conifera vegetation*

This type of vegetation is characteristic for the large open stretches of the dry white-sand savanna (photographs 2, 3 and 4; fig. 29). It is a very open vegetation with a degree of cover of but a few per cent. The "*typical* variant" is characterized by the high abundance of *Bulbostylis conifera* (on the average 140 tufts per square metre), whereas of *Lagenocarpus weigelti* on the average but one tuft is found in a plot of 4 sq. metres, and of *Schizaea incurvata* and *Trachypogon plumosus* one example in every square metre; especially *Trachypogon plumosus* is, moreover, in a poor condition. Scattered shrublets of *Cassia ramosa* var. *ramosa, Licania incana* and *Byrsonima crassifolia* and an occasional plant of *Bulbostylis fasciculata, Borreria suaveolens* and *Schwenckia americana* figure also on the species list of the community. On somewhat smaller open stretches *Axonopus attenuatus* appears in fairly large numbers.

In the "*Axonopus pulcher* variant" *Bulbostylis conifera* is less frequent (0–60 tufts per square metre), whereas *B. fasciculata* and *Trachypogon* are better represented. It differs from the typical variant by the presence of *Axonopus pulcher* and *Mesosetum loliiforme*; where the latter becomes more numerous, and its stolons, which may reach a length of several metres and creep over the bare sand in every direction, a "*Mesosetum* facies" may be distinguished.

In the uppermost centimetre of the soil a micropodzol is developed (cf. III 2.4.).

IV 4.2. *The Axonopus attenuatus – Lagenocarpus weigelti vegetation*

This kind of vegetation is best developed on small open spots between groups of shrubs or in rings around and below isolated shrubs on the dry savanna (photographs 5 and 6). Apart from the two dominant species after which this vegetation type was named, *Schizaea incurvata, Borreria suaveolens, Stylosanthes viscosa* and *Tetracera asperula* are always present.

Pteridium aquilinum is often present, and may even become dominant. In this "*Pteridium* facies" *Melampodium camphoratum* is often abundant, occasionally also *Paspalum arenarium*. These three species are found also in savanna wood that is regenerating after a fire (sites 14–20 and 17–4). They are indications of a fire which destroyed the original vegetation about 10–20 years ago.

In the *Pteridium* facies we always found a thin layer of charcoal at a depth of one to a few centimetres. Charcoal was often found in the typical facies too, not always as a continous layer but in the form of dark spots.

The species always present in this vegetation type, are also regularly found in the undergrowth of the scrub, and *Axonopus* as well as *Lagenocarpus* appear to reach their fullest development along the margin of bushes where the ground is covered by a thin layer of litter.

After a fire the *Axonopus – Lagenocarpus* vegetation may expand its area (photo 6), but when the scrub begins to recover, the *Axonopus – Lagenocarpus* vegetation retires to its previous position or disappears. A few *Pteridium* fronds may maintain themselves for a long time in the scrub as a witness of a previous stage.

Occasionally some other species may dominate on the small open spots, at site 13–10 *Bulbostylis surinamensis* and *Cassia ramosa* were very abundant; at site 10–257 *Axonopus pulcher* was dominant.

IV 4.3. *The Trachypogon plumosus vegetation* (photos 7 to 10, fig. 29)

This is the densest one-layered vegetation found on the dry sand soils. The degree of cover is about 60 %, and the plants reach a height of 60 cm not counting the flowering shoots of *Trachypogon* which reach a height of 1.5 m and those of *Axonopus* which are 1 m high. This vegetation consists in reality of two strata, a lower one formed by *Mesosetum loliiforme* together with the stolons of *Cassia hispidula*, *Aeschynomene hystrix* and *Stylosanthes viscosa*, and an upper one formed by *Trachypogon* and *Axonopus*.

To the characteristic species belong *Polygala angustifolia* var. *latifolia*, *P. longicaulis* and *Cassia hispidula*. In the "*typical* variant" *Bulbostylis fasciculata* and *Mitracarpus discolor* are constantly met with and very frequent, but *Zornia diphylla*, *Aeschynomene paniculata* and *Piriqueta cystoides* are also typical associates.

In the "*Bulbostylis conifera* variant" *Bulbostylis conifera* and *Cassia ramosa* take the place of *Bulbostylis fasciculata* and *Mitracarpus discolor*. In this variant we distinguish moreover a "*Lagenocarpus weigelti* subvariant" and a "*Cassia flexuosa* subvariant". Differential species for the first subvariant are *Lagenocarpus weigelti*, *Stylosanthes viscosa* and *Schwenckia americana*, for the second *Cassia flexuosa* and *Aeschynomene hystrix*. In the *Lagenocarpus weigelti* subvariant *Bulbostylis conifera*, *Axonopus pulcher* and *Cassia ramosa* are less abundant than in the other subvariant, but *Byrsonima crassifolia* is more abundant. Especially the *Lagenocarpus weigelti* subvariant shows in its floristic composition a near approach to the *Bulbostylis conifera* vegetation.

In the typical variant as well as in the *Lagenocarpus weigelti* subvariant a strong development of *Mesosetum* may give rise to a special "*Mesosetum* facies". The latter has about the same degree of total cover as the typical facies, but there is an increase in cover of the lower stratum at the expense of the *Trachypogon* stratum (photo 8).

The typical variant as well as the *Bulbostylis conifera* variant occur on white and on red sand, but the *Lagenocarpus weigelti* subvariant is confined to white sand, whereas the *Cassia flexuosa* subvariant is found on red sand and on the transition zone between the latter and the white sand (cf. III 3.3. and fig. 5). It is, in our opinion, not impossible that on the red sands more dew is formed, and that the micro-climate is here,

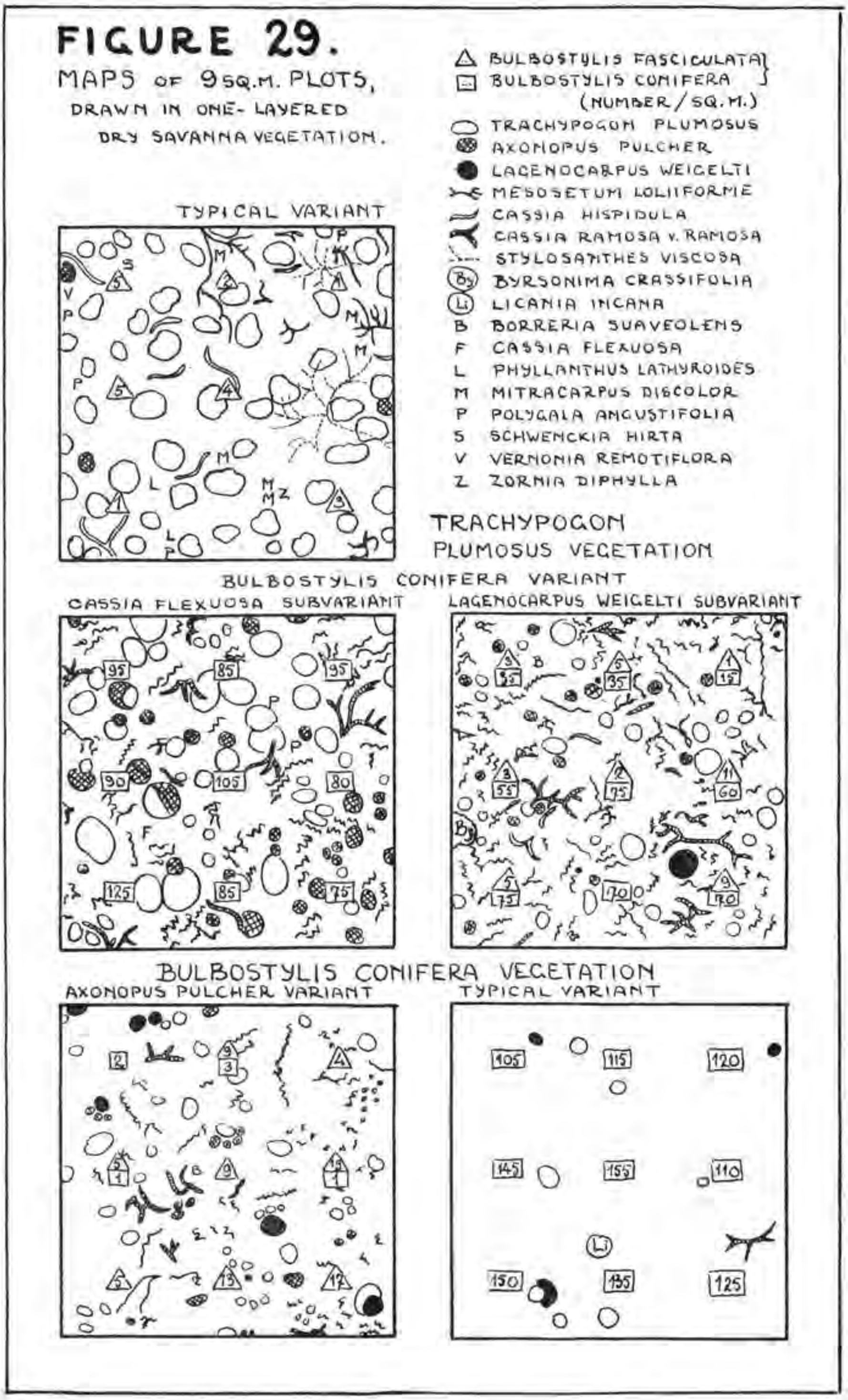
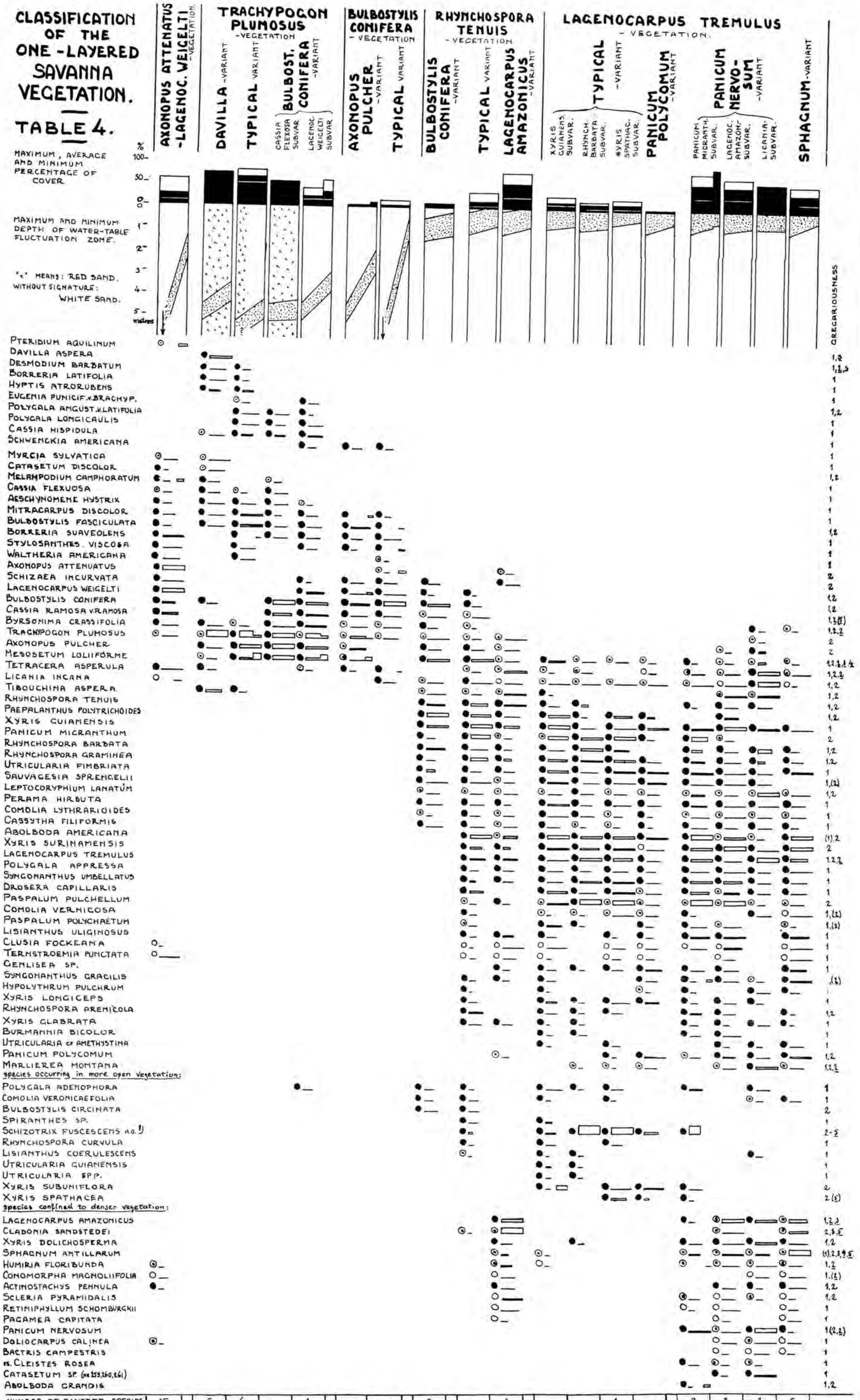


FIGURE 29.
MAPS OF 9 SQ.M. PLOTS, DRAWN IN ONE-LAYERED DRY SAVANNA VEGETATION.
BULBOSTYLIS FASCICULATA
BULBOSTYLIS CONIFERA
(NUMBER / SQ.M.)
TRACHYPOGON PLUMOSUS
AXONOPUS PULCHER
LAGENOCARPUS WEIGELTI
MESOSETUM LOLIIFORME
CASSIA HISPIDULA
CASSIA RAMOSA v. RAMOSA
STYLOSANTHES VISCOSA
BYRSONIMA CRASSIFOLIA
LICANIA INCANA
B BORRERIA SUAVEOLENS
F CASSIA FLEXUOSA
L PHYLLANTHUS LATHYROIDES
M MITRACARPUS DISCOLOR
P POLYGALA ANGUSTIFOLIA
S SCHWENCKIA HIRTA
V VERNONIA REMOTIFLORA
Z ZORNIA DIPHYLLA
TYPICAL VARIANT
TRACHYPOGON PLUMOSUS VEGETATION
BULBOSTYLIS CONIFERA VARIANT
CASSIA FLEXUOSA SUBVARIANT
LAGENOCARPUS WEIGELTI SUBVARIANT
BULBOSTYLIS CONIFERA VEGETATION
AXONOPUS PULCHER VARIANT
TYPICAL VARIANT

CLASSIFICATION OF THE ONE-LAYERED SAVANNA VEGETATION.

TABLE 4.



