AN ECOLOGICAL AND PHYTOGEOGRAPHIC STUDY OF NORTHERN SURINAM SAVANNAS

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CONTENTS

CHAPTER I

INTRODUCTION

I. 1. SCOPE OF THE INVESTIGATION

The present study deals with the flora and the vegetation of savannas in northern Surinam (Fig. 1 and 2)*. The field work was carried out from August 1958 up to June 1959.

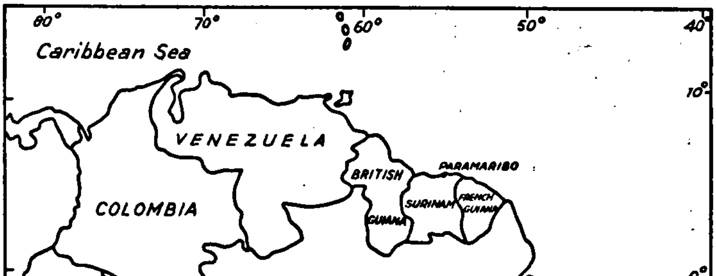

Fig. 1 Northern South America 1 : 48 000 000.

Three rather extensive savannas have been investigated in detail: the *Lobin savanna* near Zanderij, the *Coesewijne savanna* near Bigipoika¹)

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* Figure 2, Tables 6, 7, 8, 10 and the Annoted List of Species (Table 11) have been enclosed separately at the back of this issue.

¹) Spelling of Surinam words and names according to the "Glossary o the Suriname vernacular" (1961).

and the *Gros savanna* near Gros. Several other savannas, mainly smaller ones, were the object of accessory observations, viz. the *savannas of Bersaba and Vierkinderen*, the *Bigi-olo savanna* near Hanover, the *Fransina savanna* near Welgelegen, some tracts of savanna near Zanderij I, *Mimili Okili* near Powaka, the *Doti savanna* near Wisawini and the *De Jong Noord savanna.*

For the study of the flora the main work at our disposal was the "Flora of Suriname" (PULLE & coll., 1932- –).

Two publications concerning the vegetation of some northern Surinam savannas were available for comparison. LANJOUW (1936) studied some parts of the Zanderij complex and the *Patrick savanna* near Brownsweg. HEYLIGERS (1963) published the results of an elaborate study on the soil and the vegetation of the savanna complex between Jodensavanne and Kasipora.

Moreover the author had at his disposal a number of unpublished data collected in the course of time by several staff-members of the Botanical Museum and Herbarium at Utrecht. They are relevant to the *Wara savannas* and other savannas along the Marataka river, the most northern part of the Tibiti complex near Tibiti-sabana, the savanna along the Kasiwinika brook near Kopi, the hill savanna near Berg en Dal and the savannas N. of the Wane-creek.

This set of savannas may be regarded as fairly representative for the greater part of the northern Surinam savannas. Therefore the combination of his own observations and those made by others enabled the author to draw a general picture of the savanna flora and vegetation occurring in this area.

A comparison of the savannas of N. Surinam with those of other parts of tropical America was possible, only in so far as reliable literature was available. However, the author had the opportunity to learn a little more about American savannas by personal inspection during a trip of a week to the northern Rupununi savannas (British Guiana) in February 1959.

The investigation is mainly concerned with the description and classification of vegetation types on a floristic basis, with the distribution of the pertinent species and of the vegetation types and with their relation to environmental factors.

Partly parallel with this study Mrs. W. A. E. VAN DONSELAAR–TEN BOKKEL HUININK (1966) examined some other aspects of the savanna flora and vegetation, like the structure, root systems and periodicity.

I. 2. AREA OF THE INVESTIGATION

For a general description of N. Surinam from an ecological point of view and an all-over picture of the vegetation the reader is referred to LINDEMAN & MOOLENAAR (1955, 1959) and VAN DILLEWIJN (1957).

However, some particulars concerning its geology, soils and climate have to be given.

I. 2. 1. Geology and soils in general

The most recent review of the stratigraphy of Surinam is presented by Doeve (1957). In a slightly simplified form it is reproduced in Fig. 3.

Age	System	Formation	Series
Quaternary	Courantyne system	youngest f.	recent deposits
			Demerara s.
			Coropina s.*
		Bauxite f.	Zanderij s.*
Tertiary			Nickerie s.
		fracture	
Mesozoic	Post-Guyana system	fracture	
		Roraima f.*	
Paleozoic		Surinam folding (Granite 3)	
Proterozoic	Guyana system	Orapu f.	Rosebel s.*
		Guyana folding (Granite 2)	
			Bonidoro s.*
		discordance (Granite 1)	
		Balling f.*	Paramaka s.
			Nassau s.
		discordance	
Archaic	Archaic basal s.		

Fig. 3. The geologic division of Surinam, after Doeve (1957). (Units whose exposed parts may have a savanna vegetation are indicated by an asterisk.)

The classification of the soils of N. Surinam proposed by various pedologists is in fact an extension of the geological system. The main authors on this subject are Bakker (1951), Dost & Hooijsma (1957), Van der Eyk (1954, 1957), Van der Eyk & Hendriks (1953), Heyligers (1963) and Van der Voorde (1957). The quaternary "series" of Doeve are called "formations", in conformity with older geological literature (e.g. Schols & Cohen, 1953).

Within the formations are distinguished principal landscapes, landscapes, landscape elements, soil sequences and soil types (Van der Voorde, 1957), or else landscapes combined into belts, landscape elements, soil associations and soil series (Van der Eyk, 1954, 1957). The two systems cover one another but partly. In general Van der Eyk will be followed. His system is reproduced here as far as necessary with regard to the distribution of the savannas. The main units are mapped in Fig. 2.

A. The southern belt, mainly with soils from residual parent material, occupies six sevenths of the country. It is a part of the large and very old Guiana shield.

The landscapes of this belt developed from rock formations belonging to the "crystalline" basement and the "younger intrusives". In the crystalline basement two metamorphic schist formations are distinguished, viz. the *Balling* and the *Orapu formation.* The former is of volcanic-plutonic, the latter of sedimentary-clastic origin. The *Rosebel section* of the Orapu formation developed as a conglomeratic sandy facies and mainly consists of quartzites, graywackes and subgraywackes. The other section, the *Bonidoro* (or *Maäbo*) *section,* developed as a clay facies and now varies widely in the degree of metamorphism.

Both formations were folded during orogeneses accompanied by intrusions of granite or granitization. In consequence granito-dioritic rocks of variable composition are now found.

The younger intrusives occur as very long dolorite dykes running north–south. They will be left out of consideration.

The following landscapes developed from the rock formations of the basement:

a. *The granite landscapes* (see VAN DER EYK 1954, 1957).

b. *The subgraywacke landscape* (Saban-pasi landscape), belonging to the Rosebel section. "In the most characteristic part of the Saban-pasi landscape, rather low, mutual parallel, slightly bent ridges are found, which indicate the strike of this subgrauwacke formation. On them, residual soil profiles are found, consisting of mottled, kaolinic, sandy clay, covered by a layer of gravel, containing rounded and angular quartz grains and pebbles. On the flat parts of the ridges, long drawn, faintly sloping terrains are found, called ridge-feet. They are built up by colluvial material washed out during the denudation process of the ridges and deposited at their base. The soil of these ridge-feet consists of bleached fine sand." "The third landscape element is formed by the periodically submerged strips along the creeks." (VAN DER EYK, 1954) See also VAN KOOTEN (1954) and DOST & HOOIJSMA (1957).

Besides this more characteristic part, large areas belonging to this landscape do not present definite structure lines. They show less relief and have almost exclusively colluvial soils. There may be slight elevations here and there, in localities with residual soil profiles or with deeper quartz concentrations originating from quartz seams and veins (COHEN & VAN DER EYK, 1953; VAN KOOTEN, 1954).

c. *The schist-hill landscape* (Tempati landscape) ,belonging to the Bonidoro section. It consists of three elements: hills, foot plains and brook valleys.

The majority of the hills have a height varying from less than 10 m to about 60 m. The upper part is made up of the residual weathering product of the schists. There are also some higher hills occurring in groups, of which some have a laterite surface at their flat top. They may be regarded as the last remnants of a peneplain that formerly extended over a large part of the Guianas.

The foot plains are formed by colluvial material which originated from the hills. The colluvial layer consists of silty to sandy loams and very fine sands and has a thickness of 0.5 to 1.5 m. The residual schist below this layer consists of a kaolin-like clay. See also DOST & HOOIJSMA (1957).

d. *The schist-mountain landscape* (Brokolonko landscape in N. Surinam), belonging to the Balling formation. See VAN DER EYK (1954).

In the Mesozoic the *Roraima formation* was deposited on the Guiana shield. It is generally described as a formation of horizontally bedded conglomerates, sandstones and tuffs. Afterwards it was eroded for the greater part, only a few remnants being left. In Surinam these remains are found on the top of the Tafelberg, where they consist mostly of partly or wholly metamorphosed sandstone (IJZERMAN, 1931; MAGUIRE, 1945b). See also IV.5.4. However, recent observations made in the Emmaketen, a range in the interior of Surinam, raised new questions with regard to the history of the Roraima formation. Here JONKER & WENSINK (1960) found a layer of sandstone between a dolerite and a granite layer.

B. The middle belt, with mainly old soils from sedimentary parent material. The different parts belong to the *Coropina* and the *Zanderij formation.*

a. *The "dek"* (*= cover*) *landscape* (Zanderij landscape), belonging to the Zanderij formation, occupies the southern part of the belt. It comprises level and slightly undulating plains. The landscape is mainly built up by coarse sands from uncertain, tertiary to quaternary age, which lie as a cover over the crystalline basement. According to HEYLIGERS (1963) the sands are of continental origin and were deposited in several phases, the last one during the Würm glacial age.

The main soil associations are that of the bleached and that of the non-bleached soils. The bleached soils occupy the highest parts of the flat watersheds and are surrounded by the non-bleached soils.

The white sands show considerable differences in drainage; some parts are very dry, whereas some other parts are periodically very wet. The hardpans found in many localities do not necessarily affect the drainage conditions. HEYLIGERS (1963) could prove that they were formed during a phase of the deposition preceding the present one, probably during the Riss–Würm interglacial period.

DOST & HOOIJSMA (1957) described the properties of the different soil types occurring in a restricted area.

The old coastal plain, belonging to the Coropina formation, covers the northern part of the middle belt. It was deposited during a period when the sea-level was probably 10–12m higher than it is at the present. The deposition may have taken place in the Riss–Würm interglacial period.

During periodical abrasions the front part of the extensive plain was cleared away, the sand being washed out and thrown up by the dash of the waves into barriers. During the following Würm glacial age the sea-level sank considerably. In the Holocene it rose again and reached a height of 2 to 3 m above the present level. However, the water did not flood the plain, but it heavily attacked the offshore bars, partly clearing them away, and dissected the plain to the south of them with deep tidal erosion gullies. At that time the young coastal plain was deposited north of the bars and in the gullies formed in the old coastal plain.

Now two landscapes can be distinguished as the result of this process:

b. *The old offshore-bar landscape* (Lelydorp landscape). The dislocated and leveled remains of the bars themselves have to be mentioned as the main landscape element. They consist of bleached fine sands and fine-sandy loams.

c. *The old sea-clay landscape* (Para landscape) of which the most important element consists of the so-called "schols" i.e. the flat island-like remnants of the old tidal plain, separated by the slightly lower filled-up gullies.

The "schol"-soils belong to the Kasiwinika–Wakairibo association. The upper horizons consist of sandy loam to silty clay loam; the subsoil is still heavier.

On the ground of the drainage conditions two series are distinguished, the drier Kasiwinika series and the wetter Wakairibo series (see also VAN DER EYK & HENDRIKS, 1953). However, VAN DER VOORDE (1957) includes the soils of all "schols" into one series, the Wajambo series, and distinguishes several "soil phases" differing in the degree of wetness.

C. The northern belt, with young soils from sedimentary parent materials, mainly of marine and estuarine origin. This belt is identical with the young coastal plain and belongs to the *Demerara formation*. See also VAN DER VOORDE (1957).

I. 2. 2. Geology and soils of the savannas

I. 2. 2. 1. *The classification by* COHEN & VAN DER EYK

A very convenient and apprehensive survey of the Surinam savannas has been presented by COHEN & VAN DER EYK (1953). It is based on the geological division of the country and is in close agreement with the general survey given in the preceding section.

The main units of the system correspond with geological formations. These units include several savanna types associated with geomorphologic landscapes or lower entities. See Fig. 2.

I. Savannas of the Coropina formation
  1. Old offshore-bar landscape: Watamalejo-type (= Watamaleo-type)
  2. Old sea-clay landscape: Welgelegen-type

II. Savannas of the Zanderij formation, in particular the "dek" landscape
  a. Bleached soils, well drained: Kasipora-type (= Cassipora-type)

b. Bleached soils, poorly drained: Zanderij-type
c. Non-bleached soils: Coesewijne-type

III. Savannas of the Roraima formation: Tafelberg-type

IV. Savannas of the basal complex
1. Granite landscape: Paroe-type
2. Schist-hill landscape: Bosland-type
3. Subgraywacke landscape: Saban-pasi-type (= Sabanpassie type)

Watamalejo-type. Savannas of this type occur on the broad backs of the old offshore bars, in particular on soils of the Rijsdijk series. The sandy soil has an impermeable hardpan at a depth of 70 to 90 cm impeding drainage. They are found only north of the Wane-creek and have been described by BAKKER (1951, 1954; see also LINDEMAN, 1953).

Welgelegen-type. The savannas situated on the "schols" belong to this type. They have heavy soils with an impermeable subsoil of kaolinic clay. Two variations may be distinguished, viz. savannas with a relatively dry soil and savannas.with a wet soil, corresponding respectively with the soils of the Kasiwinika and the Wakairibo series. The latter variation is represented mainly north of the Wane-creek (see BAKKER, 1951, 1954; BAKKER & LANJOUW, 1947; LINDEMAN, 1953).

The middle belt, occupied by the Zanderij formation, is usually called the "savanna belt". Indeed, in this area the greater part (70 %) of the northern Surinam savannas is situated. However, this should not blind us for the factual situation. In reality only 7 % of the Zanderij formation is covered by savannas.

Kasipora-type and *Zanderij-type.* The bleached sands of the "dek" landscape are partly covered by savannas of these two types. They form extensive complexes and occupy 43 % and 25 % respectively of the total savanna area of northern Surinam. The complexes of the Zanderij-type are situated more or less north of those of the Kasipora-type. See HEYLIGERS (1963).

Coesewijne-type. Most savannas of this type, occurring only in a few places on the non-bleached soils, are situated on the northern border of the extensive complexes formed by the former two types. Some of them are isolated, i.e. surrounded by forest; others are a continuation of a white-sand savanna. A savanna of the Coesewijne-type may extend slightly over the boundary of the "dek" landscape, with the result that its lowest part actually belongs to the Coropina formation.

Tafelberg-type. Small savannas of this type are found on the top of the Tafelberg. See MAGUIRE (1945a; & coll., 1948). The Kappel savanna near the foot of this mountain may also belong to this type (KRAMER, verbal information).

Paroe-type. This type occurs only in the far interior and little is known of it. COHEN & VAN DER EYK assume that the extensive Sipaliwini savanna, on both sides of the Brazilian border (see VAN LYNDEN, 1939), has much in common with the southern Rupununi savannas in southern British Guiana. Probably the same may be said of some small savannas like the Apikalo savanna (see DE GOEJE, 1908), the Kaiser, and Palaime savannas and some similar ones.

Bosland-type. Small savannas of this type are found on the foot plains of the schist-hill landscape. Drainage is poor. This is caused either by the presence of an iron pan at a depth of 40 to 90 cm, or else by the fact that the but slightly permeable residual soil approaches the surface. See also VAN DER EYK (1954).

Saban-pasi-type. The subgraywacke landscape, its most characteristic undulating part as well as the more level parts, is covered to a great extent by savannas. On the ridges as well as on the ridge-feet a savanna vegetation is found. Only the creek valleys are occupied by forest.

I. 2. 2. 2. *Other classifications*

A quite different system of classification has been employed by BAKKER (1951). The principal criteria are purely pedologic. In particular those properties of the soil are stressed that are supposed to be of importance with respect to the origin of the savannas.

A part of this system is reproduced here as an example:

A. Sand savannas
  1. Coarse-sand savannas
    a. Loamy sands
    b. Pure sands
  2. Fine-sand savannas
    a and b as above
  Each of the four types is divided into subtypes like this:
  bh. Iron pan, completely impermeable
    bh′ at a depth of about 1 m
    bh″ at a depth of more than 4 m
    bh‴ between 1 and 4 m
  bv. Iron pan, not completely impermeable

B. Savannas on heavier soils
  a. Favourable structure down to a depth of 0.80–1.50 m
  b. Impermeable layer at a depth between 0.60–1.00 m
  c. More sandy, with favourable structure down to 0.60–1.50 m

C – E.

It must be mentioned that at the time of the publication of this system its author did not yet dispose of a complete review of all savannas found in Surinam.

In Surinam, on the one hand similar profiles developed from different parent materials, whereas on the other hand there are a large number of profiles that retain many features of their parent material and are therefore dissimilar. Both possibilities are involved in the variability shown by the savannas. In consequence the classifications of BAKKER and of COHEN & VAN DER EYK do not cover one another, nor would they have done so if the former had been completed. They can not be combined either, as is apparent from an attempt made by BAKKER in a later article (1954).

Finally LANJOUW (1954) proposes to distinguish only three principal savanna types in N. Surinam and to base the latter on the main topographic and edaphic factors that may be responsible for their origin and/or maintenance. These three types are:

1. The flat-watershed type
2. The impermeable-clay-layer type
3. The leached-soil-and-impermeable-ironpan type

The savannas of the Zanderij formation obviously belong to the first type. The Welgelegen-type of COHEN & VAN DER EYK corresponds with the second type and the Watamalejo-type with the third. The Bosland-type has to be distributed over the types 2 and 3. The place of the Saban-pasi-type is not clear.

In Section V. 2 the relation between the classification of the savanna vegetation and the geological and pedological systems will be dealt with.

In Chapter III the savannas will be arranged for convenience of survey in accordance with the system of COHEN & VAN DER EYK. As a rule the types distinguished in this system will be used in order to give a general picture of the savanna landscape.

I. 2. 3. **Climate**

The climate of the country has been dealt with by BRAAK (1935). OSTENDORF (1953–1957) has provided supplementary data and has presented reviews concerning some factors.

The main factor which varies markedly in the course of the year, is the amount of precipitation. Four periods are distinguished: a long rainy season (April–July), a long dry season (August–November), a short rainy season (December–January) and a short dry season (February–March). However, this picture is schematic. Beginning, end and duration of the periods, the heaviness of the rainy seasons and the severity of the drought may vary considerably from year to year.

The differences from place to place are not of much importance. (See also SCHULZ, 1960, p. 27). Fig. 4 presents the mean course of the rainfall at the stations Republiek and Kabel, which have a mean annual precipitation of 2071 mm and 2320 mm respectively. Between those two stations the majority of the savannas in the central part of N. Surinam are situated.

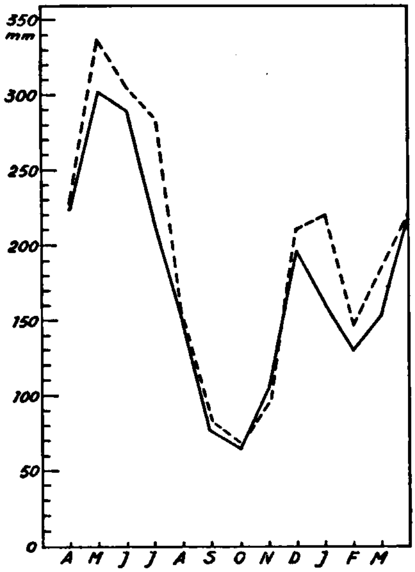


Fig. 4. Monthly rainfall at two stations (beginning with April).

——— Republiek (after Voets, 1959b)
- - - - - Kabel (after Ostendorf, 1957)

It has to be mentioned that the investigation took place after and during a period of relative dryness. Paramaribo has a mean annual rainfall of 2290 mm, but the figure for 1957 was 1597 mm and that for 1958 1757 mm. The first three months of 1959 had a deficit of 500 mm. In the rest of the country the situation was the same (Voets, 1959a,b).

CHAPTER II

STARTING-POINTS, CONCEPTIONS AND METHODS

II. 1. The savanna concept

There is no unanimity with regard to the definition of "savanna". Some noteworthy and representative definitions will be compared.

1) Lanjouw (1936). "Savannahs are plains in the West Indian Islands and Northern South America covered with more or less xeromorph herbs and small shrubs and with few trees or larger shrubs."
2) Beard (1953). "Savannas are communities in tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic plants, of which grasses and sedges are the principal components and with scattered shrubs, trees or palms sometimes present."

3) Eeckhout (1954). "Savanna: Open xerophytic herb formation in the tropics with scattered xero- or tropophytic trees or shrubs, isolated or in clumps" (translated).
4) Sillan (1958). "Formation characterized either by a continuous herb layer, mainly consisting of more or less high and more or less dense grasses, or in addition by a layer of shrubs or by a layer of trees of very variable density" (translated).
5) Dijksterhuis (1957). "Xeromorphic grassland containing isolated trees."
6) Dansereau (1951). "Savana: more or less closed ground layer, very discontinuous upper (woody) layer."

It appears that the applied criteria are partly geographic and partly derived from physiognomy and structure of the vegetation. The only point of agreement seems to be the simple fact that there is a ground layer and that this ground layer is always ecologically dominant, though this is mentioned explicitly only in the definition given by Beard. This is essential. All authors except Dansereau are of opinion that the ground layer has to be a xeromorphic herb layer. Sillan does not include the xeromorphic character in the definition itself, but he remarks that his definition includes all dry formations with a grass layer. Another point of agreement, if Dansereau is left out of consideration, is undoubtedly the important part played by grasses.

The significance of the presence of shrubs and trees is a controversial point between those who want to make a distinction between savanna (with trees or shrubs) and grassland or prairie (without trees or shrubs) and those who do not want to make this distinction.

With respect to the geographic position Lanjouw's definition is more restrictive than the other ones. This found its justification in the origin of the word savanna, which is Caraib indian, and in the state which our knowledge of this vegetation type had reached at that time (1936). The extension of the term to other parts of tropical America, as proposed by Beard, seems now fully justified. The latter author adds moreover: "If we establish the name 'savanna' as the correct one on historical grounds for neotropical grasslands, however, it will be legitimate for others to apply it to those of the old world if they consider there is sufficient affinity in physiognomy and ecological relationships". In fact, investigators of the African grasslands do already apply the name and their descriptions suggest that they are right. However, they never mention the *Cyperaceae* as a notably abundant group. On the other hand, the definition given by Sillan, who worked in Africa, takes into account that the savannas in that part of the world frequently have a more or less continuous tree layer, though the ground layer remains the dominant one. This, however, is applicable to tropical America too, though to a lesser degree, if one wants to include the campos cerrados into the definition. From their descriptions it appears that both Lanjouw and Beard want to do so, at least in so far as this vegetation type occurs in northern tropical America.

The Brazilian *campos cerrados* (*chaparrales* in the Spanish speaking countries of Latin America, *orchard savanna* in British Guiana) may have a fairly continuous layer of woody plants with a habit that escapes the distinction between trees and shrubs. This woody layer has little or no effect on the herb layer. WAIBEL (1948) and PAFFEN (1957) are of opinion that the campos cerrados of Brazil have a vegetation type sui generis and may not be identified with savannas. Most authors, however, also the Brazilian DUCKE and even DANSEREAU (see 1948), consider savanna and campo (campo cerrado inclusively) to be a single unit and for them therefore the two names are synonyms.

DANSEREAU (1951) unites all vegetation types on the ground of their structure into four entities, so-called "biochores": 1) desert: open, discontinuous cover, considerable unoccupied space; 2) grassland: no trees, rather closed, often unistratal, low plant cover; 3) savana: more or less closed ground layer, markedly discontinuous upper (woody) layer; 4) forest: continuous upper layer. The author, being aware of possible objections, says: "If it is the word savana that is employed in too broad a sense, I should be glad to have unother substituted, but it seems to me that a major structural category is involved".

Finally must be mentioned the "tentative classification of tropical vascular vegetations on a structural basis" given by FOSBERG (1958). Three "great structural groups" are distinguished, viz. closed, open and sparse vegetation. The units of the second level are "formation classes", defined by habit and structure. Vegetation types which according to the more restrictive definitions mentioned above belong to the savanna, are found in several of FOSBERG's formation classes, e.g. in open scrub with closed ground layer, in savanna (defined here as "closed grass or other herbaceous vegetation with scattered trees"), in shrub savanna, in tall grass, in short grass, in steppe savanna and even in steppe.

The way in which some German geographers (JAEGER, 1945, and after him TROLL, 1952, and LAUER, 1952) use the term savanna, may be left out of consideration. These authors have expressed very interesting ideas concerning the relation between vegetation and climate, but their nomenclature has been adapted completely to the restricted aim of their studies.

In view of the foregoing the author proposes the following definition of "savanna":

"A savanna or a campo is an area with a xeromorphic vegetation comprising an ecologically dominant ground layer consisting mainly of grasses, sometimes together with sedges, and with or without trees and/or shrubs either forming a more or less continuous layer, or occurring in groups, or isolated."

Following LANJOUW a savanna here is considered to be a concrete object, a piece of ground, but the word "plain" might be better replaced by a more general term, because savannas need not to be flat. If an abstraction is thought to be preferable, the definition might be changed into "savanna is a xeromorphic vegetation type comprising... etc."

In Surinam the name savanna is used for every stretch of ground occupied by a natural or apparently natural vegetation without a closed tree layer (as in forests and woods) and during the greater part of the year not (as in swamps) covered by water.

The vegetation types which are in accordance with the proposed definition show a great diversity. There are savannas with a closed and with a markedly discontinuous herb layer, consisting mainly of grasses or of a mixture of grasses and sedges, with or without many other low herbs and dwarf-shrubs, with or without trees and/or shrubs, some having the character of rather open or rather closed orchard savannas. All these types are considered in this study.

No genuine savannas are the "rock savannas" occurring in the interior (LINDEMAN & MOOLENAAR, 1959). FANSHAWE (1952) calls them "heaths", a name which is not suitable either, but BEARD (1955) speaks more correctly of "rock pavement vegetations".

"Swamp savannas" are not considered. LINDEMAN (1953) says of those near Nikeri: "These swamp savannas are in the wet season submerged in a shallow layer of water but in the dry season the soil is merely boggy". The vegetation consists of *Eleocharis mutata* and *Cyperus articulatus* with scattered *Avicennia nitida.*

Areas with a continuous or discontinuous scrub vegetation are called "struik-savanna", that is "shrub savanna". These vegetation types are identical with the "dry evergreen thicket" and the "evergreen bushland" of BEARD (1955). The first is left out of consideration. HEYLIGERS (1963) deals with it and calls it "savanna scrub". The second type however is taken into account. It is known in the Guianas as "muri scrub" ("xeromorphic scrub", FANSHAWE, 1952) and consists of a mosaic of dense bushes and open patches with a very sparse herbaceous vegetation. The bushes have many species in common with the isolated bushes occurring in open savannas and the vegetation of the open patches is floristically related to the vegetation of the dry open savanna itself.

II. 2. SURVEY OF THE VEGETATION

In principle the vegetation was studied according to the methods and conceptions of the Braun–Blanquet school. The reader is referred to the handbook of BRAUN–BLANQUET (1932, 1950, 1951) and to DOING KRAFT (1956) and ELLENBERG (1956).

The attention of the English speaking reader is drawn to the fact that the English edition of 1932 is not at all up to date. A brief review taking the subsequent development of the system into account is given by BECKING (1957). A recent discussion by MOORE (1962) may also be clarifying.

II. 2. 1. **Starting-points and conceptions**

With regard to the study and in particular the classification of vegetation the following statements by FOSBERG (1958) are of importance: "... (1) a uniform technique for the study of vegetation is neither possible nor desirable; (2) that a natural classification of vegetation in one of the ways this term is commonly used is inherently impossible and in the other is improbably feasible and if possible would be too complex to be readily understandable; (3) that no single artificial classification will likely be serviceable for all purposes, and that therefore no such classification will be generally accepted; (4) that a uniform nomenclature of vegetation types, being dependent on a single accepted classification, will not be feasible. It was not suggested, however, that attempts to classify vegetation be abandoned. Classifications are useful and necessary to facilitate understanding and communication."

In view of this quotation, in particular of point 3, the use of the Braun–Blanquet system in this study has to be regarded as a choice, justified by the purposes of the investigation. The main purpose is, as will be seen later, to bring to the fore the relation between the vegetation and the properties of the habitat. If the vegetation is regarded as the main object, there is no better measure for this relation than its floristic composition, at least so long as a not too wide area is considered. The Braun–Blanquet system, which is essentially floristic, in principle appears to be the most preferable.

The question whether the Braun–Blanquet system can be applied to vegetation types in the tropics, has been discussed e.g. on the *Symposium on humid tropics research* held at Kandy (Ceylon) in1956 (see BHARUCHA, 1958a,b). In this connection it may be mentioned that in fact tropical vegetation types are the object of many studies carried out according to this system. These studies are persued mainly by continental Europeans and moreover by an ever increasing number of botanists from the tropical countries themselves.

However, it is remarkable that most of the investigations in the tropics deal with relatively simple vegetations, e.g. those of swamps, steppes, savannas and paramos. As far as savannas are concerned, see e.g. LEBRUN (1947), DUVIGNEAUD (1949), HEYLIGERS (1963). This is not surprising, for these vegetations in particular are appropriate to the system.

The Braun–Blanquet system is by its method of sampling and also by its process of classification committed to vegetation types with the following properties: 1) A not too complex structure. When there are e.g. too many tree layers, it is not possible to estimate the degree of covering of every single species. 2) A moderate number of species. In the case of too many species the minimum area of a sample plot becomes too large and cannot easily be taken in. When there are too few species the floristic classification runs short of criteria. 3) A sufficiently high number of species having a not too restricted area of distribution. It is not possible to compare communities occurring in different localities on account of their floristic composition if they have very few or no species in common. The savanna vegetations of Surinam fulfill these conditions.

The description, the delimitation and the classification in a hierarchic system of the communities is based on floristic criteria. This means that whenever the floristic composition of a community and the formation to which it belongs suggest different affinities, the former property has been given precedence. In consequence alliances have been distinguished including associations both with and without an open stratum of trees, just because they have herb layers of a closely related composition.

The use of *characteristic species* (in the sense of faithful taxa as the only criteria for the distinction of vegetation units has been abandoned. The total composition of a vegetation type (qualitative and quantitative) has always been taken into consideration. The units were chosen and defined in such a way that their limits present a contrast as pronounced as possible. Species marking a limit because they occur only or mainly on one side of it, are called *differential species*. The differential species are used as the general criteria for the delimitation and classification of the vegetation units. From this point of view a characteristic species is a differential species delimiting a community with regard to every other community.

A hierarchic system of vegetation units built up in this way has to be more than just a survey expressing the variability in floristic composition within one or another type of vegetation. It has to reflect the close relation between the composition of the vegetation and the properties of the habitat. In order to achieve this aim some conceptions and methods of DUVIGNEAUD (1946, 1960) have been accepted and applied. This appeared to promise success, not in the least in view of the exemplary investigation of the savannas of Bas-Congo carried out by this Belgian author (1949), whose ideas did not yet receive the attention they deserve.

Following DUVIGNEAUD much attention has been paid to the elaboration of groups of species with a sociological affinity corresponding with an ecological one, apparently as a result of similar requirements with regard to the habitat. These groups are called *ecological groups*. The groups of differential and characteristic species, necessary for the definition, delimitation and classification of the vegetation units, have been selected mainly from these ecological groups.

An objection might be that in this way the normal and correct procedure is reversed. This is true. However, this is no difficulty so long as the main habitat factors influencing the vegetation can be traced with certainty. If this cannot be done, the system will have little value indeed. It is better to have a classification on the ground of sociological groups corresponding with principal habitat factors, though (still) unknown, than one on the ground of ecological groups corresponding with habitat factors of secondary importance. However, in the latter case, this imperfection will reveal itself in the presence of groups of species with inexplicable but nevertheless unmistakable sociological affinities.

In conformity with the generally accepted practice of the Braun-Blanquet school no highly specialized statistical methods were applied.

This point will not be discussed here, but it will be illustrated by another quotation from Fosberg (1958):

"In dealing with complex phenomena with many variables, especially when the pattern is in the form of a continuum as is usual with vegetation, the indispensable factor is the intuition or the judgement of the classifier. Some of the burden of handling the variables might be lightened by means of electronic computors, but the factor of judgement would still be essential in coding and programming, and if it were faulty, the results would be without value."

Of course the delimitation and the classification of the savanna vegetation-units of northern Surinam, as presented in this study, have to be regarded as provisional. Every conclusion in this field of study is provisional so long as the flora and the vegetation of the neotropics have not been investigated in detail.

Nevertheless the outcome of this study will be put forward in a rather definite form, with e.g. latin names. This has been done in the first place to facilitate the handling of the system and the comparison of the situation on other savannas of tropical America with that in N. Surinam. However, there are more reasons for this line of conduct. Indeed, on the one hand experience shows that a provisional classification always meets with fierce criticism from the side of those who regard it as premature, imperfect, incomplete, superficial or even quite superfluous. These critics are often right. On the other hand, however, a provisional system impels other students in the same field to realize exactly the properties of the vegetation types they are working with. The system may have the function of a challenge. In this way it may prove to be a stimulus to future work, and to function as a useful starting point.

So long as the creator, the users and the critics of a provisional classification are aware of this situation, the advantages amply outweigh the disadvantages. Then the words of Francis Bacon may be applicated: "Trueth comes out of Error much more rapidly, than out of Confusion".

II. 2. 2. **Sampling and tabulating**

With regard to the sampling method the following basal concepts may be recalled to mind.

For the analysis of a sample plot (shortly indicated as *record*) are required:

1. A scale for the *total estimate* of abundance and coverage of each species

   + sparsely present, degree of cover very small
   1 numerous, but degree of cover small; or rather sparsely, but degree of cover higher (up to 5 %)
   2 very numerous, or degree of cover 5–25 %
   3 any number, degree of cover 25–50 %
   4 any number, degree of cover 50–75 %
   5 any number, degree of cover 75–100 %

2. A scale for the *sociability* of each species

1 single specimens
2 small groups or tufts
3 larger groups or cushions
4 very large groups or carpets
5 covering the sample plot homogeneously.

The various single records obtained in a definite community may be combined. For the *presence* of a species the following scale is used.

I species present in 1– 20 % of the records
II species present in 21– 40 % of the records
III species present in 41– 60 % of the records
IV species present in 61– 80 % of the records
V species present in 81–100 % of the records

The absolute value of the presence may also be indicated by an arabic figure; this is obligatory when less than five records are available.

In the table the symbol of the presence is followed by one or more arabic figures indicating the total estimate. It is preferable to take here the normal or the characteristic value(s), not the total range or the mean value.

Different degrees of sociability within one species may be used for the delimitation of different communities with regard to one another. In this case the symbol for the sociability should in every single instance be joined to those for the presence and the total estimate. If the sociability of a species is uniform or increasing parallel to the total estimate, the figure(s) may be put at the end of the table in which the communities are comparatively arranged. Exceptional values may be added in brackets.

II. 3. SURVEY OF THE SOIL (see Tables 1 and 2)

The soil has been studied in so far as it seemed possible to correlate its properties with the floristic composition of the vegetation. The descriptions in the field and the sampling of the profiles were as a rule restricted to the upper 1.20 m.

The majority of the profiles have been described in the field by Ir. H. Dost, head of the "*Dienst Bodemkartering*" (Dept. of Soil Survey) in Surinam, and by other members of this department. The samples have been analysed in the pedological laboratory of the "*Koninklijk Instituut voor de tropen*" (Royal Institute for Research in the Tropics) at Amsterdam.

II. 3. 1. **Texture**

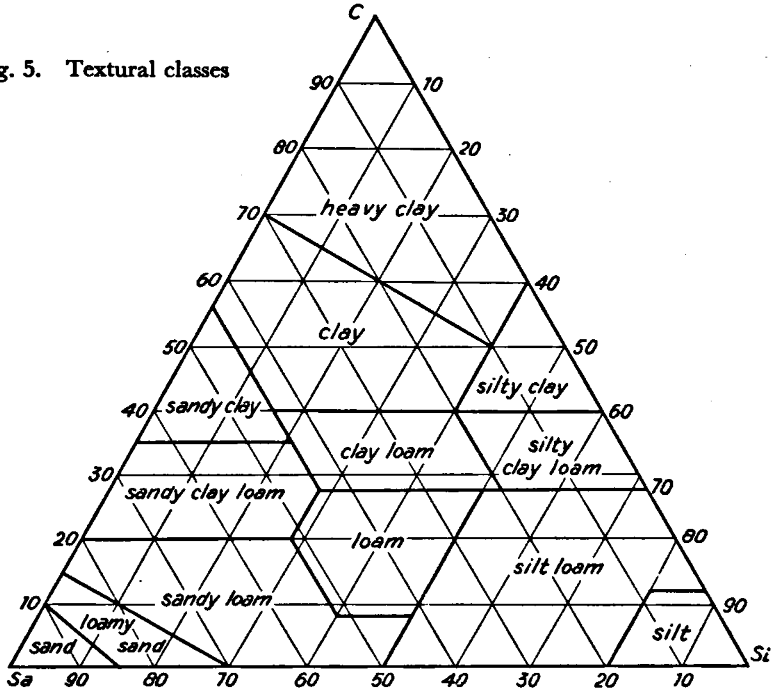
The international and the U.S. system have been taken into account. For the latter see the Soil Survey Manual of the U.S. Department of Agriculture.

μ	>2000	2000-200	200-50	50-20	20-2	<2
U.S.	gravel	(very) coarse sand	(very) fine sand	silt		clay
Intern.	gravel	coarse sand	fine sand		silt	clay

In the U.S. system the exact limit between the particles of coarse and fine sand is 297 μ, between those of sand and silt 53 μ.

In conformity with the Dept. of Soil Survey in Surinam the U.S. system has been applied. This holds also for the delimitation and the nomenclature of the *textural classes*. Only the class "clay" has been divided into "clay" and "heavy clay" after VAN DER VOORDE (1957). See Fig. 5.

Fig. 5. Textural classes



Henceforth the following abbreviations will be used:

s	sand or sandy	h	heavy
l	loam or loamy	w	white, i.e. completely bleached
si	silt of silty	r	red, i.e. not bleached
c	clay		

II. 3. 2. Water economy

Only in some instances the fluctuation of the water level has been studied with the help of vertical tubes sunk into the soil (see Figs. 8 and 11). As a rule data concerning the water economy of the soil were obtained indirectly from the observation of phenomena related with it, as the "gley" phenomenon, recognizable from colour, rusty spots and ferrugineous root-channel concretions, cracks and "kawfoetoes".

In general the *degree of moistness* is indicated with the aid of a simple scale used by the Dept. of Soil Survey. However, this scale has been slightly modified.

very dry	(vd)	upper limit of the "gley" phenomenon	> 120 cm
dry	(d)	in sand upper "gley"	> 70 cm
		in loam upper "gley"	> 50 cm
		in clay upper "gley"	> 40 cm
moist	(m)	in sand upper "gley"	70–40 cm
		in loam upper "gley"	50–30 cm
		in clay upper "gley"	40–20 cm
wet	(w)	in sand upper "gley"	< 40 cm
		in loam upper "gley"	< 30 cm
		in clay upper "gley"	< 20 cm
very wet	(vw)	kawfoetoes	
rivulet	(r)	high kawfoetoes	

The surface of the very wet soils and the rivulets has a "hog-wallow structure", i.e. a configuration of hummocks and channels. In Surinam the hummocks are called *kawfoetoes* (Photo 12).

In some instances erosion may be the cause of the kawfoetoe development. Slowly running water may wash away the upper soil layer, in particular between tufts of herbs, so that a micro-relief develops and gradually becomes more pronounced. However, kawfoetoes are found mainly on low lying, flat stretches where in the wet season pools of stagnant or hardly moving water are formed, on savannas as well as in woods. Van der Voorde (1957) proved that they are built up by worms which only in this way are able to keep their heads above the water. The higher the water rises, the higher the worms build their kawfoetoes.

In connection with the water economy, two factors have been analysed in the laboratory, viz. the percolation velocity and the moisture content.

The *percolation velocity* in situ is dependent among other things on the structure of the soil. In the laboratory it was measured after the structure had been disturbed. In the case of the savanna soils the difference may be of little importance, because these soils are hardly structured in the field. Nevertheless the figures for the percolation velocity do not present absolute but only relative values. They are useful in particular for tracing poorly permeable layers.

The figures for the *moisture content* refer to air-dried samples. On the whole they are directly proportionate to the percentages of the clay fractions. They have been added only for the sake of completeness.

The superficial way in which the water economy is treated here satisfies the purpose of this study. It does not do justice, however, to the complexity of the drainage conditions. For a more comprehensive treatment of this matter the reader is referred to Van Donselaar–ten Bokkel Huinink (1966).

II. 3. 3. **The texture-moisture diagram**

The main soil factors studied because of their influence on the plants are the texture of the upper 20 to 60 cm and the degree of moistness. In anticipation of the exposition given in the next chapters we may state that not every possible combination of these two factors is realized on the savannas studied here.

The open squares in the following *texture-moisture diagram* indicate the combinations that were actually found. All soil types heavier than sandy clay loam are taken together as "heavy" soils.

	ws	rs	ls	sl	scl	h
vd						☒
d						☒
m		☒				☒
w		☒				
vw		☒	☒		☒	
r		☒	☒	☒	☒	

II. 3. 4. **Other factors**

The differences in the *C-content* of the samples are in agreement with the estimations of the *humus content* in the field. Therefore, the humus content is taken into account when the properties of the soil are correlated with the vegetation types.

The *N-content* has been mentioned in the table only for the sake of completeness. The number of data is too small and does not permit to draw definite conclusions. The same holds for the *C/N-ratio*.

II. 3. 5. **Methods of analysis applied in the laboratory**

Granular composition. Boiling with peroxide, dispersing with Na-pyrophosphate + Na-bichromate. Fractions 2000–200 μ and 200–50 μ by sieving (wet), fraction 50–20 μ by calculation, fractions 20–2 μ and < 2 μ by precipitation, pipetting, drying and weighing. The figures refer to the percentages of the total amount of grains ranging from 0–2 mm.

Percolation velocity. Slightly shaking of the soil during at least one hour in tubes 2.1 cm in diameter until a constant height of 12 cm is obtained. Saturating the soil column with water, percolating with water (100 ml) at a constant pressure, 5 cm above the surface of the soil column. Measuring the percolated water at fixed times.

Moisture content. Loss in weight in percentage between normally air-dried soil and soil dried during 3 hours at 105°C.

C-content. Normal analysis (Walkley–Black). Oxidation with bichromate + conc. sulphuric acid. Retitrating of the surplus bichromate with ferrosulphate.

N-content. Destruction with "selenium mixture after Kjeldahl" and conc. sulphuric acid. Micro-kjeldahl analysis (steam destillation, titration of the accumulated ammonia).

The figures of the last two analyses are given as a percentage of the dried soil (105°C).

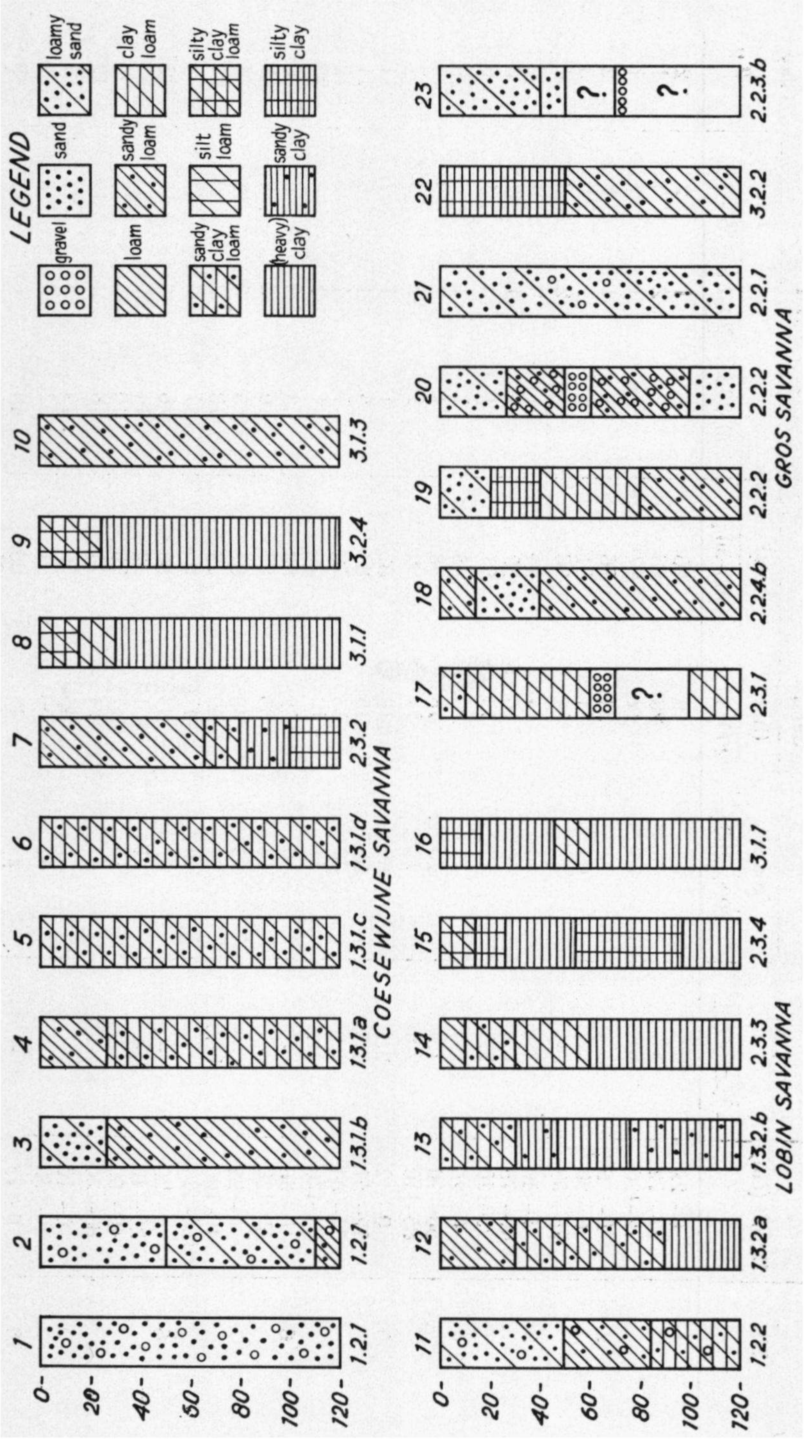


Fig. 6. Soil profiles

TABLE 1 Analyses of soil profiles I

Nr.	Depth (cm)	Gravel	Sand			Silt			Clay
			(coarse)	(fine)	total			total	
		> 2000 μ	2000–200 μ	200–50 μ	2000–50 μ	50–20 μ	20–2 μ	50–2 μ	< 2 μ
1	0– 22	0.5	77	19	96	1	1	2	2
	22– 72	–	76	20	96	1	2	3	1
	72–120	–	85	12	97	1	1	2	1
2	0– 6	–	72	24	96	1	1	2	2
	6– 28	–	69	24	91	5	1	6	3
	28– 59	–	82	14	96	1	2	3	1
3	1– 40	2.2	80	14	94	1	3	4	2
	40– 75	6.5	76	16	92	1	1	2	6
	75–120	3.8	77	13	91	1	3	4	6
4	0– 25	2.0	77	18	95	1	1	2	3
	50– 70	1.9	70	18	88	1	2	3	9
	85–110	2.6	73	17	90	1	2	3	7
5	0– 12	2.1	69	18	87	1	1	2	11
	12– 51	1.3	68	15	83	5	1	6	11
	51– 84	1.9	66	13	79	1	1	2	19
	84–120	1.9	57	13	70	1	1	2	28
6	0– 30	–	56	32	88	3	3	6	6
	65–120	–	48	35	83	6	2	8	9
7	0– 25	–	33	49	82	5	8	13	5
	40–100	11.3	24	49	73	18	2	20	7
	100–120	–	48	47	95	1	2	3	2
8	0– 20	–	47	33	80	6	9	15	5
	20– 40	–	1	1	2	14	39	53	45
	40– 80	–	19	17	36	10	25	35	29
	80–120	–	47	24	71	16	1	17	12
9	0– 10	–	31	45	76	19	4	23	1
	40– 50	–	41	50	91	2	3	5	4
10	0– 15	–	23	43	66	19	6	25	9
	15– 40	–	39	42	81	4	6	10	9
	60– 80	–	36	36	72	15	2	17	11
11	0– 25	–	51	27	78	1	1	2	20
	25– 40	–	50	23	73	4	2	6	21
	40–110	–	56	20	76	1	1	2	22
12	0– 30	–	68	10	78	1	1	2	20

	30– 60	–	68	8	76	1	2	3	21
	60– 90	–	49	12	61	1	8	9	30
	90–120	–	32	9	41	1	11	12	47
13	0– 20	–	70	13	83	1	1	2	15
	20– 50	–	65	15	80	1	5	6	14
	60– 95	–	56	20	76	1	5	6	18
14	0– 35	–	8	44	52	17	14	31	17
	50– 65	–	52	13	65	1	19	20	15
15	0– 15	–	47	20	67	1	1	2	31
	15– 45	–	43	21	64	1	1	2	34
	45– 60	–	54	22	76	1	2	3	21
16	0– 20	–	39	31	70	1	2	3	27
	20– 40	–	49	25	74	1	1	2	24
	40–120	–	43	28	71	1	1	2	27
17	0– 15	–	45	13	58	1	10	11	31
	15– 29	–	49	9	58	1	10	11	31
	29– 47	–	37	10	47	2	13	15	38
	47– 75	–	16	5	21	10	11	21	58
	100–120	–	37	11	48	1	5	6	46
18	0– 10	–	32	27	59	14	6	20	21
	20– 60	–	20	14	34	1	33	34	32
	100–120	–	3	6	9	12	49	61	30
	0– 10	–	35	6	41	3	32	35	24
	10– 30	–	45	5	50	1	25	26	24
	30– 60	–	36	6	42	13	16	29	29
	60– 95	–	8	1	9	1	11	12	79
	95–120	–	4	2	6	10	2	12	82
20	0– 13	–	4	5	9	13	39	52	39
	13– 25	–	9	3	12	10	34	44	44
	25– 54	–	3	2	5	1	32	33	62
	54– 97	–	2	2	4	4	40	44	52
	97–120	–	4	3	7	1	34	35	58
21	0– 15	–	11	4	15	18	37	55	30
	15– 30	–	23	5	28	10	31	41	31
	30– 50	–	5	2	7	7	27	34	59
22	0– 15	–	8	1	9	1	45	46	45
	15– 45	–	9	2	11	9	24	33	56
	50– 60	–	40	2	42	1	18	19	39
	90–100	–	15	2	17	1	22	23	60
23	0– 25	–	1	1	2	1	59	60	38
	25– 60	–	1	1	2	1	37	38	60
24	0– 50	–	1	1	2	18	36	54	44
	50–120	–	40	29	69	10	10	20	11

TABLE 2 Analyses of soil profiles II

Nr.	Depth (cm)	Percolation velocity (ml/h)	Moisture content	C	N	C/N	Nr. in Fig. 6	Vegetation type
1	0– 22	304	0.1	0.33	0.02	17	–	1.1.1.a.c
	22– 72	168	0.2	0.07	0.01	7		
	72–120	150	0.2	0.03	0.01	3		
2	0– 6	120	0.4	0.66	0.04	17	–	2.1.3.a
	6– 28	280	0.2	0.23	0.02	11		
	28– 59	300	0.1	0.05	0.01	5		
3	1– 40	180	0.4	0.45	0.04	11	1	1.2.1
	40– 75	320	0.4	0.36	0.02	18		
	75–120	280	0.5	0.20	0.02	10		
4	0– 25	160	0.4	0.52	0.03	17	2	1.2.1
	50– 70	200	0.4	0.41	0.03	14		
	85–110	340	0.3	0.26	0.02	13		
5	0– 12	60	1.0	1.26	0.06	21	11	1.2.2.b
	12– 51	70	1.1	0.72	0.05	14		
	51– 84	65	1.0	0.75	0.03	25		
	84–120	16	1.4	0.60	–	–		
6	0– 30	8	0.3	0.52	0.04	13	21	2.2.1
	65–120	9	0.2	0.09	0.01	9		
7	0– 25	2	0.3	0.29	–	–	20	2.2.2
	40–100	6	0.2	0.12	–	–		
	100–120	7	0.4	0.06	–	–		
8	0– 20	3	0.4	0.35	0.04	9	19	2.2.2
	20– 40	2	0.2	1.05	0.06	18		
	40– 80	1	1.0	0.14	–	–		
	80–120	3	0.3	0.09	0.01	9		
9	0– 10	9	0.3	0.32	0.03	10	23	2.2.3.b
	40– 50	9	0.3	0.17	0.02	9		
10	0– 15	4	0.3	0.47	0.04	12	18	2.2.4.b
	15– 40	3	0.3	0.21	0.02	11		
	60– 80	3	0.2	0.09	0.02	5		
11	0– 25	20	1.0	0.79	0.04	20	4	1.3.1.a
	25– 40	21	0.7	0.47	0.02	24		
	40–110	22	0.7	0.20	0.02	10		
12	0– 30	26	1.1	0.91	0.06	15	12	1.3.2.a

	30– 60	56	1.0	0.40	0.03	14		
	60– 90	33	1.2	0.24	–	–		
	90–120	21	1.7	0.24	0.03	8		
13	0– 20	24	1.2	1.06	0.06	18	10	3.1.3
	20– 50	10	0.8	0.78	0.04	20		
	60– 95	25	0.7	0.40	0.02	20		
14	0– 35	3	1.7	1.35	0.09	15	7	2.3.2
	50– 65	4	0.9	0.30	0.04	8		
15	0– 15	18	1.1	1.06	0.08	13	5	1.3.1.c
	15– 45	18	0.9	0.43	0.04	11		
	45– 60	16	0.9	0.23	0.03	18		
16	0– 20	10	1.8	0.93	0.07	13	6	1.3.1.d
	20– 40	18	1.0	0.40	0.06	7		
	40–120	18	0.7	0.24	0.03	8		
17	0– 15	42	2.0	1.00	0.11	9	13	1.3.2.b
	15– 29	45	2.0	1.00	0.07	14		
	29– 47	10	2.2	0.63	0.06	11		
	47– 75	4	3.2	0.33	0.04	8		
	100–120	6	2.2	0.12	0.03	4		
18	0– 10	3	0.8	1.13	0.08	14	17	2.3.1
	20– 60	1	1.3	0.23	0.03	8		
	100–120	2	1.6	0.12	–	–		
19	0– 10	2	2.6	2.18	0.15	15	14	2.3.3
	10– 30	6	2.1	1.16	0.08	15		
	30– 60	4	2.0	0.63	0.06	11		
	60– 95	1	3.8	0.46	–	–		
	95–120	2	3.6	0.25	0.07	4		
20	0– 13	1	3.2	2.59	0.18	14	15	2.3.4
	13– 25	3	3.1	1.56	0.13	12		
	25– 54	1	3.4	0.77	0.09	9		
	54– 97	1	2.9	0.30	0.05	6		
	97–120	1	2.8	0.26	–	–		
21	0– 15	3	2.2	1.77	0.15	12	8	3.1.1
	15– 30	1	2.1	1.37	0.10	14		
	30– 50	1	3.4	0.87	0.13	7		
22	0– 15	5	3.6	2.85	0.24	12	16	3.1.1
	15– 45	3	3.2	0.90	0.10	9		
	50– 60	< 1	2.1	0.34	0.04	9		
	90–100	< 1	3.2	0.21	–	–		
23	0– 25	1	3.0	2.55	0.26	10	9	3.2.4
	25– 60	2	3.9	0.88	0.11	8		
24	0– 50	2	2.7	2.00	0.12	17	22	3.2.2
	50–120	2	0.5	0.28	0.03	9		

DESCRIPTIONS OF SOIL PROFILES

1. Surface level. The whole profile consists of more or less bleached coarse sand.

0– 22 cm	light grey; some gravel
22– 72 cm	light brown-grey, spotted
72–120 cm	white

2. Surface level, with very low kawfoetoes. The whole profile consists of more or less bleached coarse sand.

0– 6 cm	light brown-grey, slightly spotted
6– 28 cm	grey, few lighter spots
28– cm	white

3. Surface level, slightly uneven. The whole profile consists of coarse sand with some gravel.

0– 1 cm	pink bleached grains
1– 40 cm	dark brown
40– 75 cm	dark grey-brown
75–120 cm	orange-brown

4. Surface slightly convex. The whole profile contains some fine gravel.

0– 25 cm	dark brown coarse sand with pink bleached grains
25– 50 cm	idem, without pink grains
50– 70 cm	dark grey-brown, slightly loamy coarse sand
70– 85 cm	idem, less humic
85–110 cm	idem, brown
110–120 cm	orange-brown coarse-sandy loam

5. Surface level. The whole profile contains some fine gravel.

0– 51 cm	dark grey loamy coarse sand
51– 84 cm	dark grey passing into brown-grey coarse-sandy loam
84–120 cm	brown-grey passing into yellow-brown coarse-sandy clay loam with grey and orange-yellow spots

6. Surface slightly inclined. The whole profile consists of loamy sand.

0– 30 cm	brown-grey with few rusty spots; gradually passing into
30– 40 cm	light brown-yellow with minute yellow spots
40– 65 cm	orange-yellow, minutely spotted with white and a little yellow; 1 % gravel
65–120 cm	white with minute orange-yellow spots; locally red spots beginning at 85 cm; plastic

7. Surface inclined.

0– 25 cm	light brown loamy sand, gradually passing into
25–100 cm	yellow fine-sandy loam with 10 % gravel
(50– 60 cm	gravel layer)
100–120 cm	light yellow sand with small white-yellow spots; locally red spots beginning at 80 cm

8. Surface inclined.

0– 20 cm	light brown loamy sand, abrupt transition into
20– 40 cm	yellow silty clay with minute orange-yellow and red-brown spots; gradually passing into
40– 80 cm	yellow clay loam with minute red-brown, orange-yellow, light purple and white spots
80–120 cm	coarse-sandy loam, minutely spotted white, yellow and ligh purple-red

9. Surface level.

0– 10 cm	pink-brown loamy sand with very few small greenish spots
10– 40 cm	greenish loamy sand with small light brown spots
40– 50 cm	grey-white sand, minutely spotted with green and light brown
50– 70 cm	light yellow with few minute green and light brown spots
70– cm	gravel

10. Surface slightly inclined.

0– 15 cm	light brown fine-sandy loam
15– 40 cm	yellow loamy sand
40–120 cm	sandy loam, finely spotted light red, bright red and yellow

11. Surface level.

0– 25 cm	dark brown-grey coarse-sandy loam
25– 40 cm	grey-yellow coarse-sandy clay loam
40–110 cm	orange-brown coarse-sandy clay loam
110–120 cm	pale orange coarse-sandy clay loam

12. Surface slightly inclined, partly covered by bleached coarse sand grains.

0– 30 cm	brown-grey coarse-sandy loam
30– 60 cm	grey-brown coarse-sandy clay loam
60– 90 cm	idem, with small grey spots
90–120 cm	yellow-brown clay with orange and yellow spots

13. Surface slightly inclined. The whole profile consists of coarse-sandy loam.

0– 20 cm	dark brown
20– 50 cm	dark brown-grey, with some ferruginous root-channel concretions
50– 65 cm	brown-grey, with ferruginous root-channel concretions
65– 95 cm	grey-brown, with idem
95–100 cm	light brown-grey, with idem
100–120 cm	light yellow-grey with yellow spots

14. Surface inclined, with small worm heaps.

0– 35 cm	brown-black fine-sandy loam with bleached sand grains,
35– 65 cm	gradually merging into brown-grey coarse-sandy loam, with ferruginous root-channel concretions,
65– 80 cm	gradually merging into light grey coarse-sandy clay loam with large red and yellow spots
80–100 cm	grey-white coarse-sandy clay with large red and yellow spots
100–120 cm	grey-white silty clay with large red and yellow spots

15. Surface slightly inclined, 80 % covered by bleached coarse sand grains. The whole profile consists of coarse-sandy clay loam.

0– 15 cm	dark brown-grey
15– 45 cm	grey yellow-brown
45– 60 cm	light brown-yellow,
60–110 cm	gradually passing into orange-brown
110–120 cm	pale orange-brown with few indistinct orange spots

16. Surface slightly inclined, with patches of bleached coarse sand grains. The whole profile consists of sandy clay loam.

0– 10 cm	brown-grey with few bleached sand grains
10– 20 cm	lighter brown-grey, no bleached grains
20– 40 cm	grey-brown with indistinct pale orange spots
40–120 cm	pale brown-orange

17. Surface level, partly covered by bleached coarse sand grains.

0– 15 cm	grey coarse-sandy clay loam
15– 29 cm	brown-grey coarse-sandy clay loam, gradually passing into
29– 47 cm	orange coarse-sandy clay
47– 75 cm	orange clay with dark grey and purple concretions
75–120 cm	orange coarse-sandy clay, very hard

18. Surface slightly inclined.

0– 10 cm	light brown sandy clay loam with rusty spots, plastic; abrupt transition into
10– 20 cm	orange-yellow clay loam with few minute white and purple-red spots, gradually passing into
20– 60 cm	yellow clay with small yellow-white and purple-red spots; sticky
60– 70 cm	gravel
70–100 cm	finely spotted, white, purple-red and yellow
100–120 cm	white silty clay loam with small orange-yellow and light yellow spots

19. Surface level, with worm heaps.

0– 10 cm	dark grey loam with bleached sand grains
10– 30 cm	grey to brown-grey coarse-sandy clay loam with bleached sand grains
30– 60 cm	brown-grey to orange clay loam; sticky
60– 95 cm	orange, heavy clay with yellow spots; very sticky
95–120 cm	mottled heavy clay, orange and light brown-grey with purple concretions

20. Surface level.

0– 13 cm	brown-grey silty clay loam; sticky
13– 25 cm	brown-grey passing into orange silty clay
25– 54 cm	orange heavy clay, with brownish passing into light grey spots
54– 97 cm	mottled silty clay, light grey, purple and orange
97–120 cm	heavy clay

21. Flat kawfoetoes of about 5 cm high, occupying 60 % of the surface.

0– 5 cm	dark brown-grey silty clay loam,
5– 15 cm	gradually passing into idem with ferruginous root-channel concretions
15– 30 cm	grey clay loam with indistinct grey-brown spots and with ferruginous root-channel concretions,
30– 50 cm	gradually merging into mottled heavy clay, grey, red-brown and red
50– cm	idem, light yellow, yellow-grey and red

22. Surface slightly inclined.

0– 15 cm	dark grey silty clay with ferruginous root-channel concretions
15– 45 cm	light grey heavy clay with light orange spots, especially along the root channels; gradually passing into
50– 60 cm	mottled clay loam, brown-grey and brown-yellow
60–120 cm	light grey to white heavy clay with brown-yellow and red spots

23. Surface slightly inclined. Rounded kawfoetoes of 15 to 20 cm high, occupying 50 % of the surface.

0– 25 cm	dark grey silty clay loam; abruptly changing into
25– 60 cm	heavy clay, grey with brown-grey and yellow spots
60– 65 cm	idem, with light grey spots and charcoal remains
65– 80 cm	idem, light grey with grey and red-brown spots
80– 85 cm	idem, grey with light grey and orange-grey spots
85– cm	mottled heavy clay, yellow, red, grey, and light grey

24. Kawfoetoes of 20 cm high, occupying 30 % of the surface.

0– 50 cm	dark grey silty clay with rusty spots; plastic
50–120 cm	dark grey sandy loam with yellow spots and a few remains of charcoal; sticky

CHAPTER III

THE INVESTIGATED SAVANNAS

The investigated savannas are described here in order to give a general impression of their flora and vegetation in relation to the prevailing environmental conditions.

The reader is referred to the maps 1 : 40 000 edited by the "*Centraal Bureau Luchtkaartering*" (Central Bureau of Aerial Survey), Surinam.

Historical data have been obtained from some old maps drawn by A. DE LAVAUX (about 1750), I. H. MOSEBERG (1801) and Js. VAN DEN BOSCH (1818).

Where this was possible the vegetation was described in its optimal state. However, if a savanna has received only a short visit, this was not possible. In that case the dates of the visit and of the last fire, if the latter was available, are mentioned.

A detailed review of the total flora is given in Chapter IV, whereas the vegetation types are described, compared and classified in the Chapters V and VI on the basis of the Tables 6, 7, 8 and 10. In Chapter VII an attempt is made to interpret the existence of the savanna vegetations.

In the text of this chapter a group of species is sometimes followed by a figure and a letter in brackets referring to the categories distinguished in IV. 1. The treatment of every concrete local community is followed by some figures in brackets referring to the abstract vegetation unit to which it belongs (see V. 8 and VI).

III. 1. SAVANNAS OF THE WELGELEGEN-TYPE

Four savannas of the Welgelegen-type have been visited, all belonging to the wet variation and situated along the Para river or one of its tributaries.

From the old maps it appears that they all occupy part of the grounds of former plantations. Creole descendants of the plantation labourers are still living in the old villages. However, according to ZONNEVELD & KRUYER (1951), the so-called plantations in the Para region were no true plantations but concessions for the cutting of wood.

The structure of the heavy soil is, in combination with the climate, responsible for the fact that the upper layer is alternatively desiccated and waterlogged. Kawfoetoes and deep cracks are two features characteristic of these two situations. The vegetation is burnt at least once a year.

It is very well possible that the present situation would persist even if the fires were stopped. It is not likely, however, that the former "plantations" were started under such conditions. It seems more likely that the present structure of the soil is the result of an advancing savannisation, which started either at the time of the concessions or was brought about later by shifting cultivation and periodic burning.

III. 1. 1. **The savanna of Bersaba**

III. 1. 1. 1. *General data*

Position: immediately W. of the village Bersaba
Map 1 : 40 000 : 14 c
Area: about 30 ha
Date of visit: November 8th, 1958
Last fire: September 1958

The savanna is bordered on the W. side by the village and the Coropina creek, elsewhere by secondary forest (Sur.: *kapoeweri*). It is divided by a railroad into a small western and a bigger eastern part. Some parts are traversed by remnants of ditches which are of recent date.

III. 1. 1. 2. *Vegetation*

The unburnt vegetation found on a part without remnants of ditches was very dense and very dry. It consisted mainly of grasses like *Hypogynium virgatum*, *Leptocoryphium lanatum* and *Mesosetum cayennense* and the dwarf-shrub *Tibouchina aspera*. The only flowering species were *Hypogynium*, with some 80 cm high shoots, *Rhynchospora glauca* and the yellow-flowered *Turnera guianensis*. The combination of these three species is characteristic of this savanna type and indicative of the conditions prevailing here. Two more species, *Arundinella hispida* and *Gerardia hispidula*, which were collected here in May 1956, may complete the picture. (**Ass. 3.1.1**)

The vegetation on the burnt parts was much thinner, but there all grasses were flowering. Proportionally the composition was about the same, but some species were (still) lacking. Among these was *Hypogynium*, which needs some months to recover after a fire. In the remnants of the ditches *Tibouchina* was still more numerous.

On this savanna not one tree or shrub was seen.

III. 1. 2. **The savanna of Vierkinderen** (Photo 13)

III. 1. 2. 1. *General data*

Position: some hundreds of meters W. and S. of the village Vierkinderen
Map 1 : 40 000 : 14 c
Area: about 14 ha
Date of visit: November 8th, 1958
Last fire: beginning of October 1958

On the N. and E. sides the savanna is bordered by the swampy area which surrounds the village and by the Tawajakoera creek, on the other sides by kapoeweri. The surface is notably convex. It is partly traversed by remnants of not very old ditches.

III. 1. 2. 2. *Vegetation*

The burnt herb vegetation was nearly identical with that on the savanna of Bersaba. Here too *Hypogynium virgatum* was not found, but according to HEYLIGERS (unpubl.) it locally dominated the aspect of the savanna in May 1958. Still more characteristic for this vegetation type are the species *Gerardia hispidula* and *Schultesia brachyptera*, collected here in september 1948. (**Ass. 3. 1. 1**)

On the whole savanna 2 specimens were observed of *Curatella americana*, some of *Coccoloba latifolia* and some other species.

III. 1.3. **The Bigi-olo savanna or Hanover savanna**

III. 1.3.1. *General data*

Position: immediately N. of the village Hanover
Map 1 : 40 000 : 14 c
Area: about 24 ha
Date of visit: October 30th, 1958
Last fire: ?

On the E. side the savanna is bordered by kapoeweri, on the S. side by the village, at the other sides by the *Eleocharis*-swamp of the Para river.

In 1918 a company started a project to bring the savanna into cultivation: many *Curatellas* were removed. The plan was soon given up, and only some shallow ditches and remnants of them are left as witnesses of this project.

III. 1.3.2. *Vegetation*

The greater part had the character of an orchard savanna. *Curatellas* of about 8 m high covered nearly everywhere about a fifth of the surface, whereas the herb layer did not leave a single open spot. The dominating herb was *Imperata brasiliensis*, a species which seems to have some preference for slightly shaded localities. The same holds good for *Heliconia psittacorum*, which was also well represented. Other abundant species were *Leptocoryphium lanatum*, *Tibouchina aspera* and the small sedge *Rhynchospora podosperma*. (**Ass. 2.3.3**)

Along the eastern border and on other open spots without *Curatella* the herb layer was somewhat different. *Imperata* played a minor part and the place of *Rhynchospora podosperma* was taken by *Andropogon leucostachyus*. Moreover some species were present which as a rule are bound to wetter and/or heavier soils than the former vegetation type, so e.g. *Rhynchospora glauca* and *Echinolaena inflexa*. (**Ass. 3.1.1**)

On the unburnt part the only flowering species was *Rhynchospora cephalotes*. The recently burnt part could be recognized from afar by the hairy inflorescences of *Imperata*, entitled by our creole guide as "poespoesi tere" (cat's tail).

III. 1.4. **The Fransina savanna or Welgelegen savanna**

III. 1.4.1. *General data*

Position: 2.5 km S.E. of the village Hanover
Map 1: 40 000 : 14 c
Area: about 110 ha

Date of visit: October 30th, 1958
Last fire: recently

The savanna touches with its W. side the Para river. It is surrounded by swamps and kapoeweri. One inhabited cottage near the river was the only remnant of the former village of Welgelegen, belonging to the plantation of that name.

III. 1.4.2. *Vegetation*

Nearly the whole savanna presented only a thin, green haze caused by very young blades of *Leptocoryphium lanatum* and also some that may have belonged to *Hypogynium virgatum.* Probably these two species were the first signs of the characteristic vegetation type of savannas of this kind (**ass. 3.1.1,** see the savanna of Bersaba). This idea is confirmed by the former collection of *Turnera guianensis* and of *Cassia tetraphylla* var. *brevipes* at this place.

A narrow zone of savanna cashew (*Curatella*) in the western part against the kapoeweri, contained more recognizable species. The *Curatellas* apparently had outgrown the influence of the fires, for they were about 14 m high and their appearance was strikingly slender. The thin herb layer consisted of *Imperata brasiliensis*, *Leptocoryphium lanatum*, *Tibouchina aspera*, *Heliconia psittacorum* and some other species. A remarkable species was *Hypoxis decumbens*, a small Amaryllid with the aspect of a crocus. It is likely that it belongs to the small group of species which on savannas flower only shortly after a fire, i.e. before the vegetation becomes more closed.

The vegetation as a whole looked very much like the orchard vegetation of the Bigi-olo savanna (**ass. 2.3.3**).

III. 2. SAVANNAS OF THE COESEWIJNE-TYPE

See I. 2.2.1. The vegetation of all savannas treated here is burnt at least once a year.

III. 2.1. **The Lobin savanna, loamy part**

III. 2.1.1. *General data*

Position: between Zanderij and Hanover
Map 1 : 40 000 : 14 c
Area: about 100 ha

The Lobin savanna is a narrow, north-eastern extension of the vast savanna complex south and west of Zanderij. Sometimes it is called erroneously "Hanover savanna", but this name applies to the smaller isolated savanna on the other side of the Para river, against the village of Hanover (see III.1.3). The savanna consists of a small white-sandy part (see III.3) and, more to the north-east, a larger part with a soil composed of loamy sand and heavier soil types. The latter will be called the "loamy part".

The topography is slightly rolling. In general the surface has the shape of a flat ridge, which forms the watershed between two rivulets, both tributaries of the Para river. One of the rivulets partly fringes the northern and the north-eastern extensions of the savanna.

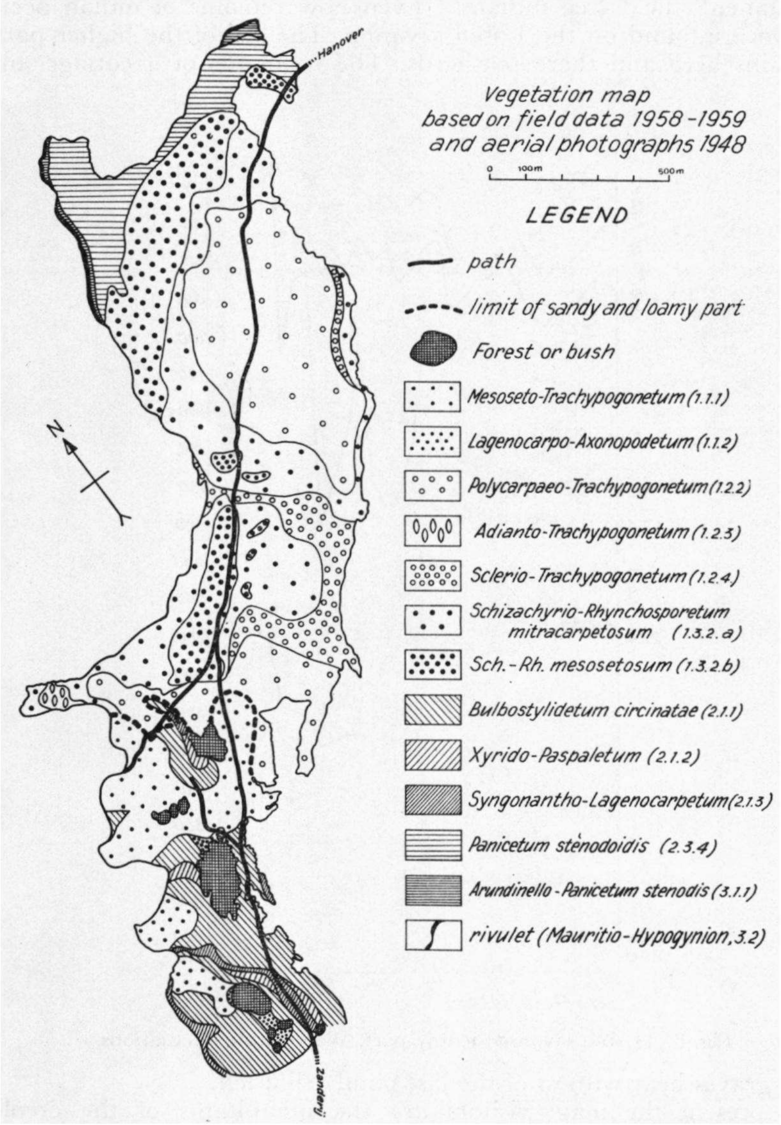


Fig. 7. Lobin savanna

It appears from old maps that the watershed formerly served as the boundary between several plantations. The greater part of the loamy savanna was occupied by the plantation Mawacabo. The "plantations" along the Para river, however, were concessions for cutting wood (see III.1).

On a map from about 1750 drawn by A. DE LAVAUX, on the savannas directly bordering on these plantations is written "Vrye Indiaanen", i.e. "free indians". Even now remains of indian occupation are found on the Lobin savanna. The soil of the higher parts contains here and there potsherds. The remnants of a cottage and some graves bear witness of the last family that left.

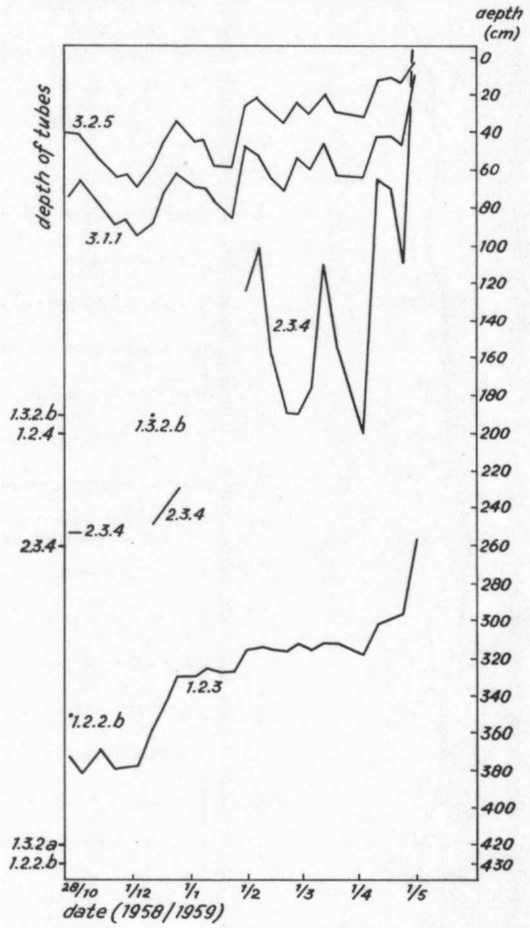


Fig. 8. Lobin savanna, loamy part. Water-table fluctuations.

At present the main visitors are the inhabitants of the creole village of Hanover. Everywhere in the surrounding forest that partly is made up of kapoeweri they have their planted clearings, in particular along the eastern border. Some of the clearings are almost bordering upon the savanna itself. The villagers also cut trees to sell them.

According to an inhabitant of Hanover the savanna has expanded recently on its north-eastern tip after a clearing had been abandoned there. A comparison of the present situation with an (indistinct) outline-map of 1922–23 (GONGGRIJP, 1923) seems to confirm this information. The same map already shows the narrow extension found on the western side.

The vegetation was sampled from August up to December; it was burnt in two phases in the first half of December and mapped after the recovering. VAN DONSELAAR–TEN BOKKEL HUININK (1966) deals with structure, root systems and periodicity of the savanna plants and vegetations and with physiognomic characters of the trees, all in relation with the habitat.