Species	Gregariousness
PTERIDIUM AQUILINUM	
DAVILLA ASPERA	1,2
DESMODIUM BARBATUM	1,2,3
BORRERIA LATIFOLIA	1
HYPTIS ATRORUBENS	1
EUGENIA PUNICIF. V. BRACHYP.	1
POLYGALA ANGUST. X LATIFOLIA	1,2
POLYGALA LONGICAULIS	1
CASSIA HISPIDULA	1
SCHWENCKIA AMERICANA	1
MYRCIA SYLVATICA	1
CATASETUM DISCOLOR	1
MELAMPODIUM CAMPHORATUM	1,2
CASSIA FLEXUOSA	1
AESCHYNOMENE HYSTRIX	1
MITRACARPUS DISCOLOR	1
BULBOSTYLIS FASCICULATA	1
BORRERIA SUAVEOLENS	1,2
STYLOSANTHES VISCOSA	1
WALTHERIA AMERICANA	1
AXONOPUS ATTENUATUS	1
SCHIZAEA INCURVATA	2
LAGENOCARPUS WEIGELTI	2
BULBOSTYLIS CONIFERA	1,2
CASSIA RAMOSA V. RAMOSA	1,2
BYRSONIMA CRASSIFOLIA	1,2,(3)
TRACHYPOGON PLUMOSUS	1,2,2
AXONOPUS PULCHER	2
MESOSETUM LOLIIFORME	2
TETRACERA ASPERULA	1,2,3,4
LICANIA INCANA	1,2,3
TIBOUCHINA ASPERA	1,2
RHYNCHOSPORA TENUIS	1,2
PAEPALANTHUS POLYTRICHOIDES	1,2
XYRIS GUIANENSIS	1,2
PANICUM MICRANTHUM	1
RHYNCHOSPORA BARBATA	2
RHYNCHOSPORA GRAMINEA	1,2
UTRICULARIA FIMBRIATA	1,2
SAUVAGESIA SPRENGELII	1
LEPTOCORYPHIUM LANATUM	1,(2)
PERAMA HIRSUTA	1,2
COMOLIA LYTHRARIOIDES	1
CASSYTHA FILIFORMIS	1
ABOLBODA AMERICANA	1
XYRIS SURINAMENSIS	(1),2
LAGENOCARPUS TREMULUS	2
POLYGALA APPRESSA	1,2,3
SYNGONANTHUS UMBELLATUS	1
DROSERA CAPILLARIS	1
PASPALUM PULCHELLUM	1
COMOLIA VERNICOSA	2
PASPALUM POLYCHAETUM	1,(2)
LISIANTHUS ULIGINOSUS	1,(2)
CLUSIA FOCKEANA	1
TERNSTROEMIA PUNCTATA	1
GENLISEA SP.	1
SYNGONANTHUS GRACILIS	1
HYPOLYTHRUM PULCHRUM	,(2)
XYRIS LONGICEPS	1
RHYNCHOSPORA ARENICOLA	1,2
XYRIS GLABRATA	1
BURMANNIA BICOLOR	1
UTRICULARIA cf AMETHYSTINA	1
PANICUM POLYCOMUM	1,2
MARLIEREA MONTANA	1,2,3
species occurring in more open vegetation:	
POLYGALA ADENOPHORA	1
COMOLIA VERONICAEFOLIA	1
BULBOSTYLIS CIRCINATA	2
SPIRANTHES SP.	1
SCHIZOTRIX FUSCESCENS a.o.[1]	2-5
RHYNCHOSPORA CURVULA	1
LISIANTHUS COERULESCENS	1
UTRICULARIA GUIANENSIS	1
UTRICULARIA SPP.	1
XYRIS SUBUNIFLORA	2
XYRIS SPATHACEA	2(3)
species confined to denser vegetation:	
LAGENOCARPUS AMAZONICUS	1,2,3
CLADONIA SANDSTEDEI	2,3,5
XYRIS DOLICHOSPERMA	1,2
SPHAGNUM ANTILLARUM	(1),2,3,4,5
HUMIRIA FLORIBUNDA	1,2
CONOMORPHA MAGNOLIIFOLIA	1,(2)
ACTINOSTACHYS PENNULA	1,2
SCLERIA PYRAMIDALIS	1,2
RETINIPHYLLUM SCHOMBURGKII	1
PAGAMEA CAPITATA	1
PANICUM NERVOSUM	1(2,3)
DOLIOCARPUS CALINEA	1
BACTRIS CAMPESTRIS	1
vs. CLEISTES ROSEA	1
CATASETUM SP. (nr. 159,160,161)	1
ABOLBODA GRANDIS	1,2

NUMBER OF OMITTED SPECIES	15	5	6	–	1	–	–	2	–	1	–	–	1	–	3	3	1	5
NUMBER OF RECORDS	12 (7+5)	4	8 (5+3)	7	9 (6+3)	8 (6+2)	12 (8+4)	8	14	6	12 (6+6)	8	10	9	8	7	3	9

LEGEND FOR SYMBOLS:
● FLOWERING SPECIMENS OBSERVED WITHIN THE VEGETATION TYPE
⊙ VEGETATIVE PARTS FULLY DEVELOPED, EVENT. ASEXUAL REPRODUCTION
○ SPECIMENS OF REDUCED VITALITY OR ONLY JUVENILE PLANTS PRESENT.
▭ AVERAGE FIGURE FOR ESTIMATION OF ABUNDANCE-DOMINANCE (HEIGHT) AND VALUE FOR PRESENCE (LENGTH) ⟼ = 100%
x, x-1, 1, 1-2, 2, 3, 4 — COMPARE TABLE 3.

SCALE FOR GREGARIOUSNESS
1: SINGLE SPECIMENS.
2: OCCURRING IN SMALL GROUPS.
3: OCC. IN LARGER GROUPS.
4: OCC. AS A CARPET OR IN VERY LARGE GROUPS.
5: THE WHOLE GROUND HOMOGENEOUSLY COVERING.
_: GROUP NOT CLOSED, BUT SPECIMENS SINGLE OCCURRING VERY NEAR EACH OTHER.
( ): VALUE OF RARE OCCURRENCE.

[1] THE COVER OF THE CYANOPHYCEAE-LAYER IS NOT INCLUDED IN THE COVER OF HERBS, MENTIONED IN THE GRAPH.

therefore, less extremely dry; this would explain the higher abundance of *Bulbostylis conifera* and its associates. It does not look probable that differences of the soil in exchangeable ions would be responsible (cf. III 2.7. and 3.2.).

Where on the red sand the *Trachypogon* vegetation borders on a secondary forest of *Matayba*, sometimes a "*Davilla* variant" is developed. In this variant *Davilla aspera* is found in greater or smaller numbers, whereas *Tibouchina aspera* too may be abundant. Young woody plants from the secondary forest, like *Ternstroemia dentata*, *Aulomyrcia hostmanniana* and *Roupala montana*, are also found.

Trachypogon vegetations were found exclusively on soils with a deep water-table where, moreover, the influence of man was very strong, i.e. in the vicinity of villages or in that of secondary forest (sites 11–8 to 14, and 66 to 86; 12–20 to 32; 15–220 to 250; cf. fig. 7).

IV 4.4. *The Rhynchospora tenuis vegetation* (photo 11)

The vegetations consisting of a single stratum found on the wet savanna show an aspect which is totally different from that shown by vegetations of this kind occurring on the dry savanna. The two main types of the wet savanna have many species in common, but their species lists show only little resemblance to those of the vegetations found on the dry savanna.

The *Rhynchospora tenuis* vegetation still has some species in common with the *Bulbostylis conifera* vegetation of the dry savanna, although these species have, as a rule, a low presence. There is, however, a transitional type, distinguished as the "*Bulbostylis conifera* variant", in which only a part of the species of the typical variant is found, which, however, are accompanied here by a larger number of species from the *Bulbostylis conifera* vegetation.

Species which occur in the "*typical* variant" as well as in the one-layered vegetation of the dry savanna, are *Trachypogon*, *Mesosetum*, *Axonopus pulcher*, *Bulbostylis conifera* and, in the form of small shrubs, *Cassia ramosa*, *Licania* and *Tetracera*. With the exception of *Mesosetum* these species are scarce and have often a low presence. The following species are characteristic for the wet savanna and occur in fairly large to large numbers: *Paepalanthus polytrichoides*, *Xyris guianensis* and *X. surinamensis*, *Abolboda americana*, *Drosera capillaris*, *Rhynchospora tenuis*, *Rh. graminea* and *Rh. arenaria* and *Lagenocarpus tremulus*. They are accompanied by a number of species that are less abundant, and among which *Rhynchospora barbata*, *Sauvagesia sprengelii* and *Perama hirsuta* are most often seen.

Of the species which are characteristic for the *Bulbostylis conifera* variant as well as for the typical variant, viz. *Bulbostylis circinata* and *B. junciformis*, *Stylosanthes angustifolia* and *Polygala galioides*, *Bulbostylis circinata* is the only one which recurs in more than half the records.

The "*Lagenocarpus amazonicus* variant" has a much higher degree of cover than the typical one, viz. on the average 55 % against 14 % in the latter. It is found in the form of a narrow, ca. 0.5 m wide belt round bushes growing on a savanna with a *Rhynchospora tenuis* vegetation; these bushes usually represent the *Ilex* variant of the *Clusia* – *Scleria* scrub or, more rarely, the *Ormosia* thicket, one of the variants of the wet savanna wood. Between the herbs the ground is covered with some litter, with the result that completely bare spots are rare. Some species are absent in this variant, whereas some other ones occur in smaller numbers and with a lower presence. These species apparently prefer the more open variants of the *Rhynchospora tenuis* vegetation, which get no shade from bushes. On the other hand this marginal vegetation is characterized by some sciophilous species, viz. *Lagenocarpus amazonicus* and *Cladonia sandstedei*. Especially *Cladonia* may give this marginal zone a characteristic aspect because it is apt to form a carpet. This zone shows an approach to the *Axonopus attenuatus* – *Lagenocarpus weigelti* vegetation by the occurence of *Axonopus attenuatus*, *Schizaea incurvata* and *Actinostachys pennula*. *Tetracera* may occupy an important part of the space in this zone, and seedlings and young specimens of species from the bushes may also be present.

In the rainy season the water-table rises in the *Bulbostylis conifera* variant to a height of 40 to 20 cm below the surface, and in the typical variant and in the *Lagenocarpus amazonicus* variant to a level of 20 cm below to just at the surface.

The *Rhynchospora tenuis* vegetation is met everywhere where the dry savanna passes into the wet one, e.g. in area 1 along transect 10–52 to 72, in various parts of area 2, and in area 3 along transect 30–70 to 78, and at 32–4 and 32–70.

A kind of vegetation of which only one record was obtained and which is not considered in table 4, was preliminarily included in the *Rhynchospora tenuis* vegetation as "*Leptocoryphium lanatum* facies" (photo 17). The floristic composition is poor; flowering plants of *Leptocoryphium lanatum* are dominant (2.5); *Rhynchospora tenuis* (x–1.2), *Rh. barbata* (1.1), and *Mesosetum* (x–1.1) are fairly abundant, and they are accompanied by *Trachypogon*, *Panicum nervosum*, *P. micranthum*, *Paspalum pulchellum*, *Lagenocarpus tremulus*, *Rhynchospora arenaria* and *Hypolythrum pulchrum* (*Panicum nervosum* and *Hypolythrum pulchrum* have x.1, the other species x.2 in Braun Blanquet's notation). Locally the ground may be covered with a film of Algae (cf. IV 4.5.). The degree of cover was as a rule 7 %, but the plants were very regularly spaced; at other places the degree of cover was somewhat higher, in which case *Trachypogon* and *Panicum nervosum* were more abundant.

That this facies consists exclusively of grasses and Cyperaceae is to be ascribed to fires, which caused the disappearance of such species as *Xyris guianensis* and *X. surinamensis*, *Abolboda americana*, *Drosera* and *Sauvagesia*. A few dead plants of *Syngonanthus umbellatus* were still present, and the small bushes found in this vegetation showed unmistakable signs of damage by fire. In the herbaceous vegetation locally charred plant remains were also seen.

This facies was found along transect 32 between the pickets 200 and 210. The fluctuations of the water-table, which in the rainy season reaches the surface, are larger than those measured below the typical facies, viz. 150 cm instead of 100 cm (cf. III 6.2. and fig. 17).

IV 4.5. *The Lagenocarpus tremulus vegetation*

This type of vegetation differs from the *Rhynchospora tenuis* vegetation by the absence of almost all the species which the latter has in common with the dry savanna and by the presence of some new species which usually differentiate special variants. Such species are *Panicum nervosum*, *P. polycomum*, *Paspalum polychaetum*, *Xyris uniflora* and *X. spathacea*. Some other species are more regularly found or more abundant. *Lagenocarpus tremulus*, for instance, is always present and, as a rule, abundant or very abundant, and under such circumstances its panicles determine the aspect of this vegetation type (photo 12). *Paspalum pulchellum* too is always present and abundant to very abundant. *Perama hirsuta*, *Polygala appressa*, *Drosera capillaris* and *Syngonanthus umbellatus* are more often present. *Rhynchospora tenuis*, on the other hand, is rare or absent.

In the *Lagenocarpus tremulus* vegetation the water-table rises often above the surface; only at the end of long periods of drought it sinks to a depth of 60 to 80 cm, rarely to 100 cm or even deeper. For this reason the *Lagenocarpus tremulus* vegetation is to be regarded as the typical vegetation of the wet savanna. It occurs along transect 32 between the pickets 10 and 250, along transect 10 between the pickets 33 and 56, and in the lower part of area 2.

We divided the *Lagenocarpus tremulus* vegetation into four variants: the "*typical* variant", the "*Panicum polycomum* variant", the "*Panicum nervosum* variant" and the "*Sphagnum antillarum* variant".

IV 4.5.1. The typical variant

In the typical variant the herbs cover about 13 % of the soil surface, whereas 10 to 90 % of the latter is covered by a film of Algae, mainly of Cyanophyceae; among these *Schizothrix fuscescens* is the dominant species, and *Stigonema minutum* one of its most important associates.

In the "*Xyris spathacea* subvariant" on the average 50 % of the soil is covered by this film of Algae. The dominant herbs of this subvariant are *Paspalum pulchellum*, *Panicum micranthum*, *Lagenocarpus tremulus*, *Rhynchospora graminea* and *Abolboda americana*, whereas the associates are *Xyris guianensis*, *X. surinamensis*, *X. longiceps*, *X. paraënsis*, *X. subuniflora* and *X. spathacea*, *Rhynchospora barbata* and *Rh. curvula*, *Utricularia fimbriata*, *Sauvagesia sprengelii*, *Paepalanthus polytrichoides*, *Perama hirsuta*, *Polygala adenophora* and *P. appressa*, *Syngonanthus* *umbellatus*, *Drosera capillaris*, small shrubs of *Licania incana* and *Comolia vernicosa*, and seedlings of *Clusia fockeana*.

In the "*Rhynchospora barbata* subvariant" (photo 14) the film of Algae covers usually more than two thirds of the soil surface. *Rhynchospora barbata* is here abundant, whereas *Xyris subuniflora* and *X. spathacea*, *Rhynchospora curvula* and seedlings of *Clusia* and of *Ternstroemia* are lacking. *Paepalanthus*, *Polygala adenophora*, *Xyris guianensis* and *X. longiceps*, *Rhynchospora arenicola*, *Perama hirsuta* as well as *Comolia vernicosa* are far less often present. In half the records unmistakable signs of a fire were found, and it is therefore not unexpected that in these records some of the species that are most easily destroyed by a fire were sometimes absent, viz. *Paepalanthus*, *Xyris surinamensis* and *X. guianensis*, *Sauvagesia*, *Utricularia* and *Perama hirsuta*, perhaps still more of the species mentioned above. Of *Syngonanthus* and *Abolboda* dead tufts were found. After a recent fire *Paspalum pulchellum* showed mass-flowering, with the result that such stretches were already recognizable from afar by their brownish-red tinge. Whether the total absence of *Xyris subuniflora* and of the other species mentioned above may be ascribed to repeated burning, is a question that requires a special investigation.

The "*Xyris guianensis* subvariant" differs from the other two subvariants in the main by differences in the proportion in which the various species are represented. *Mesosetum*, *Xyris guianensis*, *Sauvagesia*, *Perama*, *Abolboda*, *Paspalum polychaetum* and *Xyris longiceps* are relatively better represented, *Lagenocarpus tremulus*, *Paspalum pulchellum* and *Syngonanthus* relatively less well. The film of Algae is poorly developed or lacking. In about half the records *Xyris subuniflora* is so abundant that it is permissible to speak of a "*Xyris subuniflora* facies"; *Xyris spathacea*, on the other hand, is entirely lacking. The approach to the typical variant of the *Rhynchospora tenuis* vegetation is in this subvariant more obvious than in the other two. A small terrestrial orchid belonging to the genus *Spiranthes*, which is found in the typical *Rhynchospora tenuis* vegetation, turns up again in this subvariant.

IV 4.5.2. The Panicum polycomum variant

This variant is the "white border" vegetation found on the barren zones by which many bushes in the wet savanna are surrounded (photo 15). The degree of cover is very small, viz. 2 to 7 %. The number of species is small, but *Panicum polycomum*, *Xyris guianensis*, *X. subuniflora* and *X. longiceps*, *Utricularia fimbriata*, *Sauvagesia*, *Abolboda* and *Genlisea* sp. are rather frequent. Sporadically a fragment of the algal film sticks to the base of a plant, where it was left by a passing flow of rain water running off along the surface. Occasionally *Xyris spathacea* or *X. subuniflora* may cover an area of some square metres in such abundance that we may speak of a special facies. Frequently the plants are poorly developed and especially *Xyris surinamensis* is found only in a depauperated form. At a depth of about 1 cm below the surface we find a thin light green layer in the sand, which appears to be caused by the presence of Cyanophyceae, of which *Fischerella ambigua* is the most important one.

IV 4.5.3. The Panicum nervosum variant

This variant forms a very dense vegetation. It occurs in three subvariants which we have named each after a dominant species: *Panicum micranthum*, *Lagenocarpus amazonicus* and *Licania incana*, respectively. The species which distinguish this variant as a whole from the typical variant and from the *Panicum polycomum* variant are besides *Panicum nervosum Xyris dolichosperma*, a plant preliminarily identified as *Cleistes rosea*, and *Sphagnum antillarum*; the latter may be present in small amounts only, sometimes even in the form of scattered leafy shoots. Pedologically important is the rather considerable amount of organic matter found in the top soil, and the usually slightly hogwallowed surface (cf. III 2.5.).

In its typical aspect the "*Panicum micranthum* subvariant" (photo 16) has a degree of cover varying between 30 and 85 %, and is rich in grasses. Especially *Paspalum pulchellum* is abundant, and *Leptocoryphium* is here somewhat more abundant than it is in other vegetations. This subvariant differs from the other ones also in the presence of *Lycopodium meridionale*, whereas the soil, especially in the little holes, is covered to some extent with a film of Algae. Occasionally *Abolboda grandis* may become so numerous that we may speak of an "*Abolboda grandis* facies"; *Lindsaea stricta* var. *parvula* is in this facies an associate. The large rosettes of *Abolboda* may leave little room between them; this happens especially in the zone round bushes, and in such zones also some other species are present, e.g. *Lagenocarpus amazonicus* and *Andropogon leucostachyus*. The records of such marginal zones are not included in table 4.