III. 2.1.2. *Soil* (Figs. 6 and 8)

There is a close correlation between the elevation, the texture and the degree of humidity of the soil in different spots. The texture of the upper layers ranges from loamy sand via sandy loam, sandy clay loam and silty clay loam to silty clay, whereas the degree of humidity in this sequence ranges from dry to very wet. As a rule the soils have a normal profile, becoming heavier with increasing depth and consequently also less permeable. In accordance with the increasing heaviness and humidity observed down the slight slopes, the upper limit of the "gley"-phenomenon and the mottling too are found at a higher level in the profile.

The stretch from about the centre of the loamy part into the northern and north-eastern extensions presents the whole sequence and may be considered to be a slightly developed catena.

The outer edge of the northern extension has a very wet silty clay soil. Here the savanna just passes the limit of the "dek" landscape and advances slightly on the adjoining "gully swamp soil" that belongs to the "old sea-clay landscape" (map in VAN DER EYK, 1957).

III. 2.1.3. *Vegetation*

III. 2.1.3.1. Orchard savanna and one-layered communities (Fig. 7)

Two relatively elevated, sandy parts are occupied by a more or less closed, very attractive orchard-savanna vegetation. Large patches dominated by gnarled, up to 8 m high savanna cashews (*Curatella*) are intermingled with open spots, where only low and burnt down trunks are found. The only notable epiphyte on the trees is the orchid *Polystachya luteola.*

The herb layer is closed or nearly so, but not dense, varied and altogether luxuriant, at least for a savanna vegetation.

Trachypogon plumosus is dominating; other important grasses are *Axonopus pulcher* and *Schizachyrium riedelii*; the sedge *Bulbostylis junciformis* has to be mentioned too. Among the many forbs ¹) the portion

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1) WEAVER and his collaborators apply this useful word to all herbs, except grasses and sedges. However, a definition could not be found.

of the Papilionaceae is by far the largest with 22 species: *Cassia* 4, *Aeschynomene* 3, *Stylosanthes*, *Tephrosia*, *Desmodium*, *Eriosema*, the climbing *Phaseolus* and *Centrosema* each 2, and 3 other genera each 1. There are 9 species of Compositae of which 2 are *Eupatoriums*. The shadow-loving *Heliconia psittacorum* may also occupy an important place, but only under the *Curatellas*. In the open spots *Axonopus pulcher* is more numerous. In general the vegetation of the open spots is a little more uniform, mainly owing to the very high abundance of *Trachypogon*.

There are some weeds among the forbs, e.g. *Crotalaria stipularia* and *Euphorbia brasiliensis*, but it is uncertain where the original habitat of these species is to be found.

Though the mean height lies between 80 and 100 cm, there are also low herbs like *Mitracarpus microspermus*, *Cyperus amabilis* and *Polycarpaea corymbosa*, of which the last one is characteristic for this vegetation type. On the other hand there are some species with high overtopping shoots like *Desmodium asperum* and *Aeschynomene paniculata*.

Some species are represented so long as the vegetation is fully developed in a more or less degenerated state or only by a radical rosette, e.g. *Hybanthus ipecacuanha*, *Ayenia tomentosa*, *Oxypetalum capitatum* and *Conyza chilensis*. *Myrosma cannifolia* even has retired completely into the soil and can be found only by digging up the small tubers. All these species, of which the examples mentioned are characteristic for this community, start flowering shortly after the vegetation has been burnt. (**Ass. 1.2.2,** Photo 1)

Starting from the largest *Curatella* vegetation to the north and following down the catena, one finds a rather abrupt transition to the next vegetation type. As soon as the savanna cashews are left behind and the soil has changed into a sandy loam, two thirds of the number of species disappear. Little is left from the bunch of pretty forbs. As the vegetation becomes thinner and lower, shade-loving species cannot maintain themselves any more. The main grasses however remain the same, but *Trachypogon* becomes less, *Axonopus pulcher* more abundant. The persistence of *Schizachyrium*, *Bulbostylis junciformis* and some other species is in agreement with the corresponding dryness of the soil. *Tibouchina aspera* comes to the fore; quite new species are *Rhynchospora barbata*, *Aristida tincta* and *Axonopus purpusii*. The latter two indicate the changed texture of the soil. (**Ass. 1.3.2, subass. a,** Photo 4)

The next change, corresponding once more with a somewhat heavier texture of the soil, is the appearance of *Mesosetum cayennense* and, a little further on, of *Leptocoryphium lanatum*. From the decrease in number of *Bulbostylis junciformis* and *Schizachyrium* and the disappearance of *Mitracarpus microspermus*, all indicators of dry soils, we may conclude that the habitat becomes slightly more humid. The part of *Tibouchina* is smaller again, but now it is concentrated on low termitaries. (**Ass. 1.3.2, subass. b**)

Gradually the soil becomes still heavier and consequently the impermeability of the subsoil increases. In the northern and eastern extensions of the savanna the upper layer consists of wet silty clay loam, which cracks in the dry season. The vegetation becomes rather low, but very dense. *Trachypogon* disappears first, *Axonopus pulcher* next, *Leptocoryphium* becomes slightly more frequent. Some quite new species, indicators of a wet soil, begin to play a part in the bulk of the vegetation, viz. *Rhynchospora globosa* and *Panicum stenodoides*.

Axonopus purpusii is represented only by the form with narrow leaves and this too seems to be correlated with the water economy of the soil. *Andropogon leucostachyus* is another notable new species. (**Ass. 2.3.4**)

Along the edge of this part of the savanna, in those localities where the border is formed by a rivulet, a narrow zone is occupied by still another vegetation type. The main species of the former community are present, except *Mesosetum cayennense*. The new species are indicators of very wet and heavy soils with pronounced kawfoetoes. They are *Rhynchospora glauca*, *Echinolaena inflexa*, *Panicum nervosum* and locally some *Hypogynium virgatum*. This community is identical with that which is common on the savannas belonging to the Welgelegen-type, but it is not very well developed here. (**Ass. 3.1.1**, Photo 3)

The rivulets themselves have a quite different vegetation. In the one along the N.W. side the four last mentioned species are present, but the real savanna plants are on the whole in the minority. The tall grass *Ischaemum guianense* is dominating. This species is characteristic for savanna rivulets, together with e.g. *Scleria notoptera*. For the rest there is a strikingly high number of species that are found also in swamps, as *Montrichardia arborescens*, *Scleria microcarpa*, *Blechnum indicum* and the palm *Mauritia flexuosa*. (**Ass. 3.2.1**)

Along the most eastern tip of the savanna the (deeper) rivulet contains hardly other than swamp species. *Lagenocarpus guianensis* and *Scleria notoptera* are the most abundant ones. (**Comm. 3.2.5,** see Photo 3)

The last community that has to be mentioned from this part of the savanna, occupies small patches in the associations 1.3.2.b and 2.3.4, in particular near the western forest border. It consists of small groups of *Curatella*, rather close together, with an undergrowth of *Imperata brasiliensis*, *Tibouchina*, *Heliconia* and *Scleria bracteata* as its main participants. Though it is not quite the same, it has much in common with the orchard-savanna type occurring on the Bigi-olo savanna (**ass. 2.3.3**), though the latter occupies more space.

On other parts of the savanna the community bordering the rich vegetation with savanna cashews is different as a rule. It may be described as an impoverished form of the herb layer under the *Curatellas*, with a little less *Trachypogon* but a little more *Axonopus pulcher*. *Tibouchina* and *Symplocos guianensis*. The only new species found here, the tiny *Scleria micrococca*, appears to have its optimum in this vegetation type (**ass. 1.2.4**). It is followed by association 1.3.2.a etc. (Photo 2).

The narrow extension on the western side presents another type of orchard savanna. Here the loamy sand is moister than in the central part and consequently there is a shifting in the composition of the herb layer. A number of the forbs is absent and *Trachypogon* may be less abundant. On the other hand some species are more numerous or even new here, mainly belonging to the "shadow-loving" group e.g. *Paspalum plicatulum*, *Imperata brasiliensis* and the small fern *Adiantum serrato-dentatum*. Characteristic for this vegetation type is *Cassia faginoides*. **(Ass. 1.2.3)**

Where the vegetation touches upon the forest border, it is always a little more shrubby and here *Tibouchina aspera* belongs always to the participating species. In this habitat the older specimens often are infected with the half-parasite *Oryctanthus florentulus*.

Main correlations of the vegetation types with the properties of the soil:

Ass. 1.2.2 – dry loamy sand
Ass. 1.2.3 – dry to moist loamy sand, very humic
Ass. 1.2.4 – dry to moist loamy sand, humic
Ass. 1.3.2, subass. a – dry to moist sandy loam
subass. b – moist sandy clay loam
Ass. 2.3.4 – wet to very wet silty clay loam
Ass. 3.1.1 – very wet silty clay

III. 2.1.3.2. Bushes (see also VI.5 and Table 10)

There are many bushes on the savanna, in particular in the southern and eastern part and near the S.E. border. As a rule they are more or less rounded with a maximum size of a hundred square meters. **(Type B 3)**

There are mostly some small – up to about 15 m high – trees in the centre. The most common among them are *Byrsonima crassifolia*, *Maprounea guianensis*, *Protium heptaphyllum*, *Pithecellobium jupunba* and also *Curatella*. These species may also be present as shrubs. The same holds for *Xylopia frutescens*, *Miconia ciliata*, *Siparuna guianensis*, *Tapirira guianensis*, the characteristic species *Cupania scrobiculata* var. *frondosa* and several others. The bushes are usually surrounded by a belt of the rough-leaved *Davilla aspera*.

The species mentioned so far are either characteristic for savanna bushes in general (2a) or they are normal species on the savannas in another way (2 b–f). This is also true for species like *Rollinia exsucca* and *Isertia parviflora*, which belong to the flora of the rain forest, but flourish in the bushes too, though they remain low (2g). There are, however, some species that do not flower here and obviously have to be regarded as pure forest plants, so e.g. *Pithecellobium jupunba*, *Virola sebifera* and the climbing *Doliocarpus guianensis* (3). It is noteworthy that many of the woody species of these bushes are common in kapoeweri too.

The sparse undergrowth mainly consists of species which are known also from the open savanna, e.g. *Tibouchina aspera*, *Rhynchospora cephalotes*, *Heliconia psittacorum* and *Trachypogon*.

The distribution of the bushes is more or less correlated with that of association 1.3.2.a. The concentration along the S.E. border is due to the fact that on account of the prevailing eastern winds this part of the savanna is reached less frequently by fires.

III. 2.1.3.3. Single trees

Small, single trees and palms are found nearly everywhere. Only the northern part and the western extension are treeless. In general the height of the trees is not more than 15 m.

In total 33 species were observed, but only 15 of them were represented by more than 5 specimens. The majority is also present in the bushes, either as trees or as shrubs. The main exceptions are *Licania divaricata*, *Vismia angusta* and the spiny awara (*Astrocaryum segregatum*). A small group of another palm species, *Acrocomia lasiospatha*, was found between the *Curatellas* in association 1.2.2. Its vernacular name is "nengrekondre awara".

The most frequent species is *Byrsonima crassifolia*. It is present everywhere, least in the orchard associations 1.2.2 and 1.2.3. The other main trees with their abundance and with their distribution over the vegetation and the soil types are given in the following list.

	Association soil type	1.2.2 ls	1.2.4 ls	1.3.2.a s(c)l	1.3.2.b scl
Tapirira guianensis	very numerous	×	×	×	×
Maprounea guianensis	numerous	×	×	×	×
Astrocaryum segregatum	numerous	×	×	×	×
Pithecellobium jupunba	28 specimens	×	.	×	.
Licania divaricata	20 specimens	×	×	×	×
Araliacea spec.	17 specimens	(×)	.	×	.
Himatanthus articulatus	12 specimens	×	.	×	×
cf. *Casearia* spec.	10 specimens	×	(×)	(×)	.
Vismia angusta	9 specimens	×	×	×	.
Rollinia exsucca	6 specimens	.	.	×	×
Rapanea guianensis	6 specimens	×	×	.	.
Trattinickia burserifolia	6 specimens	.	.	×	(×)

It is noteworthy that in the areas occupied by the association 1.2.2 the trees do not occur in the centre but only near and in the transition zone to the adjoining community.

Astrocaryum segregatum is most numerous near the path.

The tree-like *Ravenala guianensis* with its large banana-leaves is seen at many places along the wetter stretches of the forest border and moreover here and there in small groups in association 1.3.2.a.

It is striking that, just as the bushes, the trees are most numerous in association 1.3.2.a on sandy loam, and that the highest concentration (of species and specimens as well) is found along the S.E. border.

Most of the tree species are common in savanna wood and/or forest, and many of them also belong to the flora of the rain forest. The majority is also common in kapoeweri.

Very remarkable were two specimens of *Hymenolobium petraeum*. Up till now this tree has been found in Surinam only here and on the Coesewijne savanna.

The other rare trees not mentioned before are *Protium heptaphyllum* (5), *Symplocos guianensis* (4), *Clusia* spec. (4), *Cecropia* vs. *surinamensis* (4), *Lacistema aggregatum* (3), *Mapouria opaca* (2), *Myrcia fallax* (2), *Bombax nervosum* (2), *Maximiliana maripa* (2), *Xylopia frutescens* (2), *Goupia glabra* (1), *Piratinera velutina* (1), *Tabebuia capitata* (1), *Cupania scrobiculata* (1), *Ocotea* spec. (1), *Torrubia* spec. (1), *Virola* spec. (1).

III. 2.2. **The savanna Mimili Okili** (Fig. 9)

III. 2.2.1. *General data*

Position: 2.2 km N.E. of the Arowak indian village Powaka, on the eastern side of the Siparipabo creek.
Map 1 : 40 000 : 14 c
Area: 140 ha
Dates of visit: March 26th and 28th, 1959
Last fire: November 1958

The savanna presents a slightly undulating aspect. In general it is sloping to the south and the west. It is surrounded by forest.

Old maps show that the former plantations along the Suriname river extended more or less to the northern border of this savanna.

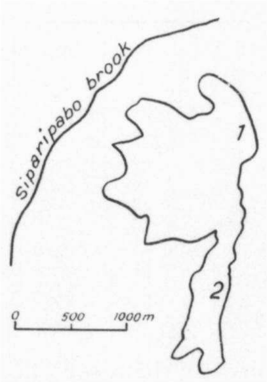

Fig. 9. Mimili Okili.

1 = Adianto-Trachypogonetum (1.2.3)
2 = Polycarpaeo-Trachypogonetum (1.2.2) + Sclerio-Trachypogonetum (1.2.4)

Muller (1945) carried out soil analyses from four different spots. As far as a comparison is possible, the results seem to indicate a sandy clay loam. Frickers (1945) mentions that at a depth of 30 to 60 cm the subsoil becomes impervious.

In the years 1936–1940 it was tried to raise cattle on this savanna, but without success (Frickers).

Sometimes the savanna is wrongly called "Powaka savanna". This name should be applied only to the extensive white-sand savanna S. of the village. The indians of Powaka give the savanna to the N.E. of the village the name of Mimili Okili, which means in the Arowak language: "place where the mimili (= *Curatella*) grows".

III. 2.2.2. *Vegetation*

The savanna is for the greater part occupied by a relatively low herbaceous vegetation without trees or shrubs. Abundant species occurring everywhere are *Trachypogon plumosus*, *Axonopus pulcher*, *Leptocoryphium lanatum*, *Aristida tincta*, *Rhynchospora* spec. and *Tibouchina aspera*.

However, on closer examination it appears that two communities may be distinguished with a continuous transition between them. In the first one the species mentioned so far are slightly more abundant, while *Polygala longicaulis* and the typical form of *Axonopus purpusii* are found only here. This vegetation type occurs on the higher parts. The other community is characterised by very much *Panicum stenodoides*, much *Rhynchospora globosa*, some *Andropogon leucostachyus* and the form of *Axonopus purpusii* with narrow leaves. These too types are identical with the **associations 1.3.2.b** and **2.3.4** respectively, of the Lobin savanna. It is remarkable that MULLER's results of the soil analyses are in agreement only with the former of these two communities.

Along the eastern side of the northern part there is a large orchard vegetation of *Curatella* mixed with other trees and shrubs. It has some western extensions in shallow depressions. The soil in these depressions appears to be more sandy and moist than in the adjoining parts. The undergrowth contains many fine Leguminous and other forbs and also much *Imperata brasiliensis*, *Paspalum plicatulum* and *Trachypogon*. It is clearly the same vegetation as that growing under the same conditions on the Lobin savanna (**ass. 1.2.3**).

Near the eastern side of the southern extension there is another stretch of orchard savanna, but here the soil seems to be drier. The savanna cashews locally cover about 5 % of the surface; the undergrowth is rather dense and rich in species. The community is obviously related to the former one. Though but one of the characteristic species is present (*Conyza chilensis*), the total floristic composition indicates that it is indeed an example of the main orchard type of the Lobin savanna (**ass. 1.2.2**).

The larger open spots in this area are occupied by a vegetation with some, but not all of the species found in the undergrowth of the *Curatellas*. It corresponds very well with the **association 1.2.4** of the Lobin savanna. Along the forest border it is very rich in *Tibouchina*.

In the lower parts more to the east, which usually assume the form of long depressions provided with kawfoetoes obviously serving as drainage channels, the dense vegetation consists mainly of quite other species. Besides *Imperata* and *Andropogon leucostachyus*, the dominating grass may be *Andropogon selloanus*. Other notable species are *Axonopus chrysites*, *Arundinella hispida*, *Echinolaena inflexa* and *Rhynchospora glauca*. This vegetation too is to be regarded as another form of a common association occurring on very wet and heavy soils (**ass. 3.1.1**). It has been mentioned already several times from other savannas.

III. 2.3. **The Doti savanna**

III. 2.3.1. *General data*

Position: between Karolina and Wisawini
Map 1 : 40 000 : 14 c and 22 a

Area: 75 ha
Date of visit: December 30th, 1958
Last fire: September–November 1958

The savanna is surrounded by forest. Former plantations along the Suriname river extended more or less to the eastern border of the present savanna.

III. 2.3.2. *Vegetation*

The main vegetation type consisted of much *Mesosetum cayennense*, *Aristida tincta*, *Rhynchospora globosa*, *R.* spec., *Panicum stenodoides*, *P. nervosum* and *Axonopus pulcher* with scattered *Curatellas*. On some lower places *Andropogon leucostachyus* might be dominating. It was obviously the community characterized by *Panicum stenodoides* (**ass. 2.3.4**) that had been found already on the Lobin savanna and on Mimili Okili.

A depression with low kawfoetoes in the western part of the savanna presented a vegetation mainly of *Panicum stenodes*, the narrow-leaved form of *Axonopus purpusii* and *Rhynchospora* spec. with some *Panicum nervosum*, *Echinolaena inflexa*, *Andropogon selloanus*, *Odontadenia nitida*, etc. This too represented the community usually found on very wet and heavy soils (**ass. 3.1.1**).

Along a part of the eastern side, against the forest border, there was a low-lying zone of about 60 m wide with high kawfoetoes. Here the most common species was *Axonopus surinamensis* and the second place was taken by *Leptocoryphium lanatum*. Other well represented species were *Eriochrysis cayennensis*, *Panicum nervosum*, *P. stenodes*, *Imperata brasiliensis*, *Scleria bracteata*, *Heliconia psittacorum* and *Blechnum indicum*. This vegetation resembled the community with *Ischaemum guianense* (**ass. 3.2.1**) found on the Lobin savanna, but it was not quite identical with it.

III. 2.4. **The Coesewijne savanna**

III. 2.4.1. *General data*

Position: 6.5 km S.W. of the village Bigipoika (or Gran-Poika)
Map 1 : 40 000 : 21 a
Area: about 1200 ha

The large Coesewijne savanna may be considered as a northwestern outpost of an extensive savanna complex W. of the Saramacca river. This complex consists of white-sandy savannas, except a northern extension occupied by the indian village Bigipoika, that belongs to the Coesewijne type too (see Fig. 2). The Coesewijne savanna is separated from the nearby Wana and Poika savannes by savanna forest. On the savanna itself too some large patches of forest are found. An extension in S.W. direction ends upon the swamp along the Coesewijne river.

The surface is undulating, varying in height from about 12 to 20 m above sea-level, but the S.W. extension slopes down to the 8 m level of the swamp. In general the central part is higher than the edges. There is only one short rivulet, which disappears in the forest at the northern side. It appears from a map of 1923 (GONGGRIJP, 1923) that already at that time the savanna had its present contour.

At the time of the investigation no indians were living on the savanna. So far as the memory of the present generation goes, the inhabitants of Bigipoika have always been the only visitors, but an old woman remembered that in her youth, some 60 years ago, people of another tribe were living there. Potsherds of a very large pot found under an awara-tree give evidence of this former occupation.

The people of Bigipoika have no planted clearings in the forests surrounding the savanna. They only traverse it on the way to their hunting-grounds and fishing-camps along the Coesewijne river. However, according to SCHULZ (1960) patches of secondary forest and many pieces of charcoal and potsherds in the soil bear witness of a more widely distributed population in this region very long ago as well as more recently.

The vegetation was sampled during the months of December, January, February and March with some interruptions. It was mapped afterwards with the aid of aerial photographs on the basis of the field observations.

III. 2.4.2. *Soil* (Fig. 6)

With regard to the soil the same may be mentioned in many respects as for the Lobin savanna (see III.2.1.2). However, the Coesewijne savanna is drier.

The greater part of the savanna has a dry to very dry soil with an upper layer of red sand, loamy sand or sandy loam. More to the west sandy clay loam may prevail and along the western forest border the soil may be locally very wet and humic. In the dry season the surface of the loamy parts is very hard.

The S.W. extension presents a slightly developed catena with upper layers changing in texture from sandy loam to silty clay loam and in humidity from very dry to very wet. However, according to the map of VAN DER EYK (1957) the illuvial material of the outermost zone belongs to the sediments of the Coropina formation.

III. 2.4.3. *Vegetation*

III. 2.4.3.1. Orchard savanna and one-layered communities (Fig. 10)

As a whole this savanna perfectly answers the usual definition of the savanna concept. It is a large, slightly undulating plain with a vegetation dominated by grasses and scattered with trees and bushes.

However, there are some stretches of orchard savanna. Though this vegetation type does not determine the aspect of the savanna, it has to be mentioned first because it represents ecologically one of the ends of the series of communities found here.

The orchard vegetation occupies the highest and most sandy places in the centre of the savanna. It is also present on both sides but at some distance of the rivulet. Probably the drainage is deep here.

The orchard trees are *Curatella americana* and *Byrsonima coccolobifolia* in about equal numbers. The degree of covering varies strongly from place to place, but this does not affect distinctly the composition of the herb layer.

The rather open herbaceous layer is dominated by *Trachypogon plumosus* and/or *Thrasya petrosa*. *Galactia jussieuana* too is always abundant. There are some more remarkable small shrubs that are restricted to these parts of the savanna, viz. *Pavonia speciosa* var. *hostmanni* with its large pink flowers, *Casearia silvestris* var. *lingua* and *Psidium grandifolium* with very thick and hairy leaves. The last species was found here for the first time in Surinam. Other species that may locally attain a high abundance are *Mesosetum cayennense*, *Bulbostylis fasciculata* and *Heliconia psittacorum* (Photo 9).

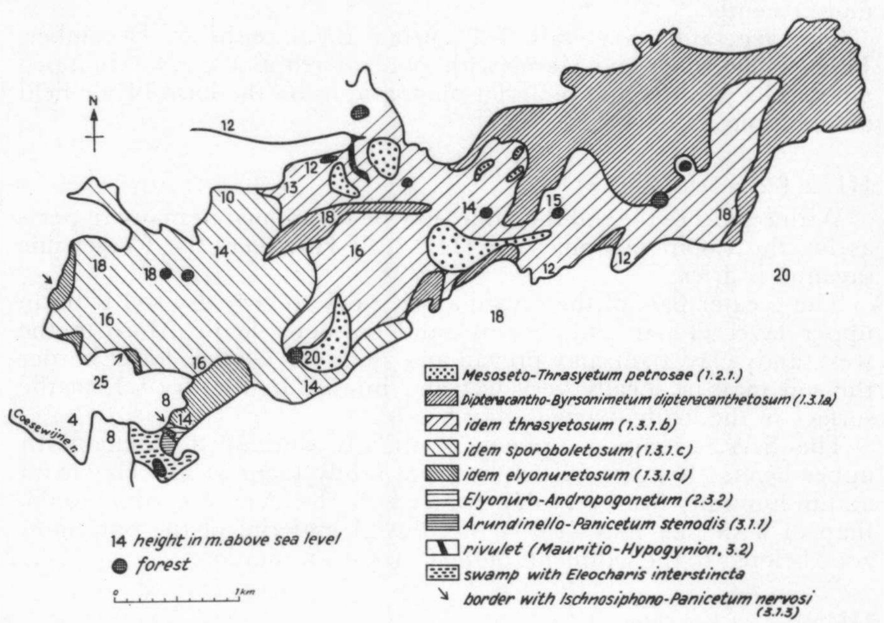

Fig. 10. Coesewijne savanna. Vegetation map based on field data of 1958–1959 and aerial photographs of 1947.

The vegetation reflects very well the properties of its habitat. Though it is not by far so rich in species, this community (**ass. 1.2.1**) clearly shows its affinity to the orchard vegetations of the other Coesewijne-type savannas (ass. 1.2.2 and 1.2.3).

Outside this community nearly the whole savanna is covered by a herbaceous vegetation with only here and there one of the orchard trees (**ass. 1.3.1**). The most remarkable species is the low *Byrsonima verbascifolia* (var. *villosa* fo. *spathulata*) with its long grey-hairy leaves resembling the ears of a donkey. When it produces its yellow flowers it gives the savanna a very pretty appearance. This flowering takes place a few months after the burning of the vegetation. Later on other, more numerous, but not so conspicuous species are going to determine the aspect of the savanna.

At first sight the vegetation gives the impression of being rather uniform. *Trachypogon* and *Mesosetum cayennense* are the most abundant species occurring everywhere. *Axonopus pulcher* and *Bulbostylis conifera* come in the second place, *Axonopus purpusii* and *Mesosetum loliiforme* in the third. Other species may be abundant too, but they are not so equally distributed.

In the centre and in the S.E. part, where the soil consists of loamy sand to sandy loam, the vegetation still shows some elements of the orchard vegetation which it surrounds, e.g. *Schwenckia americana, Mitracarpus discolor, Cassia flexuosa, Zornia diphylla* and some *Thrasya petrosa*. (**Subass. b**)

In the vegetation of the N.E. part, on slightly heavier soil, these species are (nearly) absent. Here *Leptocoryphium lanatum* and *Rhynchospora barbata* (var. *barbata*) join the group of abundant species. *Byrsonima verbascifolia* is not common, but the characteristic *Dipteracanthus angustifolius* has its optimum here. (**Subass. a**) There occur ant-hills and/or termitaries in this area, which are about 40 cm high. Their vegetation is different and consists mainly of *Tibouchina aspera, Rhynchospora cephalotes* and sometimes of *Panicum rudgei.*

In the western part of the savanna, where the soil is not so very dry, the vegetation has about the same composition, but *Trachypogon* is less abundant, whereas *Andropogon leucostachyus, Tibouchina aspera* and *Byrsonima verbascifolia* become important. A quite new and numerous species is the grass *Sporobolus cubensis*. (**Subass. c,** Photo 8) This vegetation spreads equally over the numerous small ant-hills and termitaries, that are found here.

Where the communities mentioned so far are in contact with the forest border, the vegetation is characterized by the abundance of *Davilla aspera* and, to a lesser degree, of *Vismia guianensis, Miconia ciliata* and *Byrsonima crassifolia*. In a few spots the fern *Pteridium aquilinum* (var. *arachnoideum*) was observed. (See also Photo 11)

The S.W. extension of the savanna has a still heavier and moister soil. The vegetation of the greater part does not differ much from the former one, but most indicators of dryness have disappeared. A new species is the grass *Elyonurus adustus; Axonopus purpusii* is present with normal and with narrow leaves. *Byrsonima verbascifolia* may be numerous. (**Subass. d**) This vegetation type is transitional between the former one and the next one.

In the subassociations c and d an unknown *Ryhnchospora* was collected. Later on it was described by LINDEMAN (1966) as *R. rhizomatosa.*

The community as a whole has affinity to the association 1.3.2 of the Lobin savanna and Mimili Okili.

Following down the S.W. extension one observes a considerable change. The majority of the abundant species disappears. *Mesosetum cayennense* and *Sporobolus cubensis* stay and are now the main species, followed by *Andropogon leucostachyus, Elyonurus adustus* (optimal here), *Leptocoryphium*, *Tibouchina*, the narrow-leaved *Axonopus purpusii*, *Rhynchospora globosa*, *Paspalum pulchellum*, *Panicum nervosum* and some *P. stenodoides*. The last four species indicate that the soil is wet. (**Ass. 2.3.2**) This community resembles the one with *Panicum stenodoides* (ass. 2.3.4) found on the other savannas of the Coesewijne-type.

About 100 m further there is again a remarkable change in the soil as well as in the vegetation. The soil becomes heavier and it consists now of a layer of silty (clay) loam on heavy clay; the presence of kawfoetoes shows that it is very wet. *Sporobolus* and *Elyonurus* have vanished completely, *Andropogon leucostachyus* nearly. New species are in the first place the grasses *Hvpogynium virgatum* and *Axonopus chrysites*, in the second place *Echinolaena inflexa*, *Panicum stenodes*, *Turnera guianensis* and *Cassia tetraphylla* var. *brevipes*. It is the normal community of very wet and heavy soils (**ass. 3.1.1**) in a rich form.

The very edge of the savanna, against the swamp with *Eleocharis interstincta*, presents a quite different type of vegetation. It has affinity to the former one and to the vegetation of rivulets, as is apparent from the occurrence e.g. of *Panicum stenodes* together with *Ischaemum guianense* and some swamp species as *Rhynchospora cyperoides* and *Scleria microcarpa*. There are, however, four species which are typical for the borders of swamps, pools, ditches and the like, viz. *Dalbergia glauca*, *Buettneria scabra*, *Paspalum pumilum* and *Panicum parvifolium*. (**Comm. 3.2.4**)

At some places along the low lying western border, adjoining the association of *Elyonurus adustus* (ass. 2.3.2), a special community is found. The combination of species like *Hypogynium virgatum*, *Rhynchospora glauca*, *Echinolaena inflexa* and *Cassia tetraphylla* var. *brevipes* with e.g. *Leptocoryphium lanatum*, *Panicum nervosum* (much) and *Andropogon leucostachyus* shows that it is related to the common association 3.1.1 and that the soil is very wet and heavy. However, there are no kawfoetoes, though the soil is very humic or even peaty. The shadow of the forest border favours species like *Heliconia psittacorum*, which is very numerous, *Imperata brasiliensis* and *Paspalum plicatulum*.
Ischnosiphon leucophaeus is found only on this part of the savanna. (**Ass. 3.1.3**)

At the time of the investigation the vegetation of the rivulet and of the adjoining zones was still recovering from fires. Nevertheless it could be seen that some interesting problems were coming up here. The following zones may be distinguished:

1) The rivulet itself. The upper 20 cm of the peat soil were burnt over large stretches and had been blown away. The remaining parts, like islands in a sea of black ash, consisted of large, flat kawfoetoes with narrow channels between them. Here the vegetation was regenerating. Under a peat layer of about 50 cm the soil consisted of sandy loam, at a greater depth of loamy sand and still further downwards of pure coarse sand.

2) The transition between 1) and 3): a thin (burnt) peat layer on sand.

Photo 1. Lobin savanna, loamy part. Orchard-savanna vegetation of *Curatella americana* (Polycarpaeo—Trachypogonetum curatelletosum, 1.2.2.a).

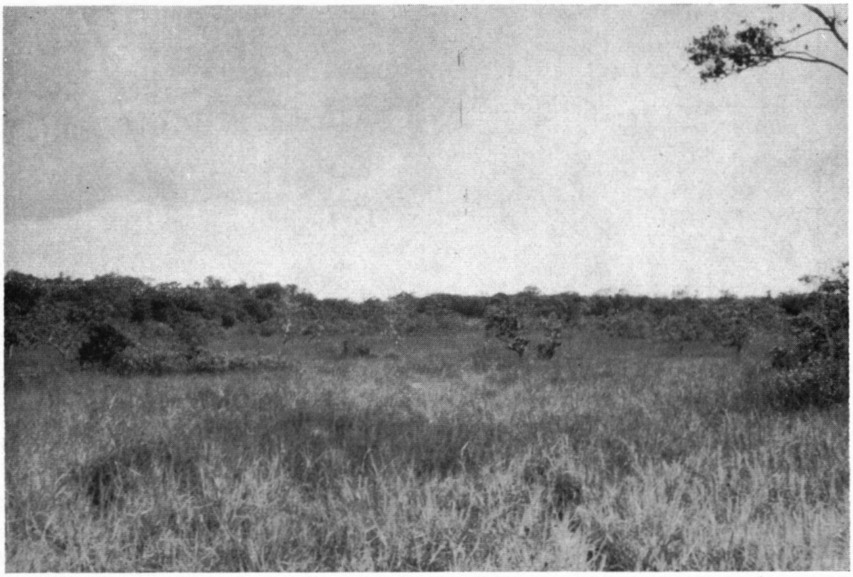

Photo 2. Lobin savanna, loamy part. Schizachyrio—Rhynchosporetum (1.3.2). On the background *Curatellas* in the Polycarpaeo—Trachypogonetum (1.2.2).

Photo 3. Lobin savanna, loamy part. Arundinello—Panicetum stenodis (3.1.1) in the N.E. extension. On the background *Mauritia flexuosa* palms in a rivulet along the forest border.

Photo 4. Lobin savanna, loamy part. The savanna on fire (Schizachyrio—Rhynchosporetum barbatae, 1.3.2.a).

Photo 5. Lobin savanna, white-sandy part. *Trachypogon plumosus* vegetation (Mesoseto—Trachypogonetum, 1.1.1).

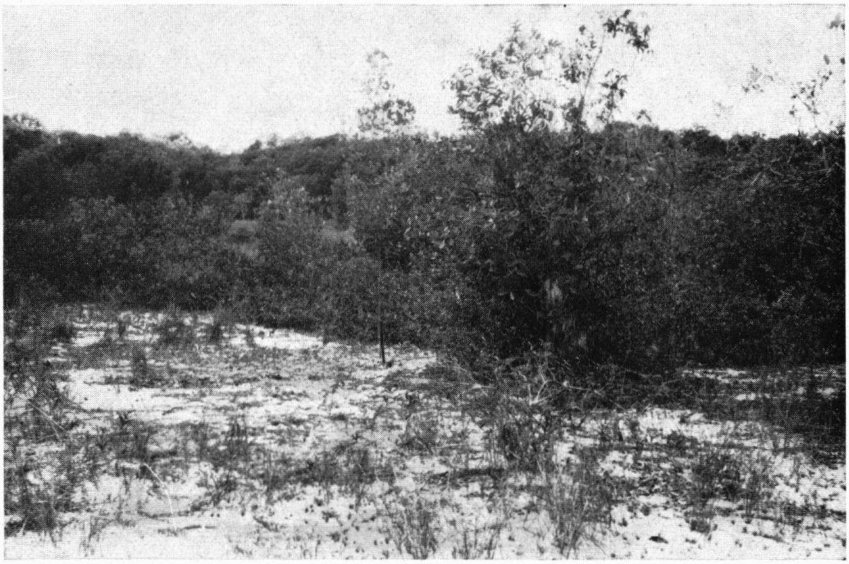

Photo 6. Lobin savanna, white-sandy part. Savanna bushes of the *Ternstroemia—Matayba* type (B 1); open patches with sparse vegetation of the Lagenocarpo—Axonopodetum attenuati (1.1.2).

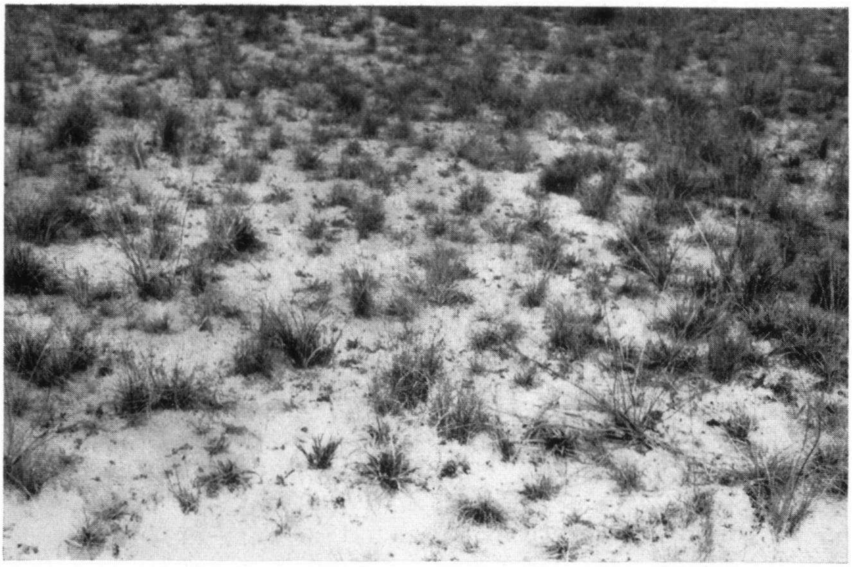

Photo 7. Lobin savanna, white-sandy part. Xyrido—Paspaletum (2.1.2). The high grass is *Leptocoryphium lanatum*, the small tufts belong to several species of grasses and sedges.

Photo 8. Coesewijne savanna, W. part. Vegetation with much *Byrsonima verbascifolia* (Dipteracantho—Byrsonimetum verbascifoliae sporoboletosum, 1.3.1.c).

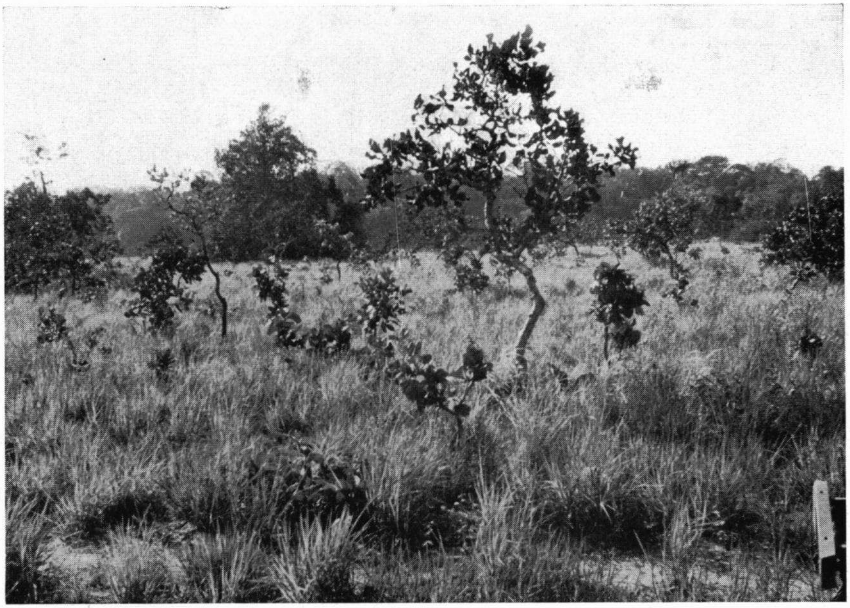

Photo 9. Coesewijne savanna, central part. Open orchard-savanna vegetation with *Curatella americana* and *Byrsonima coccolobifolia*; herb layer with much *Trachypogon plumosus* and *Thrasya petrosa* (Mesoseto—Thrasyetum, 1.2.1). On the background a bush of the *Rapanea* type (B 2).

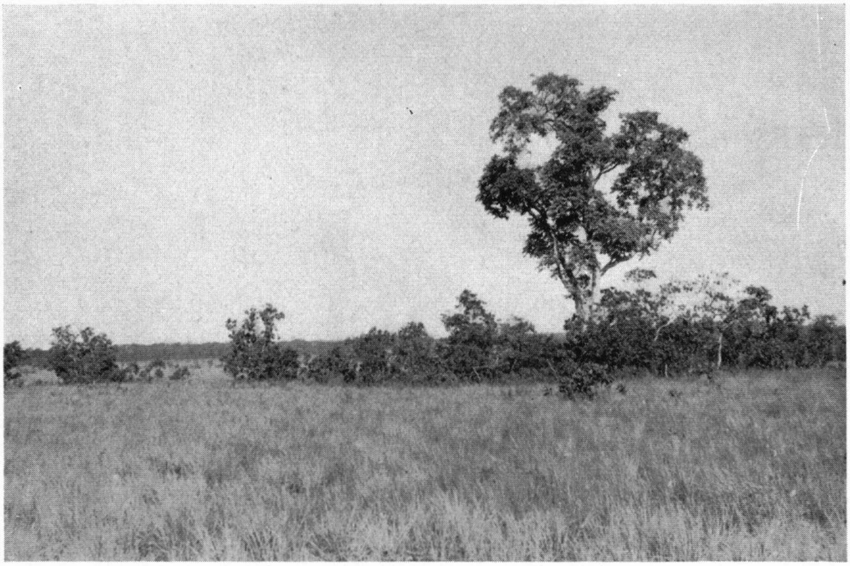

Photo 10. Coesewijne savanna, E. part. A bush of the *Rapanea* type (B 2), with a high tree (*Trattinickia burserifolia*) in the centre.

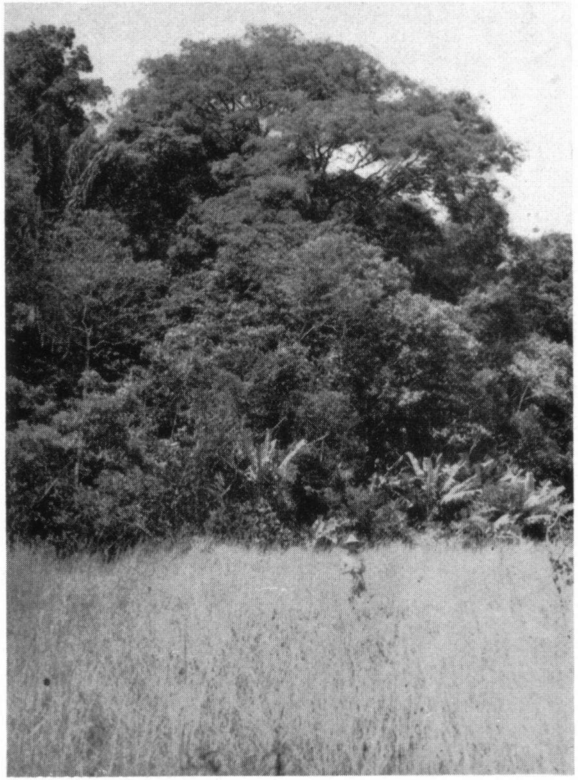

Photo 11. Coesewijne savanna. Forest border with the banana-like *Ravenala guianensis*. The tall tree with wide crown is a *Parkia nitida*.

Photo 12. Fransina savanna. Kawfoetoes with regenerating vegetation of the Arundinello—Panicetum stenodis (3.1.1).

Photo 13. Savanna of Vierkinderen. Uniform vegetation of the Arundinello-Panicetum stenodis (3.1.1). The flowering grasses are *Leptocoryphium lanatum* and *Andropogon leucostachyus.*

Photo 14. Gros savanna, N.W. part. Pebble-knoll with bushes of the *Roupala—Antonia* type (B 6) and open patches with a low and scanty vegetation (Bulbostylidetum coniferae minoris, 2.2.5).

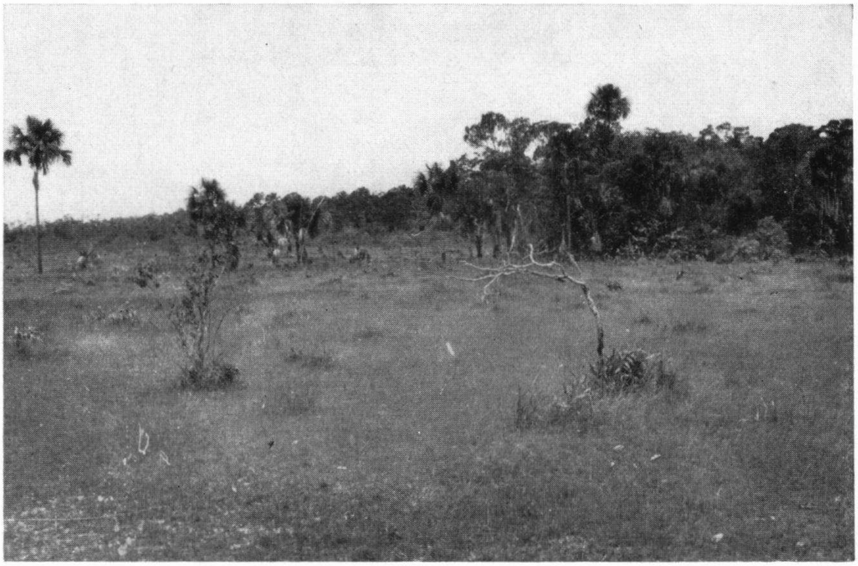

Photo 15. Gros savanna, N.W. part. Slope with low vegetation containing much *Rhynchospora curvula* (Rhynchosporetum curvulae, 2.2.3). On the background *Mauritia flexuosa* in a rivulet.

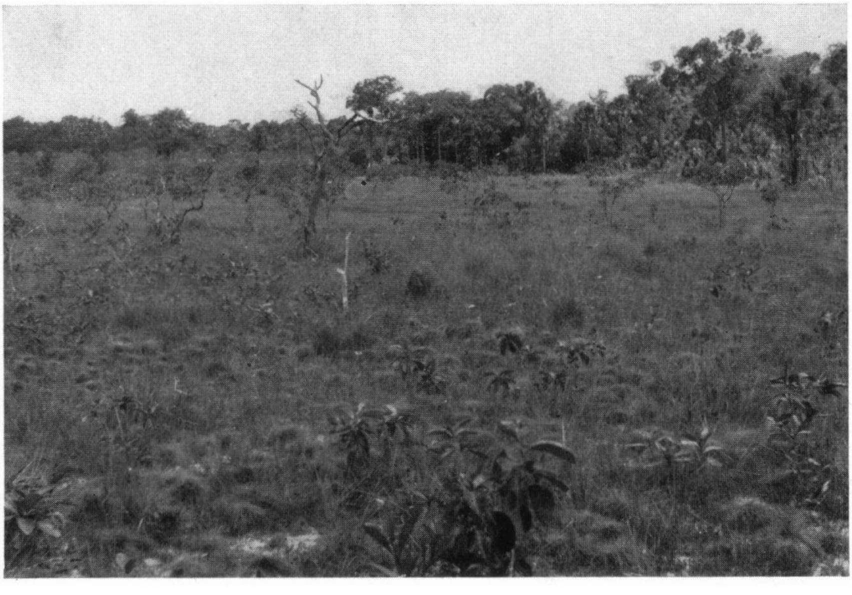

Photo 16. Gros savanna, E. part. Slope with, on the foreground a vegetation with much *Bulbostylis spadicea* (Bulbostylidetum spadiceae, 2.2.4) and, on the background an orchard-savanna vegetation with gnarled *Byrsonima crassifolia* (Byrsonimetum crassifoliae malosae, 2.2.2).

3) A zone of about 20 m wide with a soil apparently consisting of coarse sand.

The next table gives the species with their total estimate. One has to keep in mind that the vegetations were not yet completely restored.

zone total cover	1 40 %	2 30 %	3 30 %
Echinolaena inflexa	1	.	.
Hypogynium virgatum	+	.	.
Phyllanthus hyssopifolioides	+	.	.
Imperata brasiliensis	1	.	.
Desmodium barbatum	+	.	.
Heliconia psittacorum	2	.	.
Blechnum indicum	2	.	.
Lindsaea stricta var. *parvula*	+	.	.
Phyllanthus lathyroides	+	+	.
Cassia tetraphylla var. *brevipes*	+	+	.
Panicum nervosum	.	+	.
Odontadenia nitida	.	+	.
Bulbostylis surinamensis	+	1	.
Panicum errabundum	+	+	.
Zornia tenuifolia	+	+	.
Leptocoryphium lanatum	1	3	+
Andropogon leucostachyus	1	+	+
Axonopus pulcher	.	+	.
Rhynchospora barbata/arenicola	.	+	.
Cassia hispidula	.	+	.
Tibouchina aspera	.	+	.
Paspalum carinatum	.	+	+
Bulbostylis circinata		+	2
Panicum micranthum	.	.	1
Trachypogon plumosus	.	.	1
Mesosetum loliiforme	.	.	2
Bulbostylis conifera	.	.	+
Mesosetum cayennense	.	.	+
Cassia cultrifolia	.	.	+
Turnera ulmifolia var. *surinamensis*	.	.	+
Byrsonima crassifolia juv.	.	.	+

The vegetation of the rivulet resembles the association of *Ischaemum guianense* (**ass. 3.2.1**), though this species itself was not found.

The vegetation of the bordering zone 3) is very remarkable by the combination of *Bulbostylis circinata* and *Panicum micranthum* on the one hand, with *Mesosetum cayennense*, *Turnera ulmifolia* and *Cassia cultrifolia* on the other. This indicates that the soil here is wet and consists of loamy sand, a type of habitat that is rare in the savannas of the Zanderij formation.

Panicum errabundum and *Zornia tenuifolia* were collected resp. for the second and first time in Surinam. No peculiarities are known from the first collection of the former. The complete lists of the three zones are given here to indicate under what conditions and in what combination these two curious species occur. It is likely that their rarity in Surinam is caused by the rarity of their habitat.

Main correlations of the vegetation types with the properties of the soil:

Ass. 1.2.1 – very dry to dry, red, pure or loamy sand
Ass. 1.3.1, subass. b – very dry loamy sand to sandy loam
subass. a – very dry sandy (clay) loam
subass. c – dry sandy (clay) loam
subass. d – dry to moist sandy clay loam
Ass. 2.3.1 – wet sandy loam
Ass. 3.1.1 – very wet silt loam to silty clay loam on clay
Comm. 3.2.4 – silty clay loam, still wetter than the preceding
Ass. 3.1.3 – very wet sandy loam, very humic

III. 2.4.3.2. Bushes (see also VI.4 and Table 10)

Bushes are mainly found in the central and eastern part of the savanna. They are surrounded by the orchard vegetation and by the association 1.3.1 (a and b), as far as these communities occur on loamy sand or sandy loam. They vary in size from some tens to some hundreds of square meters. The height of the higher trees in the centre is more or less proportionate to the size of the bushes. (**Type B 2,** Photo 10)

The highest trees are usually *Byrsonima crassifolia*, *Tapirira guianensis*, *Trattinickia burserifolia* and a still undetermined species called "koemete" in the Caraib indian language.

Besides these four, the most frequent species present in the form of small trees or of shrubs, are *Astrocaryum segregatum*, *Rapanea guianensis*, *Miconia rubiginosa*, *Symplocos guianensis* (sometimes set with *Phthirusa theobromae*), *Curatella* and *Byrsonima coccolobifolia*. The last three are often found on the outside of the bush only, together with much *Davilla aspera*.

Many species are the same as in the bushes on the Lobin savanna, but as a whole the vegetation is less varied and this applies also to the undergrowth. That the soil is drier here is indicated most conspicuously by the occurrence of *Trattinickia*, *Torrubia olfersiana* and *Ternstroemia dentata*. Other species by which these bushes differ are e.g. *Rapanea guianensis*, *Miconia rubiginosa* and "koemete".

With regard to the general habitat of the species the same can be said as for the Lobin savanna. Here too there are species characteristic for the savanna bushes (2a), whereas others may be found also in savanna wood and forest or even in rain forest (2c-g). However, the share of forest species that do not flower in the bushes (3) is smaller.

III. 2.4.3.3. High trees

The number of single trees belonging to different species that are scattered in the open vegetations is not so large as it is in the Lobin savanna. In this savanna occur here and there some high trees, standing alone or in small groups, sometimes with some lower trees and shrubs at their feet. They give the impression that they were the central individuals of a small bush and the only ones that have escaped the influence of the fires (Photo 10).

Trattinickia burserifolia is the most common tree, *Byrsonima crassifolia* and *Tapirira guianensis* are numerous too, but only a few specimens of other species reach a great height.

Some small groups of *Acrocomia lasiospatha* were observed, without a special undergrowth. The other "awara", *Astrocaryum segregatum*, is also present in separate clumps, but as a rule it seems to prefer the bushes.

At one place near the northern border a 20 m high specimen was found of the very rare *Hymenolobium petraeum*. It was accompanied by some other high trees, viz. *Trattinickia burserifolia* (20 m), *Himatanthus articulatus* (18 m) and *Ternstroemia dentata* (15 m). A second layer, very open and about 10 m high, was formed by *Curatella*, *Byrsonima coccolobifolia*, *B. crassifolia*, *Miconia rubiginosa* and *Astrocaryum segregatum*. The lowermost story of woody species, reaching a height of 2 m, consisted of much *Siparuna guianensis*, *Xylopia frutescens* and *Tibouchina aspera*, less *Maprounea guianensis*, *Miconia rufescens*, *Eugenia punicifolia*, *E. compta*, *Tapirira guianensis*, *Casearia javitensis*, *Clidemia rubra*, *Davilla aspera*, *Pagamea guianensis* and *Protium heptaphyllum*. Among the herbs *Rhynchospora cephalotes* and *Scleria bracteata* were dominating.

III. 3. A SAVANNA OF THE KASIPORA- AND THE ZANDERIJ-TYPE: **The Lobin savanna, white-sandy part**

III. 3.1. *General data*

See the loamy part: III.2.1.1

Area: about 42 ha

The distinction of dry and wet white-sand savannas is in general very well possible and justifies the recognition of two separate types, the Kasipora- and the Zanderij-type respectively. However, there are stretches of savanna where dry and wet sites intermingle; the white-sandy part of the Lobin savanna is an example.

III. 3.2. *Soil* (Fig. 11)

The soil consists of pure bleached sand. The degree of humidity varies from place to place, ranging from dry, in the highest parts, to very wet. There is a depression near the transition to the loamy savanna of which the deepest part has the properties of a rivulet. In the wetter spots the upper layer is more humic.

A hardpan, found on the lower spots within reach of the soil-auger, probably underlies the whole white-sandy part.

III. 3.3. *Vegetation*

III. 3.3.1. One-layered communities (Fig. 7)

The driest parts are mainly occupied by extensive and rather thin *Trachypogon plumosus* vegetations with much *Axonopus pulcher* and *Bulbostylis conifera* (**ass. 1.1.1**, Photo 5). The other, less abundant herbs are mainly indicators of a dry soil, e.g. *Bulbostylis junciformis*, *Cassia hispidula*, *Mitracarpus discolor* and *Paepalanthus subtilis*, of which the last one is restricted to this association. Some fine little shrubs occur, e.g. *Cassia ramosa*, a typical species of dry white sands, and a low form of *Byrsonima crassifolia*.

At the time of the investigation the most notable variation observed within this vegetation type was caused by *Mesosetum loliiforme*. This low, creeping grass was either absent or covering at least 5 % of the surface. However, no correlation of this difference with any environmental factor could be traced. Maybe that it was due to local differences in the influence of the most recent fires.

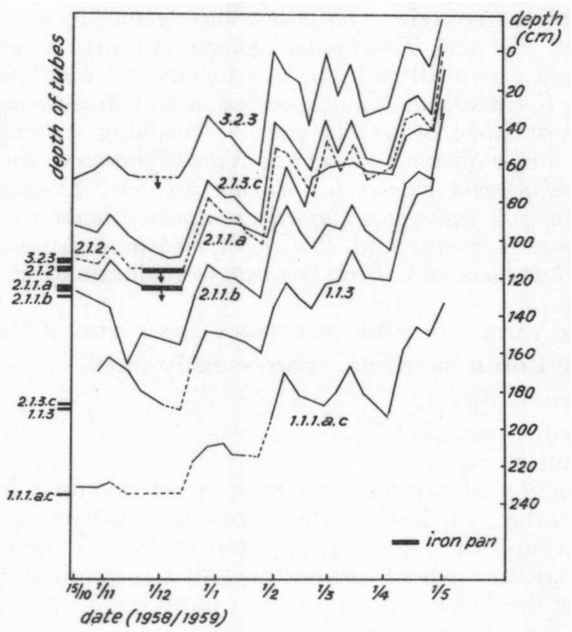

Fig. 11. Lobin savanna, white-sandy part. Water-table fluctuations.

Another variety of an apparently more constant character is related with the properties of the soil. There is a transitional zone to the dry loamy sand with a soil consisting of slightly reddish sand. Here some typical species of the adjoining orchard-savanna vegetation (ass. 1,2.2) are found, like *Polycarpaea corymbosa* and *Desmodium barbatum* and also some low *Curatellas*. Only here *Vernonia remotiflora* occurs. (**Subass. c**)

At one spot where the shrubby *Byrsonima crassifolia* was more abundant, *Borreria suaveolens* was present.

The transition from this dry vegetation to those of the wet sand is nicely displayed in the depression mentioned in the preceding section. Going down the slight slope one observes the quick fading-out of most dryness-indicators. *Cassia ramosa*, however, and the main species of the *Trachypogon* vegetation maintain their position for a while, though the tufts of *Trachypogon* itself are scattered here. They mix with a number of new species, of which the most numerous are *Bulbo-*

stylis circinata, *Rhynchospora barbata* (var. *glabra*) and *Leptocoryphium lanatum* (**ass. 2.1.1, subass. b**). This zone is transitional to another thin vegetation (**subass. a**) dominated by the last mentioned group of species together with some other low grasses and sedges, viz. *Paspalum pulchellum*, *Panicum micranthum* and *Rhynchospora graminea.* The degree of cover is about 40 to 70 %. *Bulbostylis conifera*, *Axonopus pulcher* and some small forbs are now the only links with the *Trachvpogon* vegetation. The group of species for the first time appearing in this vegetation, consists mainly of small and delicate forbs, as *Curtia tenuifolia*, *Lisianthus coerulescens*, *Perama hirsuta*, *Xyris savanensis* and some other Xyrids. Most of them are characteristic for the whole group of vegetation types on wet white sand (**all. 2.1**). In the wet season the groundwater just reaches the surface here.

The adjoining centre of the depression is flooded in the wet season during and after heavy showers. The vegetation is still more open than the preceding one, but the participating species are mainly the same. However, *Axonopus pulcher* and *Bulbostylis circinata* are found no more, whereas the number of wet-white-sand species has increased a little, e.g. by some *Utricularias.* (**Ass. 2.1.2,** Photo 7)

In this and the preceding vegetation low humps may occur, caused by termites nesting in the ground. Here some higher and shrubby species are gathered as *Tibouchina aspera*, *Tetracera asperula* and *Byrsonima crassifolia.* Some of them belong to drier vegetation types, e.g. *Trachypogon* and *Cassia ramosa*, others to wetter ones, e.g. *Panicum nervosum* and *Lagenocarpus tremulus.*

On its northern side the depression is still deeper, presenting a surface with low kawfoetoes. In the wet season water fills the narrow gullies. The aspect of the vegetation is determined by the high shoots of *Lagenocarpus tremulus.* Some species, in the first place *Paspalum pulchellum* and *Rhynchospora tenuis*, reach their highest degree of cover here, so that the vegetation as a whole is denser (degree of cover 70–85 %). The floristic composition does not differ much from that of the preceding type. (**Ass. 2.1.3**)

Two patches within the *Lagenocarpus tremulus* vegetation are still wetter. A single morisi-palm even indicates slightly swampy conditions. The dense vegetation appears to resemble that of rivulets draining white-sand savannas. Everywhere the high kawfoetoes are set with *Panicum nervosum*, *Hypolytrum pulchrum* and *Blechnum indicum*, whereas locally *Ischaemum guianense* and *Calyptrocarya poeppigiana* are of importance. (**Ass. 3.2.3**)

The vegetation types described up till now are distributed over the savanna in accordance with the local differences in drainage (see Fig. 7). Here and there slight deviations from the normal composition are found along the borders of the bushes. However, only in one case a difference was found worth mentioning:

A characteristic vegetation surrounds the bushes on dry sand and occurs also on the small open patches between them (**ass. 1.1.2,** Photo 6). It consists of few widely scattered species of which *Lagenocarpus weigeltii* and the slender ferns *Schizaea incurvata* and *Actinostachys pennula* are the most notable. The other species are the same as those of the *Trachypogon* vegetation, but they occur only in small numbers.

Main correlations of the vegetation types with the properties of the habitat during the wet season:

Ass. 1.1.1 – dry soil; water table never reaching the surface
Ass. 1.1.2 – idem; along and between bushes
Ass. 2.1.1 – wet soil; water table just reaching the surface
Ass. 2.1.2 – periodical flooding
Ass. 2.1.3 – idem; lasting longer, but confined to the gullies between the low kawfoetoes
Ass. 3.2.3 – permanently water in the gullies between the high kawfoetoes

III. 3.3.2. Bushes (see also VI.2 and 3; Table 10)

The number of bushes is relatively small and they are not very well developed.

On dry places some nice rounded bushes are found, with shrubs and small trees in the centre and a belt of procumbent *Humiria balsamifera* (var. *guianensis*) along the margin. The majority, however, has an irregular shape, covering about hundred square meters; the height is about 10 m. (**Type B 1**, Photo 6)

The small trees mostly belong to the species *Trattinickia burserifolia* and *Matayba opaca*, indicating a dry soil, and *Pagamea guianensis*; all three species occur also in savanna wood and forest (2d). To the same group belong some other common and dominating species of the bushes, viz. *Clusia fockeana*, *Licania incana* and the already mentioned *Humiria*. The common *Ternstroemia punctata*, however, is restricted to savanna wood (2c).

Of all these species only *Matayba opaca* (var. *opaca*) is restricted to this type of bushes. This holds for *Myrcia sylvatica* too, a species occurring in several forest types, also in rain forest (2e).

Smaller species, partly climbing, partly belonging to the sparse undergrowth, are e.g. *Tetracera asperula*, *Doliocarpus calinea* and *Tibouchina aspera*. In particular in the outer zone some species of the adjoining open-savanna vegetation (ass. 1.1.2) are present, e.g. *Schizaea incurvata*.

There is a remarkable amount of epiphytes and (half-)parasites on the woody species. Most common is *Phthirusa squamulosa*, bound to *Licania incana*. Other species are the ferns *Polypodium ciliatum* and *P. lycopodioides* var. *salicifolium*, the Bromeliads *Tillandsia bulbosa*, *Aechmea mertensii* and *Catopsis sessiliflora*, further *Anthurium gracile*, one or more *Campylocentrum* sp. and some other (undetermined) orchids and Loranthaceae and the omnipresent *Cassytha filiformis*. *Marlierea montana* is preferred by most of them, but also *Clusia fockeana* and *Licania incana* may bear several species.

The bushes of the wet sand are lower, as a rule not exceeding 4 m, and cover only a few square meters. The number of species is small and not one of them grows out to a tree. (**Type B 4**)

Dominating species may be *Clusia fockeana* and *Licania incana*, of which the former is most common. Other species with a high presence are *Humiria balsamifera* (var. *guianensis*) and *Tetracera asperula. Bactris campestris*, *Comolia vernicosa* and, to a lesser degree, *Marlierea montana* are indicators of a wet habitat. The climbing *Philodendron latifolium* was collected here for the first time in Surinam.

Nearly all participating species are found outside the bushes in savanna wood and/or forest, some even in rain forest (2c, d, e). Only two of them are present also in kapoeweri.

The undergrowth consists of some species common in open savanna and bushes as well (1/2) and some genuine open-savanna species (1a). *Lagenocarpus tremulus* is the most common one.

It is remarkable that the two types of bushes on the white sand do not derive any species directly from the rain forest (2b and 3 absent).

III. 4. SAVANNAS OF THE SABAN-PASI-TYPE

See VAN DER EYK (1954), COHEN & VAN DER EYK (1953), VAN KOOTEN (1953, 1954), and section I. 2.2.1.

The soil profiles of the savannas belonging to the Saban-pasi-type vary widely from place to place.

The savannas are found mainly on the tops and slopes of subgraywacke hills. The fresh weathering product of the subgraywacke is very plastic and poorly permeable. Normal profiles are hardly or not developed on it because of strong sheet erosion. On the one hand the higher parts of the steeper slopes show bare rock and the profiles on the somewhat lower levels are "decapitated". On the other hand, the weathered subgraywacke on the lower part of the slopes and in the valleys of the savanna rivulets is covered by a layer of colluvial or illuvial material respectively. The upper limit of the subgraywacke may be recognized by a layer of gravel.

Local accumulations of pebbles or bigger rocks may impede the erosion and give rise to small hills. The pebbles may either be the weathering products of quartz seams or remnants of decomposed conglomerate that was mixed among the subgraywacke.

The highest hills of the landscape (the Brinckheuvel, Klaiberheuvel and Loblesheuvel) have a flat top covered with about 6 m of bleached sand. It is supposed that these sand caps are remnants of a formerly more extensive covering layer. The sand is also found on the slopes and in the valleys in the vicinity of the high hills. The texture of it appears to be identical with that of the white sands of the Zanderij formation (VAN KOOTEN, 1954).

Up till world war II several companies practised gold-mining in this area. Some hundreds of labourers lived at that time in a number of settlements situated on the savannas along the railroad (e.g. Guyana Placer, Gros, De Jong Noord and De Jong Zuid). At the moment only a few cottages are left of the formerly prosperous villages. Nevertheless the scanty population of the region keeps the savannas under a severe regime of burning.

At present no indians inhabit this region and they do not live in the neighbourhood either. However, VAN KOOTEN (1954) found potsherds and other remnants of human occupation in the soil. They occurred in the valleys of the savanna rivulets, mostly under the illuvial cover, down to a depth of 2 m, but sometimes also in this layer. VAN KOOTEN concludes from these finds that the filling-up of the valleys has taken place recently and quickly, but it might be assumed as well that the remnants are very old.

III. 4.1. **The Gros savanna** (Fig. 12)

III. 4.1.1. *General data*

Position: W. of Gros (km 103.5 along the railroad)
Map 1 : 40 000 : 21 d
Area: about 400 ha

The savanna is surrounded by forest. It is slightly accidented but as a whole slopes down and drains to the west and the south.

Three parts may be distinguished: an eastern, a north-western and a south-western part. A few cottages are found in the eastern part near the railroad. The inhabitants, mainly private gold-miners, set fire to the savanna vegetation every year.

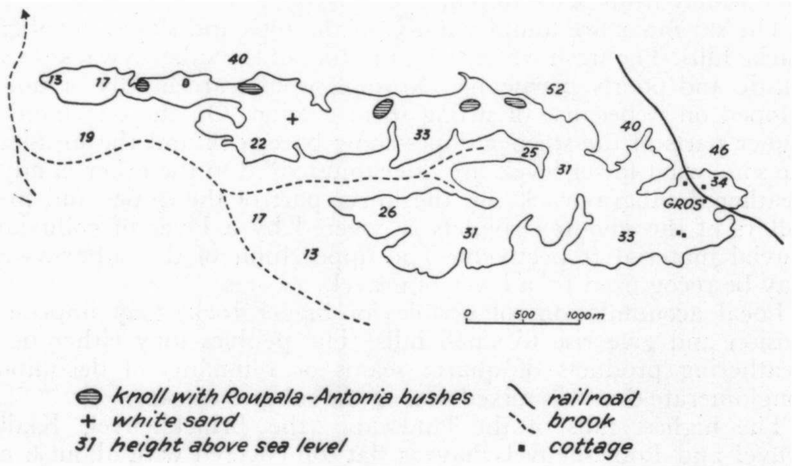

Fig. 12. Gros savanna

Here and there traces are recognizable of the former activities of the gold-companies, e.g. the tracks of some lorry railroads that disappear into the forest. No digging of importance has taken place in the savanna itself.

The vegetation has been investigated in April 1959.

III. 4.1.2. *Soil* (Fig. 6)

In many places it is difficult to recognize the simple picture of a subsoil consisting of weathered subgraywacke covered by a layer of colluvial or illuvial material and separated from the latter by a layer of gravel.

Small knolls with relatively steep slopes occur only near the northern border of the north-western part. A map in VAN KOOTEN (1954), presumably drawn from an aerial photograph, indicates in these spots "probably conglomerate". On the tops the soil is impenetrable, consisting of pebbles with a maximum size of 15 cm, embedded in sandy loam or perhaps in a heavier soil type.

The soil of the slopes consists of loamy sand, usually with relatively much gravel in it and often with a definite layer of gravel at a depth of 60 cm or deeper. At the bases of the slopes the texture of the upper soil is still the same except for the lower gravel-content.

On the rest of the savanna the low hills have more rounded tops and long, gentle slopes. The topsoil on the tops consists of sandy clay loam. As a rule there is a layer of gravel, sometimes near the surface. In some places big rocks cropp out. On the slopes no gravel is found higher than 1 m below the surface. The upper part of the slopes has an upper layer consisting of sandy loam, but downhill this gradually changes into a loamy sand.

The narrow rivulets along the feet of both types of hill have a heavier soil, consisting of silty clay.

Approximately in the centre of the north-western part there is a spot with pure white sand down to a depth of at least 120 cm. It may be assumed that this sand has the same origin as that of the sand caps on the high hills mentioned in section III.4, but its texture is finer than that of the white sands of the Zanderij formation.

All direct and indirect observations with regard to the water economy show that in nearly every part of the savanna, also on the tops of the hills, the soil may be considered to be wet. Only the bordering zones of the rivulets are very wet.

III. 4.1.3. *Vegetation*

III. 4.1.3.1. Orchard savanna and one-layered communities

The tops of the pebble-knolls in the north-western part present a mosaic of bushes and open patches of about equal size (Photo 14). The vegetation of the open patches is very scanty and covers half of the surface at the most. It has a very remarkable composition. The most abundant species are *Trachypogon plumosus* and a tiny sedge that on closer examination appears to be the common *Bulbostylis conifera*. This small form ("*minor*") has been collected in Surinam only on these knolls. The rest of the vegetation consists mainly of a mixture of species that on the savannas described above are found either on wet white sand or on another type of soil, but never together. Compare e.g. on the one hand *Bulbostylis circinata*, *Paspalum pulchellum*, *Lagenocarpus tremulus* and *Panicum micranthum* with, on the other hand, *Rhynchospora podosperma*, *Sipanea pratensis*, *Coutoubea spicata*, *Aristida tincta* and *Mesosetum cayennense*. (There is one exception: see III.2.4.3.1.) Two other remarkable species are *Mesosetum tenuifolium*, that had not been collected in Surinam before, and *Rhynchospora rhizomatosa*, the newly found species of the Coesewijne savanna (see p. 47). (**Ass. 2.2.5**)

The vegetation on the slopes of these knolls is slightly denser. In principle it presents the same mixture as the former type, but more species are partaking, e.g. *Comolia lythrarioides*, *Panicum nervosum* and *P. stenodoides*. Its most characteristic feature is the high abundance of the tiny *Rhynchospora curvula*. Other numerous participants are *Panicum micranthum*, *Paspalum pulchellum*, *Rhynchospora barbata* (var. *barbata*) and *Hypolytrum pulchrum*. Some species that did not turn up before, are the big *Bulbostylis lanata* and the deep-blue-flowered *Abolboda pulchella*. (**Ass. 2.2.3, subass. a,** Photo 15) The latter species is found in particular near to the tops in a transition zone between the former association and the present one (**subass. b**).

Here and there in this vegetation bushes occur.

The tops of the flat hills are covered by a one-layered herb vegetation and some scattered trees. The most abundant species is *Trachypogon plumosus*, but as a rule it does not cover more than a third of the surface. Another frequent grass is *Axonopus purpusii* that appears to have its optimum in this type of vegetation. For the rest the majority of the species are the same as those of the former two types, but there are important quantitative differences. *Mesosetum cayennense* and *Aristida tincta* come to the fore and, like the high abundance of *Axonopus purpusii*, this is in agreement with the relatively heavy texture of the soil. The preponderance of these species and of *Rhynchospora glubosa* and the presence of some *Sporobolus cubensis* and *Andropogon leucostachyus* place this vegetation nearer the one with *Panicum stenodoides* (ass. 2.3.4) of the Lobin savanna and the one with *Elyonurus adustus* (ass. 2.3.2) of the Coesewijne savanna, rather than the other vegetations of the Gros savanna itself. (**Ass. 2.3.1**)

The long slopes of these hills present again a vegetation type that belongs to the same group as those of the pebble-knolls described above (**all. 2.2**). *Trachypogon plumosus*, *Rhynchospora barbata*, *R. rhizomatosa*, *Mesosetum tenuifolium*, *Panicum micranthum*, *Hypolytrum pulchrum* and *Bulbostylis spadicea* may be numerous. The last species, a thick-stemmed sedge with in vegetative state the shape of an old shaving-brush, determines the aspect of the vegetation. (**Ass. 2.2.4,** Photo 16)

On closer examination this vegetation type appears to be divisible into two sections occurring on the higher and the lower parts of the slopes,where the topsoil consists of sandy loam and loamy sand, respectively. Differential species of the former section (**subass. b**) are e.g. *Sporobolus cubensis* and *Aristida tincta*, of the latter section (**subass. a**) *Paspalum pulchellum* and *Bulbostylis circinata*.

Nearly everywhere in the savanna *Byrsonima crassifolia* is widely scattered in the form of a small orchard tree ("*malosa*"). However, on the lowest part of the long slopes these treelets are more concentrated, covering up to a tenth of the surface and forming a very attractive type of orchard vegetation. The shape of the trees, however, is not identical with the well-known form found e.g. in *Curatella*, *Byrsonima coccolobifolia* and, at least outside N. Surinam, also in *B. crassifolia*. Here the specimens have a low and fairly erect trunk, but the branches have the usual gnarled form.

The herb layer of this vegetation resembles that of the former one closely, but *Rhynchospora globosa* and *Hypolytrum pulchrum* are slightly more abundant. (**Ass. 2.2.2,** Photo 16)

The vegetation at the feet of the hills of both types is identical, bordering in the one case on the association of *Rhynchospora curvula* (ass. 2.2.3), in the other case on the orchard vegetation just mentioned (ass. 2.2.2). *Trachypogon plumosus* and *Rhynchospora rhizomatosa* are not or hardly present here, but the conspicuous *Bulbostylis lanata* is more abundant. A frequent species that has its optimum in this habitat is *Rhynchospora podosperma.* (**Ass. 2.2.1**)

A luxuriant vegetation is developed in the savanna rivulets. The main constituents are high grasses and sedges like *Hypogynium virgatum, Leptocoryphium lanatum, Rhynchospora globosa* and *Hypolytrum pulchrum. Tibouchina aspera* too is always very abundant and this locally may give the vegetation a slightly scrubby character, in particular if the small palm *Bactris campestris* is also present. Another remarkable feature is the local dominance of *Heliconia psittacorum.* The small grass *Raddia nana* is present in the narrow gullies on the sides of the kawfoetoes.

There are some species by which these rivulets differ from all other rivulets mentioned so far: *Rolandra fruticosa* (outside the savannas found as a weed!) and four climbers, *Dioscorea megacarpa, Odontadenia nitida, O. geminata* and *Prestonia perplexa.* In N. Surinam the last species has not (yet) been found outside this savanna.

The morisi-palms (*Mauritia flexuosa*) are taller here than in the savanna rivulets more to the north. Their crown commonly supports the epiphytic orchid *Catasetum longifolium,* a species with extraordinarily long, linear leaves. Except for this palm, all species that may be found in rivulets as well as in swamps (group 1d) are lacking.

This vegetation type is more or less intermediary between those of very wet localities and those of more pronounced drainage channels, but as a whole it has more in common with the latter. (**Ass. 3.2.2**)

Along some of the rivulets there is a narrow transition zone to the adjoining savanna vegetation (ass. 2.2.1). It is characterized by the dominance of *Rhynchospora globosa.* Other abundant species are *Leptocoryphium lanatum, Paspalum pulchellum* and *Tibouchina aspera.* The total composition bears the strongest resemblance to that of the common vegetation type of very wet and heavy soils reported already from several savannas of the Welgelegen- and the Coesewijne-type (ass. 3.1.1). The principal species by which it differs from the latter are *Hypolytrum pulchrum* and *Scleria cyperina.* (**Ass. 3.1.2**)

The stretch of white sand, in the centre of the north-western part, bears quite different types of vegetation from the rest of the savanna. Formerly a junction of lorry railroads was present here, but it may be assumed that the vegetation has recovered since.

Exactly on the spot of the turn-table the following vegetation-record was made (30 m^2):

Shrub layer (1–3 m high, covering 40 %): *Humiria balsamifera* 3
Herb layer (< 50 cm high, covering 60 %):

Abolboda killipii	3	*Comolia lythrarioides*	1
Xyris guianensis	2	*Sauvagesia sprengelii*	1
Panicum polycomum	2	*Schizaea incurvata*	+
Perama hirsuta	1	*Utricularia* spec.	+
Lagenocarpus tremulus	1	*Humiria balsamifera* juv.	+
Lagenocarpus amazonicus	1		

The stemless lilac-flowered *Abolboda killipii* is the most striking species. As a whole the vegetation is clearly related to the associations of the wet white-sand savannas of the Zanderij-type (all. 2.1, in particular ass. 2.1.3, subass. b).

On a slightly higher spot here is a fairly dense tree layer of *Humiria*, covering about 80 % of the surface and mixed with some other species (*Marlierea montana*, *Pagamea guianensis* and *Clusia* spec.). Here the undergrowth, in agreement with the shadyness of the habitat, consists of a uniform and nearly closed stratum of *Lagenocarpus amazonicus*, mixed with a few specimens of some of the species mentioned above and besides of *Burmannia bicolor*, *Syngonanthus gracilis* and *Scleria pyramidalis*.

Correlations of the main vegetation types with the main habitat factors:

Pebble-knolls with rather steep slopes:
Ass. 2.2.5 – on the tops; soil of gravel embedded in sandy loam
Ass. 2.2.3 – on the slopes; soil of loamy sand with relatively much gravel
Ass. 2.2.1 – at the feet of the hills; loamy sand
Ass. 3.1.2 – along the rivulets; very wet
Ass. 3.2.2 – in the rivulets; silty clay loam, kawfoetoes

Rounded hills with long slopes:
Ass. 2.3.1 – on the tops; soil of sandy clay loam, layer of gravel in the subsoil, sometimes close to the surface
Ass. 2.2.4, subass. b – upper part of the slopes; sandy loam
subass. a – lower part of the slopes; loamy sand
Ass. 2.2.2 – near the feet; loamy sand
Ass. 2.2.1, 3.1.2 and 3.2.2: see above

III. 4.1.3.2. Bushes (see also VI.6 and 7; Table 10)

The bushes on the pebble-knolls in the north-western part of the savanna occupy about half of the surface of the tops and have an irregular shape (Photo 14). The highest species are usually some small trees with a height of up to 8 m, belonging to *Roupala montana* and *Antonia ovata*. The other woody species have the form of shrubs. Most abundant are *Davilla aspera*, *Licania incana* and *Marlierea montana*. The last one indicates the wetness of the soil; the same holds for some other species, e.g. *Roupala montana* and *Bactris campestris* and for the rather dense undergrowth that consists mainly of *Scleria cyperina* and *Hypolytrum pulchrum*. *Davilla aspera*, *Coccoloba marginata*, *Siparuna guianensis* and some other species connect this type of bushes with other types occurring on not-purely-sandy soils.