At site 32–228 the *Panicum micranthum* subvariant was found in a shallow elongated depression of the savanna. No hogwallowed surface was seen here. The cause of this extension over a larger surface than is usually occupied by this kind of vegetation, which, as a rule, is confined to small areas situated near and between bushes, may perhaps be sought in the fact that this particular part of the savanna had repeatedly been subjected to fires. Where the soil became better drained, this vegetation passed into the *Leptocoryphium* facies of the *Rhynchospora tenuis* vegetation (photo 17).

In the "*Licania incana* subvariant" (photos 14 and 17) again indications of fires are often noted; charred stumps may be seen even between the roots. This subvariant occurs, as a rule, in the form of very small bushes, often not more than 0.5 m in diameter and 40 cm high, in vegetations belonging to the *Rhynchospora barbata* subvariant or in the *Leptocoryphium* facies and in the adjoining *Panicum micranthum* vegetation mentioned in the preceding paragraph. That we have here a kind of "bushes" before us, follows from the abundance of *Licania*, *Tetracera*, *Marlierea* and *Tibouchina*. Dominant herbs are *Lagenocarpus tremulus* and *L. amazonicus*, *Panicum nervosum*, *Leptocoryphium lanatum*, *Xyris dolichosperma* and *X. guianensis*.

Occasionally the small shrubs are growing so closely together that the whole vegetation assumes the character of the *Licania incana* subvariant but with a smaller abundance of *Lagenocarpus amazonicus* and *Marlierea* (site 32–236; cf. the *Comolia* variant of the *Clusia* – *Scleria* scrub, IV 3.2.5.4.). In this plot we also found *Axonopus pulcher*, *Mesosetum*, *Trachypogon*, *Byrsonima crassifolia*, *Paepalanthus* and *Rhynchospora tenuis*. This indicates an affinity with the *Lagenocarpus amazonicus* variant of the *Rhynchospora tenuis* vegetation and with the *Leptocoryphium* facies of the typical variant of the same vegetation. The water-table fluctuates in the same way as that in the last-mentioned vegetation type. The soil surface does not show a hogwallowed aspect.

The "*Lagenocarpus amazonicus* subvariant" is a vegetation confined to the zone surrounding the bushes of the *Clusia* – *Scleria* scrub, no matter wether the latter belong to the typical variant or to the *Bactris* variant, and also around bushes belonging to the *Ormosia* thicket (photo 18). It looks much like the *Panicum micranthum* subvariant, but it differs from the latter by the presence of *Lagenocarpus amazonicus*, *Cladonia sandstedei*, *Paepalanthus* and *Tibouchina*; *Panicum micranthum* is practically absent, but *Xyris surinamensis* is abundant. Neither *Cladonia* nor *Sphagnum* determine, as a rule, the aspect. The soil may be covered at the most for one third by litter, and when the surface is hogwallowed, in the depressions some Algae are found. Usually, however, the surface is flat and the soil contains less organic matter than it does in the adjoining bushes.

IV 4.5.4. The Sphagnum antillarum variant

This variant is found where bushes belonging to the *Comolia* variant or occasionally to the typical variant of the *Clusia* – *Scleria* scrub occur in the *Lagenocarpus tremulus* vegetation. This variant is, in fact, to be regarded as the undergrowth of these bushes (cf. IV 3.2.5.2. and 4). In the central part of these rather open bushes the soil is still covered with a layer of litter, and here the *Sphagnum* variant is, of course, absent. The remaining part of the surface in such a bush is covered for one to four fifths with litter, and here the degree of cover of the *Sphagnum* variant rose to about 40 %. *Sphagnum* itself, occasionally together with *Cladonia* and with *Octoblepharum cocuiense*, proved to play an important part, whereas among the herbs *Abolboda americana*, *Xyris surinamensis*, *Panicum polycomum*, *Lagenocarpus amazonicus* and *L. tremulus* were dominant.

When the degree of cover of the shrub stratum reaches a value of about 50 %, the amount of litter on the ground becomes so considerable that only fragments of the *Sphagnum* variant are left. This depauperated aspect has not been included in table 4. The degree of cover is reduced to 10 or even to 5 %, and *Sphagnum* does no longer appear in the form of large cushions. *Lagenocarpus amazonicus* and *Actinostachys pennula* are almost entirely or even totally absent in these fragments.

IV 4.6. *The vegetation of the open tracts along which the rain water runs off*

This vegetation, with the palm *Mauritia flexuosa* towering high above it (photo 14), differs markedly from the one-layered vegetations discussed above. Some high grasses and sedges are abundant, viz. *Hypogynium virgatum*, *Ischaemum guianense*, *Panicum nervosum*, *Rhynchospora cyperoides* and *Hypolythrum pulchrum*. *Paspalum pulchellum* is still present, but *Lagenocarpus tremulus* has become very rare and *Panicum micranthum*, *Paspalum polychaetum*, *Drosera capillaris*, *Abolboda americana* and the various *Xyris* species, with the exception of *X. dolichosperma*, are entirely absent. The soil surface showed a deep, hogwallowed relief along which the rain water ran off (site 38–210; the record of this plot is not included in table 4).

IV 5. Ground-water and fire damage as ecological factors

The aim of this investigation was "to describe the vegetation of the savanna against an ecological background" (I 2). The description of the vegetation has been given in the preceding sections, and in this section I will try to do justice to the "ecological background" by an attempt to establish a relation between the vegetation and the hydrological conditions, and to analyse the processes which set in when the vegetation has been visited by a fire.

IV 5.1. *The influence of the hydrological conditions*

In III 7 the hydrological condition of the soil in the areas which form the subject of this publication, has been discussed. In the first place the important differences between the dry and the wet savanna were emphasized, and it was pointed out that the degree of drainage depends entirely on the topography. The wet savanna was characterized as that part of the savanna in which the groundwater (at least in the rainy season) reaches the surface, and the dry savanna as the part in which the water-table never reaches the surface.

Where a hardpan proved to be present, it is conceivable that the latter may have a local effect on the position of the water-table, but this effect is apparently not very important in these parts, and insofar as my experience goes, this effect was never reflected in the composition of the vegetation.

IV 5.1.1. The wet savanna

In the wet savanna the water-table is often found so near the surface that changes in its position do not necessarily reflect changes in the

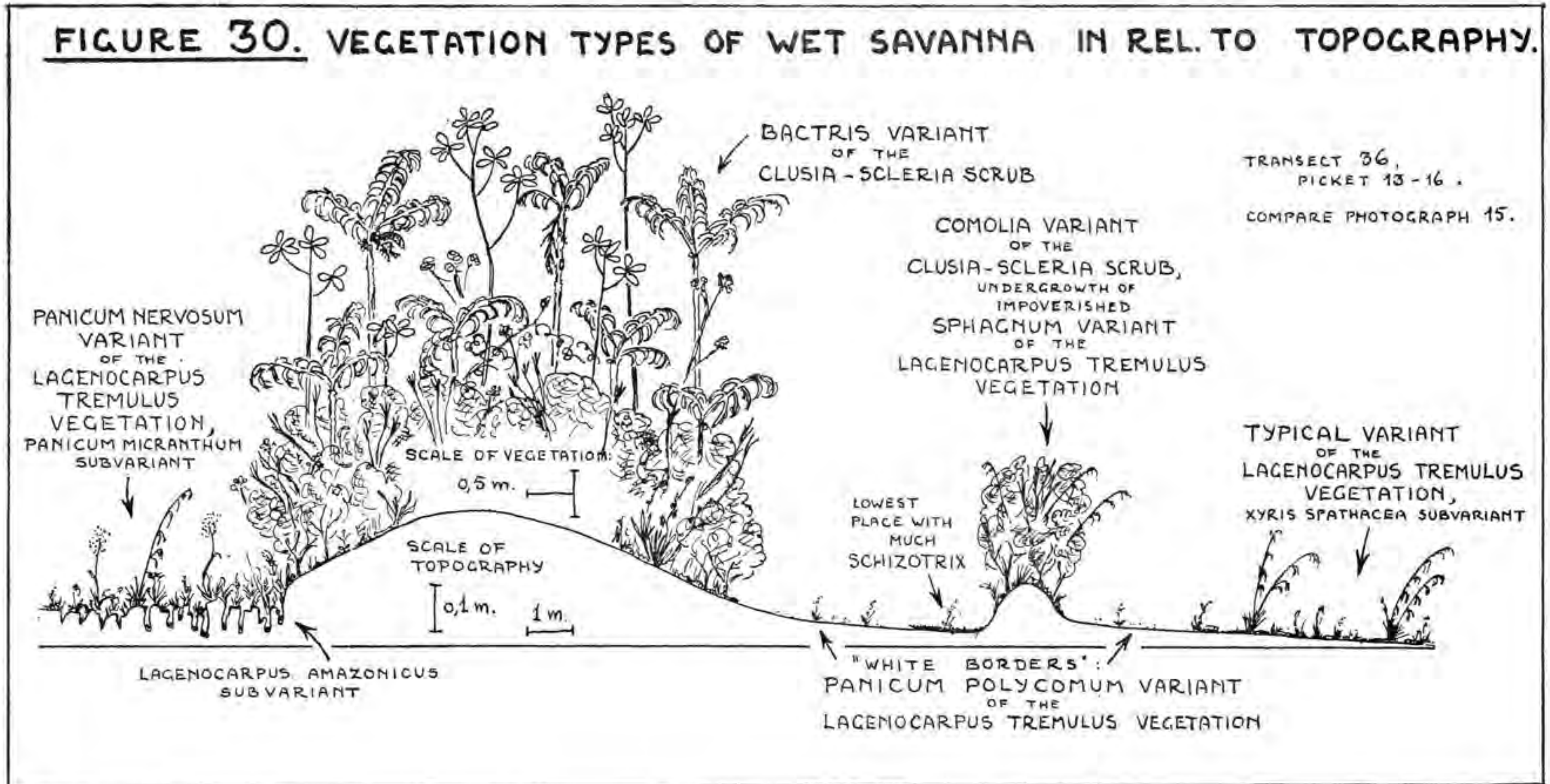


FIGURE 30. VEGETATION TYPES OF WET SAVANNA IN REL. TO TOPOGRAPHY.
BACTRIS VARIANT OF THE CLUSIA - SCLERIA SCRUB
TRANSECT 36, PICKET 13 - 16.
COMPARE PHOTOGRAPH 15.
COMOLIA VARIANT OF THE CLUSIA-SCLERIA SCRUB, UNDERGROWTH OF IMPOVERISHED SPHAGNUM VARIANT OF THE LAGENOCARPUS TREMULUS VEGETATION
PANICUM NERVOSUM VARIANT OF THE LAGENOCARPUS TREMULUS VEGETATION, PANICUM MICRANTHUM SUBVARIANT
SCALE OF VEGETATION:
0,5 m.
SCALE OF TOPOGRAPHY
0,1 m.
1 m.
LOWEST PLACE WITH MUCH SCHIZOTRIX
TYPICAL VARIANT OF THE LAGENOCARPUS TREMULUS VEGETATION, XYRIS SPATHACEA SUBVARIANT
LAGENOCARPUS AMAZONICUS SUBVARIANT
"WHITE BORDERS": PANICUM POLYCOMUM VARIANT OF THE LAGENOCARPUS TREMULUS VEGETATION

amount of groundwater available to the vegetation (cf. III 7.1.). If the depth at which the water-table is found, is less than 40 cm, and in large parts of the area this is actually so for long periods (fig. 18), the structureless sand will be saturated with water. Under such circumstances the roots remain confined to the upper layers of the soil, for roots, as a rule, do not penetrate into the zone beneath the water-table nor in that part of the capillary zone which is continually saturated with water. This was found in experiments with cultivated plants grown in sand that was free of silt and humus (cf. GOEDEWAGEN, 1952).

From time to time extremely dry periods may occur, of which the length may vary considerably in different places (compare the figures given by SCHULZ, 1960, for the rainfall measured during 1957 at Mapane camp and at Republiek, figs. 7 and 9). During such periods the water-table sinks to a deeper level and the surplus of water makes place for a deficit. On account of the fact that their root system does not extend beyond the uppermost layer of the soil, several species can no longer reach the groundwater with the result that the aerial parts wither and die off, sometimes with fatal results to the whole plant. In area 3 I noted at some places a scrub-like vegetation which from a distance looked quite grey. It appeared to represent the *Ternstroemia* facies of the *Comolia* – *Clusia* – *Scleria* scrub, but the about 1.5 m high *Ternstroemia* shrubs were all completely leafless, except for some offshoots arising from the base. They had probably lost their leaves during the severe drought of 1947. *Bactris* stems which had lost their rozette of leaves, were not rare either (photo 15), and it seems probable that this is not always an effect of age, but that it may also be due to drought.

The bushes belonging to the *Clusia* – *Scleria* scrub are always found on slight elevations (fig. 30), which are doubtless somewhat better drained than the surrounding parts. The height of these elevations varies from a few centimetres to 20 centimetres. Whether these elevations were already present before the bushes established themselves at these sites or whether they owe their origin to the development of the bushes, is at present unknown.

As soon as a rain shower of some importance is descending, the wet savanna is flooded, the surplus of water running off along the surface. This, however, does not lead to a strong erosion, as the plain is almost completely level. It is nevertheless not improbable that the micro-relief owes its origin to this factor, which will have continued its action for a very long time.

On the open parts of the savanna the water which runs off exercises an important influence on the vegetation. Its most conspicuous effect are the "white borders" found round bushes (cf. photographs 1, 2 and 15 and fig. 30). When the savanna is nearly horizontal, e.g. in the central part of area 3 (fig. 3), the bushes, which belong here to the *Comolia* variant of the *Clusia* – *Scleria* scrub, are entirely surrounded by such a white border, which in this case is rather narrow. However, where the savanna is somewhat sloping, the white borders are wider, but now they are restricted to the lower side of the bushes, which here represent the *Bactris* variant of the *Clusia* – *Scleria* scrub (transects 36–0 to 40, and 37–0 to 40). These white borders bear a very scanty vegetation, which we have described as the *Panicum polycomum* variant of the *Lagenocarpus tremulus* vegetation. The water which runs off from the elevations on which the bushes are situated, probably washes away part of the seeds which are lying on the sand, and may prevent the development of some other species by its mechanical action. Round the base of the plants often detached fragments of the algal film are found, which indicate by their direction the side where the water did come from. The rest of the detached fragments accumulates against obstacles further away, e.g. against small bushes. This run-off then also explains the circular shape of the white borders on the horizontal part of the savanna and the elliptic shape with the small bush around the upper focus on the slightly sloping part.

The elongated bushes belonging to the *Bactris* variant of the *Clusia* – *Scleria* scrub act at the higher side as a barrier against the water which runs off from the higher up plain. As this water, on account of the absence of differences in height in the direction perpendicular to that in which it is running, can not turn aside it begins to stagnate in front of this barrier, with the result that the soil here assumes a hogwallowed appearance. On such places we find the *Panicum nervosum* variant of the *Lagenocarpus tremulus* vegetation. At those of the above-mentioned *Bactris* bushes, where the difference in level between the bush and the place where the water stagnates, is rather considerable, the hogwallow relief is very strongly developed, and covered with the *Panicum micranthum* subvariant (photo 16). However, immediately against the margin of the bush, where the soil is partly covered with leaf litter, and where it is moreover shaded by the overhanging branches of the shrubs, we find the sciophilous *Lagenocarpus amazonicus* subvariant. Where the bushes are not distinctly elongated, as for instance in the case of the bushes belonging to the typical variant of the *Clusia* – *Scleria* scrub found along transects 10–47 to 52, and 21–6 to 8, and the water does not stagnate so much, and here the hogwallow relief may be entirely absent. The differences in height inside and outside the bushes are also less considerable. Around these bushes the *Lagenocarpus amazonicus* subvariant is the only one that is represented; here it forms a narrow marginal zone which differs conspicuously from the rest of the open savanna by its greater density.

The *Panicum micranthum* variant may also be found in sites which have nothing to do with bushes; in that case too there is an accumulation of water, sometimes accompanied by the development of a hogwallow relief (sites 10–40, and 32–170 and 228).

From what has been said above, we may conclude that there exists a relation between the hydrology and the nature of the vegetation on the one hand, and the development of a hogwallow relief on the other. What in this case is to be regarded as cause and what as the effect, requires further investigation (cf. III 5).