Some species only found in this type are *Psychotria cordifolia*, *Aulomyrcia hostmanniana* and *Antonia ovata*.

It should be observed that no species are present that are restricted to savanna bushes and rain forest together (groups 2g and 3 absent). **(Type B 6)**

The bushes occurring on the slopes with a *Rhynchospora curvula* vegetation may be up to 4 m high and cover an area up to about 50 m². Sometimes, however, they occupy only small elevations of a few sq.m each. Their composition differs from those on the tops; this probably has to be accounted for by the difference in the texture of the soil (here loamy sand) and in the water economy of the site.

The number of woody species is small and all are shrubby. The dominant species is in general *Marlierea montana*, whereas *Bactris campestris* comes in the second place, followed by *Licania incana* and *Tetracera asperula*. The last species and *Marlierea* are the only constituents that may occur in rain forest too (2e). For the rest all species are either restricted to savanna bushes (2a) or do occur in savanna wood and/or forest (2c,d).

The undergrowth may be relatively rich, in particular if the bushes are small. It consists mainly of species from the surrounding open-savanna vegetation. Most abundant are *Hypolytrum pulchrum*, *Scleria cyperina* and *Lagenocarpus tremulus*. **(Type B 5)**

Small trees are scattered here and there in the open-savanna vegetations, mainly belonging to *Roupala montana* and *Antonia ovata*. Very few tall trees are found. The only noteworthy species is *Platonia insignis* which occurs in small groups near the rivulets and along the margins of the savanna. These trees have no marked effect on the composition of the vegetation at their foot.

III. 4.2. The De Jong Noord savanna

III. 4.2.1. *General data*

Position: immediately S.W. of the village De Jong Noord (km 99.5 along the railroad)
Map 1 : 40 000 : 21 d
Area: about 325 ha
Date of visit: April 26th, 1959

This savanna is separated from the Gros savanna by a strip of forest. It lies a few m higher and is more hilly than the latter, but in principle it presents the same conditions for plant-growth.

On a map in VAN KOOTEN (1954) "probably conglomerate" is frequently indicated in lines running parallel to those on the Gros savanna. It appears that these indications correspond with the same type of pebble-knolls.

III. 4.2.2. *Vegetation*

In general the same vegetation types were observed as on the Gros savanna.

On one of the pebble-knolls the bushes were examined. It appeared that the most abundant species were *Antonia ovata*, *Marlierea montana* and *Humiria balsamifera* (**type B 6**). The vegetation of the open patches was characterized by the small form of *Bulbolstylis conifera* (**ass. 2.2.5**). This vegetation type, however, was also found on flat tops and gentle slopes, provided that they had pebbles at their surface.

On the steeper slopes with gravel in (not on) the soil the *Rhynchospora curvula* vegetation (**ass. 2.2.3**) was very well developed with relatively much *Bulbostylis lanata*. On one spot in the transition zone with much *Abolboda pulchella* (**subass. b**) a single specimen of *Byrsonima verbascifolia* was observed.

In the *Marlierea* bushes (**type B 5**) some species were present that connect this vegetation type more closely with the bushes on wet white sand, viz. *Retiniphyllum schomburgkii* and *Pagamea capitata*.

Two flat tops were examined. They had an impenetrable layer of gravel as deep as 5 to 10 cm down. Nevertheless the *Axonopus purpusii* vegetation (**ass. 2.3.1**) was present with much *Mesosetum cayennense*, *Aristida tincta*, *Leptocoryphium lanatum* and *Trachypogon plumosus*.

On many slopes vegetations with *Bulbostylis spadicea* (**ass. 2.2.4**) were observed.

III. 5. COMPARISON WITH OTHER SAVANNAS IN SURINAM

Welgelegen-type

HEYLIGERS visited the small savanna north of the village Berlijn in 1956. *Leptocoryphium lanatum* was the most abundant grass. Other species with an ecologically indicative value are e.g. *Rhynchospora glauca*, *Schultesia brachyptera* and *Desmocelis villosa*. His species list, together with earlier incidentally collected species, suggests that this savanna is covered for the greater part by the same vegetation type as the other wet savannas of the Welgelegen-type (ass. 3.1.1). The same holds for a savanna on the E. bank of the Marataka river in the N.W. part of Surinam where Mr. and Mrs. FLORSCHÜTZ collected a number of species in 1951.

A savanna belonging to the dry variant of the Welgelegen-type is situated on the E. side of the Kasiwinika river S.W. of the village Kopi. It was visited by LINDEMAN in 1953. It appears from his data that this savanna resembles more or less those of the Coesewijne-type. There occur vegetations resembling the dry orchard-savanna vegetations (all. 1.2) in which *Thrasya petrosa* was found. On some spots a combination of species was found closely similar to the association of *Elyonurus adustus* on the Coesewijne savanna (ass. 2.3.2), though *Elyonurus* itself was not observed, whereas other spots presented a vegetation with *Panicum stenodoides*, probably similar to the one on the Lobin savanna (ass. 2.3.4). A vegetation type on lower stretches obviously belongs to the common association of very wet and heavy soils mentioned above (ass. 3.1.1), here with e.g. *Rhynchanthera grandiflora*, *Scleria setacea* and *Desmocelis villosa*. There is a small swampy depression. In a zone with kawfoetoes surrounding it the vegetation is probably identical with the *Ischaemum guianense* vegetation (ass. 3.2.1) in the rivulet along the Lobin savanna (loamy part). Here it is rich in *Rhynchospora podosperma*. In the centre of the depression, on high kawfoetoes, *Lagenocarpus guianensis* is the most abundant species (cf. comm. 3.2.5). On one spot near the Kasiwinika river there is a vegetation consisting mainly of *Eleocharis* spec., *Rhynchospora cyperoides* and *Dalbergia glauca*. It is probably related to the community of *Dalbergia glauca* (3.2.4) on the outermost edge of the Coesewijne savanna.

In 1948 LANJOUW and LINDEMAN crossed the extensive savanna complex north of the Wane-creek (see LINDEMAN, 1953). The topsoil of the Welgelegen-savannas in this region may be more or less sandy. Possible explanations for this phenomenon were reviewed by VAN DER EYK (1957). Though as a rule the surface is flat, the ecological conditions on those savannas seem to resemble those on the Gros savanna. In principle the same combination of species was found here (all. 2.2). Compare e.g. on the one hand *Paspalum pulchellum*, *Panicum micranthum*, *Lagenocarpus tremulus*, *Perama hirsuta*, *Xyris spathacea* and *X. paraënsis* with, on the other hand, *Aristida tincta*, *Panicum stenodoides*, *Rhynchospora globosa* and *Hypolytrum pulchrum*. *Abolboda pulchella* was found too, but *Mesosetum tenuifolium*, *Rhynchospora rhizomatosa* and *Bulbostylis lanata* were lacking. The composition of the bushes on these savannas also brings the Gros savanna to mind. Among the collected species are *Antonia ovata* and *Psychotria cordifolia*.

Watamalejo-type

On the same expedition LANJOUW and LINDEMAN made an inventory of the species of a savanna on one of the old offshore bars. The list nearly completely corresponds with one of the associations found on the savannas of the Zanderij-type, e.g. in the centre of the depression in the Lobin savanna (see III.3.3.1, ass. 2.1.2). Only *Aristida tincta* (rare) and *Bulbolstylis lanata* (common) do not fit into this picture.

Coesewijne-type

The most northern part of the white-sandy Tibiti complex, near the village Tibiti-sabana, belongs to the Coesewijne-type, not to the Welgelegen-type as was assumed by COHEN & VAN DER EYK (1953; see BAKKER, 1954). LINDEMAN visited this savanna in 1949. His data indicate that its drier parts have much in common with the Lobin savanna. There is an orchard-savanna vegetation with *Curatella* resembling the one in the centre of the Lobin savanna (see III. 2.1.3.1, ass. 1.2.2). Another type found here is the combination of *Trachypogon plumosus* with *Rhynchospora barbata*, *Mesosetum cayennense*, *Aristida tincta* and *Leptocoryphium lanatum* (ass. 1.3.2, subass. b). Probably the association of *Panicum stenodoides* (2.3.4) or a more or less similar one is also present.

The Wara savannas and the other savannas on the western bank of the Marataka river were the object of a brief study by Mrs. and Mr. FLORSCHÜTZ in 1951. In general the collected species indicate that the vegetation on several spots belongs to the same group as the well-developed orchard vegetations on the savannas of this type (all. 1.2), though a tree layer was not observed.

Among the species met with were *Pavonia speciosa*, *Phaseolus longepedunculatus*, *Tephrosia purpurea*, *T. sessiliflora*, *Aeschynomene paniculata* and *Cassia faginoides*.

Kasipora- and Zanderij-type

HEYLIGERS (1963) studied an extensive complex of white-sand savannas between Jodensavanna and Kasipora. All types of one-layered vegetations as well as bushes of the Lobin savanna (white-sandy part) are also found in that region and as a rule are much better developed there. HEYLIGERS deals with them in detail. The only types that could be studied better on the Lobin savanna are the *Trachypogon* vegetation (ass. 1.1.1) and the vegetation of *Bulbostylis circinata* (ass. 2.1.1).

LANJOUW (1936) paid attention to the white-sand savannas in the surroundings of Zanderij. Near Sectie O this author found a vegetation type dominated by *Gymnopogon foliosus* that probably belongs to the group of associations on dry white sand (all. 1.1). So far it has not been found outside this locality.

Saban-pasi-type

Another savanna visited by LANJOUW (1936) is the Patrick savanna, a small savanna by the railroad near Brownsweg. The list of collected species, though short, shows clearly that the vegetation types of this savanna correspond with some of those described from the other investigated savannas of the Saban-pasi-type. He collected e.g. *Bulbostylis lanata*, *Rhynchospora curvula*, *Scleria cyperina* and *Hypolytrum pulchrum*.

It appears from the description by VAN KOOTEN (1954) that the Rosebel savanna presents the same ecological conditions as the Gros and the De Jong Noord savanna. On some of the photographs published by this author the same type of pebble-knolls may be recognized, covered partly by bushes, partly by a scanty one-layered vegetation.

The present author made a trip of one day to the Brinckheuvel and the savanna south of it in August 1958 before the actual investigation was started. A small collection was made. In general the species collected on the slopes indicate the presence of some of the vegetation types studied afterwards on the Gros savanna. However, it may be taken for granted that in this area sites occur with a topsoil of pure white sand and covered with a corresponding type of vegetation (all. 2.1). See VAN KOOTEN (1954).

Bosland-type

In 1956 HEYLIGERS collected some species on the hill-savanna near Berg en Dal on the western side of the Suriname river. The list of species indicates a dry soil of loamy sand or another, not too heavy type of soil. This, however, is not at all in agreement with the descriptions of these savannas by VAN DER EYK (1954) and COHEN & VAN DER EYK (1953). HEYLIGERS found e.g. *Bulbostylis junciformis*, *Borreria latifolia*, *Panicum rudgei*, *Paspalum plicatulum* and *Schizachyrium brevifolium*.

Paroe-type

In 1952 GEIJSKES made a collection of plants on the Palaime savanna, N. of the Upper Sipaliwini river in the extreme south of Surinam. The combination of e.g. *Tibouchina aspera*, *Sipanea pratensis*, *Aristida tincta*, *Rhynchospora globosa*; *Lagenocarpus tremulus* and *Perama hirsuta*; and *Scleria cyperina*, *Hypolytrum pulchrum* and *Bulbostylis lanata*, appears to indicate vegetation types that are described here from the savannas of the Saban-pasi-type (all. 2.2).

A collection made by ROMBOUTS in 1935 and 1936 on the Sipaliwini savanna near the Brazilian border suggests that many vegetation types are found there that correspond largely with those of the savannas of the Coesewijne- and the Saban-pasi-type.

Tafelberg-type

MAGUIRE & coll. (1948) published on the collections made by the first author a.o. on the small savannas on the top of the Tafelberg. As far as the species are identical with savanna species of N. Surinam they occur on wet white-sand savannas of the Zanderij- and the Watamalejo-type (all. 2.1). These species, forming one-layered vegetations, are *Raddia nana*, *Panicum nervosum*, *Paspalum polychaetum* (erroneously published as *Paspalum pulchellum*), *Lagenocarpus tremulus*, *L. amazonicus*, *Rhynchospora barbata*, *R. tenuis*, *Abolboda americana*, *A. grandis*, *Xyris dolichosperma*, *Syngonanthus gracilis*, *Burmannia capitata*, *B. bicolor*, *Polygala appressa*, *Sauvagesia sprengelii*, *Perama hirsuta*, *Siphanthera hostmannii* and *Catasetum discolor*. The presence of *Scleria micrococca* and *Borreria capitata* is more difficult to explain. The main species of the scrub and the bushes, found also in N. Surinam, are *Ormosia costulata*, *Ternstroemia punctata*, *Retiniphyllum schomburgkii*, *Pagamea capitata*, *Licania incana*, *Clusia fockeana*, *Humiria balsamifera* and *Byrsonima crassifolia*. It has to be remarked that on the white-sand savannas of N. Surinam some of these species are restricted to bushes on dry soil (type B 1) and others to bushes on wet soil (type B 4).

CHAPTER IV

THE SAVANNA FLORA

IV. 1. FLORISTIC NOTES

An unknown *Rhynchospora* has been collected, first on the Coesewijne savanna (see III.2.4.3.1), later also on the Gros savanna (see III.4.1.3.1), LINDEMAN (1965) described it as *Rhynchospora rhizomatosa*.

In one of the bushes on the Lobin savanna a *Humiria* was found that could not be determined with CUATRECASAS' (1961) monograph. Together with three older specimens of the Utrecht herbarium exhibiting the same features, it was send to Mr. Cuatrecasas, who considered it to be a new taxon for which he proposed the name *Humiria balsamifera* (Aubl.) St. Hil. var. *balsamifera* fo. *acuminata* Cuatr.

The following species were collected for the first time in Surinam:

Philodendron latifolium C. Koch – Lobin savanna; white-sandy part
Heliotropium fruticosum L. – Lobin savanna; loamy part
Ayenia tomentosa L. – Lobin savanna; loamy part
Paspalum gardnerianum Nees – Coesewijne savanna
Psidium grandifolium Mart. – Coesewijne savanna
Zornia tenuifolia Moricand – Coesewijne savanna
Prestonia perplexa Woods. – Gros savanna
Mesosetum tenuifolium Swallen – Gros savanna

Within the following taxa morphologic variations appeared to be correlated with differences in habitat. In general the reader is referred to appendage 3.

Two varieties of *Rhynchospora barbata* (Vahl) Kunth are clearly distinguishable, viz. the typical variety and the var. *glabra* Maury, which ecologically exclude one another. During our study in the field unfortunately the former one and *R. arenicola* Uitt. have been confused in some localities.

Two forms of *Bulbostylis capillaris* (L.) Kunth var. *capillaris* were observed, viz. a small one with a height of 5–25 cm and a higher one reaching a height of 30–45 cm. The length of the leaves is about proportional to the length of the stem.

The normal *Bulbostylis conifera* Kunth is 15–40 cm high. On the tops of the pebble-knolls of the Gros and the De Jong Noord savanna a very small form ("*minor*") is found with stems of about 11 cm and leaves of 2–2.5 cm, while the generative parts are relatively tiny too. There is a gradual transition to the normal form in intermediary habitats (see III.4.1.3.1).

Axonopus purpusii (Mez) Chase may have leaves with a width up to 6 mm, but in N. Surinam 4 mm is rarely exceeded. There is, moreover, a certain variability in the width corresponding with the habitat. In general specimens with narrower leaves occupy heavier and wetter soils. It appeared reasonable to take a width of 2 mm as a limit for the distinction of two forms.

A very variable taxon is *Byrsonima crassifolia* (L.) Rich. var. *crassifolia*. Small trees and normal shrubs are found in open savanna and in bushes as well. The orchard-tree form ("*malosa*") in N. Surinam seems to be restricted to very special habitats (see III.4.1.3.1). Very small shrubs are present on dry white sand (see III.3.3.1). In all these cases the specimens may have flowers and fruits.

IV. 2. HABITAT IN GENERAL

Not every species occurring on savannas may be regarded as a genuine savanna species. The savanna flora partly consists of species which are found also in other habitats. Some of them have their optimum elsewhere, and there even are a few not developing completely on the savannas.

The data for the elaboration of the following survey are derived, besides from own observations, from LINDEMAN (1953), HEINSDIJK (1953), LINDEMAN & MOOLENAAR (1955, 1959), SCHULZ (1960), HEYLIGERS (1963), the herbarium at Utrecht and unpublished observations of Dr. J. C. Lindeman. For the description of the forest types one is referred to these authors, for the nomenclature in particular to LINDEMAN & MOOLENAAR and for criticism of the latter to AUBRÉVILLE (1961a).

It is evident that all species of the open-savanna vegetations, but not occurring in the bushes (**1**), are heliophilous. Among them the real savanna species (**1a**) form by far the largest group. Nearly all species which quantitatively may play an important part belong to it, e.g. *Trachypogon plumosus*, *Mesosetum loliiforme*, *Bulbostylis conifera* and *Lagenocarpus tremulus*. Some trees and shrubs restricted to open savannas (orchard savannas included) also have to be referred to this group (e.g. *Curatella americana* and *Byrsonima coccolobifolia*).

There is a group of species occurring on all sorts of open localities so long as the latter are not too wet (**1b**). Some of them, e.g. *Zornia diphylla* and *Crotalaria stipularia*, are outside the savannas restricted to natural habitats like river banks and beach ridges. However, most of them are weeds, occurring on the savannas only under rather special conditions (mainly on dry sandy soils), though elsewhere they appear to be less fastidious. Examples are *Melampodium camphoratum*, *Euphorbia brasiliensis*, *Piriqueta cistoides* and *Desmocelis villosa*. Probably these weeds were originally confined to the savanna. It even seems allowed to assume that most weeds with a wide distribution over tropical and even subtropical America originated from the savannas, for the savannas as habitats for plants have many properties in common with all sorts of secundary habitats.

The species of very wet savannas and savanna rivulets partly occur also on the borders of swamps and pools, along rivers and ditches and the like (**1c**). Examples are *Conobea aquatica*, *Buettneria scabra* and *Calyptrocarya glomerulata*.

The vegetation on the savanna rivulets consists for a large part of species which are sometimes very common in swamps (**1d**). Though the rivulets represent only small areas of the proper habitat, the majority of these species nevertheless flourish here; e.g. *Blechnum indicum*, *Rhynchospora cyperoides* and *Scleria microcarpa*.

The savanna bushes on white sand may be regarded physiognomically as the one end of the series savanna forest – savanna wood – savanna scrub – savanna bushes. There are, apart from the physiognomy, floristic differences between forest, wood and scrub. The bushes, however, are mere fragments of the scrub and they have no species of their own (HEYLIGERS). Therefore in the next classification scrub and bushes will be treated as a single entity. As the bushes on the other soil types do not have a scrub-equivalent, the species of the whole group will be indicated as "species of the savanna bushes".

Nearly all the species of the savanna bushes complete their life-cycle in these bushes, and may be included in the savanna flora (**2**). A small number, however, belongs to the forests and does not flower in the bushes (**3**).

Real savanna-bush species are in the minority (**2a**). *Xylopia frutescens*, *Rapanea guianensis*, *Roupala montana*, *Davilla aspera* and *Doliocarpus calinea* belong to this category. The last two are lianas which may occur, though less frequently, in open-savanna vegetations, and in that case they have the form of small shrubs. The only herbaceous plants restricted to the undergrowth of the bushes are *Scleria pyramidalis* and *Schizaea elegans*. The undergrowth of the bushes, which is of importance only in the more open types, consists mainly of species having their optimum in open savanna vegetations (**1a**).

There are species which occur on all sorts of open, sunny spots, so long as they can find a support. They are found not only in savanna bushes, but also along forest edges and in several types of secondary habitat. Examples are *Allamanda cathartica*, *Philodendron latifolium* and *Gonolobus ligustrinus* (**2b**).

The majority of the species occurring in the bushes as shrubs or small trees are found in several forest types in the form of higher trees. Some are restricted to the one-layered savanna wood, e.g. *Ternstroemia punctata*, *Retiniphyllum schomburgkii* and *Miconia ciliata* (**2c**), but most of them occur also in the two-layered savanna forest, so e.g. *Trattinickia burserifolia*, *Licania incana*, *Clusia fockeana* and *Ilex jenmani* (**2d**). Another group shows a still greater adaptibility and is found not only in the light forest types already mentioned, but also in the heavier forest types taken together here as rain forest. Examples are *Maprounea guianensis*, *Tapirira guianensis*, *Marlierea montana* and the climbing *Tetracera asperula* (**2e**). A few of them are lacking in the savanna wood, e.g. *Antonia ovata* and *Protium heptaphyllum* (**2f**). Finally there is a group of species, which occur only in the savanna bushes and in rain forest, e.g. *Ternstroemia dentata* and *Ocotea neesiana* (**2g**).

The group of species which are found only in a sterile condition in the bushes (**3**), has only one representative occurring in all forest types mentioned, viz. *Doliocarpus guianensis* (**3a**). The other species occur either in savanna forest and rain forest (e.g. *Pithecellobium jupunba* and young specimens of *Oenocarpus bacaba*, **3b**), or in rain forest alone (e.g. *Pera glabrata*, *Virola sebifera* and young specimens of *Euterpe oleracea*, **3c**).

Part of the species found in the bushes occur not only in primary woods and forests but also in other habitats. Some are found also in swamps, e.g. *Clusia nemorosa* and *Pithecellobium jupunba* (**S**), whereas several others, all belonging to the groups 2e, f, g and 3, are found also in marsh forest, e.g. *Marlierea montana*, *Parinari campestris* and again *Pithecellobium jupunba* (**M**). Many species, also of the groups 2a, b, c and d, occur in one or another type of the secondary forest which in Surinam is called *kapoeweri*. ("capoeira" in Brazil) (**K**). Species with a high abundance in kapoeweri are e.g. *Tapirira guianensis*, *Protium heptaphyllum*, *Clusia fockeana* and *Xylopia frutescens*.

A group left out of consideration up to now, consists of those species occurring in optimal condition both in open-savanna vegetations and in savanna bushes (1/2). Most of these do not occur outside the savannas (1a/2a). There are several small shrubs among them, e.g. *Tibouchina aspera*, *Symplocos guianensis* and *Miconia rufescens*, and some herbs, e.g. *Actinostachys pennula* and *Scleria cyperina*. There are only few species which occur not only in open savanna and savanna bushes, but also in a type of forest. An example is *Wulffia baccata*, which may be found in savanna wood (1a/2c).

Only few of the species rooting in the soil can not be classified with the aid of this survey. An example is *Heliconia psittacorum*, which is common on savannas, in swamps, in several types of light forest and in all sorts of secondary habitats.

A quite separate group is formed by the epiphytes, half-parasites and parasites found on the aerial parts of other plants; they are all of minor importance (4). Most epiphytes are Bromeliads, orchids and ferns. Of these only *Polystachya luteola* (Orch.) is rather common on *Curatella americana*. All half-parasites belong to the Loranthaceae; *Phthirusa squamulosa* is common, namely on *Licania incana*. The only parasite of this group is the ubiquitous *Cassytha filiformis* (Laur.), which is present in nearly every type of savanna vegetation.

The following list gives the numbers and percentages of the different groups. Column 3 of Table 11 presents the group(s) to which the various species belong.

Open savanna (272 species in total)		
1a	only in open savanna	197 = 72 %
1b	open savanna and other open spots	23 = 8 %
1c	very wet savanna and other very wet spots	8 = 3 %
1d	savanna rivulets and swamps	19 = 7 %
1/2	open savanna and savanna bushes	23 = 8 %
Savanna bushes (117 species in total)		
2a	only in savanna bushes	18 = 15 %
2b	savanna bushes, forest borders, etc.	9 = 8 %
2c	savanna bushes and savanna wood	8 = 7 %
2d	idem and savanna forest	19 = 16 %
2e	idem, idem and rain forest	15 = 13 %
2f	savanna bushes, savanna forest and rain forest	4 = 3 %
2g	savanna bushes and rain forest	7 = 6 %
1/2	savanna bushes and open savanna	23 = 20 %
2 + 1/2	(species of the bushes flora)	103
3a	savanna wood and forest, rain forest	1 = 1 %
3b	savanna forest and rain forest	5 = 4 %
3e	rain forest	8 = 7 %

K	kapoeweri	37 = 31 %
M	marsh forest	10 = 9 %
S	swamp	4 = 3 %

Epiphytes and (half-)parasites 4 19 species

IV. 3. HABITAT IN PARTICULAR ON THE SAVANNAS

It has been shown in section II.3 that the savanna soil everywhere can be defined with the aid of a moisture scale and a texture scale. However, not every theoretically possible combination of moisture and texture has been met with in the field.

It is possible to indicate the factual behaviour of a species with regard to these two factors by plotting it in the texture–moisture diagram (see II.3.3). There are many possibilities.

a. Species with a narrow ecological amplitude will fill only one, two or three of the squares. Some of them, each indicated by a different letter, are put together in the next diagram, explained in II.3.3.

	ws	rs	ls	sl	scl	h
vd	a		b	b		☒
d	c		d			☒
m	e	☒		f		☒
w	g	☒	h	f		
vw	i	☒	☒		☒	j
r	i	☒	☒	☒	☒	j

a. *Polygala angustifolia* var. *latifolia*
b. *Dipteracanthus angustifolius*
c. *Paepalanthus subtilis*
d. *Polycarpaea corymbosa*
e. *Stylosanthes angustifolius*
f. *Elyonurus adustus*
g. *Xyris spathacea*
h. *Bulbostylis lanata*
i. *Burmannia capitata*
j. *Sauvagesia rubiginosa*

b. There are species with a wider ecological range; the latter nevertheless seems to be clearly defined.

	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h
vd						☒		+	+	+	+	☒		+	+			☒
d						☒		+	+	+	+	☒		+	+			☒
m		☒				☒		☒	+	+	+	☒		☒	+			☒
w	+	☒	+	+	+	+		☒	+	+	+	+		☒				
vw	+	☒	☒	+	☒	+		☒	☒	+	☒	+		☒	☒		☒	
r	+	☒	☒	☒	☒	+		☒	☒	☒	☒	+		☒	☒	☒	☒	

Panicum nervosum *Sipanea pratensis* *Bulbostylis capillaris* var. *tenuifolia*

The first example suggests as determining factor the degree of moistness, the second example the texture or a factor corresponding with the latter, whereas the third suggests that the two factors are of equal importance.

c. Many species, however, do not show an ecological range which can be interpreted so easily. Consider e.g. the next two examples.

	ws	rs	ls	sl	scl	h
vd	+					☒
d	+		+			☒
m		☒	+			☒
w		☒				
vw		☒	☒	+	☒	+
r	+	☒	☒	☒	☒	+

Desmodium barbatum

ws	rs	ls	sl	scl	h
+					☒
+		+	+	+	☒
	☒	+	+	+	☒
	☒	+	+	+	+
	☒	+		☒	+
	☒	+	☒	☒	+

Polygala longicaulis

The distribution of these two species over the savannas is determined obviously by more factors than soil texture and moisture alone.

In the case of *Desmodium barbatum* it is more or less possible to point out what these factors are. The species is confined to the denser and higher vegetation types and other habitats with some shadow provided either by associated plants or by a forest border or a similar agent. It is not certain that the shadow itself is the actual determining factor. Probably it is correlated with lower temperature and a higher humidity of the air.

There are quite a number of species which show more or less the same behaviour in this respect as *Desmodium barbatum*, e.g. *Eriosema violaceum*, *Cyperus amabilis*, *Imperata brasiliensis* and *Paspalum plicatulum*. In neither of these cases it has been determined which factor or combination of factors of the "shadow-complex" is responsible. However, not all of them are indifferent to the moisture and the texture of the soil, as *Desmodium barbatum* seems to be to a certain degree.

An explanation of the behaviour of *Polygala longicaulis* can not be given here. Probably the distribution of this annual species is mainly determined by environmental conditions favourable to its germination. On the other hand, competition of other species also may be important.

The example of *Desmodium barbatum*, and especially that of *Polygala longicaulis*, stresses the fact that in general it is not possible to explain the ecological behaviour of plants by the aid of field observations alone. The main difficulty is that the influence which the plants exert on one another, has to be taken into account, and this very diversified complex of factors mostly escapes the means of a study in the field.

Only in some instances field observations may clarify some of the relations between a species and its abiotic environment. E.g. *Melampodium camphoratum* appears to be restricted on the savannas to very dry white and red sands. This, however, has nothing to do with preference, for as a weed outside the savannas the species occurs also on wet and heavy soils. *Phyllanthus orbicularis*, on the other hand, exhibits as a savanna plant and as a weed the same behaviour, viz. it is confined to dry sandy soils. This suggests a distinct preference for the latter.

In general, field data can only contribute to a picture of the *factual* amplitude of a species with regard to an abiotic factor or a complex of such factors. The *potential* amplitude which can appear only if the influence of biotic factors has been excluded, has, as a rule, to be studied experimentally. The difference between factual and potential ecological amplitude had been recognized since long, but the terms were introduced only recently by HEIJBROEK (1955).

The amplitude of the species with regard to granular composition and humidity of the soil as given in the previous examples, refers of course to the factual situation and the same holds for the columns 4 and 5 of table 11. In the table gaps in the picture are not taken into account, so e.g. *Polygala longicaulis* is simply indicated as occurring on all soil types with every degree of humidity. In such cases more detailed information can be obtained only from the vegetation tables.

Column 6 of table 11 indicates the species which are correlated with the "shadow-complex".

Finally the subjoined diagrams present the number of species occurring at every actually observed combination of soil texture and moisture.

	ws	rs	ls	sl	scl	h
vd	39	54	56	44	20	☒
d	40	55	99	59	25	☒
m	37	☒	82	60	27	☒
w	62	☒	67	64	39	41
vw	52	☒	☒	57	☒	66
r	35	☒	☒	☒	☒	61

Open savanna (272 species)

ws	ls	sl
☒	☒	☒
43	46	40
30	45	52
32	32	40
☒	☒	☒
☒	☒	☒

Savanna bushes (103 species)

IV. 4. DISPERSAL TYPES

The best known and most generally applied system of dispersal types is the one proposed by MOLINIER & MÜLLER (1938). It is used in the first place for the calculation of dispersal spectra of plant communities.

DANSEREAU & LEMS (1957), in criticizing this system, are of opinion that the criteria have not been chosen objectively and not in a consequent way. They want to make a clear distinction between actual agents of dispersal and presumed adaptations of the diaspores themselves. They therefore elaborate a new system which is based only on visible adaptational features, whether these turn out to fulfil their obvious function or not. This system is simple, clear and logical and therefore will be used here.

In short the system is like this:

A. Autochores – Diaspores without obvious adaptation to any external agent
  1. Barochores – D. heavy
  2. Sclerochores – D. lighter than 1
  3. Semachores – D. shaken out by swaying motion of parent-plant
  4. Auxochores – D. deposited by parent-plant
  5. Ballochores – D. forcibly ejected from parent-plant

B. Heterochores – Diaspores either with appendages, or extremely light, or provided with fleshy outer layers
  6. Cyclochores – D. largely consisting of accessory parts, forming a voluminous spherical frame
  7. Saccochores – D. within a loose covering
  8. Pterochores – D. with scarious winglike appendages

9. Pogonochores – D. with plumose appendages, hairs, aigrettes
10. Ascochores – D. of low density
11. Sporochores – D. very minute
12. Ixochores – D. glandular, viscous
13. Acanthochores – D. spiny, hooked or bristled
14. Sarcochores – D. with soft and fleshy outer layers

If a species can be included in more than one of these groups, preference should be given according to the following sequence: 4 - 6 - 8/7 - 9 - 12/13 - 14 - 11 - 2/10 - 1 - 5/3.

The types, represented on the savannas are: 1, 2, 8, 9, 11, 13 and 14.

The flora of the open savannas consists for three quarters of sclerochores (2). To this group belong e.g. nearly all sedges and Papilionaceae, all Eriocaulaceae, Euphorbiaceae, Polygalaceae, Xyridaceae, and many grasses. The pogonochores (9) are represented mainly by Compositae and grasses. The orchids and the cryptogamic species are sporochores (11). Finally there are some sarcochores (14) with edible fruits (e.g. *Eugenia punicifolia*, *Psidium guineense* and *Erythroxylum citrifolium*), some pterochores (8, e.g. *Burmannia bicolor*, *B. capitata* and *Rhynchospora barbata*) and two Acanthochores (13, *Zornia diphylla* and *Echinolaena inflexa*).

Among the species of the bushes the sarcochores (14) take the first place, followed by the sclerochores (2). To group 14 belong all Myrtaceae and Rubiaceae, but the Melastomataceae are divided over the two groups. The only barochores (1) are *Anacardium occidentale* and *Rollinia exsucca*. There are a few pterochores (8), e.g. *Himatanthus articulatus*, and also a few pogonochores (9), e.g. *Mandevilla scabra*. Sporochores (11) are only present in the undergrowth.

Column 8 of table 11 presents the dispersal type to which a species belongs. The distribution of the species over the types is as follows:

	Open savanna (256 species)	Savanna bushes (91 species)
1. barochores	—	2 = 2 %
2. sclerochores	181 = 71 %	34 = 36 %
8. pterochores	13 = 5 %	3 = 3 %
9. pogonochores	29 = 11 %	2 = 2 %
11. sporochores	15 = 6 %	6 = 7 %
13. acanthochores	2 = 1 %	—
14. sarcochores	16 = 6 %	45 = 50 %

Section IV.6 deals with the question of the effectiveness of the supposed adaptations.

IV. 5. DISTRIBUTION

The distribution of the species has been studied with the aid of the Utrecht herbarium, floras, monographs, enumerations and other taxonomic publications, which in general are not mentioned in the listed references. Some recent plant geographic and ecological papers provided additional information concerning the savanna flora, viz. DE ANDRADE LIMA (1959), ARISTEGUIETA (1959), BLYDENSTEIN (1962), CUATRECASAS (1958), LASSER (1955), TAKEUCHI (1960a, b), TAMAYO (1956, 1960) and WILLIAMS (1940, 1941, 1942).

IV. 5.1. Geographic affinities in general

The next table gives the opportunity to compare the distribution of the savanna flora of N. Surinam with that of the Surinam flora as a whole.

The figures in the first column refer to 1270 species, covering about a third of the total number collected; they belong to 43 representative families. The choice of the families was restricted because not all of them have been treated already in the "Flora of Surinam". For this reason the important family of the *Orchidaceae* had to be excluded. Families with many introduced representatives (weeds, cultivated plants) have been left out of consideration (e.g. *Gramineae* and *Euphorbiaceae*) and within the other families this category has been excluded too.

The total picture should be considered with some caution, not only for its incompleteness, but also because it is based on our present-day knowledge with regard to the distribution of the included species, which is not always quite sufficient.

The selected 43 families are: *Alismataceae*, *Annonaceae*, *Aquifoliaceae*, *Araceae*, *Araliaceae*, *Bignoniaceae*, *Bombacaceae*, *Bromeliaceae*, *Burmanniaceae*, *Burseraceae*, *Caryocaraceae*, *Combretaceae*, *Connaraceae*, *Cyperaceae*, *Dilleniaceae*, *Droseraceae*, *Eriocaulaceae*, *Flacourtiaceae*, *Gesneriaceae*, *Guttiferae*, *Humiriaceae*, *Lauraceae*, *Lecythidaceae*, *Loganiaceae*, *Malpighiaceae*, *Marantaceae*, *Melastomataceae*, *Myristicaceae*, *Myrsinaceae*, *Myrtaceae*, *Ochnaceae*, *Olacaceae*, *Passifloraceae*, *Piperaceae*, *Polygalaceae*, *Quiinaceae*, *Rapateaceae*, *Rosaceae*, *Rubiaceae*, *Sapindaceae*, *Turneraceae*, *Vochysiaceae* and *Xyridaceae*.

	1	2	3
Endemics	13 %	1 %	3 %
occurring in Guiana	81	97	97
occurring in another part of extra-Amazonian northern S. America, incl. Trinidad and Tobago	39	84	71
occurring in the Amazon region	50	70	60
occurring in another part of S. America	28	72	48
occurring in Central America	21	41	19
occurring in the West Indies, excl. Trinidad and Tobago	19	42	17
occurring outside America	3	4	1

column 1. The whole flora of Surinam
column 2. The species of the open-savanna vegetations in N. Surinam
column 3. The species of the savanna bushes in N. Surinam.

Even when allowance is made for a possible shifting in column 1, it may be concluded that the flora of the savannas, in particular that of the open savanna, has a markedly wider distribution than the Surinam flora as a whole.

In addition the subjoined list gives a more detailed survey of the geographic affinities of the savanna flora. It shows the percentages of the savanna species of northern Surinam, present in some other regions.

	Open savanna	Savanna bushes
French Guiana	63 %	74 %
British Guiana	87	87
Venezuelan Guiana	61	45
rest of Venezuela, Trinidad, Tobago	72	55
Colombia	15	18
Amazonian Brazil	70	60
eastern Brazil	73	43
Bolivia	30	24
subtropical South America	20	2
Central America	41	19
West Indies, excl. Trinidad and Tobago	42	17
subtropical North America	7	—

It is obvious that of the two groups the flora of the savanna bushes has a more distinctly tropical South-American character.

IV. 5.2. **Areas of distribution**

In order to arrive at the distinction of geographic elements the following regions (in combination with Surinam) have been considered.

Sur	Surinam
BG	British Guiana
wGui	western Guiana: BG, Venezuelan Guiana and Rio Branco
FG	French Guiana
eGui	eastern Guiana: FG and Amapa
Gui	wGui and eGui
nSA s.s.	northern South America sensu stricto: Gui, the rest of Venezuela, Trinidad and Tobago, Colombia and Equador
nSA	northern South America: nSA s.s., Amazonian Peru and Brazil (Amazonas and Pará)
wSA	western South America: the rest of Peru, W. Matto Grosso, Bolivia and N. Chile
eSA	eastern South America: Maranhão, E. Matto Grosso, Goiás, Minas Gerais, S. Paulo and the other E. Brazilian states
cSA	central South America: Matto Grosso
tSA	tropical South America: n, w, e and cSA
sSA	subtropical South America: Paraná, S. Catarina, Rio Grande do Sul, Uruguay, N. Argentina, etc.
SA	South America: tSA and sSA
CA	Central America: tropical Mexico up to and including Panama
WI	West Indies: all Caribbean islands except Trinidad and Tobago
tA	tropical America: tSA, CA and WI
sNA	subtropical North America: subtropical Mexico and USA
Afr	Africa
pt	pantropic: American, African and other tropics

The area of distribution of every species can be indicated by one symbol or by a combination of several of the symbols. Column 1b of table 11 in this way presents all areas. It must, however, be born in mind that our knowledge on this point is not complete. Many parts of Latin America have been hardly or not at all investigated. Moreover, incorrect data may have been published, for in many of the taxa there are still difficulties to be cleared up. However, it is not probable that the number of possible mistakes should disturb the general picture concerning the geographic aspects of the savanna flora.

Some examples of species with an interesting distribution must be mentioned.