The remainder of the open spaces in the wet savanna is covered by the typical variant of the *Lagenocarpus tremulus* vegetation. The *Xyris spathacea* subvariant of this variant is found on those sites where the surface of the soil remains in reach of the groundwater the whole year round, whereas the *Xyris guianensis* subvariant occurs on sites where during the dry season the surface of the soil lies above the maximum height to which the groundwater may rise by capillarity.

IV 5.1.2. The transition between the wet and the dry savanna

This part of the savanna is characterized by strong fluctuations in the water-table and by the fact that in the rainy season the latter rises almost to the surface and that it may even reach the surface, whereas in the dry season it sinks more or less deep beneath the zone in which the roots are found. These fluctuations of the water-table are shown in fig. 14 for two sites on transect 10, viz. at picket 69 and at picket 55, and should be compared with those at picket 97, which shows the fluctuations in the dry savanna. As on transect 10, the high position of the water-table is due to a depression in the surface relief (fig. 19); the contrast is not so great here as in the savannas found in area 3, where the fluctuations of the water-table are larger (figs. 17 and 18). The small tracts of "dry savanna" that are found in this area, are all of this transitional type; as they do not rise above the surrounding part of the savanna, they receive, apart from rain, a continuous lateral supply of water; during the dry season, on the other hand, they are strongly drained.

The typical vegetation types of this transitional region are the *Rhynchospora tenuis* vegetation and bushes belonging to the *Ilex* variant of the *Clusia* – *Scleria* scrub. By charting the vegetation along transect 10 between the pickets 64 and 84, data were obtained which I will discuss here in some detail; they indicate that each species reacts in its own way on differences in moisture conditions in the zone in which its roots are found. In fig. 31 A the changes in the water-table are illustrated in two maps based on the measurements at two days, the one at the end of the short dry period, and the other when the long rainy season had passed its maximum. In both maps depth-lines of the water-table have been drawn for intervals of 25 cm. In fig. 31 B and C are shown the boundary lines of the areas occupied by various species of plants some of which have their main distribution in the dry savanna and others in the wet savanna. Comparing fig. 31 A with fig. 31 B and C, it appears that there is on the whole a high degree of coincidence between certain boundary lines indicating the position of the water-table and those indicating the utmost limit of the area occupied by these species. This,

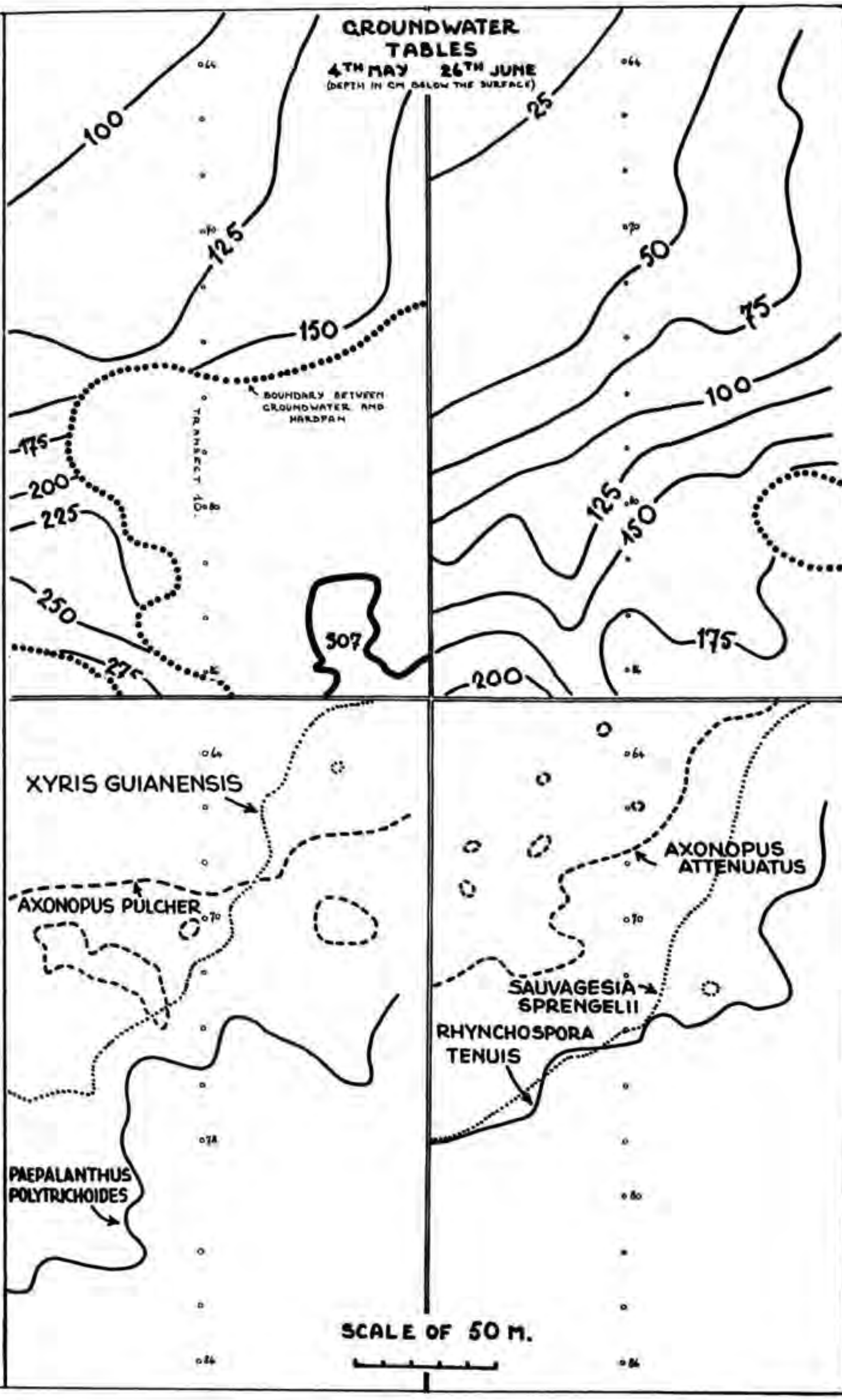


FIGURE 31. DISTRIBUTION LIMITS IN RELATION TO DEPTH OF GROUNDWATER TABLE, (COMPARE FIGURE 6) MAPPED OUT AT THE 4-HA-INVESTIGATION PLOT ROUND SITE 10-80.

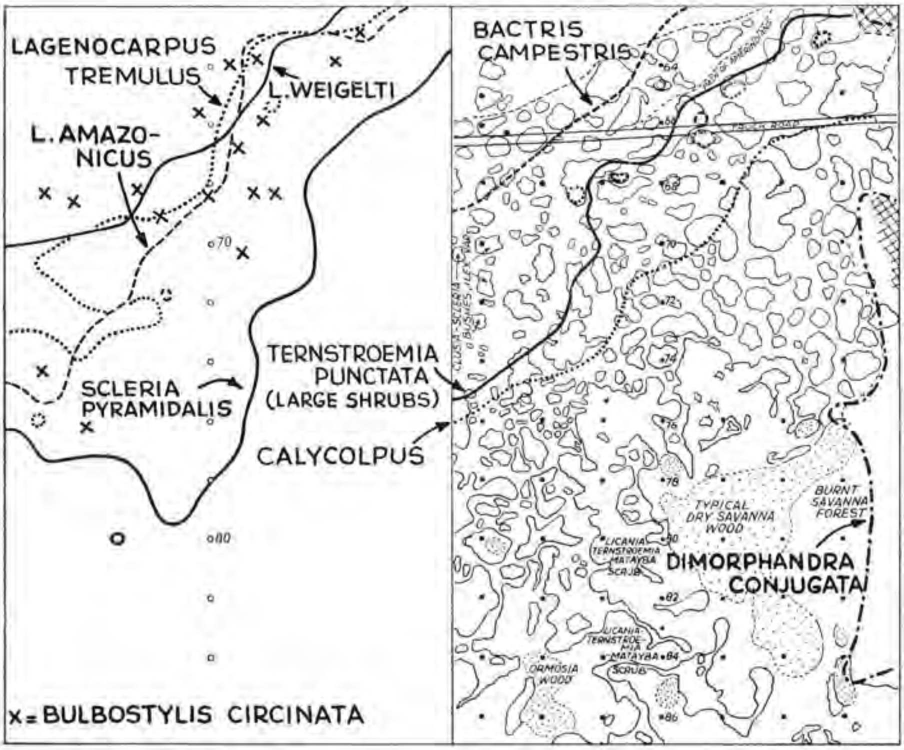


Fig. 31C. Compare left page, where the upper half is A and the lower half B.

however, does not apply to the boundary lines of *Dimorphandra conjugata* and *Axonopus pulcher*. The ecological requirements of *Dimorphandra* will be discussed further on (IV 5.2.3.), and with reference to *Axonopus*, which occurs sporadically in the marginal zone around the bushes on the wet savanna and also in the *Rhynchospora tenuis* vegetation, we may perhaps assume that it reached these places as a result of the construction of the truckroad which runs more or less parallel to the borderline of the area occupied by this species. An argument in favour of this assumption is that this species is found also in the *Trachypogon* vegetation, of which it cannot be doubted that its development is strongly favoured by human activity.

In the vicinity of the line where in the rainy season the water-table is found at a depth of 50 cm, which implies that the zone of capillary water reaches the surface, some species of the dry savanna, viz. *Ternstroemia punctata* (large shrubs), *Calycolpus revolutus*, *Axonopus attenuatus* and *Lagenocarpus weigelti*, as well as some species of the wet savanna, viz. *Sauvagesia sprengelii*, *Xyris guianensis* and *Lagenocarpus amazonicus* reach the limit of their area of distribution. *Bactris* can only attain maturity in a soil with a still higher water-table; at the spots indicated in fig. 31 C outside the boundary line of its area it is found only in the form of juvenile plants. *Scleria pyramidalis* and *Rhynchospora tenuis*, on the other hand, occur already in places where the water-table is found at a somewhat greater depth, and *Paepalanthus polytrichoides* may be regarded as a reliable indicator of the dry savanna (the incurvation of the boundary line near picket 82 is due to the fact that *Paepalanthus* is unable to thrive in the dense shade of the scrub found here). In no satisfactory way, however, can be explained how the position of the groundwater can be of ecological significance for *Paepalanthus* as the water-table near the boundary line of its area of distribution on the side of the wet savanna is found in the rainy season at a depth of about 1 m. It might be that, after very heavy rains, the groundwater rises to a sufficient height to enable the seeds of this plant to germinate; as soon as they are rooted, the plants may maintain themselves for several years; in fact, they may probably reach an age of ten or more years.

Finally I should like to draw attention to the fact that the boundary lines of the areas occupied by the three *Lagenocarpus* species largely coincide with definite isohypses. It will hardly be possible to find species which possess in this respect a higher diagnostic value than these three.

The number of species restricted to the transitional region is apparently very small. *Bulbostylis circinata* and *Stylosanthes angustifolia* are good examples; *Bulbostylis junciformis* and *Polygala galioides* may also belong to this group, but because they are comparatively rare, this is difficult to say.

The different vegetation types owe their origin to the simultaneous action of various factors that are of importance to the life of the plants. The dry savanna wood at site 10–80 is surrounded by the *Clusia* facies of the *Licania* variant of the *Ternstroemia* – *Matayba* scrub. Towards the North-west this continuous scrub zone is broken up into bushes; especially *Licania* and *Ternstroemia* occur in the form of large single shrubs which may reach a height of 3 m and which grow often so closely together that they touch each other; *Clusia* remains in the undergrowth and forms the nucleus of the denser bushes. Nearer to the wet savanna and on the latter itself *Clusia* maintains itself in this position, but *Calycolpus* and *Myrcia* disappear from the undergrowth of the bushes, where, in the meantime, *Scleria* has made its appearance. *Matayba* has also disappeared, and *Ternstroemia* and *Pagamea capitata* change their aspect; instead of large shrubs or small trees they appear now as small, sparsely ramified shrubs. *Licania*, on the other hand, does not change its habit, and together with *Ilex* and *Conomorpha* it overtops the *Clusia* shrubs; this means that the *Licania* variant of the *Ternstroemia* – *Matayba* scrub has passed into the *Ilex* variant of the *Clusia* – *Scleria* scrub. Subsequently the last elements of the dry savanna vegetation disappear, and *Bactris* comes to the fore; in this way the *Ilex* variant is replaced by the typical variant. At the same time the *Axonopus attenuatus* – *Lagenocarpus weigelti* vegetation, which occurred along the margin of the *Licania* variant of the *Ternstroemia* – *Matayba* scrub and in open spots in the latter, is replaced in the zone around the dense *Clusia* bushes by the *Lagenocarpus amazonicus* variant of the *Rhynchospora tenuis* vegetation; this happens more or less at the place where *Ternstroemia* begins to show a marked decrease in vitality.

In the open spaces the change in the composition of the vegetation proceeds in a similar way. In the *Bulbostylis conifera* vegetation, which is found in the open stretches at the sites 10–88 and 10–86, *Paepalanthus* already makes its appearance. At a distance of 50 m follow *Xyris guianensis*, *Sauvagesia*, *Rhynchospora tenuis* and *Bulbostylis circinata*. This means that the *Bulbostylis conifera* vegetation passes into the *Bulbostylis conifera* variant of the *Rhynchospora tenuis* vegetation. *Bulbostylis conifera* remains rather abundant, although gradually less so, but we have to go on for about 200 m, viz. to site 10–62, before it disappears; the border of its area coincides more or less with the line at which *Bactris* makes its appearance.

The same regularity in the sequence of the species which we met in passing from the dry part of area 1 to the wet part, was found also in the areas 2 and 3; this may be learned from the description of the various vegetation types (IV 3.1.9.; IV 3.2.3.2.; IV 3.2.4.2.; IV 3.2.4.3.; IV 3.2.5.1., and IV 4.4.).

IV 5.1.3. The dry savanna

Here the water-table is found at a considerable depth, because on account of differences in relief the drainage is more effective (cf. III 1. and III 7.2.). For the herbs the groundwater is out of reach, and so it is probably also for most, and perhaps even for all woody plants occurring in the dry savanna. The latter are provided with an extensive root system, which is found at a depth of about 10 cm below the surface, and which absorbs the percolating rain water (photographs 23 and 24, cf. III 4.1.). However, as soon as this water has passed the root mat, it is lost to the plants. On the other hand, of some of the species occurring in the forests that cover the slopes towards the creeks, we may assume that they profit from the groundwater, because in these forests thick roots have been found to a depth of 3 m.

On the dry south-eastern savanna in area 1 *Swartzia* may perhaps profit by the presence of a clay subsoil at a depth of a few metres, as this puts a stop to the passage of the rain water (cf. IV 3.1.9.). In the transition zone between sand and clay dark spots of organic origin were noted, which might represent the remains of roots, but this point requires further investigation (cf. IV 2.3.).

Summarizing we may say that the distribution and the vitality of the species occurring on the dry savanna is not governed by the position and the fluctuations of the water-table, but by other factors. Apart from the to some extent passing influence of fires which will be discussed in the next section, the nature of the factors which determine the presence and the abundance of these species is still unknown. Here as elsewhere the various species must possess the faculty to tolerate the presence of other ones and the faculty to compete with them, but with regard to the differences in the environment which enable them to use these faculties to the best of their power, we are in this case as yet completely in the dark.

IV 5.2. *The influence on the vegetation exercised by fires*

When preparing grounds for the growing of food plants by felling the trees, the Amerindians get rid of the branches and leaves by burning them. This is usually done in the dry season, and it sometimes happens that the flames attack the rest of the forest, and that the fire spreads over a large area. Moreover, occasionally the *Dimorphandra* scrub is set on fire, in which case the twigs and leaves are consumed by the flames, but the older woody parts are spared, and are afterwards felled to be used as fire-wood. Sometimes fire is set also to the wet savanna; this is done to facilitate the capture of tortoises. Finally the *Trachypogon plumosus* vegetation is regularly burnt down, usually once a year, because "the high grass is so troublesome". Lighting a fire for ceremonial purposes is, at least in the region round Jodensavanne, an unknown practice; so, at least, I was told by one of the inhabitants of Pierre-kondre.

When describing the various types of vegetation we have already more than once drawn attention to the effects of fires. At this place we will enter somewhat deeper into this problem.

IV 5.2.1. The effects of fires on the wet savanna

Especially in the north-eastern part of area 3 everywhere on the wet savanna indications of fires are met. Because of the presence of the two centuries old "cordonpad" (the cordon path, cf. I 5.8.) the influence of man here was stronger than elsewhere, and it is in the neighbourhood of this old road that the tracts along which the surface water runs off appear in the form of open stretches studded with *Mauritia* palms. The recurring fires not only prevent the regeneration of the forest in these tracts, but also attack the margins of the gallery forest (cf. IV 2.3.; photo 14).