Bulbostylis fasciculata, a common species of the open savannas, has never been found outside N. Surinam. The same holds for *Scleria pyramidalis*, a characteristic sedge in the undergrowth of certain savanna bushes, and for *Rhynchospora rhizomatosa* (see IV.1). Other endemics of the bushes are the shrubs *Mapouria opaca* and *Humiria balsamifera* var. *balsamifera* fo. *acuminata.*

There are some species with a Caribbean distribution, i.e. a combination of Gui or nSA (s.s.) with CA, WI and/or sNA, but not enough to justify the distinction of a Caribbean element within the savanna flora. Examples are *Paspalum pulchellum*, *Panicum stenodes* and *P. stenodoides*, *Apteria aphylla* var. *hymenanthera* and *Rourea surinamensis.*

JOHNSTON (1935) did not believe that *Heliotropium fruticosum* would occur in French Guiana, though it is mentioned by AUBLET. His doubt may have been unfounded as the species is now known to occur in Bolivia, Columbia, Venezuela, Central America and Texas, on Cuba, Trinidad, Aruba, Curaçao and Bonaire; recently it has been found in Surinam.

The "Flora Brasiliensis" mentions *Psidium grandifolium* from E. Brazil; since then it never has been cited, but in 1958 it was collected on the Coesewijne savanna. The orchid *Lyroglossa euglossa*, also present on the Coesewijne savanna, shows the same gap in its distribution.

Habenaria platydactyla shows a disjunction which is even more striking. According to the "Flora Brasiliana" it has been found only twice in Paraná. Now it was collected in 1959 on the Coesewijne and on the Lobin savanna. The distance between Surinam and the S. Brazilian stations is so large that this seems hardly believable.

As a rule there is no marked correlation between the taxonomic affinities and the distributional similarities within the savanna flora. However, in this respect it is notable that in general the areas of the *Gramineae* and the herbaceous *Papilionaceae* are relatively wide, those of the *Xyridaceae* relatively small.

IV. 5.3. **Geographic elements**

A geographic element can be defined as a group of species with the same area of distribution. A classification might have been carried out here on the basis of the previously mentioned regions. In that case, however, the majority of the elements would contain so few species that it would in many instances not be possible to draw fully reliable conclusions from them. Therefore it has been necessary to choose ampler criteria in order to obtain geographic elements with some statistical value. The following choice has been made:

G Guianan element, including species with areas symbolized by Sur, wGui, eGui and Gui

N northern South-American element: nSA and nSA s.s.

NE	northern-eastern South-American element: any of the areas of N or G in combination with eSA
MNE	Middle and northern-eastern South-American element: NE in combination with CA and/or WI
S	South-American element: any other combination of S. American areas than G, N or NE
A	American element: any combination of areas other than those symbolized by the foregoing five

In general these elements consist of a large group of species occupying the same area, in combination with a number of smaller, more or less corresponding groups. E.g. the NE-element on the open savannas is composed of 29 species neSA; 5 species nSA s.s., eSA; 2 species Sur, eSA; 1 species BG, eSA; 1 species FG, eSA; 1 species wGui, eSA. This example also shows that disjunct areas are not taken into consideration separately. There are only few species presenting this phenomenon and it may be asked in how many cases it is only a false picture which results from lack of information concerning the region figuring as the missing link.

The justification of our choice of the elements can not be understood completely unless we consider the relations existing between distribution and other aspects of the species. These relations will be dealt with in section IV.7 and in Chapter VIII.

The distribution of the species over the geographic elements is shown in the following table. (See also Table 11, column 1a)

	Open savanna (256 species)	Savanna bushes (91 species)
G	29 = 12 %	24 = 26 %
N	27 = 11 %	16 = 18 %
NE	39 = 16 %	12 = 13 %
MNE	26 = 10 %	3 = 3 %
S	23 = 9 %	16 = 18 %
A	112 = 42 %	20 = 22 %

A comparison between the two series again stresses the differences between the two groups of savanna inhabitants. Of the species of the bushes 75 % is in one or another way restricted to South America, whereas this percentage for the open-savanna species is only 48.

IV. 5.4. The Roraima element

The sediments from which the Roraima sandstones originated, were deposited on the Guiana shield either during the Upper Triassic (Weeks, 1948) or the Cretaceous (Tate, 1938; Darrah, 1945). According to Weeks these sandstones are similar to the widespread sandstones of central and southern Brazil. Next the Roraima plateau was gradually broken down. This breakdown resulted from a slow raising accompanied by climatic changes in the direction of increased rainfall. TATE, speaking of Auyán-tepuí in Venezuela, remarks: "The rate of uplift (which may be still going on) was possibly great enough to raise the general surface 2400 meters in spite of the increased rate of denudation."

The greater part of the sandstone cap has been eroded and transported in the form of sand to the edges of the shield. The basement rocks now are exposed nearly everywhere. The main remnants of the formerly extensive Roraima sandstone formation are a number of sandstone mountains and plateaus or table mountains.

On the flat tops of the latter and also on other more or less level spots, the soil may consist of a thin layer of whitish or reddish sand mixed with (or covered by) a greater or smaller amount of humus, but there are also stretches with only a slight amount of soil in the fissures of the sandstone rock. As a rule these stretches are occupied by open savanna and in the depressions by small bogs.

The climate of the tops has a relatively short dry season (3 months on Cerro Duida), during which the humidity of the air may remain high in consequence of the frequent fogs. See JENMAN (1882), BROWN (1901), HITCHCOCK in GLEASON (1931), TATE (1938), MAGUIRE (1945a, b).

FANSHAWE (1952) makes use of the simple but generally accepted view of the Roraima history to divide the flora of British Guiana into three entities. He distinguishes (1) the Pakaraima flora, occurring on the rests of the Pakaraima (= Roraima) plateau, the Kaieteurian series, (2) the Upland flora of the exposed basement rocks and (3) the Lowland flora on the White-Sand series. It is FANSHAWE's opinion, based on the great similarity of the three floras, that the Upland flora was derived from the Pakaraima flora, and the Lowland flora from the Upland flora. This idea may be a little too simple, as the possibility of immigration from entirely other regions has not been taken into consideration, yet it stresses the prominent part that must be ascribed to the flora of the table mountains if we wish to interpret the origin and the geographic relationships of the Guianan flora or of a part of it.

Anyhow it seems to be right to distinguish the table-mountain species as a separate group within the savanna flora of N. Surinam. Here this group will be called the *Roraima element.* This element is no geographic element like the groups distinguished above, and it is quite independent of them. The species composing it do not have similar areas. Perhaps in the long run it will turn out to be a genoelement or a migro-element in the sense of KLEOPOV (1941), that is either a group of species with the same area of origin or a group of species which reached an area coming from the same direction. At the moment nothing positive can be said in this respect.

MAGUIRE, COWAN, WURDACK & coll. (1953) enumerate 22 table-mountains from Surinam, British Guiana, Venezuela and Colombia. At the moment there are botanical data available from 13 of them. The authors say that the interpretation of the phytogeography and ecology of the flora of the "Guayana Highlands" may be more succesfully made at the conclusion of their program of exploration and after the completion of the review of the collected material. This is certainly true. Nevertheless it will be tried here to interpret the occurrence of the Roraima element on the N. Surinam savannas, at least from an ecological point of view.

The following sources were at our disposal:
Surinam: Tafelberg (MAGUIRE & coll., 1948)
British Guiana: Kaieteur savanna (JENMAN, 1882; MARTYN, 1937; MAGUIRE & coll., 1948); Mount Roraima (BROWN, 1901; GLEASON, 1929; STEYERMARK & coll., 1957)
Venezuela: Auyán-tepuí (TATE, 1938; GLEASON & KILLIP, 1939); Ptari-tepuí (STEYERMARK & coll., 1957); Cerro Duida (GLEASON, 1931; STEYERMARK & coll., 1957); Cerro Yaví (LASSER & MAGUIRE, 1950); Cerro Sipapo (MAGUIRE, COWAN, WURDACK & coll., 1953); Uaipán-tepuí (MAGUIRE & WURDACK, 1957); Chimantá-tepuí (MAGUIRE, STEYERMARK, WURDACK & coll., 1957); general (MAGUIRE & PHELPS, 1953)
Colombia: three table-mountains (SCHULTES, 1951)
General: MAGUIRE, COWAN, WURDACK & coll., 1953; MAGUIRE, WURDACK & coll., 1957.

The first eight areas have (collected and published) species in common with N. Surinam savannas. This is indicated in column 2 of Table 11. Up till now the list contains 72 species of the open savannas, that is 26 % of the total number, and 32 species of the savanna bushes, that is 31 % of the total number.

There are many grasses and sedges among them. The element is also relatively well represented among the Eriocaulaceae, the Melastomataceae and Rubiaceae, but poorly among the Papilionaceae.

In the next list the distribution of the Roraima element over the geographic elements is given.

	Open savannas	Savanna bushes
G	8 = 11 %	5 = 16 %
N	8 = 11 %	5 = 16 %
NE	15 = 21 %	4 = 13 %
MNE	7 = 10 %	5 = 16 %
S	9 = 12 %	—
A	25 = 35 %	13 = 39 %

It appears from these figures that a high percentage of the Roraima element consists of species with a rather wide distribution. Probably there was already a basis for this distribution before the Roraima plateau was completely dissolved into isolated mountains. This means that not all these species necessarily reached N. Surinam directly from the sandstone remnants. Other consequences will be discussed in Chapter VIII.

IV. 6. RELATION BETWEEN DISPERSAL TYPE AND DISTRIBUTION

One of the factors determining the distribution of a species is its capability of dispersal. In this respect it may be asked how far a feature that is supposed to be adaptational to an agent of dispersal actually is effective. This question may be approached by the calculation of the relation between the dispersal types and the geographic elements. This has been done in Table 3.

TABLE 3

Relation between dispersal type and geographic element (in absolute figures)

		Total	Geographic elements					
			G	N	NE	MNE	S	A
Species of open savanna vegetations	Total	256	29	27	39	26	23	112
	Dispersal types 2	181	26	23	31	18	15	68
	8	13	1	–	–	2	–	10
	9	29	1	1	3	3	5	16
	11	15	–	1	2	1	3	8
	13	2	–	–	1	–	–	1
	14	16	1	2	2	2	–	9
Species of savanna bushes	Total	91	24	16	12	3	16	20
	Dispersal types 1	2	–	–	–	–	1	1
	2	32	14	5	5	2	6	–
	8	3	–	1	1	1	–	–
	9	2	–	–	–	–	–	2
	11	6	–	–	–	–	–	6
	14	45	10	10	6	–	9	11

It is evident that the species with adapted diaspores (types 8–14) in general have wider areas than those without (types 1–2). However, the numbers of species possessing a definite kind of specialized diaspores are so small that a comparison between the different types is not well possible. Therefore it is better to contract the table in such a way that only two dispersal types are distinguished, viz. one with non-adapted diaspores (types 1–2) and one with adapted ones (types 8–14). In the same way the number of geographic elements can be reduced to two, viz. the species with a relatively small (G and N) and those with a relatively wide distribution (NE, MNE, S and A).

Now the picture becomes as follows:

	Open savanna			Savanna bushes		
	total	area		total	area	
		small	wide		small	wide
diaspores						
non-adapted	181	59 = 33 %	122 = 67 %	34	19 = 35 %	15 = 47 %
adapted	75	7 = 9 %	68 = 91 %	55	21 = 38 %	34 = 62 %

Among the open-savanna species the correlation between adaptation to dispersal and a wide area is striking. However, the non-adapted species too comprise a high percentage with wide distribution. The latter species probably have had a long period of potential distribution, and, at least temporarily, favourable circumstances for it.

The species of the bushes hardly show any correlation, and their numbers moreover are too small.

Nevertheless there seems to be a real difference between the open-savanna species and the species of the bushes as a whole, which in general means a difference between the herbs and the shrubs. This, however, can not be explained at present.

IV. 7. RELATION BETWEEN HABITAT ON THE SAVANNAS AND DISTRIBUTION

In order to investigate the relation between the ecology of the species (i.e. their factual amplitude with regard to soil texture and soil moisture) and their distribution, the geographic elements have been plotted in the texture-moisture-diagram of II.3.3 (Table 4).

Among the species of the open savannas the G-element appears to be represented best on wet and very wet white sands and on wet loamy sand. The N-element restricts its preference to (very) wet white sand. This may be due to the fact that at least wet white sand savannas hardly occur outside Guiana and the adjoining parts of the Amazon region.

The NE-element finds within the white sands its optimum on the wet to very wet soils, but on the other soil types it is a little more numerous on loamy sand and sandy loam, independent of the degree of moistness. The MNE-element is most numerous on dry and moist loamy sand, but shows more preference for dry and sandy soils in general.

The S-element has less affinity to the white sands than the other elements. It shows some preference for dry to wet loamy sand and sandy loam, and for the wet savannas and rivulets on heavy soils. The A-element behaves more or less in the same way, but corresponds moreover with the MNE-element with regard to the top on dry and moist loamy sands.

It is remarkable that all elements are represented poorly on the very dry to moist white sands and on the sandy clay-loam soils.

In general it may be said that the elements with a smaller distribution are most numerous on savannas with wet to very wet sandy (in particular white-sandy) soils. The elements with a wider distribution, on the other hand, have more representatives on dry and moist coloured sands and loams, and on very wet soils and their rivulets, but there is a preference-top on dry and moist loamy sand. The NE-element occupies an intermediary position. Consequently one obtains the impression that there are two focal points in the open-savanna flora as a whole: one group of species with a northern South-American distribution, concentrated on wet to very wet white sands, and another

TABLE 4

Relation between ecology and distribution (in absolute figures)

Species of open savannas (total 256)

	G-element (29 sp.)						N-element (27 sp.)						NE-element (39 sp.)						MNE-element (26 sp.)					
	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h
vd	4	4	4	2	–	X	2	2	2	2	–	X	4	8	8	10	4	X	7	9	10	5	2	X
d	2	4	5	3	–	X	4	2	4	3	–	X	4	8	10	10	4	X	7	9	18	6	2	X
m	5	X	4	4	–	X	4	X	2	2	–	X	5	X	8	9	4	X	6	X	13	6	2	X
w	15	X	10	6	2	2	11	X	2	1	–	1	10	X	10	10	6	7	4	X	6	5	3	3
vw	8	X	X	6	X	5	7	X	X	1	X	3	9	X	X	10	X	12	4	X	X	4	X	5
r	4	X	X	X	X	3	2	X	X	X	X	5	4	X	X	X	X	7	4	X	X	X	X	2

	S-element (23 sp.)						A-element (112 sp.)							R-element (72 sp.)					
	ws	rs	ls	sl	scl	h	ws	rs	ls	sl	scl	h		ws	rs	ls	sl	scl	h
vd	3	6	6	3	2	X	19	25	26	22	12	X		10	16	16	16	9	X
d	4	6	10	5	3	X	19	26	52	32	16	X		13	18	21	20	11	X
m	2	X	7	7	4	X	15	X	44	32	18	X		17	X	21	22	11	X
w	4	X	8	8	5	5	18	X	31	34	23	23		35	X	29	27	19	19
vw	4	X	X	6	X	9	20	X	X	30	X	32		30	X	X	26	X	24
r	2	X	X	X	X	7	20	X	X	X	X	36		20	X	X	X	X	26

Species of savanna bushes (total 91)

	G (24 sp.)			N (16 sp.)			NE (12 sp.)			MNE (3 sp.)			S (16 sp.)			A (20 sp.)				R 32 (sp.)		
	ws	ls	sl	ws	ls	sl	ws	ls	sl	ws	ls	sl	ws	ls	sl	ws	ls	sl		ws	ls	sl
d	14	10	8	8	8	7	6	7	7	1	1	1	6	9	7	8	11	10		19	19	20
m	10	8	10	5	7	8	5	7	8	–	2	2	4	9	11	6	12	13		17	18	21
w	12	9	11	6	4	7	6	7	9	–	–	–	2	5	6	6	7	7		16	17	20

group of species with a tropical (ev. also subtropical) South-American to American distribution, concentrated on dry to moist loamy sands.

The further elaboration of this idea may be more successfully undertaken after we have seen to what results the treatment of the plant communities in the next chapter leads.

The number of species found in the bushes is so small that a more detailed analysis would be waste of time. The general impression confirms to a certain degree the tendencies prevailing within flora of the open savanna.

Among the species of the bushes the Roraima element does not show any clear differentiation. Among the species of the open savanna the element is more numerous on the wetter soil types than on the drier ones and has its top on wet white sand. The table however does not show that moreover 60 of the 72 open-savanna species occur on wet white and/or loamy sand, whereas among the 32 species of the bushes this number is 25. This corresponds with the expectation, based on the descriptions of the table-mountain savannas. The broken-down sandstone gives a soil of pure sand or loamy sand and as the thin layer of this soil rests on the unweathered sandstone rock it is badly drained. Therefore ecologically these savannas show a strong resemblance with the wet sand savannas of N. Surinam.

That a minority of the species of the Roraima element does not fit into this general picture, may be interpreted in different ways. Species like *Axonopus attenuatus*, *Vernonia remotiflora*, *Thrasya petrosa* and *Myrcia silvatica*, which in N. Surinam are restricted to dry sandy soils, perhaps prove that on the table-mountains the environment is locally dry. However, species like *Buchnera rosea*, *Rhynchanthera grandiflora*, *Ischaemum guianense* and *Roupala montana* can not be taken to indicate the presence of loam or clay at the top of the table mountains, for these soil types are never correlated with sandstone. In these cases there is obviously a difference between the factual ecological behaviour of the species in N. Surinam and their potential capacities.

The similarity in the ecological behaviour of the G- and the N-elements on the one hand and of the Roraima element on the other, might suggest that these two categories are very similar. This is not so, as can be seen from the review given in section IV.5.4. In addition it may be mentioned that 27 % of the species of the G- and the N-element belong to the Roraima-element. This will be discussed further in Chapter VIII.

CHAPTER V

THE OPEN-SAVANNA VEGETATION
CLASS LEPTOCORYPHIO—TRACHYPOGONETEA

V. 1. INTRODUCTION – THE CLASSIFICATION

In spite of their great variety, all communities found on the open savannas can be united into a single class. There are enough species occurring in all or in nearly all these different vegetation types, so e.g. *Trachypogon plumosus*, *Leptocoryphium lanatum*, *Axonopus pulcher*, *Rhynchospora barbata*, *Sipanea pratensis*, *Hyptis atrorubens*, *Buchnera palustris*, *Polygala adenophora* and *P. longicaulis*. The class may be named after the first two species: *Leptocoryphio—Trachypogonetea*. In every community one of these two or both may be present and may show a considerable degree of cover.

Within this class the communities have to be classified on floristic grounds in a hierarchic system. The object of this system has to be to stress the relation between the floristic composition of the different communities and the properties of their habitat (see II.2.1).

The main habitat factors that have been studied, are texture and degree of moistness of the soil. Nearly all species present one or another (factual) amplitude with regard to these two factors or to one of them, as has been shown in the preceding chapter. Of course texture itself is not necessarily the decisive factor in all cases. On the savannas the lighter soil types in general have a looser consistency, whereas the heavier types are firmer. There is also a correlation with the fertility of the soil. However, because of lack of information on these and other points, the apparent preference of a species or a community in the field will be expressed mainly in terms of texture and degree of moistness.

The occurrence of most species seems to be related to a combination of these two factors. This holds for 183 out of the 197 genuine open-savanna species (group 1a). Only 6 species seem to be dependent exclusively on the degree of moistness, 3 only on the texture, whereas 5 species show no correlation with either.

It is clear that both factors have more or less the same influence on the composition of the savanna vegetation. This is not surprising if one realizes that there is in general an obvious relation between texture and degree of moisture. Except on the white sands and in the rivulets, this relation can be seen also on the savannas to a certain degree. The loamy sands are only very dry to wet and soils which are heavier than sandy clay loam are only wet to very wet (see II.3.3).

This means that it is possible to make two systems: one in which the groups are arranged hierarchically in such a way that the degree of moistness comes to the fore as the factor superposed on the texture, and another one with the opposite arrangement.

A comparison of the results leads to the conclusion that the first classification is preferable. This will not be discussed in detail. A good reason is e.g. that there are no species restricted to communities found on dry and on wet sand, whereas the dry as well as the wet sand communities have many typical species in common with communities occurring respectively on dry and on wet loamy sands, etc. Another reason is that the rivulets obviously have to be taken together on the ground that they have several species in common, which occur also in swamps (group 1d).

In short the system is as follows:

1. Order *Trachypogonetalia plumosi* – very dry the moist
    - 1.1. Alliance *Cassio (ramosae)—Trachypogonion*: 3 associations – white sand
    - 1.2. Alliance *Curatello—Trachypogonion*: 4 associations – red sand and loamy sand
    - 1.3. *Rhynchosporo (barbatae)—Trachypogonion*: 2 associations – sandy (clay) loam
2. Order *Paspaletalia pulchelli* – wet (to very wet)
    - 2.1. Alliance *Syngonantho—Xyridion*: 3 associations – white sand
    - 2.2. Alliance *Bulbostylidion lanatae*: 5 associations – loamy sand and sandy loam
    - 2.3. Alliance *Imperato—Mesosetion cayennensis*: 4 associations – sandy (clay) loam and heavier soils
3. Order *Panicetalia stenodis* – very wet soils and rivulets
    - 3.1. Alliance *Axonopodion chrysitis*: 3 associations – very wet, sandy loam and heavier soils
    - 3.2. Alliance *Mauritio—Hvpogynion virgati*: 3 associations – rivulets

All communities with their main ecological relationships are arranged schematically in Fig. 13.

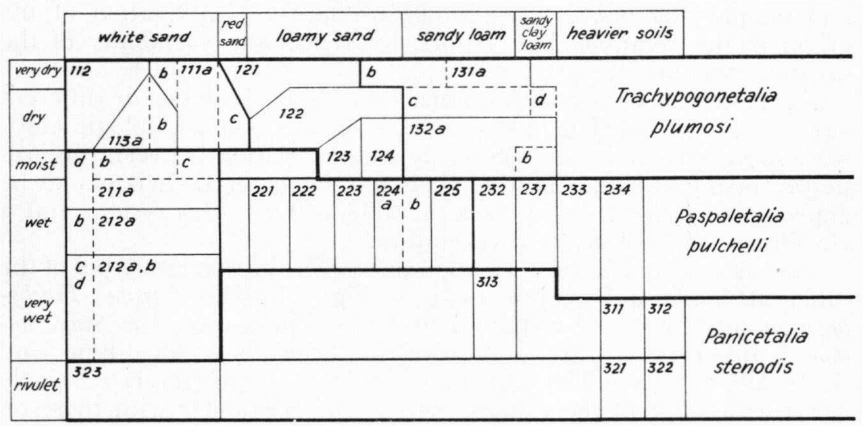

Fig. 13. Ecological range of the open-savanna vegetation-units.

——— limit between orders ——— limit between associations
——— limit between alliances .... limit between subassociations

V. 2. RELATION WITH GEOLOGICAL AND PEDOLOGICAL SYSTEMS

It is evident that there is a relation between the floristic composition of the vegetation and the properties of the soil. The best way to trace this relation in detail is to study the vegetation and the soil in close connection. The properties of both have to be considered without any prejudice. As a rule it will be possible to establish basic vegetation and soil units that cover one another fairly well. However, it depends on the aim of the student how the more general lines of the relation will be presented. The botanist will try to classify the basic units distinguished on floristic grounds, in such a way that the larger units correspond with larger soil units. If necessary he will adapt the floristic criteria more or less to this aim. The main contents of this chapter are the result of such a procedure. However, the pedologist will do the opposite, and beforehand it is quite uncertain whether independently drafted vegetation and soil classifications will turn out to be correlated. In many instances it will not be possible to make a combined system that satisfies botanical as well as pedologic standards. In the case of the savanna, for instance, probably no pedologist would agree with an arrangement of the soils resting in the first place on the degree of moistness and only in the second place on texture.

In view of the foregoing it is not surprising to find that the present classification of vegetation types corresponds neither with the system of BAKKER (1951) nor with that of LANJOUW (1954). The first one ranks the texture in general higher than the drainage conditions. Much emphasis is laid on the presence of impermeable layers and the depth at which they are found. These layers are not so important for the drainage conditions as has formerly been assumed. HEYLIGERS (1963) showed that they even do not affect at all the vegetation of the white sand savannas near Jodensavanne.

The system of LANJOUW, based on a combination of topographic and edaphic factors, is very important for the explanation of the origin of the savannas, but it does not reflect the variability of the savanna vegetation.

The system of COHEN & VAN DER EYK (1953) is of a quite different nature, as it is based in the first place on the geomorphologic landscapes. Since there is not necessarily a close relation between the properties of the soil and those of their parent material, it is not to be expected that there will be any parallel between this system and a classification of the savanna vegetation.

The distribution of the vegetation units over the savanna types of the different landscapes is presented in Fig. 14. The *Cassio—Trachypogonion* appears to be restricted to the Kasipora-type, the *Syngonantho—Xyridion* (nearly) to the Zanderij- and the Watamalejo-type (and the Tafelberg-type). The communities of the Welgelegen-type largely agree with those of the Coesewijne-type, in particular with those on the heavier and wetter soil types. As far as the Saban-pasi-type corresponds with the former two, this holds for the alliances but in general not for the associations; this will be seen later.

<table>
<tr><th></th><th>White sand</th><th>Loamy sand</th><th>Sandy (clay) loam</th><th>Heavier soils</th><th></th></tr>
<tr><td rowspan="5">Dry</td><td>Cassio-Trachypogonion</td><td>Curatello-Trachypogonion</td><td>Rhynchosporo-Trachypogonion</td><td></td><td></td></tr>
<tr><td></td><td>Welgelegen</td><td></td><td></td><td>I</td></tr>
<tr><td>Kasipora</td><td colspan="2">Coesewijne</td><td></td><td>II</td></tr>
<tr><td></td><td colspan="2">(Paroe)</td><td></td><td>IV</td></tr>
<tr><td></td><td>Bosland</td><td></td><td></td><td>IV</td></tr>
<tr><td rowspan="6">Wet</td><td>Syngonantho-Xyridion</td><td colspan="2">Bulbostylidion lanatae</td><td>Imperato-Mesosetion</td><td></td></tr>
<tr><td>Watamalejo</td><td colspan="3">Welgelegen</td><td>I</td></tr>
<tr><td>Zanderij</td><td></td><td colspan="2">Coesewijne</td><td>II</td></tr>
<tr><td>(Tafelberg)</td><td></td><td></td><td></td><td>III</td></tr>
<tr><td></td><td colspan="2">(Paroe)</td><td></td><td>IV</td></tr>
<tr><td colspan="3">Saban-pasi</td><td></td><td>IV</td></tr>
<tr><td rowspan="6">Very wet</td><td>Syngonantho-Xyridion</td><td></td><td colspan="2">Axonopodion chrysitis</td><td></td></tr>
<tr><td></td><td></td><td></td><td>Welgelegen</td><td>I</td></tr>
<tr><td>Zanderij</td><td></td><td colspan="2">Coesewijne</td><td>II</td></tr>
<tr><td>(Tafelberg)</td><td></td><td></td><td></td><td>III</td></tr>
<tr><td></td><td></td><td></td><td>(Paroe)</td><td>IV</td></tr>
<tr><td></td><td></td><td></td><td>Saban-pasi</td><td>IV</td></tr>
<tr><td rowspan="5">Rivulet</td><td colspan="4">Mauritio-Hypogynion</td><td></td></tr>
<tr><td rowspan="4">Zanderij</td><td></td><td></td><td>Welgelegen</td><td>I</td></tr>
<tr><td></td><td></td><td>Coesewijne</td><td>II</td></tr>
<tr><td></td><td></td><td>(Paroe)</td><td>IV</td></tr>
<tr><td></td><td colspan="2">Saban-pasi</td><td>IV</td></tr>
</table>

Fig. 14. Environmental factors and open-savanna vegetation-units (alliances) in relation to the savanna types of COHEN & VAN DER EYK.

V. 3. DISTRIBUTION

The geographic distribution of the communities of different rank corresponds in so far with the hierarchy of the latter that the alliances occupy definite geographic areas, but that this is not so with the orders.

The *Syngonantho—Xyridion* and the *Bulbostylidion lanatae* are represented on the table-mountains of the Guiana interior. Together with the *Cassio—Trachypogonion* they are restricted to Guiana s.l. and the adjoining parts of Brazil. The *Curatello—Trachypogonion* has about the same distribution, but has moreover affinities to the chaparrales of the central Venezuelan llanos and the campos cerrados of eastern Brazil.

The other four alliances seem to have their main distribution in and W. of Surinam. As far as can be judged, the *Rhynchosporo—Trachy-*

TABLE 5 Chorologic spectra and dispersal spectra of the vegetation types of open savanna in percentages, and the percentage of the Roraima element in a separate column R

Vegetation type	Number of species	Geographical elements						R	Dispersal types					
		G	N	NE	MNE	S	A		2	8	9	11	13	14
Total of all types	256	12	11	16	10	9	42	29	74	2	11	6	1	6
1.1.1.a.a	18	5	5	17	34	–	39	22	85	–	5	–	5	5
1.1.1.a.c	28	11	7	10	25	4	43	25	81	–	4	–	4	11
1.1.2.a	23	17	13	13	13	13	31	26	61	–	4	27	–	8
1.1.3.a	15	13	13	13	13	13	35	33	72	–	7	7	–	14
1.2.1	52	6	4	17	9	9	55	21	66	–	17	–	2	15
1.2.2.a	73	5	3	13	18	7	54	14	65	–	23	–	2	10
1.2.2.b	61	3	3	14	22	3	55	14	79	–	16	–	2	3
1.2.3	68	6	3	9	19	6	57	13	73	–	13	1	1	12
1.2.4	40	5	5	15	15	3	57	30	78	–	9	–	3	10
1.3.1.a	29	3	3	27	18	7	42	31	77	3	14	3	–	3
1.3.1.b	31	6	6	27	22	6	33	24	73	–	21	–	3	3
1.3.1.c	33	9	3	24	15	6	43	27	70	3	15	3	–	9
1.3.1.d	21	9	5	19	14	9	44	29	65	5	20	–	–	10
1.3.2.a	28	4	8	19	15	4	50	39	70	3	14	–	3	10
1.3.2.b	22	–	5	23	14	9	49	45	76	3	14	–	–	5
2.1.1.a	35	17	20	20	9	9	25	80	88	3	6	–	–	3
2.1.2.a	39	17	23	21	10	5	24	74	85	8	5	–	–	2
2.1.3.a	35	16	20	22	12	5	25	83	82	9	6	–	–	3
2.2.1	25	8	4	12	20	12	44	52	84	4	8	–	–	4
2.2.2.	29	18	3	10	14	10	45	45	70	5	10	–	–	15
2.2.3.a	33	15	6	12	15	12	40	51	72	3	6	–	–	9
2.2.4.a	29	14	3	14	10	18	41	41	70	5	10	–	–	15
2.2.4.b	27	7	4	18	11	18	42	48	80	4	8	–	–	8
2.2.5	18	11	5	22	22	11	29	55	80	5	10	–	–	5
2.3.1	30	7	3	16	10	14	50	57	76	3	14	–	–	7
2.3.2.	23	–	–	13	4	17	66	39	63	4	29	–	–	4
2.3.3	23	–	–	13	9	9	69	30	63	–	25	–	–	12
2.3.4	27	4	–	14	11	14	57	44	60	4	19	6	–	11
3.1.1	53	4	6	13	10	13	54	26	67	2	19	6	–	6
3.1.2	28	–	–	21	11	14	54	57	73	3	17	–	–	7
3.1.3	38	5	3	13	8	10	61	34	66	3	18	5	–	8
3.2.1	32	10	13	10	6	6	55	31	73	–	12	6	–	9
3.2.2	37	5	11	16	5	13	50	46	67	3	19	–	–	11
3.2.3	30	3	13	11	7	7	60	60	74	3	3	7	–	13

pogonion and the *Imperato—Mesosetion* are restricted to W. Guiana, but the latter has affinities to communities found on the llanos and even in Petén (Guatemala). The two alliances of the *Panicetalia stenodis* both occur on the llanos and have moreover affinity to some communities found on some of the W.I. islands.

It is likely that the distinction of a class of *Leptocoryphio—Trachypogonetea* and the classification of its subdivisions as far down as the alliances may be applicable to the savanna vegetations of the whole of Guiana.

V. 4. CHOROLOGIC SPECTRA (Table 5)

The chorologic spectra of the communities are partly in agreement with their distribution.

The three alliances with a Guianan distribution comprise relatively high percentages of the Guianan element, in particular the *Syngonantho—Xyridion*. Moreover, the latter alliance is the only one with a high percentage of the northern South-American element.

In the *Curatello—Trachypogonion*, the alliance which has affinities with communities in very remote areas, the American element dominates. The same holds for the *Imperato—Mesosetion* and the two alliances of the *Panicetalia stenodis* which all have a western trend and show affinities to communities outside Guiana.

For the rest the interpretation of the chorologic spectra meets many difficulties. In several instances the relations between the percentage of a certain element and other properties of a community are not clear.

V. 5. THE RORAIMA ELEMENT (Table 5)

The representation of the Roraima element is by far the best in the *Syngonantho—Xyridion*. Its representation in the *Bulbostylidion lanatae* comes second. It is noteworthy that these two alliances probably include some communities of the table-mountain savannas.

For the rest it appears that the Roraima element attains in general lower figures in communities bound to heavier soils and still lower ones in those bound to drier soils.

V. 6. DISPERSAL SPECTRA (Table 5)

The only category of plants with diaspores not adapted to any agent of dispersal is formed by the sclerochores. We will do well to compare the percentages of this group with those of the other categories taken together. The correlation, if any, between the percentage of the species with adapted diaspores and the distribution of the communities is positive. The *Curatello—Trachypogonion*, however, with its wide area of distribution and with its relatively large number of sclerochores, spoils the picture.

V. 7. NOTES TO THE DESCRIPTION OF THE COMMUNITIES

1) The description of the vegetation tries to evoke a general image. The degree of cover and the height of the different layers refer to a

vegetation which is completely developed. For information concerning characteristic species, differential species and the like the reader is referred as a rule to the table. For the position the communities occupy with regard to each other in the field, the description of the savannas given in Chapter III should be compared.

2) The soil is described in so far as its properties are brought into correlation with the floristic composition. For a more detailed analysis of a representative example, if available, the reader is referred to Tables 1 and 2 and Fig. 5, 6, 8 and 11.

For a more detailed interpretation of the relation between the vegetation and the habitat of some communities see VAN DONSELAAR–TEN BOKKEL HUININK (1966).

3) Remarks on the chorologic spectra, the presence of the Roraima element and the dispersal spectra of a community of higher rank are as a rule not repeated under the communities hierarchically subordinated to it.

V. 8. THE COMMUNITIES

(V. 8.)1. **Order Trachypogonetalia plumosi** (Table 6*)

Vegetation

The order comprises communities with a relatively high herb layer, mainly consisting of grasses, from which the most generally present and abundant species is *Trachypogon plumosus*. The second place is occupied by *Axonopus pulcher*. Another generally present species with sometimes a relatively high abundance is *Bulbostylis junciformis*. All other species which quantitatively may be of importance, are restricted either to one or to two of the three alliances.

In some communities there is a more or less closed tree layer, usually consisting of gnarled *Curatellas*, so that the vegetation has the character of an orchard savanna.

The order has a large group of characteristic species. A quarter is present in all three alliances, the others are absent either in the *Cassio—Trachypogonion* or in the *Rhynchosporo—Trachypogonion*. Therefore, from a floristic point of view the *Curatello—Trachypogonion* occupies a central position in the order. It is also the alliance with the highest number of characteristic species of its own.

The distribution of the characteristic species of the class gives a different picture. There are a number of them occurring in all three the alliances belonging to the order, then a number which are found in the *Curatello—Trachypogonion* as well as in the *Rhynchosporo—Trachypogonion*, and still another number which is found in the latter alliance only. There is only one species occurring in the *Cassio—Trachypogonion* as well as in the *Rhynchosporo—Trachypogonion* and (nearly) absent in the *Curatello—Trachypogonion*, viz. *Bulbostylis conifera*.

The distribution of the different groups of species is correlated with their apparent preference in the field.

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* Table 6 has been enclosed separately at the back of this issue.

Descriptions given by MYERS (1936) and FANSHAWE (1952) of savannas found high in the Kanuku and Pakaraima Mountains (B.G.), suggest that in these regions communities are present which might perhaps be taken to represent a fourth alliance of this order. This alliance would be characterized by the combination of *Trachypogon plumosus* and *Byrsonima verbascifolia* with *Paspalum contractum.*

Habitat

The communities of the order are found on very dry to moist soils. The texture of these soils ranges from bleached coarse white sand (in the *Cassio—Trachypogonion*) and red coarse sand to loamy coarse sand (in the *Curatello—Trachypogonion*), and to coarse-sandy (clay) loam (in the *Rhynchosporo—Trachypogonion*). In the latter two cases the profiles become heavier with increasing depth, but generally they retain, at least down to a depth of 120 cm, a small amount of sand. As a rule the upper layer is humic.

Distribution

The order appears to be present in Guiana in the widest sense and in the adjoining parts of Brazil, and maybe also in the central parts of Venezuela. The *Curatello—Trachypogonion* seems to occur everywhere in this area. The *Cassio—Trachypogonion* is restricted to the white sands of northern British Guiana, northern Surinam (northern French Guiana?), and the campinas in the state of Pará. The *Rhynchosporo—Trachypogonion* shows a more western trend, occurring from French Guiana to the Rupununi and the Rio Branco savannas in British Guiana and adjacent Brazil, and probably also in Venezuelan Guiana. See further the description of the alliances.

Chorologic spectra

Nearly all communities of this order have a relatively high percentage of the MNE-element and relatively low percentages of the Guianan element and the northern S.-American element. Exceptions are two associations of the *Cassio—Trachypogonion* (1.1.2 and 1.1.3).

(V. 8.)1.1. *Alliance Cassio (ramosae)—Trachypogonion*

Vegetation

The alliance is represented by rather open vegetation types in which some grasses and sedges are the most important species. The aspect of the various vegetation types is rather different.

In the group of characteristic species, besides those which have already been mentioned in the table, *Borreria capitata* and *Lisianthus chelonoides*, both rare species, have to be included.

Nearly all species composing the communities are true savanna species. There are a few species occurring also in open places elsewhere (group 1b), among which *Waltheria americana* is a differential species of the alliance.

Three associations are distinguished here, but perhaps a fourth has to be added. A description by LANJOUW (1936) of a stretch or savanna near Sectie O suggests that there a community is present dominated by *Gymnopogon foliosus*, which might belong to this alliance.

Habitat

The communities occur on coarse bleached, very dry to dry white sand, with a water table that never reaches the surface.

Distribution

In N. Surinam three or four associations of the alliance occur in the savanna belt on savannas of the Kasipora-type.

Outside Surinam the alliance seems to be restricted to Guiana and the adjoining parts of Brazil.

MARTYN (1931) describes a vegetation type associated with the muri scrub on the Wiruni-Ituni savannas (Berbice, B.G.), which probably corresponds with one or two of our associations (1.1.2 and 1.1.3). This vegetation type may be present everywhere in northern B.G. where the white sands of the Tiwiwid series occur (STARK c.s., 1959).

Photo 631 in BOUILLENNE (1930) of the Campina de Pôrto de Móz shows a vegetation that very probably belongs to this alliance, and the descriptions given by DUCKE & BLACK (1953) suggest that it is found also on many other campinas in Pará.