The general aspect of the wet savanna too is changed by the fires (see the aerial photograph of the region shown in fig. 2D). The *Clusia* – *Scleria* scrub can no longer maintain itself, and the small elevations on which the bushes were standing, often with a surface of less than 1 sq. metre, are now occupied by the *Licania* subvariant of the *Panicum nervosum* – *Lagenocarpus tremulus* vegetation, which consists of less than 0.5 m high shrublets of *Licania*, *Marlierea* and *Tetracera*, far overtopped by the panicles of *Panicum* and *Lagenocarpus*. Where the flat parts are somewhat better drained than they usually are (cf. IV 5.1.2. and fig. 18), this vegetation may cover larger stretches. One of its most striking features is in this case the abundance of *Axonopus pulcher* and *Mesosetum*, and the presence of *Trachypogon*, three species which determine the aspect of the *Trachypogon* vegetation of the dry savanna. That *Axonopus* and *Trachypogon* can maintain themselves on this part of the wet savanna, is in my opinion due to the recurrent fires. Under normal circumstances they would not be able to compete with the typical representatives of the wet-savanna flora, simply because the environment is too wet for them. At a lower level the *Licania* subvariant of the *Panicum nervosum* variant is replaced by the *Panicum micranthum* subvariant.

Another vegetation type that was found on better drained parts between the drainage tracts is the *Leptocoryphium* facies of the typical *Rhynchospora tenuis* vegetation. The position of this vegetation, which contains but a comparatively small number of species, is rather difficult to determine. It may locally contain an admixture of elements belonging to the *Panicum nervosum* variant of the *Lagenocarpus tremulus* vegetation. The number of records made of this vegetation type, which belongs to those whose development is influenced by fires, is too small to allow a definite conclusion.

Where the surface becomes more level we find the *Rhynchospora barbata* subvariant of the typical *Lagenocarpus tremulus* vegetation. This subvariant may be regarded as a typical fire-induced modification of the typical variant. When dealing with this vegetation type I have already drawn attention to the destructive influence which fires exercise on the Xyridaceae, Eriocaulaceae and Dicotyledones of the typical variant. Grasses like *Paspalum pulchellum* and *Leptocoryphium*, on the other hand, are not killed by a fire; on the contrary, they put forth new shoots which leads to a mass production of inflorescences. This is still more remarkable as they are hardly ever seen in flower in parts of the savanna that did not suffer from a fire (IV 4.5.).

These vegetation types, whose aberrant composition is due to the influence of fires, were seen exclusively along transect 32 between the pickets 184 and 260. Near picket 184 bushes belonging to the *Swartzia – Ormosia* variant of the wet savanna wood and to the *Bactris* variant of the *Clusia – Scleria* scrub appeared to form a barrier against the spreading of the fires in a southern direction; the influence of the fires remained confined in this way to the north-eastern part of the savanna.

From what has been said above we may conclude that fires may cause a shift in the position of the various vegetation types, that they cause a decrease in the number of their species and change the proportion in which the remaining species are represented.

IV 5.2.2. The effects of fires on the dry savanna

On the dry savanna the *Trachypogon plumosus* vegetation is the one which is most markedly influenced by fires. It owes not only its origin to fires, but at least in the case of the typical variant, fires are also required to maintain it. In the absence of fires this vegetation type passes via the *Bulbostylis conifera* variant into the *Bulbostylis conifera* vegetation, at least when it borders on a part of the savanna which is covered by this type of vegetation. When this is not so, i.e. when the *Trachypogon plumosus* vegetation covers but a small patch and is surrounded by wood, it is not excluded that it will in the end be replaced by the latter.

The *Trachypogon plumosus* vegetation south of Redidoti belongs entirely to the typical variant (fig. 21). This vegetation contains several "weeds" which were not found in any of the other types of savanne vegetation. The grasses *Trachypogon*, *Axonopus pulcher* and *Mesosetum* are dominant and determine its aspect; it is therefore a typical "grass savanna". In the centre of this savanna a bush is found which represents the *Inga* variant of the dry savanna wood; part of it is well-developed, another part strongly damaged by fire; it has an *Axonopus attenuatus – Lagenocarpus weigelti* vegetation as undergrowth in those places where the canopy is more open and where larger gaps are present in the latter. The smaller bushes that are seen here and there, often contain species like *Astrocaryum segregatum*, *Anacardium occidentale*, and *Himatanthus articulata*, which are typical for the secondary forest, and also the lower bushes of *Miconia albicans* are entirely different in composition from the bushes belonging to the *Ternstroemia – Matayba* scrub. This savanna is entirely surrounded by secondary forest and it can not be doubted that originally the whole neighbourhood consisted of savanna forest, and that the latter was destroyed by fire. The regeneration of this forest was made impossible by the ever recurring fires. This follows from the fact that in several of the savanna forests of which records were made, indications were found that they had recovered after a fire. We may assume therefore that a regeneration of the burned savanna forest would have been possible too on the site of this savanna.

The same situation is found in the grass savannas along the margin of the terrace, e.g. along the transects 11–8 to 26 and 12–20 to 32. Two generations ago the savanna along transect 12 was still inhabited. Here too we see remains of the savanna wood in the form of bushes belonging to the *Inga* variant of the dry savanna wood, but also bushes consisting of species belonging to the secondary forest. Here fires are more rare, with the result that *Bulbostylis conifera*, *Cassia ramosa* and *Lagenocarpus weigelti* succeeded once more in establishing themselves, whereas several of the "weeds" disappeared. Where this vegetation borders on the open savanna, it passes into the *Axonopus pulcher* variant of the *Bulbostylis conifera* vegetation.

We have already dealt at some length with the influence of fires on the secondary forests and on the dry savanna forest (IV 2.3.), on the bushes representing the dry savanna wood (IV 3.1.2.), on the *Dimorphandra* scrub (IV 3.2.3.) and on the *Licania* variant of the *Ternstroemia – Matayba* scrub (IV 3.2.4.3.). At site 17–6, where ten years ago the forest, probably consisting of the *Dimorphandra* facies of the *Cupania* variant of the dry savanna forest and of the typical variant of the dry savanna wood, was destroyed by a fire, the "pioneer vegetation" still bore an irregular character, and contained several elements which one would not have expected here, e.g. *Vismia cayennensis*, *Byrsonima coriacea*, *Xylopia* spec., *Amajoua guianensis*, *Miconia lepidota* and *Cecropia* spec.; however, most of the specimens by which they were represented, were already dead. Between the shrubs the *Pteridium* facies of the *Axonopus attenuatus – Lagenocarpus weigelti* vegetation had established itself.

Along transect 14 between the pickets 0 and 16 the influence exercised by a past fire manifested itself clearly by the presence of the *Pteridium* facies of the *Axonopus – Lagenocarpus* vegetation, although the composition of the bushes appeared to be already more or less stabilized; elements not belonging to the savanna vegetation proper had become rare, and bushes and scrub had already established themselves to some extent, e.g. in the form of an incomplete stage of the *Ternstroemia – Matayba* scrub (IV 3.2.4.4.) and of the *Clusia* facies of the *Licania* variant of this kind of scrub (IV 3.2.4.3.). The adjoining dry savanna wood (transect 14–16 to 26) had also been partly destroyed by fire. The composition of the shrub vegetation was not yet fully stabilized, because large parts of it were not fully closed (IV 3.1.2.). Much longer ago – according to the wood-expert HELSTONE in 1918 – the other part of this wood had also been burnt down, but here it had completely regenerated and was almost indistinguishable from other woods of this type; a sporadical *Pteridium* frond in the undergrowth was the only evidence of the changes through which it had passed.

The vegetation which I described as the *Licania* variant of the *Ternstroemia – Matayba* scrub (IV 3.2.4.3.) is probably intermediate between the incomplete stage described above and the completely regenerated scrub. It is a vegetation consisting of scattered higher clumps in the midst of low shrubs. If this interpretation is correct, we may assume that the savanna scrub, just like the savanna wood, regains its former composition and aspect after a fire.

The intensity of the fire is also an important factor, for it determines the extent to which the vegetation is destroyed, i.e. how much of the aerial as well as of the underground parts may survive. It does not seem impossible that the presence of isolated bushes on a savanna is to be ascribed to the fact that the original vegetation was not completely destroyed, but that in a few spots one or a few of the shrubs were still sufficiently viable and recovered; these spots subsequently functioned as "regeneration centres". Here and in their immediate vicinity the chance for a seedling to survive was far better than it was on the completely bare parts of the savanna, and in this way round these centres bushes developed. That the open parts between the bushes may persist for a very long time, was seen in the *Dimorphandra* scrub (cf. IV 3.2.3.1.). Where the scrub does not recover, an *Axonopus* – *Lagenocarpus* vegetation is found, or in more extensive stretches a *Bulbostylis conifera* vegetation studded with a few *Ternstroemia* or *Licania* shrubs. In such a way the south-eastern savanna in area 1 (along transects 17–80 to 120, and 16–14 to 44) may have arisen. The presence of numerous bushes with comparatively large trees belonging to species found in the forest to the North-east of the savanna, as well as the presence of a sharply demarcated, completely closed forest margin to the South suggest that this savanna owes its origin to the destruction of the forest which originally must have occupied its place, a destruction which can only have been effected by a severe fire. The decaying stems which occasionally are found under the litter of the bushes, are perhaps the last witnesses of this original forest. A vegetation like that of this south-eastern savanna does not seem to offer the fires much chance to spread; even where it bordered on the *Trachypogon plumosus* savanna which is regularly set on fire, I found no indications of recent fires.

Do the bushes on the savanna always owe their origin to fires or is it possible that they arise also as the result of a succession in which fires play no part? It seems to me that the latter possibility is not excluded. There appears to be no reason to assume that the edaphically determined succession "savanna forest" → "savanna wood" → "savanna scrub" should end with the latter, and that it might not proceed to "bushes of savanna scrub". This succession would be accelerated by fires, but the latter may, as we have seen, also change the composition of the bushes by creating conditions which favour the development of some of the species and by changing in this way the proportion in which the various species are represented.

On the dry savanna the number of species in the vegetations does not decrease under the influence of fires, but it may occasionally even be increased, e.g. in the *Trachypogon plumosus* vegetation and in the *Axonopus* – *Lagenocarpus* vegetation by the appearance of "weeds", and in the pioneer vegetations by the presence of "foreign" elements, i.e. of species which belong to a different vegetation type. Just as on the wet savanna, the ratio between the number of individuals by which the various species are represented in the vegetation types, and the way in which these types are distributed over the savanna, undergo changes under the influence of fires; moreover, some of the vegetation types found on the dry savanna, e.g. the *Trachypogon plumosus* vegetation, can maintain themselves exclusively in parts which are more or less regularly set on fire.

IV 5.2.3. The effects of fires on the Dimorphandra scrub

The influence of fires on the *Dimorphandra* scrub has already been dealt with in IV 3.2.3. On account of the fact that *Dimorphandra* recovers more easily after a fire than most other species, the vegetation type in which this species originally occurred will have passed into a new type of vegetation in which this species is the only dominant that is left; this is the typical *Dimorphandra* scrub. The circumstance that this kind of scrub is found in the immediate vicinity of the *Dimorphandra* facies of the dry savanna forest (fig. 21), makes it probable that it developed out of the latter. If *Dimorphandra* had not been present in the original vegetation, it would not have been present in the scrub which took the latter's place; in that case this would probably have been a savanna studded with bushes belonging to one of the variants of the *Ternstroemia* – *Matayba* scrub.

Although *Dimorphandra* is found also in the wet savanna forest, viz. in the *Dimorphandra* variant of the latter, *Dimorphandra* scrub develops only after the destruction by fire of the dry savanna wood, i.e. on the dry savanna. On the wet savanna it is apparently unable to compete with the other species. This is well seen along transect 21 (figs. 21 and 10B). Some metres from picket 0 (=20–54) the *Dimorphandra* scrub borders on the wet savanna (fig. 26); up to picket 13 we find wet savanna with bushes belonging to the typical variant of the *Clusia* – *Scleria* scrub and on the open stretches with the typical variant of the *Lagenocarpus tremulus* vegetation. Between pickets 13 and 19 the drainage is somewhat improved because here we are nearer to the creek and especially because the surface is somewhat less sloping, with the result that the water-table remains in the rainy season at a depth of at least 10 cm. This stretch is covered by *Dimorphandra* wood. At picket 19 the latter merges into creek forest with a very peaty soil. Some tens of metres North-east of transect 21–13 to 19, the *Dimorphandra* scrub borders on the savanna forest. At this place the soil is still better drained because we are here in the axil between two creeks.

In area 3 also *Dimorphandra* scrub and *Dimorphandra* wood are found only in those parts where in the rainy season the upper layer of the soil is somewhat better drained than it is in the wet savanna. Such parts are found in the axils between the creeks, and in places where the better drainage rests on a similar combination of factors as found along transect 21 between the pickets 13 and 19 (see also III 7.2.). However, whether the presence of the *Dimorphandra* scrub at these places may be ascribed to destruction of the original vegetation by fire, remains unknown. The dominance of *Dimorphandra* in such marginal areas of the dry savanna may be due to a stronger competing ability resulting in the replacement or prevention of colonization of species at the limit of their potential area.

IV 5.2.4. Conclusion

My observations corroborate the view that the various vegetations found in savannas on white sands are edaphically determined and that they are more or less strongly influenced by fires (cf. the review of the literature given in I 7). However, in order to determine the influence exercised by fires more accurately, a study of the succession will have to be carried out.

IV 6. The geographic distribution of the savanna types found on white sands

The literature on the savannas found in Suriname has been discussed in I 5. Cohen and Van der Eyk (1953) have mapped the savannas belonging to the types "Zanderij" and "Cassipora", mainly with the aid of aerial photographs. The type "Zanderij" comprises the savannas found on humid to wet, the type "Cassipora" those on dry white sands.

As I had no opportunity to test the comprehensiveness of the classification of the vegetation types at which I arrived by my studies in the vicinity of Jodensavanna, by direct observations in other areas, I had to confine myself to a study by means of areial photographs. On these photographs, covering the whole savanna belt of Suriname, I compared the stereoscopic images of some of the savannas belonging to the types "Zanderij" and "Cassipora". This study convinced me that the series of vegetation types which I found near Jodensavanna, do not represent the whole range of types that are found in Suriname. However, they may indeed be regarded as more or less representative for the savanna area between the Commewijne River and the Saramacca River, though it must be added that the physiognomy of the savannas near Zanderij is much more strongly affected by fire. Outside this region mainly savannas of the "Cassipora type" are found. The aerial aspect of these vegetations, e.g. in the southernmost part of the savanna near the Corantyne River, is sometimes very similar to that of certain vegetation types occurring in the vicinity of Jodensavanna. There are, however, also strongly deviating types, e.g. a savanna covered by a very dense scrub, which on the aerial photographs looks quite different from anything I have seen near Jodensavanne (southern Tibiti savanna; savanna to the West of the Nickerie River; cf. aerial photograph from the last-mentioned area on p. 23 of the publication by Van Dillewijn, 1957). The topography too is very different here from what was found East of the Saramacca River. We may safely assume that our knowledge of the floristic composition and of the ecology of the savanna vegetations would be considerably extended by field-work carried out at these places.

With regard to the occurrence of white-sand savannas outside Suriname, we may state that such vegetations have often been mentioned in the literature, but that detailed descriptions are lacking. Bouillenne (1930) gave several photographs (nos. 631–642) of the "Campina rana" near Porto de Möz in the Amazonian region, but they are not accompanied by detailed descriptions. From their general aspect and from the letterpress relating to them we may conclude that they are very similar to the savannas found in area 3 near Jodensavanne. This interpretation finds support in a remark made by Aubréville (1958), who, after mentioning the "forêts basses et fourrés amazoniens sur sables blancs" (= evergreen caatinga) which according to the short description seem to resemble our dry savanna woods and dry savanna scrub and may even be identical with them, proceeds "La flore des fourrés se retrouve conservée sur les pourtours de ces savanes (appellées "campinas") au contact de la forêt et d'évidents témoins d'incendies sont visible dans les campinas les plus récents", which means that these "campinas" show a strong resemblance to the vegetation found in our area 3. The "forêts basses et fourrés sur sables blancs" are found also in other parts of the region of the Amazon and its tributaries. Guppy (1958) gives a description of the discovery of a small, completely isolated white-sand savanna in the region round the sources of the Trombetas near the Serra Irikoumé.

Fanshawe (1952) gives a description of the "*Humiria floribunda* (Muri) Community", the vegetation type found on the white sands in the eastern district of British Guiana. This vegetation resembles that of a dry savanna studded with bushes, for: "Muri consists of roughly circular patches of scrubby vegetation separated by bare or sparsely grassed sand. The centre of each circle is occupied by one or two trees of *Clusia nemorosa*, 15–20 ft tall, surrounded by a ring of shrubs (*Pagamea capitata*, *P. guianensis*, *Retiniphyllum schomburgkii*, *Ternstroemia punctata* var. *revoluta* and *Byrsonima crassifolia*) 6–8 ft high, with outer belt of semi-prostrate *Humiria floribunda* var. *guianensis*". Some of the wood types described by FANSHAWE are probably related to types found near Jodensavanne, e.g. the *Tabebuia insignis* facies of the *Clusia-Tabebuia* assemblage with our creek savanna wood. It is rather unfortunate that a detailed map is lacking in his paper.

BLEAKLEY (1957) published a geological map, scale 1:150,000, of the coastal region of British Guiana based on aerial photographs as well as on observations in situ. On this map the vegetation is indicated too, and in the accompanying letterpress some information on this topic is given. The map includes the northern part of the "Berbice or White Sand Formation". Especially between the Courantyne River and the Berbice River "Muri" (= *Humiria floribunda*) and "Dacama" (= *Dimorphandra*) scrub is found here; between the Berbice River and the Demerara River the presence of "scrub with high bush along the creeks" is mentioned; this probably agrees with our wet savanna. The description of the Pomeroon area to the West of the Essequibo River suggests a vegetation similar to that of our area 1 near Jodensavanne, but this is for the moment no more than a supposition.

On the white sands in French Guiana open savannas are found only in the neighbourhood of settlements, but elsewhere these sands are covered by "une végétation plus rabougrie, mais qui reste dense" (BOYÉ, 1960), presumably a kind of savanna scrub.

Apart from the white sands among the mainly pleistocene sediments we know also bleached sands belonging to younger formations, e.g. those of the ridges deposited along former coast lines, as well as to older ones, for instance, the sands developed from the sandstone of the Roraima formation. The vegetation types found on these sands are sometimes very similar to those described from the pleistocene white sands, but detailed data are not yet available.

Indirectly some indications with regard to the distribution of the vegetation types described in this treatise might be obtained by studying the distribution of the species that are represented in them. Data on the distribution of these species may be found in floras and in written accounts of the vegetation, and furthermore on the labels of the specimens preserved in herbaria. In this way we also may obtain some idea of the ecological amplitude of the various species. The savannas found in the savanna belt of Suriname on other soils, have been investigated by Mr. J. VAN DONSELAAR. In his treatment he intends to apply this indirect method and will extend it to the vegetation found on the white sands. The results of his study will also be published in the series "The Vegetation of Suriname".

Summarizing, we may say that white-sand savannas are found in Suriname, British Guiana and the northern part of Brasil, but that their distribution is still imperfectly known, and that analytical vegetation descriptions are almost entirely lacking.

CHAPTER V

RECAPITULATION OF THE MAIN CONCLUSIONS

V 1. General remarks

(The figures enclosed in brackets indicate the chapter and section and when necessary the subsection where the subject has been dealt with).

Low and often open shrub vegetations are found in Guiana on soils consisting of coarse white sand. Such vegetations are known in various parts of this region by different names; in Suriname they are called "sabana", in British Guiana "muri-muri", and in Brasil (evergreen) "caatinga" and "campina rana". Attention was drawn to the fact that in this work the term "savanna" is used in a wider sense than in that of Beard, because it comprises here also various shrub vegetations, whereas Beard restricts its use to vegetations in which the herb stratum predominates. Although the white-sand savanna has been mentioned by several explorers, visited by many botanists and mapped by foresters, it has never been analysed by the aid of the methods elaborated by the plant sociologists (I 3–5; IV 6).

The aim of this investigation was to describe the vegetation types found in some typical savannas, and to consider the ecological factors by which the distribution of these types is governed. To this end a complex of savannas situated East of the Suriname River near Jodensavanne was selected. This complex is situated on a plateau formed by continental sediments consisting of rather coarse to very coarse sands (III 5.4.) and attaining an altitude of 30 m above sea level. The drainage pattern of this plateau is to a large extent determined by the relief of the bed-rock. The latter consists mainly of gneiss belonging to the so-called "Caribic granite" or "Granite 3" (III 2.8.). In the north-eastern part, where the packet of covering sands is about 20 m thick, the creeks are not deeply incised, and here we find, as a rule, wet savanna, i.e. a savanna in which in the rainy season the groundwater reaches the surface. In the southern and south-western part the bed-rock is found at a depth of 4 to 8 m, and here the drainage is determined by the presence of deeply incised creeks which discharge either in the Cassipora Creek or in the Suriname River; for this reason we meet here a dry savanna. In this part, besides white sand, occasionally red sand is seen, whereas on the slopes and at the bottom of the river and creek valleys heavier colluvial and alluvial soils are present (III 1). Along the creeks in the wet savanna and on the slopes and at the bottom of the river and creek valleys in the dry savanna area woods and forests are found. The remaining part of the area, the "true" savanna, is covered by scrub or studded with more or less crowded bushes. The space between these bushes is covered by a vegetation consisting of herbs and sub-shrubs which is rather open on the dry savanna and less so on the wet savanna (I 1).

After a reconnaissance of the area by means of aerial photographs as well as by direct observation, a system of transects was cut through it with a total length of approximately 30 km. By means of this complex of transects as much different vegetation types as possible were made accessible (II 1.). Along these transects records of the vegetation were made according to the methods elaborated by the French-Swiss school of plant sociologists, but with regard to the adjoining woods and forests we contented ourselves with a list of species. In the vegetation as a whole some "main vegetation types" were distinguished, and in each of these main types some "variants", "subvariants" and "facies". The elaboration of a classification according to the synsystematic scheme of the French-Swiss school would, in our opinion, have been premature.

The classification of the vegetation types is expounded in table 2 (forests and woods), table 3 (scrub and bushes) and table 4 (one-layered vegetations) (II 3).

The structure and composition of the soil were studied by means of bore holes made with an auger as well as in pits. Special attention was paid to the fluctuations of the water-table. The transects were levelled by a geometer (II 2).

V 2. Pedological aspects

A 1 to 2 m thick upper layer of the white-sand soils consists of rather coarse, but moderately assorted sand (average diameter of the grains about 0.3 mm) passing into, as a rule, badly or not at all assorted coarse to very coarse sand with an average diameter of the grains varying between 0.5 and 1.3 mm. According to the type of vegetation the amount of organic matter varies in the upper layer between 0.05 and 4 per cent, whereas the thickness of this layer, which shows a red-brown colour, varies between 0.4 and 2.5 m. Below this layer the sand is perfectly white. Under woods and under scrub we occasionally find in the lower part of the zone in which the water-table fluctuates a layer containing humus and accordingly showing a brown colour: this layer may reach a thickness of some tens of centimetres (III 2).

In the uppermost part of the slopes towards the river valley locally red sands are found. The size of the grains does not differ from that seen in the white sand; they owe their colour to a coating with iron compounds. With increasing depth the colour of the sand becomes more intense. However, at a depth of about 4.5 m, i.e. in the zone just above the bedrock, a "pale" layer is found which may be white, light brown or orange. The red sands differ from the white ones especially by their higher iron and aluminum content (III 3.1.2.).

Between the white and the red sand we find a zone of transition which, however, is but a few metres wide. When the adjoining red sand bears a grass savanna, an accumulation of humus and of compounds of iron and aluminum was observed at a depth of about 1 m (III 3.3.). This has been formed after the disappearance of the wood in a recent past and is to be regarded as a kind of podzolization. In contrast to what is usually observed in tropical regions, it is independent of the groundwater (III 6).

The sharpness of the boundary line between the red and the white sands may, in my opinion, be explained by assuming that on the originally red sands, on account of differences in texture, different vegetations developed. The forest on the slightly loamy soils has the tendency to invade the adjoining lighter soil. This may result in a sharp boundary line with the rest of the vegetation, partly perhaps under the influence of fires. The soil below the more open vegetation would have been bleached by the more rapid leaching, whereas the sand beneath the invading forest retained its red colour; this would account for the sharpness of the boundary line between the red and the white sand (III 6.).

In parts where the bed-rock is found at a great depth, in various places an indurated, usually dark coffee-brown layer was observed. An investigation carried out with the aid of borings made at a short distance from each other, showed that this layer is separated from the white sand which elsewhere is found at the same depth by a sharp almost vertical border (III 2.2.). Where the bed-rock was found nearer to the surface, it appeared to be covered in various places by a layer of loamy sand with a thickness of some tens of centimetres; this layer was coloured light yellow to dark brown by humus and iron compounds (III 2.4.). As it appeared that these illuvial layers show no relation to the present groundwater regime, the geogenesis of these soils was studied by means of estimations of the grain size, and of the distribution and composition of the heavy-mineral assemblage in the various strata (III 5.). In this way we arrived at the following conclusion. After a long pluvial period, during which the heavy rains caused a strong erosion of the rocks that were found here and in the immediate vicinity, which in turn led to the deposition of a thick packet of detritic sands, a less wet climate developed gradually. During this period finer sands and sands containing silt were deposited on top of these coarse detritic sands. Subsequently, during the period in which the climate became drier, the upper part of the sediments was leached out, and the products of this process were precipitated in the zone in which the water-table fluctuated. Where the soil contained silt, the precipitates caused a cementation of the grains. From the position which the remnants of these dark-coloured layers now occupy, we may conclude that also in that period the drainage was determined by the relief of the bed-rock.

The last-mentioned period, i.e. that in which the hardpan was formed, was probably the Riss-Würm Interglacial. It was followed by a wetter period, during which the upper layers were exposed to pluvial erosion. In the northern part of the area investigated by us the hardpan was in this time attacked and removed. Subsequently the whole area was covered by a 1 to 1.5 m thick layer of sand derived from the local sediments deposited under fluvial or pluvial circumstances. The valleys formed by erosion during this period – probably the last pluvial period of the Würm Glacial – are still locally recognizable as depressions (III 2.8.). In the next period, the period which is still continuing, the sediments were transformed by leaching to the white sands of the present. The conditions for the development of dark-coloured illuvial layers were now no longer fulfilled. The hardpan and a few dark-coloured layers offered sufficient resistance to this leaching to maintain themselves. The white sands can therefore not be regarded as podzols, but are merely bleached sand soils.

The differences in drainage are entirely determined by the topography. The isolated remains of the hardpan are in this respect of no importance. Where in the rainy season the groundwater does not reach the surface, i.e. in the dry savanna, the highest differences found between the water-table in the rainy season and that in the dry season amount to 1 to 1.5 m. Where in the rainy season the groundwater does reach the surface, i.e. in the wet savanna, the fluctuations of the water-table are, on account of the retarded drainage, as a rule smaller. By the aid of measurements carried out during the various seasons a hydrological map could be drawn up (III 7).

V 3. THE VEGETATION

Where the savanna does not border on secondary forests on heavier soils it is surrounded by a xeromorphic vegetation for which we use the name savanna forest when the canopy shows a vertical differentiation and the name savanna wood when the latter consists of a single stratum. Characteristic species for the savanna forests and woods are *Clusia fockeana* and *Cl. nemorosa*, *Licania incana*, *Conomorpha magnoliifolia*, *Bombax flaviflorum*, *Pagamea guianensis*, *Matayba opaca*, *Ocotea schomburgkiana* and *Humiria floribunda*, whereas *Swartzia bannia*, *Ormosia costulata* and *Dimorphandra conjugata* may occupy a dominant position. In these savanna forests and woods four main vegetation types were distinguished, viz. dry savanna forest and dry savanna wood with as differentiating species *Ilex jenmanii* and *Trattinickia burserifolia*, and wet savanna forest and wet savanna wood with *Marlierea montana* and *Bactris campestris*. The creek forests are regarded as variants of the wet savanna forest and the wet savanna wood, differentiated by e.g. *Mauritia flexuosa* and *Symphonia globulifera* (IV 2.).

The scrub vegetation on the savanna proper reaches a height of 3 to 5 m, and consists of shrubs and small trees with poorly developed crowns. It is not always closed, but often split up into more or less crowded bushes. The canopy, the part which catches the sunlight, shows in such cases no level surface, but is dome-shaped with the margin descending to near the ground, and often the bush is enclosed by a fringe of *Humiria* *floribunda*, which appears here in the form of a low shrub with partly decumbent branches. The species that were mentioned above as characteristic for the savanna forests and woods, are found here too, though often in a more or less strongly aberrant habit (IV 3.2.1.). Apart from these species there are also some species that are characteristic for the scrub vegetation itself, e.g. *Ternstroemia punctata*, *Pagamea capitata* and *Retiniphyllum schomburgkii*. In some of the bushes *Clusia fockeana* forms a dense shrub stratum and then the canopy appears to be more open. On the wet savanna the canopy of such bushes is usually very open and it consists here of *Licania incana*, *Conomorpha magnoliifolia* and *Bactris campestris*.

The bushes appear to be of two different kinds. Sometimes they are isolated patches of savanna wood covering an area of 50 to 1,000 sq. metres and surrounded sometimes by a belt of savanna scrub (IV 3.1.). The other kind of bushes represent vegetation types belonging to the savanna scrub (IV 3.2.).

In the savanna scrub we distinguished three main types, viz. the *Dimorphandra* scrub, the *Ternstroemia* – *Matayba* scrub and the *Clusia* – *Scleria* scrub. The *Dimorphandra* scrub comes nearest to the *Ternstroemia* – *Matayba* scrub in its floristic composition, but differs from it in the strong dominance of *Dimorphandra conjugata*. The *Ternstroemia* – *Matayba* scrub is characterized by the abundance of *Ternstroemia punctata* and the presence of *Pagamea capitata*, *Humiria floribunda*, *Licania incana* and *Clusia fockeana*; each of the latter species may become co-dominant and this enabled us to distinguish a number of variants. Associate species which are very often present are *Matayba opaca*, *Calycolpus revolutus*, *Pisonia* sp. and *Bredemeyera densiflora*, together with *Pagamea guianensis*, *Protium heptaphyllum*, *Trattinickia burserifolia*, *Mapouria chlorantha*, *Myrcia sylvatica* and *Aulomyrcia obtusa* they distinguish this vegetation type from the *Clusia* – *Scleria* scrub. In the latter *Clusia fockeana* and *Scleria pyramidalis* are the dominants, and by the presence of *Scleria pyramidalis* this vegetation type is at once distinguishable from the two other kinds of scrub. Differentiating associates are *Bactris campestris*, *Tibouchina aspera*, *Miconia ciliata* and *Comolia vernicosa*. *Marlierea montana* is here more often met with, but *Ternstroemia*, *Humiria* and *Pagamea capitata* are seen only in the form of depauperated specimens. In contrast to the *Ternstroemia* – *Matayba* scrub the *Clusia* – *Scleria* scrub is found almost exclusively in the form of bushes which are, as a rule, much less than 100 sq. metres in extent. Four variants were distinguished, viz. a typical variant, a *Bactris* variant, a *Comolia* variant and an *Ilex jenmani* variant. The *Ilex jenmani* variant represents the transition between the typical *Clusia*–*Scleria* scrub and the *Ternstroemia* – *Matayba* scrub.

With regard to the distribution of the bushes and scrub vegetations belonging to the types mentioned above we may say that the savannawood bushes are to be found in the vicinity of the related savanna woods. The *Dimorphandra* scrub and the *Ternstroemia* – *Matayba* scrub occur on the dry savanna, and the *Clusia* – *Scleria* scrub on the wet savanna.

In the vegetation found between the bushes and in larger open spaces, five main types were distinguished (IV 4). The open stretches in the dry savanna are sparsely covered by the *Bulbostylis conifera* vegetation. In the marginal part of the bushes and where the bushes are strongly crowded, in the whole space between them the denser *Axonopus attenuatus* – *Lagenocarpus weigelti* vegetation is found. In areas strongly affected by human activities we find a "grass savanna", i.e. the *Trachypogon plumosus* vegetation; this is the only type that is found also on red sand.

Where the dry savanna passes into the wet one, and on the somewhat better drained parts of the latter, we meet the *Rhynchospora tenuis* vegetation. The *Lagenocarpus amazonicus* variant of the latter is found round bushes which mostly belong to the *Ilex* variant of the *Clusia* – *Scleria* scrub; it has a higher degree of cover than the typical variant.

Typical for the wet savanna is the fifth type, the *Lagenocarpus tremulus* vegetation. Within this vegetation type the occurrence of the variants appeared to be determined to a high degree by the way in which the rain water runs off along the surface. Where the surface is nearly level, the typical variant is found; the herb stratum covers here about 15 per cent and a film formed by Algae 20 to 90 per cent of the surface. In the narrow "white border" which surrounds the slight elevations by which the bushes belonging to the *Comolia* variant of the *Clusia* – *Scleria* scrub are borne, the *Panicum polycomum* variant is found, which covers only a few per cent of the surface. The white border owes its origin to the flow of rain water which runs off from the higher part on which the bush stands. On the slightly sloping parts of the savanna the water stagnates at the upper end of the oblong bushes of the *Bactris* variant of the *Clusia* – *Scleria* scrub. This stagnating water causes the development of a "hog-wallowed" or "kawfoetoe" surface, i.e. with channels, pits, and humps in the surface layer of the soil, and here the *Panicum nervosum* variant is found, which covers about 60 per cent of the surface. At the lower end of these oblong bushes a wide white border is found (IV 5.1.1.).