1.1.1. Association Mesoseto (loliiformis) — Trachypogonetum (HEYLIGERS: *Trachypogon plumosus* vegetation)

Vegetation

The association is represented by *Trachypogon* vegetations with *Axonopus pulcher*, *Bulbostylis conifera* and *Mesosetum loliiforme* as co-dominants, covering 40 to 60 % of the surface and with a height of 50 to 70 cm, apart from overtopping flowering shoots.

Of the characteristic species *Paepalanthus subtilis* is lacking near Jodensavanne and *Polygala angustifolia* var. *latifolia* on the Lobin savanna. This may be due to the difference in soil moisture between these two places (see below).

Habitat

The association has been studied near Jodensavanne and on the Lobin savanna, occurring under very dry and dry conditions respectively. The soil consists of coarse white sand; the upper 30 to 70 cm may be slightly humic and light grey. Soil: Tables 1 and 2 nr. 1. Water table: Fig. 11; HEYLIGERS, Table 4.

Subdivision

HEYLIGERS mainly stresses the difference between a part without and a part with the codominant *Bulbostylis conifera*, the latter being a transition to the *Bulbostylidetum coniferae axonopodetosum pulchri* (1.1.3.b). On the Lobin savanna *Bulbostylis conifera* is present everywhere, also on places where this transition apparently is not found. Here, however, *Mesosetum loliiforme* is either absent or codominant, but no factor is known to be responsable for this difference. Perhaps the way and/or the frequency and/or the intensity of the fires during the last dry season may have been of influence.

On the Lobin savanna the association can be divided into two main parts, viz. one without and one with a greater or smaller number of species having their optimum in communities of the *Curatello—Trachypogonion* on red and loamy sand, e.g. *Polycarpaea corymbosa*, *Phaseolus peduncularis* and *Cyperus flavus*. On closer examination it appears from HEYLIGERS' basic data that his records can be divided in the same way. This differentiation, correlated with the soil type, has been applied in the following subdivision.

1.1.1.a. Subassociation *typicum*: see above. The habitats of the variants do not show differences of importance.
1.1.1.a.a. Variant with *Bulbostylis conifera*. The small number of participating species (18) is remarkable. Vegetation: Table 6 (Lobin savanna).
1.1.1.a.b. Variant with *Mesosetum loliiforme*. Vegetation: HEYLIGERS, Table 4 (typical variant p.p.).
1.1.1.a.c. Variant with *Mesosetum loliiforme* and *Bulbostylis conifera*. Vegetation: Table 6 (Lobin savanna, Photo 5).

1.1.1.b. Subassociation *lagenocarpetosum weigeltii*. Transition to *Lagenocarpo—Axonopodetum attenuati* (1.1.2). Vegetation: HEYLIGERS, Table 4 (*Lagenocarpus weigeltii* subvariant of the *Bulbostylis conifera* variant).

1.1.1.c. Subassociation *curatelletosum*. Transition to the *Curatello—Trachypogonion* (1.2) on slightly red sand. Differential species (i.a.) *Vernonia remotiflora*.
1.1.1.c.a. Variant with *Mesosotum loliiforme*
1.1.1.c.b. Variant with *Mesosetum loliiforme* and *Bulbostylis conifera*

1.1.1.d. Subassociation *davilletosum* (*asperae*)

Along forest borders on slightly red sand. Vegetation: HEYLIGERS, Table 4 (*Davilla* variant).

Distribution: the association is rather common in N. Surinam on the savannas of the Kasipora-type. In view of its origin (see VII.2) it may be expected in the first place in the neighbourhood of villages.
Chorologic spectra: a high percentage of the species has a wide distribution. In particular the MNE-element is relatively well represented.
Dispersal spectra: the great majority of the species is not adapted to any agent of dispersal.

1.1.2. Association Lagenocarpo (weigeltii)—Axonopodetum attenuati (HEYLIGERS: *Axonopus attenuatus—Lagenocarpus weigeltii* vegetation, q.v.)

Vegetation

The rather thin vegetation is dominated by *Axonopus attenuatus* and *Lagenocarpus weigeltii*. The occurrence of some species of the bushes is due to the close relation between the community and the bushes which it surrounds. The column in Table 6 is derived from HEYLIGERS (Jodensavanne).

Habitat

Very dry to dry, coarse white sand, the upper 30 cm sometimes humic and light grey, covered with some litter. On small open patches between groups of bushes of the *Ternstroemia—Matayba* type (Photo 6), and in circular zones around isolated bushes, sometimes under the overhanging branches.

Subdivision

1.1.2.a. Typical variant: see above.

1.1.2.b. Variant with *Pteridium aquilinum*. First stage after burning (see HEYLIGERS). *Pteridium* has its optimum here and may be considered to be a characteristic species of the association.

Distribution: in N. Surinam the association is present everywhere on the savannas of the Kasipora-type.
Chorologic spectrum: nearly a third of the species belongs to the Guiana and the northern S.-American element, which within this order is relatively much.
Dispersal spectrum: relatively many species are adapted to a way of dispersal; among the latter there are six cryptogamic sporochores.

1.1.3. Association Bulbostylidetum coniferae
(HEYLIGERS: *Bulbostylis conifera* vegetation, q.v.)

Vegetation

The vegetations are very scanty and poor in species (15); only *Bulbostylis conifera* may be numerous. The column in Table 6 is derived from HEYLIGERS (Jodensavanne).

Habitat

Very dry to dry, coarse white sand, with a micropodzol developed in the uppermost centimeter. On large open stretches between bushes of the *Ternstroemia—Matayba* type. Water table: Fig. 11.

Subdivision

1.1.3.a. Subassociation *typicum*: see above.

1.1.3.b. Subassociation *axonopodetosum pulchri*. (HEYLIGERS: *Axonopus pulcher* variant, q.v.). Richer in species. Probably a transition to the *Mesoseto—Trachypogonetum* (1.1.1).

Distribution: As the former association.

(V. 8.)1.2. *Alliance Curatello—Trachypogonion*

Vegetation

The alliance comprises communities with a rather dense and high herb stratum, usually dominated by grasses among which *Trachypogon plumosus* is always present and mostly abundant. *Schizachyrium riedelii*, *Axonopus pulcher* and *Heliconia psittacorum* occupy the second place. There may be a more or less closed stratum of gnarled trees, in N. Surinam usually *Curatellas*, giving rise to a kind of orchard savanna.

The communities are the richest in species of all savanna vegetation-types in N. Surinam. Apart from a great number of characteristic species, the most characteristic part of the alliance (the associations 1.2.2 and 1.2.3) is also distinguished from the rest of the order by a number of shadow-loving species and from all savanna alliances by a number of species typical of open places in general, partly weeds (group 1b). Moreover it is differentiated from the *Cassio—Trachypogonion* by a group of species avoiding white sand, e.g. *Cassia cultrifolia*, *Eriosema crinitum* and *Sipanea pratensis*.

Habitat

The communities occur on very dry to moist coarse-sandy soils of which at least the upper 50 cm consist of red, pure or loamy sand. The surface is covered, at least locally, with a thin layer of pink bleached grains.

Distribution

Four associations have been studied: on the Lobin savanna, the Coesewijne savanna and on Mimili Okili, all being savannas of the Coesewijne-type. From unpublished data it appears that the alliance is also present on other savannas of this type, though the associations can not be named with certainty, viz. in the most northern part of the Tibiti complex (LINDEMAN), on the second Wara savanna and another savanna on the western bank of the Marataka river (FLORSCHÜTZ, unpubl.). The same holds for a savanna of the Welgelegen-type, viz. a savanna near Kopi (LINDEMAN, unpubl.) and for the hill-savanna near Berg en Dal, belonging to the Bosland-type (HEYLIGERS, unpubl.).

Outside Surinam the alliance is probably present in B.G. on the Oreala savanna (LINDEMAN, unpubl.) and on the Wiruni-Ituni savannas (MARTYN, 1931).

The following species have been collected in February 1959 on the Rupununi savannas, on a fine piece of orchard savanna, S.E. of Lethem at the foot of the Kanuku Mountains (B.G.):

1a. Ch. class: *Curatella americana* (tree layer, 8 m high, covering locally 100 %), *Trachypogon plumosus* (dom. in the herb layer); D. shadow: *Imperata brasiliensis*, *Paspalum plicatulum*, *Desmodium barbatum*, *Eriosema violaceum*, *Melochia villosa*, *Adiantum serrato-dentatum*; Ch. order: *Dichromena ciliata*, *Phaseolus linearis*; Ch. alliance and associations: *Schizachyrium riedelii* var. *multirameum*, *Elephantopus angustifolius*, *Conyza chilensis*, *Byrsonima coccolobifolia*. 1b: *Euphorbia brasiliensis*, *Sauvagesia erecta*, *Waltheria americana*. 1/2: *Rhynchospora cephalotes*. Other species: *Aeschynomene americana*, *Galactia tenuifolia*, *Indigofera pascuorum*, *Pavonia sessiliflora*, *Rhynchosia schomburgkiana*, *Cissus salutaris*, *Lygodium venustum*, *Borreria* spec. and Compos. spec.

From Venezuelan Guiana WILLIAMS (1940, 1942) mentions vegetations which are closely related to the *Curatello—Trachypogonion*, in particular on the Sabana de Maripa, Est. Bolivar. The same holds for the savanna vegetations near La Trinidad, Est. Miranda (ARISTEGUIETA, 1959) and the "pastizal" of the "alto llano" near Calabozo, Est. Guárico (BLYDENSTEIN, 1962). In Venezuela and other spanish speaking countries of Latin America, orchard savanna is called "chaparral".

In Brazil the alliance is probably represented in the E. Amazonian region (Pará), e.g. on the island of Marajó on the "tesos" of the "campos altos" (CHERMONT DE MIRANDA, 1908), on the isolated Campos de Vigia and Campos de Monte Allegre (DE ANDRADE LIMA, 1959). Here "campo cerrado" is the equivalent of orchard savanna.

From descriptions of campos cerrados in central and eastern Brazil it is clear that on floristic grounds their vegetations can not be brought in the same group as the savanna communities of northern S. America, mainly because they are much richer in species. WARMING (1892) e.g. enumerates in his magnificent work on the campos of Lagoa Santa (Minas Gerais) 730 species from this region, which is mainly occupied by orchard savanna, whereas on the northern Surinam savannas there occur all together about 400 species.

However, 30 of the 45 species which the savannas of Lagoa Santa and of N. Surinam have in common, participate in the *Curatello—Trachypogonion*, that is about 30 % of all species composing the communities of this alliance. These 30 species are mainly characteristic either for the alliance or one of its associations, or for the order. Moreover WARMING mentions 10 species which near Lagoa Santa behave as weeds only, but which in N. Surinam (also) occur in *Curatello—Trachypogonion* communities. It is clear anyhow that of all vegetation-units of the northern Surinam savannas the *Curatello—Trachypogonion* has the strongest affinities to the campos of E. Brazil. For the interpretation see Chapter VIII.

Chorologic spectra: The associations have in common a high percentage of the American element and low percentages of the Guianan and of the northern S.-America element.
Roraima element: It is very weakly represented in three of the four associations.

1.2.1. Association Mesoseto (cayennensis)—Thrasyetum petrosae

Vegetation

Rather open orchard savanna, with scattered 3 to 12 m high trees of *Curatella* and *Byrsonima coccolobifolia*, as a rule covering only a few percents, but locally more concentrated and then covering up to 70 % of the surface.

The herb layer covers 50 to 80 % and is dominated by *Trachypogon plumosus*, *Thrasya petrosa* and *Galactia jussieuana*. It is 80 to 100 cm high (Photo 9).

Table 6: Coesewijne savanna

Habitat

Very dry to dry, red, pure or loamy, coarse sand, slightly humic. The colour of the profile is passing with increasing depth from dark brown into grey-brown and still deeper into orange-brown. Soil: Tables 1 and 2 nr. 3 and 4; Fig. 6 nrs. 1 and 2.

Distribution: The association has been studied on the Coesewijne savanna. It is possible that it is also found on the savanna along the Kasiwinika river near Kopi (LINDEMAN, unpubl.).

Chorologic spectrum: In comparison with other associations of the same alliance the MNE-element is rather poorly represented. Dispersal spectrum: A third of the species has adapted diaspores; this is a relatively high fraction.

1.2.2. Association Polycarpaeo—Trachypogonetum

Vegetation

Rather closed orchard savanna, presenting a mosaic of patches without and with a tree layer or *Curatella americana*. It is the most luxuriant of all savanna vegetation-types found in N.Surinam (Photo 1).

Habitat

Dry loamy coarse sand, humic. At a depth between 50 and 100 cm transition into sandy loam, the colour passing from grey via brown into yellow-brown, and at a greater depth into mottled sandy clay loam. Soil: Tables 1 and 2 nr. 5; Fig. 6 nr. 11. Water table: Fig. 8.

Subdivision

1.2.2.a. Subassociation *curatelletosum*

The vegetation is richest in species (73) of all communities. The *Curatellas* are 4 to 8 m high and cover 30 to 70 % of the surface. In the herb layer, 80 to 100 cm high and covering 85 to 95 %, *Trachypogon* and *Axonopus pulcher* are less abundant than in the other subassociation, giving more room to the many forbs, among which there is a number preferring this subassociation, e.g. *Commelina erecta*, *Conyza chilensis* and the shadow-loving *Heliconia psittacorum*. *Schizachyrium riedelii* var. *multirameum* is another differential species.

Table 6: 10 records from the Lobin savanna and 1 record from Mimili Okili.

1.2.2.b. Subassociation *cyperetosum amabilis*

Only low trunks of *Curatella* are present. The herb layer covers 70 to 95 % and is 70 to 100 cm high. *Trachypogon* is nearly always dominant. *Axonopus pulcher* and *Schizachyrium* codominant. *Cyperus amabilis* is the only species showing some preference for this subassociation.

Table 6: 10 records from the Lobin savanna, 1 record from Mimili Okili.

Distribution: Lobin savanna and Mimili Okili; probably also northern Tibiti savanna (LINDEMAN, unpubl.).
Chorologic spectra: The MNE-element is relatively well represented, the Guianan and the northern S.-American element badly.
Roraima element: Only 14 % of the species belong to it.
Dispersal spectra: Of the subassociation *curatelletosum* about a third of the species has adapted diaspores and the majority of them are pogonochores. In the subassociation *cyperetosum amabilis* these figures are lower.

1.2.3. Association Adianto—Trachypogonetum

Vegetation

Rather closed orchard vegetation with 7 to 8 m high *Curatellas* covering 40 to 60 % of the surface. The rich herb layer, covering 80 to 100 % and at least 1 m high, is dominated by *Trachypogon plumosus*, whereas *Paspalum plicatulum*, *Imperata brasiliensis* and *Heliconia psittacorum* may be codominant.

Table 6: 5 records from the Lobin savanna and 1 record from Mimili Okili.

Habitat

Dry to moist loamy sand, very humic. At a depth of 50 cm transition into sandy loam and at a still greater depth into sandy clay loam, the colour passing at the same time from dark brown via grey-brown into brown-yellow with mottling.

Water table: Fig. 8.

Distribution: Lobin savanna and Mimili Okili; perhaps also on the second Wara savanna (FLORSCHÜTZ, unpubl.).
Chorologic spectrum: more or less the same as in the former association.
Dispersal spectrum: no particular features.

1.2.4. Association Sclerio (micrococcae)—Trachypogonetum

Vegetation

One-layered vegetation, covering 60 to 80 % and 70 to 90 cm high, dominated by *Trachypogon* or *Axonopus pulcher* or, near forest borders and bushes, by *Tibouchina aspera*.

Scleria micrococca, though occurring in other associations, has its optimum in this community.

Table 6: 6 records from the Lobin savanna, 1 record from Mimili Okili.

Habitat

Dry to moist loamy sand, humic. At a depth of about 50 cm transition into sandy loam, the colour passing from brown-grey into brown-yellow. At a still greater depth sometimes transition into brown-yellow to orange sandy clay loam. Red spots beginning at about 80 cm. The surface is partly covered with pink bleached sand grains. The upper layer is in the dry season rather hard. Water table: Fig. 8.

Distribution: The association has been studied on the Lobin savanna and on Mimili Okili. It is likely that it occurs also on other savannas of the Coesewijne-type.

Chorologic and dispersal spectra: more or less the same as in the former association.

(V. 8.) 1.3. *Alliance Rhynchosporo* (*barbatae*)—*Trachypogonion*

Vegetation

The communities of the alliance have in common a one-layered vegetation which is lower than those of the *Cassio—Trachypogonion* and the *Curatello—Trachypogonion*, but which in the degree of cover is intermediary between those two.

Here too grasses are the most important species, e.g. *Trachypogon plumosus*, *Axonopus pulcher*, *Mesosetum cayennense* and *Leptocoryphium lanatum*, but some sedges have to be mentioned as well, viz. *Rhynchospora barbata* (var. *barbata*) and *Bulbostylis conifera*.

The only characteristic species, *Buchnera rosea*, is very rare. Besides, the alliance is distinguished positively from the rest of the order by some differential species, e.g. *Mesosetum cayennense*, *Leptocoryphium lanatum*, *Axonopus purpusii* (in particular the typical form) and *Rhynchospora barbata*.

All species composing the communities of the alliance are real savanna species.

Habitat

Very dry to moist. At least the upper 25 cm consist of coarse-sandy loam or clay loam; at a greater depth the soil may be heavier, but it generally contains some sand. The surface may be covered locally with a thin layer of bleached coarse sand grains. The soil is sticky and in the dry season very dry and hard.

Distribution

In N. Surinam two associations of the alliance have been met with on savannas of the Coesewijne-type, viz. the Coesewijne savanna, the Lobin savanna, Mimili Okili and also the northern Tibiti savanna (by LINDEMAN, unpubl.). An undetermined community seems to be present on the first Wara savanna (FLORSCHÜTZ, unpubl.).

In southern Surinam the alliance may be represented on the Sipaliwini savanna, as is indicated by a collection of plants made by ROMBOUTS in 1935 and 1936 (unpubl.).

On the Rupununi savannas near Lethem (B.G.) in two places specimens were collected in communities which might also be included in the alliance (see also DIRVEN & VAN DER EYK, 1952):

a) On a large open stretch of uniform savanna. Soil: Lethem–Burru association (LOXTON c.s., 1958).

Herb layer: 1a. Ch. class: *Trachypogon plumosus* (dom.), *Axonopus pulcher* (codom.), *Bulbostylis conifera* (codom.), *Mesosetum cayennense* (D. alliance), *Eriosema crinitum*; Ch. order: *Cassia hispidula, C. flexuosa, Schizachyrium riedelii*: Ch. alliance: *Byrsonima verbascifolia* var. *villosa* fo. *spathulata*; Ch. other units: *Galactia jussieuana, Scleria micrococca, Bulbostylis spadicea* (codom.), *Elyonurus adustus* (codom.). 1/2: *Scleria bracteata, Rhynchospora cephalotes*. Other species: *Cassytha filiformis, Merremia aturensis, Aristida recurvata, Buchnera elongata, Diodia rigida.*

Widely scattered trees (orchard type) and shrubs: *Curatella americana, Byrsonima coccolobifolia, B. crassifolia, Himatanthus articulatus, Antonia ovata, Roupala montana, Bowdichia virgilioides, Casearia celastroides, Connarus incomptus* var. *subcordata, Rosenbergiodendron formosum, Hirtella* spec., 2 spec. indet.

b) On a small hill with ironstone pebbles at the surface, surrounded by the former vegetation type. Soil: St. Ignatius series (LOXTON c.s., 1958).

Herb layer: 1a. Ch. class: *Bulbostylis conifera* (codom.); Ch. order: *Bulbostylis junciformis, Cassia flexuosa, Mitracarpus discolor, Aeschynomene hystrix, Schizachyrium riedelii*; Ch. alliance: *Byrsonima verbascifolia*; Ch. other units: *Galactia jussieuana*. Other species: *Cassytha filiformis, Mesosetum longifolium* (dom.), Gram. spec. (codom.), Labiat. spec.

Scattered trees (orchard type) and shrubs: *Curatella americana, Byrsonima coccolobifolia, B. crassifolia, Bowdichia virgilioides, Casearia celastroides,* Myrtac. spec.

Similar and closely related vegetation types from the adjoining Rio Branco savannas are dealt with by TAKEUCHI (1960a, b). Maybe that also on the lower levels of the Pakaraima and the Kanuku Mountains vegetations are found belonging to this alliance (MYERS, 1936; FANSHAWE, 1952).

There are indications that communities of the alliance occur in Venezuelan Guiana, Est. Bolivar, e.g. on the Sabana de Maripa (WILLIAMS, 1942), near Santa Elena (TAMAYO, 1962) and on the Gran Sabana (BEARD, 1952).

For French Guiana: see the *Dipteracantho—Byrsonimetum.*

CIFERRI (1936) mentions some vegetation types from the savannas on the island of Hispaniola which are related to this alliance, viz. the (drier) "*Sporobolus indicus—Paspalum plicatulum association*" and the moist, but not inundated parts of the "*Scleria—Rhynchospora savanna*".

Chorologic spectra: the communities present low percentages of the Guianan and the northern South-American element. The NE-element has its highest percentages in this alliance.

1.3.1. Association Dipteracantho—Byrsonimetum verbascifoliae

The association comprises one-layered vegetations dominated by grasses, in particular *Trachypogon* and *Mesosetum cayennense.* The aspect may be determined by the low *Byrsonima verbascifolia* (var. *villosa* fo. *spathulata*), especially when it is flowering.

The community is rather diversified and occurs on several soil types, ranging from loamy sand to sandy loam and from very dry to moist. In the dry season the soil is very hard.

1.3.1.a. Subassociation *dipteracanthetosum* (*angustifoliae*)

Vegetation

The vegetation covers 70 to 95 % of the surface and is not higher than 50 cm, if overtopping flowering shoots of the grasses are left out of consideration. *Trachypogon plumosus* and *Mesosetum cayennense* are equally abundant, the codominants are *Axonopus pulcher, Leptocoryphium lanatum, Bulbostylis conifera* and *Rhynchospora barbata.* Of the characteristic species *Byrsonima verbascifolia* is scarce, but *Dipteracanthus angustifolius* has its optimum in this subassociation.

Where a vegetation of this subassociation touches upon the forest border, it is distinguished by a high abundance of *Davilla aspera* in the first place, and further of *Miconia ciliata, Tibouchina aspera* and *Rhynchospora cephalotes.* The latter two species are dominating on humps caused by underground nests of ants and termites.

Table 6: Coesewijne savanna.

Habitat

The whole profile consists of coarse-sandy loam or coarse-sandy clay-loam, or the former is overlying the latter. Down to a depth of about 25 cm the soil is humic and coloured dark brown-grey, passing into light grey-yellow and at a greater depth into (pale) orange-brown. In the dry season the soil is very dry, the surface very hard and impenetrable. Soil: Tables 1 and 2 nr. 11; Fig. 6 nr. 4.

1.3.1.b. Subassociation *thrasyetosum* (*petrosae*)

Transition between the former subassociation and the *Mesoseto—Thrasyetum* (1.2.1), occurring on very dry loamy sand or sandy loam. Vegetation: Table 6 (Coesewijne savanna).

1.3.1.c. Subassociation *sporoboletosum* (*cubensis*)

Vegetation

Mesosetum cayennense is the most important grass, but it is followed immediately by the other dominant and codominant grasses and sedges of the subassociation *dipteracanthetosum,* and in addition by the differential species *Sporobolus cubensis. Byrsonima verbascifolia* has a relatively high presence and a high abundance (Photo 8).

Table 6: Coesewijne savanna.

Habitat

The granular composition and the colour of the soil are the same as in the subassociation *dipteracanthetosum*, but it is dry and only the upper 15 cm are humic and coloured dark brown-grey. About 80 % of the surface is covered with a thin layer of bleached coarse sand grains. Soil: Tables 1 and 2 nr. 15; Fig. 6 nr. 5.

1.3.1.d. Subassociation *elyonuretosum* (*adusti*)

Transition from the former subassociation into the *Elyonuro—Andropogonetum leucostachyi* (2.3.2), occurring on dry to moist sandy clay loam. Vegetation: Table 6 (Coesewijne savanna). Soil: Tables 1 and 2 nr. 16; Fig. 6 nr. 6.

Distribution: In N. Surinam the association seems to be restricted to the Coesewijne savanna, but there are indications that it occurs in French Guiana on a savanna near the Crique des Pères, river Kourou (Benoist, 1925). The presence of some closely related communities in other regions has already been dealt with (see under the alliance). Chorologic spectra: The species with a relatively wide area are well represented, in particular by the NE- and the MNE-elements. The Guianan and the northern S.-American element are on the low side. Roraima element: the percentages are near the mean value.

1.3.2. Association Schizachyrio—Rhynchosporetum barbatae

The association consists of one-layered vegetations dominated by grasses and sedges. Besides the rare characteristic species *Aristida capillacea*, it is differentiated from the *Dipteracantho—Byrsonimetum* mainly by the presence of *Schizachyrium riedelii*, *Aristida tincta*, *Polygala longicaulis* and *P. adenophora*, and by the absence of *Mesosetum loliiforme* and *Bulbostylis conifera*.

It occurs on dry to moist sandy (clay) loam, which is very hard in the dry season.

The association can clearly be divided into two subassociations.

1.3.2.a. Subassociation *mitracarpetosum microspermi*

Vegetation

The vegetation is 50 to 70 cm high and covers 60 to 90 % of the surface. *Trachypogon plumosus* and *Axonopus pulcher* are either dominant or codominant whereas *Schizachyrium*, *Tibouchina aspera* and *Rhynchospora barbata* may be codominants too. The only species which is positively differential with regard to the other subassociation, is *Mitracarpus microspermus* (Photo 4).

On the Lobin savanna the community is more or less correlated with bushes of the *Cupania*-type. In contact with these bushes and with the forest border the vegetation is distinguished by the dominance of *Davilla aspera* and the high abundance of *Miconia ciliata* and *Tibouchina aspera.*

Table 6: Lobin savanna.

Habitat

Dry to moist coarse-sandy loam, humic. At a depth of 30 to 40 cm sandy clay loam, sometimes at 90 cm or deeper, passing into sandy clay. Sometimes sandy clay loam at the surface. Colour brown-grey passing with increasing depth via grey-brown into mottled grey and yellow in the lower half. The mean depth on which red spots begin is 50 cm. The surface is partly covered with bleached coarse sand grains. Soil: Tables 1 and 2 nr. 12; Fig. 6 nr. 12. Water table: Fig. 8.

Distribution: The subassociation has not been met with outside the Lobin savanna.

1.3.2.b. Subassociation *mesosetosum cayennensis*

Vegetation

The degree of cover and the height of the vegetation are similar to those of the former subassociation. The same species are the most important ones, but in addition *Leptocoryphium lanatum* and *Mesosetum cayennense* are differential species, and the latter may be dominant. *Tibouchina* is mainly concentrated on small and low humps caused by underground nests of termites and ants. On aerial photographs the vegetation therefore looks spotted.

Table 6: 10 records from Lobin savanna and 2 records from Mimili Okili.

Habitat

Moist coarse-sandy clay loam, humic. The colour is grey to brown-grey down to a depth of about 25 cm; there is a transition into orange sandy clay, more or less mottled in the deeper part; at about 80 cm a transition into mottled clay. Red spots begin at a depth of about 30 cm. Bleached sand grains are covering part of the surface. Soil: Tables 1 and 2 nr. 17; Fig. 6 nr. 13 (not very typical). Water table: Fig. 8.

Distribution: Lobin savanna, Mimili Okili; northern Tibiti savanna (LINDEMAN, unpubl.).

Chorologic spectra: In both subassociations the species with a wide distribution are well represented, in particular by the American and the NE-element.

Roraima element: In this association the percentages are far higher (39 and 45 %) than in all other associations of the order.

(V. 8.)2. **Order Paspaletalia pulchelli** (Table 7*)

Vegetation

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* Table 7 has been enclosed separately at the back of this issue.

The communities of this order have a herb layer that in general is lower and a little thinner than in the other two orders.

There is not a single species or a small group of species that determines in the field the aspect of all communities. The most generally present and abundant species throughout the order are found among the grasses and the sedges. The same holds for the different species forming the bulk of the vegetation of the different communities. *Leptocoryphium lanatum* is the only species with a high presence in all of them.

Only a few communities have a layer of gnarled trees; the majority has a discontinuous algal layer.

There are three alliances: the *Syngonantho—Xyridion*, the *Bulbostylidion lanatae* and the *Imperato—Mesosetion.* Nearly all characteristic species of the order occur in the first two alliances but in only one of the four associations of the third one. Some of them show a preference for the communities on sand soils. The position of *Rhynchospora arenicola* is not clear, because it has not been separated from *Rhynchospora barbata* var. *barbata* (see IV.1). Possibly it is present in more communities than is indicated in the table.

The distribution of the characteristic species of the class is essentially the same as that in the *Trachypogonetalia plumosi*, i.e. one group occurs in all three alliances, another group is lacking in the first one, and finally there is a group occurring only in the third one and therefore differential for this alliance with regard to the rest of the order. (The *Imperato—Mesosetion* has no characteristic species.) Among the first and the second group there are species which the order has in common either with the *Trachypogonetalia plumosi* or with the *Panicetalia stenodis.* As these species are present also in the *Imperato—Mesosetion*, this alliance appears to be rightly included in the *Paspaletalia pulchelli.*

Habitat

The soils of the communities are wet, in some cases tending to very wet. The topsoil is more or less humic, if very wet sometimes strongly humic.

The granular composition of the topsoil varies widely but it is never as heavy as clay. The differences between the vegetation of the alliances correspond mainly with differences in the composition of the topsoil. It consists of white sand in the *Syngonantho—Xyridion*, of loamy sand to sandy loam in the *Bulbostylidion lanatae.* The soils in the *Imperato—Mesosetion* are heavier and/or wetter and more humic than the wet sandy loam soils of the *Bulbostylidion lanatae.*

Distribution

Communities of the order occur throughout the Guianas, in adjoining parts of Brazil and probably in the llanos of Venezuela. The *Syngonantho—Xyridion* is present on the tops of the Roraima table-mountains and on the white-sand savannas near the edges of the Guiana shield in N.E. Guiana and Brazil. The *Bulbostylidion lanatae* too may be represented on some table-mountains. For the rest it seems to be restricted to British Guiana, Surinam and French Guiana, where it mainly occurs in the interior. The *Imperato—Mesosetion* is found in Surinam and probably extends in a western direction as far as the llanos in central Venezuela. See further the alliances.

Roraima element: It is well represented in most communities, but there are in this respect considerable differences between them.

(V. 8.)2.1. *Alliance Syngonantho—Xyridion*

Vegetation

The vegetations belonging to this alliance have an open herb layer that as a rule does not cover more than 50 % of the surface. The height in most instances is less than 50 cm, except when higher shrubs are present or when flowering *Lagenocarpus tremulus* is dominant.

In general no species can be indicated as dominating. The most abundant species rarely cover more than 25 % of the surface. To this group belong *Panicum micranthum*, *Rhynchospora graminea*, *Xyris guianensis* and *Abolboda americana* and, to a lesser degree, *Paspalum pulchellum*, *Rhynchospora barbata* var. *glabra* and *Lagenocarpus tremulus*.

The alliance has a large group of characteristic species. Three of them, viz. *Curtia tenuifolia*, *Xyris savanensis* and *Syngonanthus simplex*, were not found by HEYLIGERS (1963) near Jodensavanne. This is surprising with regard to the former two, for those are common savanna species. On the other hand, HEYLIGERS mentions a number of (characteristic) species which are absent or nearly so on the Lobin savanna: *Panicum polycomum*, *Syngonanthus gracilis* (which is var. *koernickeanus*), *Utricularia fimbriata*, *Xyris longiceps*, *Comolia vernicosa* and *C. veronicifolia*. In general the vegetations of this alliance near Jodensavanne are richer in small forbs, like *Xyrids*, *Abolbodas* and *Eriocaulaceae*, and shrubs. On the Lobin savanna grasses and sedges are more abundant; only here *Rhynchospora tenuis* and *Leptocoryphium lanatum* may reach a considerable degree of cover. These differences are pronounced in particular in the association *Xyrido—Paspaletum pulchelli* (2.1.2); probable explanations will be dealt with under this head.

Another characteristic species lacking in the table is the stemless *Abolboda killipii*. It is present in communities of the alliance near Zanderij I, together with *Abolboda americana*. On the Gros savanna it was found as the most abundant species in a very peculiar vegetation type; see III.4.1.3.1.

Habitat

The alliance represents the communities characteristic for the wet to very wet white-sand savannas. This sand is coarse and completely bleached.

Distribution

In N. Surinam the communities probably occupy all savannas of the Zanderij-type completely. Moreover the alliance is present on the

Gros savanna and perhaps locally also on other savannas of the Sabanpasi-type. LANJOUW & LINDEMAN (unpubl.) found vegetations belonging to the alliance on savannas of the Watamalejo-type, N. of the Wane-creek.

On the table-mountains and other sandstone remains of the "Guayana highlands" there are savannas covered by vegetation types belonging to this alliance or at least closely related to it: Tafelberg (MAGUIRE, 1945a, b; idem & coll., 1948), Kaieteur savanna (JENMAN, 1882; MAGUIRE & coll., 1948), Auyán-tepuí (GLEASON & KILLIP, 1939).

In the Brazilian state of Pará the alliance is represented on so-called campinas, e.g. on a part of the Campos de Vigia (DE ANDRADE LIMA, 1959), on the campos near Ariramba (EGLER, 1960), on the Campina de Pôrto de Móz (BOUILLENNE, 1930, Photo 632) and probably in other localities (DUCKE & BLACK, 1953).

Chorologic spectra: Species with relatively small areas are most numerously represented in this alliance, in particular the northern S.-American element. The American element has its lowest figures here.
Roraima element: The percentage is much larger than in any other savanna community (74–83 %).
Dispersal spectra: The percentage of the sclerochores, species with not-adapted diaspores, is relatively high.

The differences found between the associations with regard to the dispersal and chorologic spectra and to the percentage of the Roraima element are of no importance.

2.1.1. Association Bulbostylidetum circinatae (HEYLIGERS: *Rhynchospora tenuis* vegetation)

Vegetation

The rather thin vegetation usually covers 20 to 50 %, sometimes up to 70 % of the surface and has a maximum height of 50 cm.

It has been studied near Jodensavanne and on the Lobin savanna. In both areas *Panicum micranthum* and *Rhynchospora graminea* belong to the most abundant species, but for the rest there are several differences with regard to the abundance of the participating species. Near Jodensavanne *Mesosetum loliiforme*, *Xyris guianensis* and *Abolboda americana* come to the fore, on the Lobin savanna their places are taken by *Paspalum pulchellum*, *Rhynchospora barbata*, *Bulbostylis conifera* and *B. circinata*. The latter species has its optimum in this association. *Rhynchospora tenuis* may have its optimum in the community near Jodensavanne, but in general it has a somewhat wider range (characteristic species of the alliance).

The community is also distinguished from the rest of the alliance by the nearly complete absence of a layer of algae.

The only really characteristic species, the scarce *Stylosanthes angustifolia*, is restricted to two not typical subassociations (b and c) and does not occur therefore in the column in Table 7 (Lobin savanna).

Habitat

Wet, coarse, bleached white sand, the upper part mostly light grey and slightly humic. The water table just reaches the surface in the wet season. Water table: Fig. 11; HEYLIGERS, Table 4.

Subdivision

2.1.1.a. Subassociation *typicum*: see above. (HEYLIGERS: typical variant). Vegetation: Table 7 (Lobin savanna). Water table: Fig. 11; HEYLIGERS, Table 4.

2.1.1.b. Subassociation *trachypogonetosum*. Transition to the *Mesoseto—Trachypogonetum* (1.1.1). The main differential species is *Trachypogon plumosus* (total estimate 2). Water table: Fig. 11.

2.1.1.c. Subassociation *bulbostylidetosum coniferae*. (HEYLIGERS: *Bulbostylis conifera* variant, q.v.). Transition to the *Bulbostylidetum coniferae* (1.1.3).

2.1.1.d. Subassociation *lagenocarpetosum amazonici* (HEYLIGERS: *Lagenocarpus amazonicus* variant, q.v.). Along the borders of *Clusia—Scleria* bushes. Differential species are the shadow-plant *Lagenocarpus amazonicus* and some species which (also) occur in the bushes (groups 1a/2 and 2). May be transitional to the *Lagenocarpo—Axonopodetum attenuati* (1.1.2).

Distribution: Besides on the Lobin savanna and near Jodensavanne the association is probably present in the savanna belt in all localities where dry and wet white-sand savannas meet each other.

2.1.2. Association Xyrido—Paspaletum pulchelli
(HEYLIGERS: *Lagenocarpus tremulus* vegetation, typical variant and *Panicum polycomum* variant)

Vegetation

The herb layer covers only 10 to 50 % of the surface and does not exceed a height of 50 cm, at least if long flowering shoots of *Lagenocarpus tremulus* are left out of consideration.

The most present and abundant species are in general *Paspalum pulchellum*, *Panicum micranthum*, *Rhynchospora graminea* and *Abolboda americana*. Characteristic species are *Xyris spathacea*, *X. paraënsis*, *X. subuniflora* and *Utricularia guyanensis*.

On the Lobin savanna the latter two species were not found, and many other fine forbs occurring in large numbers near Jodensavanne were either not or rarely found. Examples: *Xyris guianensis*, *X. surinamensis*, *X. longiceps*, *Polygala appressa*, *Drosera capillaris* and *Perama hirsuta*. On the other hand, on the Lobin savanna a number of grasses and sedges like *Leptocoryphium lanatum*, *Rhynchospora barbata* and *Bulbostylis conifera* are more abundant, so that the mean degree of cover is higher (Photo 7).

It is possible that these differences are connected to a certain degree with the fact that the vegetation near Jodensavanne was studied in the wet season and that on the Lobin savanna in the dry season.

However, HEYLIGERS suggests that in particular the above mentioned forbs might easily be destroyed by fire. In addition fire obviously does favour most grasses and sedges. So it is likely that the relative poverty of the association on the Lobin savanna is due to the fires which undoubtedly are more frequent there than on the savannas near Jodensavanne. See also under "subdivision".

Table 7: Lobin savanna.

Habitat

Wet, coarse, bleached white sand, down to a depth of about 30 cm light grey and slightly humic. In the wet season the soil is permanently waterlogged and after every shower the water rises a few centimeters above the surface. Water table: Fig. 11; HEYLIGERS, Table 4.

Subdivision

2.1.2.a. Subassociation *typicum*; see above.
(HEYLIGERS: typical variant, q.v.).

HEYLIGERS distinguishes three subvariants, a subdivision which could not be checked on the Lobin savanna because the association is too scarcely represented there. In general the picture on the Lobin savanna corresponds with the *Rhynchospora barbata* subvariant of HEYLIGERS, the composition of which he ascribes to the influence of fires (see above).

2.1.2.b. Subassociation *panicetosum polycomi*
(HEYLIGERS: *Panicum polycomum* variant, q.v.)

Very thin vegetation along the borders of *Clusia—Scleria* bushes on places where the rain water runs off.

Distribution: The association is probably present on all savannas of the Zanderij-type. It is found also on savannas N. of the Wane-creek, belonging to the Watamalejo-type (LANJOUW & LINDEMAN, unpubl.).

2.1.3. Association Syngonantho—Lagenocarpetum tremuli
(HEYLIGERS: *Lagenocarpus tremulus* vegetation, *Panicum nervosum* variant and *Sphagnum* variant, q.v.)