In order to find out whether there is a definite relation between the height of the water-table and the composition of the vegetation, we turned our attention to the transitional zone between the dry and the wet savanna. In such a zone the position of the water-table was mapped in order to compare the isohypses with the boundary lines reached by species of the wet and of the dry savanna which penetrate in this zone. It appeared that for 13 out of the 15 mapped species the limit of the distribution area showed a very distinct correlation with certain isohypses of the water-table (IV 5.1.2.). Especially noteworthy is the coincidence of the limits of the three *Lagenocarpus* species, of which *L. weigelti* is found on the dry savanna, whereas *L. tremulus* and *L. amazonicus* occur on the wet savanna.

With regard to the species which are confined to the dry savanna it was pointed out that it is hardly conceivable that the delimitation of their area of distribution would depend on the position of the water-table, which is found here far beneath the zone in which their roots are spreading.

Finally, the influence which is exercised on the vegetation by fires, was examined (IV 5.2.). However, although I had noted in various vegetation types vestiges of fire damage, and was able to study some stages in the regeneration of the savanna wood and of the savanna scrub, these considerations bear in the main a speculative character, as the determination of the influence exercised by fires requires in the first place a careful study of the succession.

It could be shown that on the wet savanna fire exercises a fatal influence on the bushes, of which only poor remains are left, viz. in the form of the *Licania* subvariant of the *Panicum nervosum – Lagenocarpus tremulus* vegetation. Various grasses and sedges, on the other hand, benefit by a fire, because this gives them an opportunity to spread; in the case of some of them it causes a mass-flowering. Other herbs disappear entirely, and can re-establish themselves only when new diaspores are imported. As inside a vegetation in this way important changes may be effected, it is easily conceivable that the extent of the areas occupied by them may change. Apart from the above-mentioned *Licania* subvariant of the *Panicum nervosum – Lagenocarpus tremulus* vegetation, the *Rhynchospora barbata* subvariant of the typical *Lagenocarpus tremulus* vegetation and the *Leptocoryphium lanatum* facies of the typical *Rhynchospora tenuis* vegetation were recognized as vegetation types that owe their special character to the influence of fires.

On the dry savanna the vegetation type that is most strongly influenced by fire is the *Trachypogon plumosus* vegetation, the grass savanna. This type of vegetation can maintain itself only where the savanna is regularly set on fire. That the bushes belonging to the *Inga* variant of the dry savanna wood are always found either within this type of vegetation or along its margin, seems to prove that the *Trachypogon plumosus* vegetation owes its origin to the destruction of the dry savanna wood and the prevention of its regeneration by repeated burning.

When dry savanna wood or savanna scrub has been destroyed by fire, at first patches of shrub vegetation with an indefinite composition develop while on the open stretches the *Pteridium* facies of the *Axonopus attenuatus – Lagenocarpus weigelti* vegetation is found. The woody vegetation, however, is gradually stabilized by the disappearance of the elements which do not belong to the savanna flora proper. We assume that the development of the woody species depends upon the preservation of regeneration centres, i.e. places where rests of the original vegetation have been spared, and that the development either of an open savanna studded with bushes or of a closed scrub depends upon the number of these regeneration centres.

Whether bushes always owe their origin to fires is, however, by no means certain. Theoretically there is no reason to assume that the edaphically determined series savanna forest → savanna wood → savanna scrub would end with the latter and that it might not possess a further term, viz. open savanna studded with bushes. Fires would not only cause a shift in the direction of the latter, but they might also give rise to the development of different kinds of bushes by favouring the development of definite components of these bushes and by hindering the development of others. The *Dimorphandra* scrub, for instance, may doubtless arise, as the result of repeated firing, out of the *Dimorphandra* facies of the *Cupania* variant of the dry savanna forest, but it is not excluded that it may arise also in another way, without the interference of fire, in places where *Dimorphandra* can compete very successfully with species which are in a less favourable condition, because they attain here the limit of their area of distribution. This might apply to the small groups of often very old bushes of *Dimorphandra* found on the transition between dry and wet savanna (IV 5.2.3.).

SUMMARY

This thesis describes the vegetation and discusses the prevailing ecological factors of a savanna region near Jodensavanne, Suriname; savanna being defined in this context as a landscape with low and often open woody vegetation, relieved by tracts with a thin to dense cover of herbs.

The methodology of the French-Swiss school of phytosociologists appeared appropriate for semi-quantitative description of the vegetation but, because of the limited scope of the study, it was considered premature to apply the synsystematic rules of this school, so the established units are called "major vegetation types", with "variants", "subvariants" and "facies" as subunits. Three major vegetation types of scrub and five of herb vegetation are described in detail and some attention has been given to the surrounding woods and forests.

Except for small fringe areas, the savanna is limited to rather coarse white-sandy soils, the characteristics and genesis of which are discussed. It is demonstrated that the hardpan which occurs in places is a paleopedogenetic feature and that this hardpan does not influence the present-day drainage conditions, for the drainage pattern could be explained on the basis of topography alone. The drainage condition which is one of the more important edaphic factors affecting the vegetation, allows a division of the vegetation types into two groups, one representing the "dry savanna" and the other the "wet savanna". On the wet savanna much of the differentiation in the herb vegetation is produced by water flowing over the soil.

Some direct results of burning could be analyzed, but about the long term effects of fire only suppositions could be made.

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ADDITIONS TO TABLES 2, 3, AND 4

TABLE 2

More important species of the Creek Forest and Secondary Forest, which are not found in the Savanna Forests and Woods

(J = *Jacaranda* variant of Creek Forest, T = *Tabebuia* variant;
I = *Isertia* variant of Secondary Forest, M = *Matayba* variant.
2 to 5 = degree of presence, compare legend; species with presence 1 are omitted)

Species occurring in Creek Forest and Secondary Forest

Astrocaryum paramaca J5 T5 I5 M3
Conceveiba guianensis J3 T3 I2
Sloanea eichleri e.a. J3 I3 M2
Siparuna guianensis J2 I3 M2
Ambelania acida J2 I2 M2
Maximiliana maripa J2 I2 M3
Isertia coccinea J2 I5
Euterpe oleracea J3 I3
Swartzia tomentosa J3 I3
Inga stipularis J3 I2
Bonafousia undulata J2 I3
Goupia glabra J2 I2
Apeiba echinata J2 I2
Vismia cayennensis J2 I2
Casearia arborea J2 I2
Talisia macrophylla J3 M2
Mouriria sp. J2 M2

Species confined to Creek Forest

Cecropia sciadophylla J3 T2
Hirtella vs. triandra J3 T2
Carapa guianensis J2 T3
Qualea albiflora J2 T2
Bombax globosum J2 T2
Aspidosperma megalocarpon J2 T2
Jacaranda copaia J3
Casearia combaymensis J3
Licania micrantha J3
Heisteria cauliflora J3
Pouteria cladantha T4

Species confined to Secondary Forest

Casearia javitensis I4 M3
Byrsonima coriacea var. spicata and B. crassifolia I3 M3
Astrocaryum segregatum I3 M3
Roupala montana I2 M3
Brunfelsia guianensis I3 M2
Xylopia frutescens I3 M2
Ocotea guianensis I3 M2
Virola vs. sebifera I2 M2
Cordia spp. I3 M2
Vismia sp. I2 M2
Couratari spp. e.g. gloriosa I3 M2
Croton matourensis I3
Campomanesia aromatica I3
Palicourea guianensis I3
Vatairea vs. guianensis I2
Myrcia fallax I2
Inga alba I2
Eschweilera longipes I2
Didymopanax morototoni I2
Pithecellobium jupunba M3
Guarea guara M3
Byrsonima stipulacea M2
Erythroxylum citrifolium M2
Parkia nitida M2

Remarks on the main table

The species are grouped according to their occurrence in the Savanna forests and woods, irrespective of their presence in the other forest types.

In this table the typical variant of Dry Savannawood and its *Swartzia* and *Ormosia* facies are taken together. They are treated in detail in table 3. The typical variant of Wet Savannawood and its *Swartzia–Ormosia* facies are also combined.

TABLE 3

List of species which occur either in one vegetation type only or in more than one, but then only occasionally. When the combined estimate of abundance and cover is not expressed by a symbol, it is x (= very sparsely present). The presence is indicated by means of a fraction, and here as well as in the table itself species with a presence of 1/6 or less are omitted.

Species from the tree and shrub strata

Inga lateriflora: Inga sav. wood 5/6, Licania-Ternstroemia-Matayba scrub typical facies 1/2
Humiria balsamifera: same types, 2/6 and 1/5 resp.
Licania divaricata: Inga sav. wood 4/6, Ormosia sav. wood 1/5
Tapirira guianensis: Inga wood 3/6, Clusia-Dimerphandra scrub 1/5
Maprounea guianensis: same types, 2/6 and 1/5 resp.
Anacardium occidentale: Inga wood 3/6
Myrcia fallax: Inga wood 2/6
Rapanea guianensis: Swartzia thicket 1/4, Licania-Ternstroemia-Matayba scrub typical facies 2/2
Hymenolobium sp., juv.: Swartzia thicket 3/4
Tapirira guianensis var. elliptica: Ormosia wood 1/5
Ocotea glomerata: Ormosia wood 1/5
Andira surinamensis or coriacea: Ormosia wood 1/5, Ormosia thicket 1/4
Pera bicolor: same types, 1/5 and 1/4 resp., Swartzia-Ormosia wood 1/1
Coccoloba sp.: Swartzia-Ormosia wood 1/1
Ternstroemia dentata: Swartzia-Ormosia wood 1/1, Clusia-Dimorphandra scrub 1/5
Ilex martiniana: Swartzia-Ormosia wood 1/1, Comolia-Clusia-Scleria scrub Calyptrocarya monocephala facies 1/2
Himatanthus articulata: typical Dimorphandra scrub 4/9
Byrsonima coriacea: Clusia-Dimerphandra scrub 1/5

Species from the lower undergrowth, the herb stratum and the moss stratum

Bromeliaceae spp.: typical dry sav. wood 1/3, Ormosia wood 2/5, Ormosia thicket 2/4, Humiria-Ternstroemia-Matayba scrub 3/12, Bactris-Clusia-Scleria scrub 2/7
Orchidacea sp. (no. 207): Inga wood 2/6, Swartzia thicket 1/4, Ormosia thicket 1/4
Schizaea elegans: Inga wood 2/6
Octoblepharum cylindricum (moss): typical dry sav. wood 2/3
Sematophyllum subsimplex (moss): ,, ,, ,, ,, 2/3
Philodendron insigne: Swartzia thicket 1/4
Coccocypselum guianense: Ormosia wood 1/5, Ormosia thicket 1/4, Licania-Ternstroemia-Matayba scrub typical facies 1/2
Malanea macrophylla: Ormosia wood 1/5, Swartzia-Ormosia wood 1/1
Monotagma plurispicatum: Ormosia thicket 1/4
Dioclea guianensis: Swartzia thicket 1/4, Licania-Ternstroemia-Matayba scrub 2/11
Psychotria farameoides: Clusia-Dimorphandra scrub 1/5, Pagamea-Ternstroemia-Matayba scrub typical facies 2/6
Cassia ramosa: Licania-Ternstroemia-Matayba scrub 2/11
Calyptrocarya glomerulata: Bactris-Clusia-Scleria scrub 5/7 1
Perama dichotoma: ,, ,, ,, ,, 4/7
Siphanthera hostmannii: ,, ,, ,, ,, 2/7
Octoblepharum cocuiense (moss): ,, ,, ,, ,, 4/7 1
Calyptrocarya monocephala: in its facies of Comolia-Clusia-Scleria scrub 2/2 3

Xyris dolichosperma:	Clusia-Scleria scrub typical 4/10,	Bactris var. 4/7
Xyris surinamensis: x–1	,, ,, ,, ,, 4/10,	,, ,, 3/7
Syngonanthus umbellatus:	,, ,, ,, ,, 4/10,	,, ,, 3/7
Syngonanthus gracilis: x–1	,, ,, ,, ,, 3/10,	,, ,, 6/7
Comolia lytharioides:	,, ,, ,, ,, 3/10,	,, ,, 2/7
Utricularia fimbriata: x–1	,, ,, ,, ,, 2/10	,, ,, 3/7
Abolboda americana:	,, ,, ,, ,, 2/10,	,, ,, 2/7

TABLE 4

In the table species are not recorded in the column for a vegetation type when they were found but once in that particular type (except in the case of the *Licania* subvariant). Species which were found not more than once in any of the vegetation types, or which occurred only in a single vegetation type and did not play a dominant role in the latter, are omitted. Their number is recorded in the table at the foot of each column. These species are enumerated below, each followed by the quotient for the presence. The combined estimate of abundance and cover is indicated only when it was more than x.

Axonopus attenuatus-Lagenocarpus weigelti vegetation

Bredemeyera densiflora var. glabra 4/12 x–1
Matayba opaca, juvenile, 6/12
Centrosema brasilianum 4/12
Bulbostylis surinamensis 2/12
Calycolpus revolutus 2/12
Dimorphandra conjugata, juvenile, 2/12
Casearia densiflora 2/12
Frullania nodulosa (Hepat.) 3/12
Campylopus surinamensis (moss) 3/12
Octoblepharum cylindricum (moss) 3/12
Cladonia sp. sect. Clausae (Lich.) 2/12 x–1
— Pteridium facies: Paspalum arenarium 2/5
Paepalanthus bifidus 2/5
Ananas ananassoides 2/5

Trachypogon plumosus vegetation

Davilla variant: Ternstroemia dentata 3/4
Aulomyrcia obtusa 3/4
Aulomyrcia hostmanniana 2/4
Lisianthus chelonoides 2/4
Borreria capitata 2/4
typical variant: Zornia diphylla 5/8
Aeschynomene paniculata 3/8
Piriqueta cistoides 3/8
Scleria hirtella 2/8
Phyllanthus lathyroides 2/8
Astrocaryum segregatum, juvenile, 4/8
Bulbostylis conifera variant Lagenocarpus weigelti subvariant:
Polygala variabilis 3/9

Rhynchospora tenuis vegetation

Bulbostylis conifera variant: Stylosanthes angustifolia 4/8
Bulbostylis junciformis 2/8
Lagenocarpus amazonicus variant: Encyclia oncidioides 2/6

Lagenocarpus tremulus vegetation

Panicum nervosum variant typical subvar.: Lycopodium meridionale 4/8
Bombax flaviflorum, juv., 3/8
Abolboda facies: Lindsaea stricta var. parvula 2/2
Sphagnum cf. kegelianum (moss) 1/2 1–2
– Lagenocarpus amazonicus subvar.: Hyptis lantanaefolia 2/7
Miconia ciliata 5/7
Miconia sp. with brown hairs 2/7
– Licania subvariant: Heliconia psittacorum 2/3
typical variant Panicum micranthum subvar.: Xyris paraënsis 4/10
Sphagnum variant: Croton hostmannii 4/9
Siphanthera hostmannii 2/9
Cyrtopodium cristatum 2/9
Calyptrocarya glomerulata 2/9
Octoblepharum cocuiense (moss) 2/9 x–1

FIGURE 10A STRATIGRAPHY OF THE JODENSAVANNE REGION.

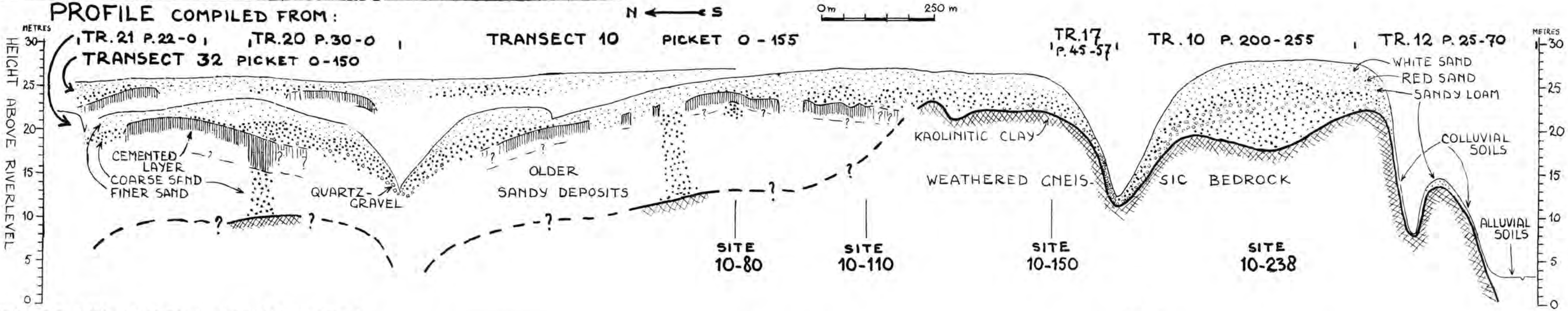
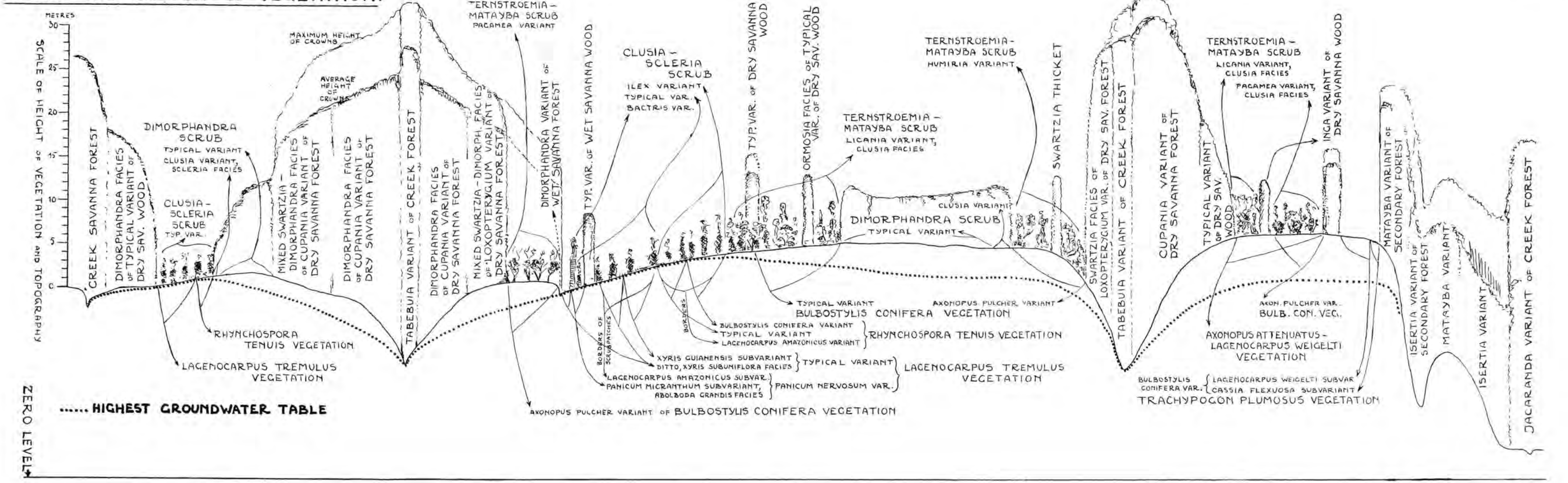


FIGURE 10B SKETCH OF VEGETATION.



Photograph 2. Open part of the dry savanna with the *Axonopus pulcher* variant of the *Bulbostylis conifera* vegetation. The bushes belong to the *Humiria floribunda* variant of the *Ternstroemia punctata — Matayba opaca* scrub. The tufts of grass are *Trachypogon plumosus*; the minute tufts are mainly *Bulbostylis conifera*. In the centre a single *Ternstroemia* whose leafy branches nearly touch the ground. In the left corner of the foreground part of a *Humiria* belt (site 17–116).

Photograph 3. Detached *Ternstroemia* shrub, surrounded by a belt of *Humiria* shrublets with decumbent branches. In the background the *Matayba* variant of the secondary forest. In the foreground the *Axonopus pulcher* variant of the *Bulbostylis conifera* vegetation (cf. fig. 29). The height of the pickets is about 1.25 m (site 11–10).

Photograph 4. Typical variant of the *Bulbostylis conifera* vegetation (cf. fig. 29). In the background once more a belt of *Humiria* round a bush belonging to the *Humiria* variant of the *Ternstroemia — Matayba* scrub. The distance between the short sticks is 2 m (130 m South of site 11–7).

Photograph 5. Two detached and densely leafy shrubs of *Clusia fockeana*, high 1.5 and 2.0 m, surrounded by the *Axonopus attenuatus — Lagenocarpus weigelti* vegetation (site 15–52).

Photograph 6. Regeneration of *Dimorphandra conjugata* scrub after a fire. The coppice shoots of *Dimorphandra* ramify already near the base, with the result that this vegetation will always remain a scrub (cf. fig. 24). Here and there in the open space the charred remains are seen of shrubs or trees and an *Axonopus attenuatus*—*Lagenocarpus weigelti* vegetation; the large tufts of *Axonopus* are a conspicuous feature of the latter. The height of the pickets is about 1.25 m (site km 3.3 on the truck road).

Photograph 7. Grass savanna South of Redidoti. Typical variant of the *Trachypogon plumosus* vegetation bordering on secondary forest; the latter is the *Matayba* variant containing *Astrocaryum segregatum* (the awara palm). The tree on the right is *Anacardium occidentale* (the cashew) (site 15–220).

Photograph 8. Typical variant of the *Trachypogon plumosus* vegetation which in the foreground is developed in the *Mesosetum loliiforme* facies. The meshes of the net that rests on the vegetation measure 1 by 1 m, cf. fig. 29 (site 15–246).

Photograph 9. Grass savanna along transect 14 seen from picket 72 towards picket 62. The vegetation is the *Lagenocarpus weigelti* subvariant of the *Bulbostylis conifera* variant of the *Trachypogon plumosus* vegetation. In the background a bush belonging to the *Inga lateriflora* variant of the dry savanna wood. In the foreground *Humiria* belts.

Photograph 10. *Bulbostylis conifera* variant of the *Trachypogon plumosus* vegetation; in the foreground the *Lagenocarpus weigelti* subvariant on white sand, in the background the denser *Cassia flexuosa* subvariant on red sand (cf. fig. 29). The high grasses are *Trachypogon plumosus* and *Axonopus pulcher*, the minute tufts *Mesosetum loliiforme* and *Bulbostylis conifera*. In the upper half at the left and at the right side a shrublet of *Byrsonima crassifolia* is seen (site 11–5).

Photograph 11. The open space bears the *Bulbostylis conifera* variant of the *Rhynchospora tenuis* vegetation with some large tufts of *Axonopus pulcher*. Near the bushes, which belong to the *Ilex jenmani* variant of the *Clusia fockeana*—*Scleria pyramidalis* scrub, the vegetation becomes denser; this is the *Lagenocarpus amazonicus* variant of the *Rhynchospora tenuis* vegetation. Transect 10 runs from the middle of the base to the right and is crossed by a path ("tjip-tjippie" or "kepkepi") of the Amerindians (site 10–65).

Photograph 12. Typical picture of a wet savanna. The open spaces are covered by the typical variant of the *Lagenocarpus tremulus* vegetation (here the *Xyris spathacea* subvariant); the bushes belong to the *Comolia vernicosa* variant of the *Clusia – Scleria* scrub. Above these bushes, which are hardly more than 1.5 m high, rise *Bactris campestris* (the keskesmaka palm) and *Conomorpha magnoliifolia* (site 32–114).

Photograph 13. Another picture of a wet savanna. The bushes belonging to the *Ternstroemia* facies of the *Comolia – Clusia – Scleria* scrub leave here so little space between them that they form an almost continuous scrub; the remaining gaps are still occupied by the *Xyris spathacea* subvariant. The depauperated *Ternstroemia* specimens should be compared with the large shrubs shown in the photographs 2 and 3. In the background the creek variant of the wet savanna wood with the characteristic emergent morisi palms, *Mauritia flexuosa* (site 32–50).

Photograph 14. Typical picture of a wet savanna which has repeatedly been burned. To the right a water course with *Mauritia flexuosa* and an undergrowth of obe palms, *Elaeis melanococca,* to the left passing into an open creek-border vegetation with high grasses such as *Hypogynium virgatum* and *Ischaemum guianense.* In the background the creek variant of the wet savanna forest deprived of its enclosing shrub belt by fire. The vegetation in the foreground is the typical *Lagenocarpus tremulus* vegetation with small isolated bushes of the *Licania incana* subvariant of the *Panicum nervosum – Lagenocarpus tremulus* vegetation (cf. photograph 17) (site 32–248).

Photograph 15. The bush in the background belongs to the *Bactris campestris* variant of the *Clusia – Scleria* scrub. It is surrounded by a "white border" bearing the *Panicum polycomum* variant of the *Lagenocarpus tremulus* vegetation. In the foreground the typical variant of the latter (cf. fig. 30) (site 37–22).

Photograph 16. The bushes represent the *Bactris* variant of the *Clusia–Scleria* scrub, and the ground between them, which shows a hogwallowed surface, is covered by the *Panicum micranthum* subvariant of the *Panicum nervosum – Lagenocarpus tremulus* vegetation. The thin grass is mainly *Paspalum pulchellum*, the coarser leaves belong to *Leptocoryphium lanatum* and to *Lagenocarpus tremulus*. The shoots with the dark capitula belong to *Xyris dolichosperma*. There are also some young specimens of *Bombax flaviflorum* (site 20–65).

Photograph 17. Another aspect of the wet savanna influenced by fire, viz. the *Leptocoryphium lanatum* facies of the typical *Rhynchospora tenuis* vegetation with low bushes belonging to the *Licania* subvariant of the *Panicum nervosum – Lagenocarpus tremulus* vegetation. In the background at the left side the creek variant of the wet savanna forest as well as water courses lined with *Mauritia flexuosa*. Far away in the background the water course shown in photograph 14 (site 32–212).

Photograph 18. *Ormosia costulata* thicket. The tree stratum is formed in this picture almost entirely by the crown of a 7.5 m high specimen of *Ormosia*, but *Conomorpha magnoliifolia* is also represented by some specimens. In the undergrowth to the left mainly *Clusia fockeana*, to the right *Licania incana*. The herbaceous vegetation in the foreground is the *Lagenocarpus amazonicus* subvariant of the *Panicum nervosum*—*Lagenocarpus tremulus* vegetation (site 23–3).

Photograph 19. Old, 5 m high scrub in which *Ternstroemia punctata* nevertheless retains the form of a shrub. It belongs to the *Pagamea capitata* variant of the *Ternstroemia—Matayba* scrub. The undergrowth consists mainly of *Pagamea capitata, Humiria floribunda* and *Tetracera asperula* (site 30–34).

Photograph 20. Bush belonging to the *Humiria* variant of the *Ternstroemia—Matayba* scrub exposed to view when transect 16 was cut. The thick stem in the foreground is a *Humiria*, the slanting one in the middle a *Ternstroemia* (site 16–24).

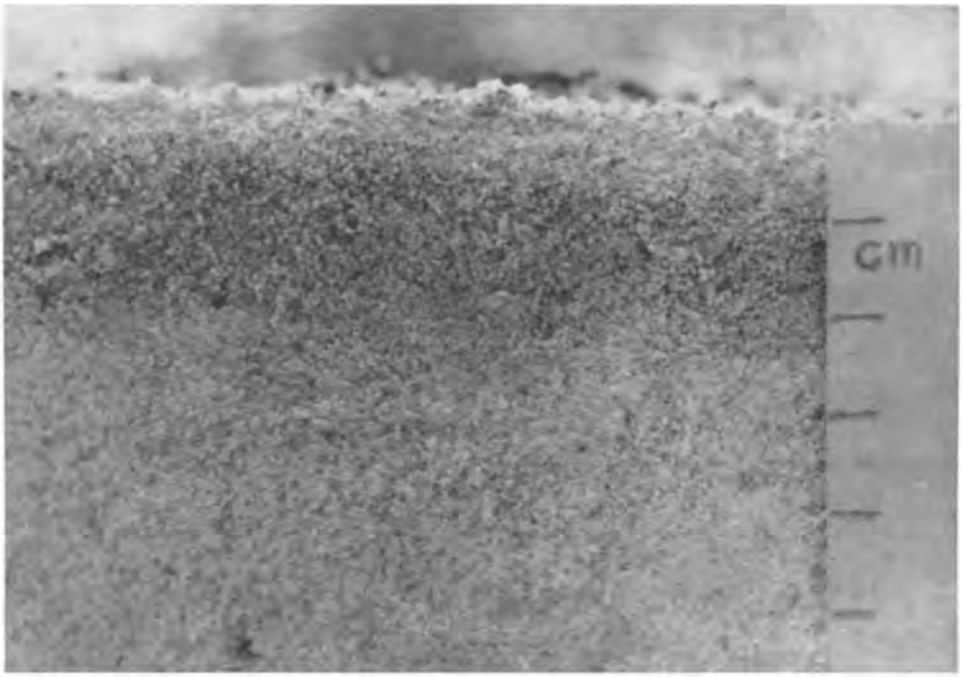
Photograph 21. *Dimorphandra conjugata* facies of the typical variant of the dry savanna wood. The large, contorted tree is a *Dimorphandra*, the erect stems belong mainly to *Licania incana* (site 30–32).

Photograph 22. Part of savanna forest in which the Amerindians have felled the trees and set the desiccated remains on fire. The plot is now ready to grow ananas (pineapple). In the background the *Cupania* variant of the dry savanna forest (North of Redidoti).

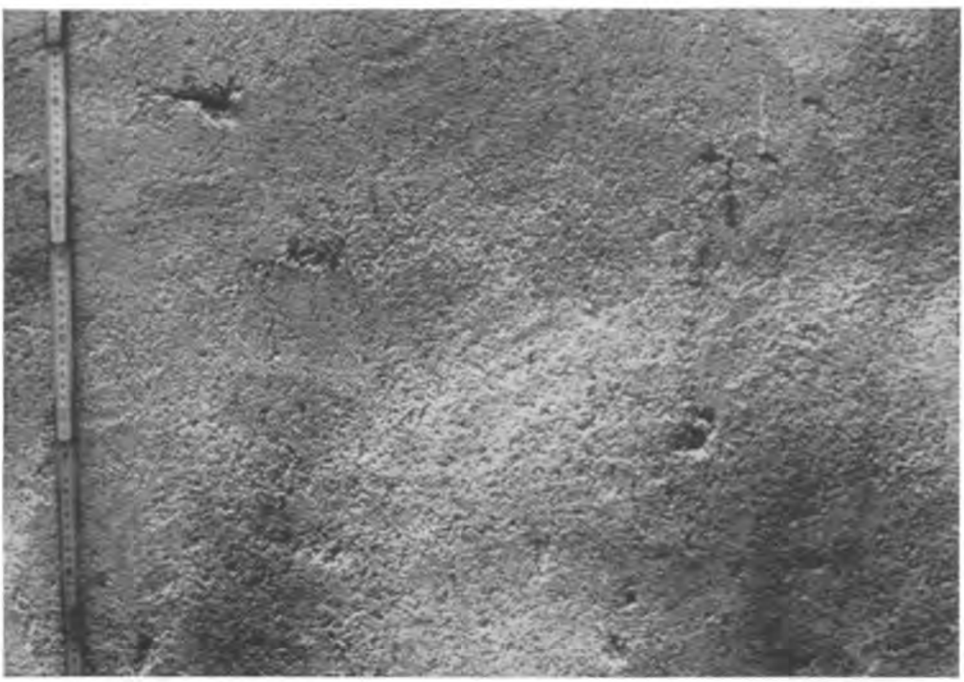
Photograph 23. Collapsed wall of the pit dug at site 10–238. The horizontally spreading roots in the layer at a depth of 10 to 20 cm are now hanging down. The sand on the surface was dug out of the pit.

Photograph 24. The upper 70 cm of the white sand soil exposed in a pit at site 10–238. Immediately below the surface an a few centimetres thick "micropodzol" has been formed; below the latter a layer of bleached sand is found. At a depth of 10 to 20 cm the sand is rich in humus and contains a large number of strong, horizontally spreading roots (cf. photo 23). Further downwards the humus content and the number of roots decrease. The horizontal stripes are artificial; they are the result of the spading.

Photograph 25. Upper part of the undulating hardpan in the pit dug at site 10–80. The rule stands approximately vertical. The uppermost layer of the hardpan is dark brown, but towards the middle the colour passes into a lighter brown. The grooves in the hardpan have been made by the pick-axe by means of which the hardpan was exposed.



Photograph 26. "Micropodzol" formed in the upper 5 cm of the white sand soil found in the open parts of the dry savanna. The thin uppermost layer, which is slightly bleached and shows a reddish hue, passes into a redbrown horizon with fine-grained illuviated material. Below the latter moderately coarse sand of a lighter colour is found (site 10–30).



Photograph 27. Wall of the pit dug at site 11–16 in the red sand; the part shown here extends from a depth of 3.3 m to a depth of 3.9 m and shows the passage of coarse red sand into still coarser white sand. In the zone of transition orange and greyish tints are seen, which penetrate as spurts into the white sand. To the left, in the red sand, the wall surface was damaged, where some roots were severed. The damaged spots in the white sand are due to the fact that pieces of quartz gravel subsided.