The association is rather diversified. In general the main species are *Lagenocarpus tremulus*, *Paspalum pulchellum*, *Abolboda americana*, *Xyris surinamensis* and *Lagenocarpus amazonicus*. There are two characteristic species, *Abolboda grandis* and *Croton hostmannii*, but these are restricted to two of the four subassociations (a and d respectively). Differential species for the whole association with regard to the rest of the alliance are *Panicum nervosum*, *Lisianthus uliginosus* (both varieties), *Cleistes rosea* and *Sphagnum kegelianum* (by HEYLIGERS erroneously called *S. antillarum*).

2.1.3.a. Subassociation *typicum*
(HEYLIGERS: *Panicum nervosum* variant *Panicum micranthum* subvariant)

Vegetation

The degree of cover of the herb layer is between 30 and 85 %. If *Lagenocarpus tremulus* is flowering, it determines the aspect of the vegetation with its 60 to 100 cm high shoots. *Paspalum pulchellum* has the highest degree of abundance. The characteristic species *Abolboda grandis* is restricted to this subassociation and was not found on the Lobin savanna. Other important species are *Panicum micranthum* and *Rhynchospora barbata*; especially near Jodensavanne *Abolboda americana*, *Xyris guianensis* and *Syngonanthus umbellatus*; especially on the Lobin savanna *Rhynchospora graminea*, *R. tenuis* and *Leptocorphium lanatum*. This difference might be explained in the same way as in the case of the *Xyrido—Paspaletum pulchelli* (2.1.2). This subassociation is the only one which may have a layer of algae.

Table 7: Lobin savanna.

Habitat

Wet to very wet, coarse, bleached sand, the upper 30 to 40 cm grey to black as a result of the high humus content. The association is found in localities where in the wet season the ground water stagnates, at least for some time, either against bushes on a slightly sloping surface (HEYLIGERS) or in low and flat stretches. In consequence the surface has low kawfoetoes; in the wet season the gullies between them mostly contain some water. Soil: Tables 1 and 2 nr. 2. Water table: HEYLIGERS, Table 4.

2.1.3.b. Subassociation *licanietosum* (*incanae*)

(HEYLIGERS: *Panicum nervosum* variant *Licania incana* subvariant; q.v.)

The vegetation consists of small, more or less bushlike islands in the typical subassociation, on slight humps caused by activities of underground animals. Differential species are some shrubs like *Licania incana*, *Tibouchina aspera* and *Tetracera asperula*.

2.1.3.c. Subassociation *lagenocarpetosum amazonici*

(HEYLIGERS: *Panicum nervosum* variant *Lagenocarpus amazonicus* subvariant; q.v.)

Along the border of *Clusia-Scleria* bushes were the surface may be partly covered with litter. Differential species with regard to the typical subassociation are some shadow-loving plants, of which *Lagenocarpus amazonicus* is the most prominent one.

Water table: Fig. 11; HEYLIGERS, Table 4.

2.1.3.d. Subassociation *sphagnetosum*

(HEYLIGERS: *Lagenocarpus tremulus* vegetation, *Sphagnum antillarum* variant; q.v.)

The vegetation is in fact the undergrowth of bushes, mostly belonging to the *Comolia* variant of the *Clusia—Scleria* scrub. Therefore its position as a subassociation of the *Syngonantho—Lagenocarpetum* is dubious. It is differentiated in general by the characteristic species *Croton hostmannii*, and with regard to the rest of the association by the high abundance of *Sphagnum kegelianum* and the presence of *Octoblepharum cocuiense*, *Calyptrocarya glomerulata* and *Siphanthera hostmannii*.

The vegetation of *Abolboda killipii* on the Gros savanna, described in III. 4.1.3.1, may be included in this alliance. It is allied to the *Xyrido—Paspaletum pulchelli* (2.1.2), in particular to the subassociation *panicetosum polycomi*. However, because it was found only once in a small area, it will for the moment be left out of consideration.

(V. 8.)2.2. *Alliance Bulbostylidion lanatae*

Vegetation

In general the vegetations have a layer of mainly low herbs covering about 50 to 80 % of the surface. The most generally present and abundant species are some grasses and sedges: *Trachypogon plumosus*, *Hypolytrum pulchrum*, *Rhynchospora barbata* var. *barbata*, *Panicum micranthum*, *Paspalum pulchellum*, *Mesosetum tenuifolium* and *Rhynchospora rhizomatosa*.

The latter two are characteristic species of the alliance, but up to now they have hardly been found outside the Gros savanna and the De Jong Noord savanna, belonging to the Saban-pasi-type (*Rhynchospora rhizomatosa* is rare on the Coesewijne savanna in the *Dipteracantho—Byrsonimetum*, 1.3.1.c and d.). From the other characteristic species at least *Bulbostylis lanata* and *Abolboda pulchella* are found on savannas of other types too. Moreover, the most characteristic feature of this alliance is the very peculiar combination of species; on the one hand there is a large group of characteristic species of the order which it only shares with the *Syngonantho—Xyridion* of the white sands, on the other hand it has many characteristic species of the class in common with the *Imperato—Mesosetion* and other communities on coloured sands and on heavier soil types.

In nearly all vegetations of the alliance here and there a small, gnarled tree of *Byrsonima crassifolia* may be found but in only one of the associations this species forms an open tree layer.

Most vegetations have a layer of algae covering part of the soil surface.

Habitat

The vegetations occur on wet soils, of which in general at least the upper 25 cm consist of slightly humic loamy sand or sandy loam. The subsoils are highly impermeable. In general the N-content seems to be very low. The differences between the associations seem to be primarily due to differences in the water economy of the soil, but this has not sufficiently been studied.

In the area studied, the Gros savanna and the adjoining De Jong

Noord savanna, the vegetations occupy the top and the slopes of low hills. For a description of the situation there one is referred to the treatment of these savannas in section III.4.

Distribution

In N. Surinam the alliance is represented on savannas of the Saban-pasi-type, viz. the Gros savanna, the De Jong Noord savanna, a small savanna S.E. of Gros, the Saban-pasi savanna, the Patrick savanna (LANJOUW, 1936) and probably also on the Rosebel savanna (see VAN KOOTEN, 1954) and other ones.

The alliance is also found on savannas of the Welgelegen-type N. of the Wane-creek (LANJOUW & LINDEMAN, unpubl.). On the Coesewijne savanna at one place a vegetation was found which might be included also in this alliance (see III.2.4.3).

The alliance seems to be restricted to Guiana. A collection made by GEIJSKES on the Palaime savanna in the interior of Surinam suggests its presence there. Further it has been found on the Rupununi savannas, B.G. (see under association 2.2.1) and in French Guiana on the Savane Blanche, the Savane des Roches and the Grande Savane (BENOIST, 1925). Probably vegetation types belonging to this alliance occur on some of the Guianan table-mountains; this at least is suggested by collections from the Kaieteur savanna (MAGUIRE & coll., 1948) and Auyán-tepuí (GLEASON & KILLIP, 1939).

Chorologic spectra: All associations have relatively low percentages of the northern South-American element, whereas the MNE- and the South-American element are on the high side.
Roraima element: It occurs with high percentages (41–55 %), though the latter are considerably lower than in the *Syngonantho—Xyridion.*
Dispersal spectre: The few species with diaspores adapted to dispersal belong to the pogonochores and the sarcochores.

2.2.1. Association Rhynchosporetum podospermae
Vegetation

The degree of cover is about 60 to 70 % and the height is not more than 40 cm.

Rhynchospora podosperma has its optimum here, and is always abundant. Other quantitatively important species are *Paspalum pulchellum* and *Rhynchospora barbata.* The relatively high abundance of *Rhynchospora globosa* and the nearly total absence of *Trachypogon plumosus* are in agreement with the fact that within the alliance this association is the one found on the wettest soil. There is no layer of algae.

Table 7: Gros savanna.

Habitat

On nearly level stretches at the foot of small hills.

Wet. At least the upper 50 cm loamy sand; at a greater depth sometimes heavier; sometimes with a layer of gravel. At least the upper 30 cm are slightly humic, homogeneously grey-brown or brown-grey with few rusty spots; at a greater depth passing into mottled orange, brown, yellow and white, the lighter colours becoming more frequent with greater depth. Red spots beginning at a depth of 75 cm or more. Soil: Tables 1 and 2 nr. 6; Fig. 6 nr. 21.

Distribution

Gros savanna and probably other savannas of the Saban-pasi-type.

On the Rupununi savannas (B.G.) in a depression N.W. of Manari, a vegetation type was met with that closely resembled this association. The following species were present (February 1959):

Ch. class: *Bulbostylis conifera*, *Rhynchospora barbata*, *R. globosa*, *Buchnera palustris*, (Ch. *Panicetalia stenodis*:) *Hypogynium virgatum*, *Panicum cyanescens*, *Scleria setacea*; Ch. order: *Rhynchospora podosperma*, *Panicum micranthum*, *Sauvagesia sprengelii*, (Ch. *Syngonantho-Xyridion*:) *Rhynchospora tenuis*, *Albolboda americana*; Ch. alliance: *Bulbostylis lanata*, *Abolboda pulchella*; other species: *Aristida setifolia*, *Mesosetum rottboellioides*.

Chorologic spectrum: In comparison with the other associations of the alliance the percentage of the Guianan element is rather low, that of the MNE-element rather high.
Dispersal spectrum: The percentage of sclerochores is very high (84 %).

2.2.2. Association Byrsonimetum crassifoliae malosae

Vegetation

There is a thin layer of 1½ to 4 m high, gnarled *Byrsonima crassifolia* trees, covering 5 to 10 % of the surface, so that the vegetation has the character of an open orchard savanna (see IV.1, Photo 16).

In the herb layer, covering 50 to 80 % and 20 to 40 cm high, the most generally present and abundant species are *Panicum micranthum*, *Paspalum pulchellum*, *Mesosetum tenuifolium*, *Rhynchospora rhizomatosa*, *R. barbata* and *Hypolytrum pulchrum*.

Algae are covering 20 to 50 % of the soil surface.

Table 7: Gros savanna.

Habitat

On inclined surfaces near the foot of small hills.

Wet. At least the upper 25 cm loamy sand, at a greater depth very variable but usually heavier; sometimes a layer of gravel in the subsoil. Down to a depth of about 25 cm slightly humic and light brown, passing into yellow and white, with or without spots. Soil: Tables 1 and 2 nr. 7 and 8; Fig. 6 nr. 19 and 20.

Distribution: Gros savanna. Further ?

2.2.3. Association Rhynchosporetum curvulae

Vegetation

The vegetation is low, the mean height of the herbs not exceeding 25 cm, and covers 50 to 60 % of the surface.

The tiny *Rhynchospora curvula*, which is present in small numbers is several communities of the *Syngonantho-Xyridion*, is always (very) abundant in this association and may be considered to be a characteristic species. A differential species with regard to the rest of the alliance is *Rhynchospora graminea*. Other species playing a considerable part are *Panicum micranthum*, *Paspalum pulchellum*, *Rhynchospora barbata* and *Hypolytrum pulchrum*.

There is rarely a layer of algae; if present, it covers only 30 to 40 % of the surface (Photo 15).

Habitat

In the area studied the vegetations of the association occur on the slopes and tops of small hills.

The soil is wet. The upper 25 to 40 cm consist of loamy sand of which at least the upper 10 cm are slightly humic and brown, sometimes with rusty spots and/or greenish spots. At a greater depth first yellow and then white is the dominating colour; there may be also red spots. Usually there is some gravel throughout the profile, beginning at 10 to 30 cm, and moreover there is often a (sometimes impenetrable) layer of gravel at 60 cm or deeper.

Outside the area studied the association is present on flat stretches with no gravel in the subsoil.

Subdivision

2.2.3.a. Subassociation *typicum*: see above. Vegetation: Table 7 (4 records of the Gros savanna and 1 record of De Jong Noord savanna).
2.2.3.b. Subassociation *bulbostylidetosum minoris*. Transition to the *Bulbostylidetum coniferae minoris* (2.2.5). *Abolboda pulchella* is found in particular in this subassociation. Soil: Tables 1 and 2 nr. 9; Fig. 6 nr. 23.

Distribution: The association has been studied on the Gros savanna and the De Jong Noord savanna. Probably it is also present on savannas N. of the Wane-creek, belonging to the Welgelegen-type (LANJOUW & LINDEMAN, unpubl.).

2.2.4. Association Bulbostylidetum spadiceae boreosurinamense

The aspect of the vegetation is strongly determined by the curiously shaped *Bulbostylis spadicea*. In the herb layer, covering 60 to 85 % and up to 40 cm high, *Rhynchospora barbata*, *R. rhizomatosa* and *Mesosetum tenuifolium* nearly always belong to the main constituents. There may be an algal layer covering up to 75 % (Photo 16).

The vegetations occur on wet soils, on long slowly rising slopes of low hills.

There are two subassociations of which one occurs near the top of hills on a more loamy soil, and the other lower on the slopes on a more sandy soil.

2.2.4.a. Subassociation *paspaletosum pulchelli*

Vegetation

The main differential species is *Paspalum pulchellum*, which is always abundant. *Bulbostylis circinata* and, to a lesser degree, *Sauvagesia sprengelii* show preference for this subassociation.

Table 7: 3 records of the Gros savanna, 1 record of the De Jong Noord savanna.

Habitat

On a lower part of the slopes than the vegetations of the other subassociation. At least the upper 20 cm of the soil, but usually more, consist of loamy sand with rusty spots; only the upper 20 cm are slightly humic and brown. At a greater depth the colour is yellow, then yellow and grey-white spotted, and finally there appear also red spots. Gravel, if present, only below a depth of 1 m.

2.2.4.b. Subassociation *sporoboletosum cubensis*

Vegetation

Differential species in the herb layer are *Sporobolus cubensis* and, to a lesser degree, *Aristida tincta* and *Leptocoryphium lanatum*. There may be some small scattered trees of *Roupala montana* and *Antonia ovata*.

Table 7: Gros savanna.

Habitat

Near the top of the low hills. The upper 15 to 30 cm sandy loam, brownish and slightly humic, then a yellow layer up to 40 to 60 cm. At a greater depth yellow and white colours dominate, usually mixed with some red. Gravel not above a depth of 1 m. Soil: Tables 1 and 2 nr. 10; Fig. 6 nr. 18.

Distribution

Bulbostylis spadicea has been observed in N. Surinam only on the slopes of the Gros savanna, the De Jong Noord savanna and a small savanna of the same type S.E. of Gros. This may indicate that these slopes present very special conditions which do not occur elsewhere in N. Surinam. There are no indications that the species is found outside N. Surinam in the combination of species which is particular for this association. It is remarkable, however, that *Bulbostylis spadicea* is widespread in tropical America and has in general a much ampler ecological range.

Chorologic spectra: Both subassociations present a rather high percentage of the South-American element. In the subassociation *sporoboletosum* the percentage of the Guianan element is low and that of the NE-element rather high in comparison with that in the rest of the alliance.

2.2.5. Association Bulbostylidetum coniferae minoris

Vegetation

The scanty herb layer covers only 30 to 50 % of the surface and has a height of 10 to 50 cm, if the flowering shoots e.g. of *Trachypogon plumosus* are left out of consideration. It is poor in species, as many of the common species of the other associations are lacking, e.g. *Comolia lythrarioides*, *Buchnera palustris* and *Panicum stenodoides*. The main plant is the small form of *Bulbostylis conifera*, which is characteristic for this association (see IV.1). Noteworthy is the relative abundance of *Trachypogon plumosus*.

Mostly young specimens of *Antonia ovata* and *Roupala montana* are present, and sometimes also some adult ones. There is no layer of algae (Photo 14).

Table 7: 2 records of the Gros savanna and of De Jong Noord savanna each.

Habitat

The vegetation occurs on the top of small hills in patches of a few square meters, forming a mosaic with bushes of the *Roupala—Antonia* type.

At the surface of the wet soil there is a closed layer of pebbles with a diameter of up to 15 cm. Below this layer the pebbles are mixed with brown, yellow or grey sandy loam or probably a heavier type of soil. Impenetrable.

Distribution

The association has been studied on the Gros savanna and on the De Jong Noord savanna. Probably it is also present on other savannas of the Saban-pasi-type, for the habitat is found e.g. on the Saban-pasi savanna and the Rosebel savanna (VAN KOOTEN, 1954).

Chorologic spectrum: Most species which appear to be lacking when this association is compared with the rest of the alliance, belong to the American element, and this element is therefore relatively poorly represented. The NE- and the MNE-element have relatively high percentages.

(V. 8.)2.3. *Alliance Imperato—Mesosetion cayennensis*

Vegetation

The four associations forming this alliance are rather different. One of them has a tree layer, two may have a layer of algae. *Leptocoryphium lanatum* is the only species that may be more or less abundant in the herb layer of all four of them. Species with a high presence and a high abundance in two or three of the associations are *Mesosetum cayennense*, *Rhynchospora barbata* (var. *barbata*) and *R. globosa*. Just like these, nearly all other species of some importance are grasses or sedges.

The alliance has no characteristic species. Differential species with regard to the rest of the order are *Mesosetum cayennense*, *Andropogon leucostachyus*, *Axonopus purpusii* and, to a lesser degree, *Turnera ulmifolia*, *Aristida tincta* and *Rhynchospora globosa*.

The characteristic species of the order are well represented in one of the associations, viz. the *Axonopodetum purpusii*, which in more respects is transitional to the *Bulbostylidion lanatae*, but they are hardly present in the other three. Nevertheless the alliance has to be included in the *Paspaletalia pulchelli*. It has, like the other two alliances of this order, two groups of characteristic species of the class which are differential with regard to the other two orders.

Habitat

The communities of this alliance occur on wet, sometimes on very wet soils, which are more humic than in the rest of the order. The upper layer consists of sandy loam or a heavier soil type, but never of sandy, silty or pure clay. In comparison with the *Axonopodion chrysitis* (3.1) the soils of the communities of this alliance are either lighter or less wet.

Distribution

In N. Surinam the alliance is represented on a number of savannas of the Coesewijne-type, the Welgelegen-type, the Saban-pasi-type, on the latter only by the *Axonopodetum purpusii*. Apart from the savannas mentioned under the associations, an undetermined community belonging to the alliance seems to be present on the northern Tibiti savanna (Coesewijne-type; LINDEMAN, unpubl.).

In S. Surinam communities of the alliance probably are found on the Sipaliwini savanna; this, at least, is suggested by the collections made by ROMBOUTS in 1935–1936 (unpubl.).

Outside Surinam vegetation types resembling this alliance are mentioned by TAMAYO (1961) from the neighbourhood of Santa Elena, Est. Bolivar in Venezuelan Guiana, by BLYDENSTEIN (1963) from the llanos S. of Calabozo, Est. Guárico, and by LUNDELL (1937) from the so-called "bobolares" in Petén, Guatemala.

Chorologic spectra: The associations have few species of the Guianan element and of the northern South-American element or even none at all. The American element is always on the high side, and in three of the associations this applies also to the South-American element.
Roraima element: The percentage is variable, but in all associations it is above the mean value.
Dispersal spectra: Apart from the *Axonopodetum purpusii*, the percentage of the species with diaspores adapted to one or another way of dispersion is relatively high, in particular that of the pogonochores.

2.3.1. Association Axonopodetum purpusii

Vegetation

The herb layer covers 60 to 80 % and has a height of up to 60 cm. The main species are *Trachypogon plumosus*, *Mesosetum cayennense* and *Aristida tincta*. *Axonopus purpusii* has its optimum in this association. The normal form and the form with narrow leaves are present together and seem to be one entity (see IV.1).

In contrast with the rest of the alliance, this association contains the majority of the characteristic species of the order.

There may be some scattered small trees, mainly of *Byrsonima crassifolia* (gnarled form) and *Roupala montana*. A layer of algae may locally cover the whole surface.

Table 7: 3 records from the Gros savanna and 2 records from the De Jong Noord savanna.

Habitat

The association is represented on the flat top of low hills. The soil is wet. As a rule there is a layer of gravel, sometimes at a depth of only 5 or 10 cm, which may be impervious. On some places large rocks, up to 80 cm in diameter, are cropping out. The upper layer of 10 to 20 cm thickness consists of light brown, humic sandy clay loam, passing into heavier soil types, first mainly spotted yellow, white and red, but at a greater depth lighter, with less red or without red. Soil: Tables 1 and 2, nr. 18; Fig. 6 nr. 17.

Distribution

Gros and De Jong Noord savanna; probably on other savannas of the Saban-pasi-type too.

Blydenstein (1963) mentions a vegetation type of the llanos S. of Calabozo (Est. Guárico) that is closely related to this association.

Chorologic spectrum: The Guianan and the northern South-American element are on the low side.

Roraima element: In this association it is better represented than in the rest of the alliance.

2.3.2. Association Elyonuro—Andropogonetum leucostachyi

Vegetation

The one-layered vegetation is dominated by grasses, mainly *Mesosetum cayennense*, *Andropogon leucostachyus* and *Sporobolus cubensis*, but *Panicum nervosum* and the characteristic species *Elyonurus adustus* together with the sedge *Rhynchospora globosa* are also numerous. The characteristic species of the order are represented by *Paspalum pulchellum* only.

The association has only been studied a few months after being burnt, and at that time the vegetation covered 25 to 60 % of the surface. The height was about 80 cm.

Table 7: Coesewijne savanna.

Habitat

Only one profile has been studied. Down to a depth of 65 cm the wet soil consisted of sandy loam of which the upper 35 cm were very humic. See Tables 1 and 2 nr. 14 and Fig. 6 nr. 7.

Distribution

The association was studied on a small area near the border of the Coesewijnse savanna. As far as known this is the only stand of *Elyonurus adustus* in N. Surinam. On a savanna near Kopi (Welgelegen-type) LINDEMAN (unpubl.) found a vegetation type that resembles this association.

Chorologic spectrum: The elements with a small area are lacking completely, whereas the great majority of the species belongs to the American and the South-American element.
Dispersal spectrum: The high percentage of the pogonochores (29 %) is striking.

2.3.3. Association Curatello—Imperatetum brasiliensis

Vegetation

A layer of *Curatella americana* covers 20 to 40 % of the surface.

The herb layer which covers up to 100 % and has a height of about 80 cm, is dominated by *Imperata brasiliensis*. This shadow-loving species has its optimum in this association. Other common species are *Heliconia psittacorum* (also shadow-loving) and *Tibouchina aspera*. For the rest there is a rather important variability, so that the three records obviously do not present an all-round picture of this association. E.g. *Rhynchospora podosperma*, the only characteristic species of the order, which is present here, occurs in but one record and there with a high abundance.

Table 7: 2 records of the Lobin savanna; 1 record from the Bigi-olo savanna.

Habitat

The vegetation may occupy a large area (Bigi-olo savanna and Fransina savanna), but it also may form small patches among a one-layered herb vegetation (Lobin savanna).

The soil is wet to very wet. On the Lobin savanna the one profile that was studied had an upper layer of humic loam passing into sandy clay loam. See Tables 1 and 2 nr. 19 and Fig. 6 nr. 14.

Distribution: Lobin savanna (Coesewijne-type), Bigi-olo and Fransina savanna (both Welgelegen-type).

Chorologic spectrum: The Guianan and the northern South-American element are absent, the percentage of the American element is relatively very high (69 %).

2.3.4. Association Panicetum stenodoidis

Vegetation

The dense herb layer (covering 90 to 100 %) is 50 to 60 cm high. The most prominent species form a rather homogeneous mixture; there are *Rhynchospora globosa*, *Panicum stenodoides* (optimum here); less prominent are *Leptocoryphium lanatum* and *Axonopus pulcher*, whereas *Mesosetum cayennense* has a very variable degree of cover. *Rhynchospora barbata* (var. *barbata*) and *R. arenicola*, the only characteristic species of the order, are both present and one or both belong to the most abundant species. In the field they were not recognized separately (see IV.1). Both forms of *Axonopus purpusii* are present, but the one with the narrow leaves is the more common one.

In particular three species of *Habenaria* have to be mentioned. These plants appear after the burning of the vegetation, but are found no more when it is completely restored.

There may be a layer of algae covering up to 60 % of the surface.

Table 7: 10 records from the Lobin savanna, 6 from Mimili Okili and 3 from Doti savanna.

Habitat

The wet to very wet soil has an upper 10 to 30 cm thick layer of dark brown and humic silty clay loam, passing quickly into heavy clay, whereas the colour changes via brown-grey into orange and at a still greater depth into mottled grey, purple and orange. Red spots may start at a depth of 10 to 30 cm.

There may be a beginning of kawfoetoe forming. In the dry season shrinkage causes cracks.

Soil: Tables 1 and 2 nr. 20; Fig. 6 nr. 15. Water table: Fig. 8.

Distribution: The association has been met with on three savannas of the Coesewijne-type: the Lobin savanna, Mimili Okili and the Doti savanna. It was found on a savanna near Kopi (Welgelegen-type) by LINDEMAN (unpubl.).

(V. 8.)3. **Order Panicetalia stenodis** (Table 8*)

Vegetation

The herb layers of the communities belonging to this order are denser than in the other two orders.

There is a group of species usually showing a high presence and often a relatively high abundance in all associations. It consists in the first place of *Leptocoryphium lanatum* and *Tibouchina aspera*, *Hypogynium virgatum*, *Panicum nervosum* and *Heliconia psittacorum* coming in the second

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* Table 8 has been enclosed separately at the back of this issue.

place. In general the vegetations consist mainly of grasses and sedges. In agreement with the density of the vegetation the part of the shadow-loving species is relatively important.

The characteristic species of the order are distributed equally over the two alliances, the *Axonopodion chrysitis* and the *Mauritio-Hypogynion virgati*. *Rhynchanthera grandiflora* and *Acisanthera recurva* belong to this group. The alliances have their own characteristic species, but the latter are rather scarcely represented. Many characteristic species of the class are restricted to the *Axonopodion chrysitis*. The associations of the *Mauritio—Hypogynion* have a very open tree layer consisting of *Mauritia flexuosa*, which exercises hardly any influence on the herb layer. Moreover this alliance has a group of differential species which it has in common with some swamp communities (group 1d). It might even be argued that the *Mauritio—Hypogynion* should be considered to be a swamp community. However, the part of the savanna species outweighs that of the swamp species, at least in the three associations of this alliance, and therefore it is included here among the savanna vegetation-types.

Habitat

Very wet, usually heavy soils (*Axonopodion chrysitis*); in savanna rivulets and similar depressions (*Mauritio—Hypogvnion*). As a rule there are kawfoetoes at the surface; the gullies between them are filled with water in the wet season only. Upper layer of the soil very humic or peaty.

Distribution

Communities of both alliances are found in N. Surinam and in a western direction up to the Rupununi savannas (B.G.) and the llanos of central Venezuela. Related vegetation types are present on some West Indian islands.

Chorologic spectra: In general the percentage of the Guianan element is low and that of the American element on the high side.
Roraima element: The percentage is in the majority of the associations above the mean value, but for the rest there are large differences.

(V. 8.)3.1. *Alliance Axonopodion chrysitis*

Vegetation

The vegetations of this alliance consist of a dense herb layer; sometimes a layer of algae is present.

The bulk of the vegetation is always formed by grasses and sedges. Of these species only *Panicum nervosum* may be abundant in all associations; the same holds for *Tibouchina aspera*. *Leptocoryphium lanatum* and *Rhynchospora globosa* may be of importance in two of the three associations.

Habitat

The communities occur on very wet soils, which mostly are heavy. The upper layer usually is very humic. Worms are always present, as is apparent from their heaps or even from a pronounced kawfoetoe-pattern at the surface.

On account of the density of the vegetation there is shadow and probably other micro-climatic conditions favourable to the development of so-called shadow-loving species. It is not clear why these species are relatively abundant in two of the associations, but lacking in the third.

Distribution

In N. Surinam savannas of the We'gelegen-type may be largely occupied by a vegetation belonging to this alliance; see the *Arundinello—Panicetum stenodis* (3.1.1). Savannas of the Coesewijne-type (Lobin, Coesewijne and Doti savanna, Mimili Okili) and of the Saban-pasi-type (Gros savanna) may also have a vegetation belonging to this alliance, but mainly along their borders and along creeks.

Communities belonging to this alliance have been found in Venezuela, viz. near Santa Elena (Est. Bolivar) in Guiana by TAMAYO (1961) and S. of Calabozo (Est. Guárico) in the llanos by BLYDENSTEIN (1963).

Related communities occur in some W.I. islands. This at least is suggested by the description of the Piarco, Mausica and O'Meara savannas on Trinidad given by BEARD (1946) and by the description of a *Panicum stenodes—Rhynchospora podosperma* association from Hispaniola given by CIFERRI (1936).

Chorologic spectra: The Guianan element and the northern S.-American element are on the low side, the American element on the high side.
Dispersal spectra: The percentages of the pogonochores are relatively high.

3.1.1. Association Arundinello—Panicetum stenodis

Vegetation

The vegetation is one-layered and consists of a dense herb layer, covering 90 to 100 % of the surface, with a height varying from 50 to 90 cm.

The floristic composition is rather variable. *Leptocoryphium lanatum* is the only species which is always present and abundant; it may even dominate the vegetation. The other species often present and abundant are mainly grasses: *Mesosetum cayennense*, *Andropogon leucostachyus*, *Panicum stenodoides* and *Axonopus purpusii* with narrow leaves. However, *Rhynchospora globosa* and *Tibouchina aspera* have to be added. *Hypogynium virgatum* may determine the aspect of the vegetation when it is flowering (Photos 3 and 13).

Table 8: 3 records from the Lobin savanna, 3 from the Coesewijne

savanna, 2 from the Doti savanna, 1 from Mimili Okili, 2 and 1 from the savannas near Bersaba and Vierkinderen respectively, 1 from the Bigi-olo savanna.

Habitat

The upper soil layer of about 15 to 25 cm thick is very humic, coloured homogeneously dark grey or brown with rusty spots, and consists of silty (clay) loam, silty clay or clay. It passes into heavier soil types, whereas there appear inconspicuous lighter spots between 15 and 45 cm, followed by a mottled layer of grey, brown, red and yellow, under which at a depth of 60 to 70 cm the colour passes into white or light grey with red spots.

The soil is very wet. In the wet season there is always water in the narrow gullies between the kawfoetoes. In the dry season shrinkage causes cracks, so that the pattern of the kawfoetoes and the gullies is accentuated.

Soil: Tables 1 and 2 nr. 21 and 22; Fig. 6 nr. 8 and 16. Water table: Fig. 8.

Distribution

In N. Surinam this association is found on savannas of the Coesewijne-type, on which it may occupy small depressions and narrow, low-lying zones along the borders or along creeks: Lobin, Coesewijne and Doti savanna, Mimili Okili. The same holds for the savanna near Kopi, belonging to the Welgelegen-type (LINDEMAN, unpubl.). Other savannas of this type may be largely or nearly completely covered by this vegetation: Bigi-olo and Fransina savanna, savannas near Bersaba, Vierkinderen and Berlijn (the last one according to HEYLIGERS, unpubl.) and a savanna on the eastern bank of the Marataka river (FLORSCHÜTZ, unpubl.).

BLYDENSTEIN (1962) mentions a vegetation type from the Venezuelan llanos near Calabozo (Est. Guárico) that might be related to this association. It occurs in depressions in the open savanna ("pastizal").

3.1.2. Association Rhynchosporetum globosae

Vegetation

The 40 to 60 cm high vegetation, covering 85 to 95 % of the surface, is dominated by *Rhynchospora globosa*. The other species with a high presence and/or abundance are *Leptocoryphium lanatum*, *Paspalum pulchellum*, *Tibouchina aspera*, *Hypolytrum pulchrum* and *Scleria cyperina*. The latter two are differential species. Further this association is distinguished from the rest of the alliance by the small part played by the characteristic species of the order, by the absence of those of the alliance and of the shadow-loving species among the characteristic species of the class.

Mostly there is a layer of algae, covering up to 75 % of the surface.

Table 8: Gros savanna.

Habitat

The soil is heavy and very wet. The upper part consists of silty loam or clay, very humic and coloured dark grey to black with rusty spots. At a depth of about 60 cm the colour becomes grey and yellow spotted and at a still greater depth it is very plastic, light grey with some yellow spots. There are small worm heaps on the surface.

Distribution: Gros savanna. Further?
Chorologic spectrum: The Guianan element and the northern S.-American element are absent.
Roraima element: The percentage is high (57 %).

3.1.3. Association Ischnosiphono—Panicetum nervosi

Vegetation

The vegetation consists of a herb layer with a height of 60 to 100 cm, covering up to 95 % of the surface.

Always present and very abundant are *Panicum nervosum* and *Heliconia psittacorum.* Other common species which may be quantitatively of importance are *Rhynchospora glauca*, *Echinolaena inflexa*, *Imperata brasiliensis* and *Tibouchina aspera*, whereas some other species, e.g. *Blechnum indicum* and *Paspalum carinatum* are very variable in their degree of cover. The last one is a differential species of this association with regard to the rest of the alliance. The association can be distinguished in general by the occurrence of *Ischnosiphon leucophaeus*, a shadow-loving species that is not restricted to open savanna vegetations. Not only the presence of this species, but also that of *Heliconia psittacorum*, *Imperata brasiliensis* and some other shadow-loving species is in accordance with the particular habitat of this community.

Table 8: Coesewijne savanna.

Habitat

The vegetation occurs in the form of a narrow zone on low-lying stretches along the forest border. At least the upper 50 cm consist of sandy loam. The upper layer of about 20 cm thickness is dark brown and very humic to black and peaty, and contains root channel concretions. At a greater depth the colour becomes gradually lighter and at a depth of about 90 cm it is grey with yellow to brown spots.

There are only small worm heaps on the surface.

Soil: Tables 1 and 2 nr. 13; Fig. 6 nr. 10.

Distribution: Coesewijne savanna. Further ?
Chorologic spectrum: The percentage of the American element is high (61 %).

(V. 8.)3.2. *Alliance Mauritio—Hypogvnion virgati*

Vegetation

Three associations have been distinguished. They have a dense and high herb layer and scattered specimens of the palm *Mauritia flexuosa.*

The species which occur usually in the herb layer and are usually abundant, are *Hypogynium virgatum* (in the first place), *Rhynchospora glauca*, *Leptocoryphium lanatum*, *Panicum nervosum*, *Tibouchina aspera* and *Heliconia psittacorum*. The alliance has some characteristic species, but they do not occur very frequently. The main group by which the alliance differs from all other savanna communities, is formed by species occurring also in swamps (group 1d). Its best representatives are *Mauritia*, *Blechnum indicum*, *Rhynchospora cyperoides* and *Scleria microcarpa*.

Habitat

Savanna rivulets and sometimes also other low spots usually showing high kawfoetoes. In the dry season there is no water above the surface.

Distribution

Rivulets with a vegetation belonging to this alliance have been met with in N. Surinam on savannas of the Zanderij-, the Coesewijne-, the Welgelegen- and the Saban-pasi-type, but they probably are present on other types too.

On the Rupununi savannas (B.G.), S.E. of Lethem near the Kanuku Mountains, in a depression a community was found, which belongs to this alliance (February 1959). Soil: Kuma Series, waterlogged in the wet season (LOXTON c.s., 1958).

1a. Ch. class: *Curatella americana* juv., *Cassia cultrifolia*, (Ch. *Paspaletalia pulchelli*:) *Rhynchospora podosperma*; Ch. order: *Panicum stenodes*, *P. cyanescens*, *Scleria setacea*, *Sauvagesia rubiginosa*, *Rhynchanthera grandiflora*. 1b: *Waltheria americana*. 1c: *Panicum parvifolium*, *Paspalum pumilum*. 1d: *Mauritia flexuosa*, *Rhynchospora cyperoides*. Other species: *Polygala subtilis*, *Xyris macrocephala*, vs. *Andropogon* spec., Gram. spec. indet.

In this alliance might be included a vegetation type occurring near Calabozo (Est. Guárico) on the Venezuelan llanos, viz. the "morichales" with *Mauritia minor* (BLYDENSTEIN, 1962).

A community more or less resembling those belonging to this alliance was found on the Aripo savanna, Trinidad (BEARD, 1946).

Note: Two communities of uncertain status provisionally have been added to this alliance. Two other vegetation types, the one found in a rivulet on the Doti savanna and the other on the Gros savanna, certainly belong to this alliance, but are left out of consideration in the following survey.

3.2.1. Association Ischaemetum guianensis

Vegetation

The herb layer is high, 100 to 140 cm, and dense, covering up to 100 % of the surface. The highest degree of cover is attained by *Ischaemum guianense*. This species has its optimum in this association and may even dominate the vegetation. It is followed by *Hypogynium virgatum*, *Heliconia psittacorum*, *Blechnum indicum* and *Montrichardia arborescens*. The latter is a differential species with regard to all other savanna communities.

Table 8: 3 records from the Lobin savanna, 1 of the Coesewijne savanna.

Habitat

Rivulets or sometimes larger low lying areas. The soil consists of sandy loam or is of a heavier type. The upper part is peaty. The kawfoetoes are 20 to 45 cm high; only in the wet season there is water in the gullies between them.

Distribution

Savannas of the Coesewijne-type: Lobin and Coesewijne savanna; of the Welgelegen-type: near Berlijn (HEYLIGERS, unpubl.), savanna near Kopi (LINDEMAN, unpubl.), Fransina savanna.

3.2.2. Association Prestonietum perplexae

Vegetation

The dense herb layer, sometimes completely covering the surface, usually does not exceed a height of 1 m.

The floristic composition is very constant; many species are always present in about the same degree. The most abundant among them are *Hypogynium virgatum*, *Leptocoryphium lanatum*, *Rhynchospora globosa*, *Hypolytrum pulchrum*, *Scleria cyperina* and *Tibouchina aspera*. The last three are differential species for this association, together with some other ones like *Scleria bracteata* and, with regard to all other savanna communities, *Rolandra fruticosa* and *Dioscorea megacarpa*. It is remarkable that apart from *Mauritia* all differential species of the alliance (group 1d) are lacking.

The vegetation may be slightly scrubby, caused by the presence of much *Tibouchina* and of such species as *Rolandra* and *Bactris campestris*.

Table 8: Gros savanna.

Habitat

Rivulets with small worm heaps or up to 20 cm high kawfoetoes. At least the upper 50 cm consist of silty clay. The upper 20 to 50 cm are (very) humic, coloured dark grey or dark brown with rusty spots. In the next layer appear yellow spots. Below 70 cm the soil may be spotted: grey, yellow and brown colours. Soil: Tables 1 and 2 nr. 24; Fig. 6 nr. 22.

Distribution: Gros savanna. *Prestonia perplexa*, the only characteristic species of the association, has not been found in other localities in N. Surinam.

Roraima element: It is relatively well represented.

Dispersal spectrum: The percentage of the pogonochores is on the high side.

3.2.3. Association Lagenocarpo—Hypogynietum virgati

Vegetation

This association has not been studied sufficiently and little can be said about its floristic composition. However, it can be taken for sure that *Hypogynium virgatum*, *Panicum nervosum* and *Blechnum indicum* are usually among the most abundant species. The characteristic species of the *Syngonantho-Xyridion* (2.1), of which a part may be present in small quantities, may be considered as differential species of this association, *Lagenocarpus tremulus* in the first place.

Table 8: Lobin savanna; not very typical, perhaps transition to the *Ischaemetum guianensis*.

Habitat

Rivulets on the wet white-sand savannas, with high kawfoetoes.

Distribution: In N. Surinam on all savannas of the Zanderij-type.

3.2.4. Community of Dalbergia glauca

See Table 8. The community occurs on the edge of the Coesewijne savanna, bordering the *Eleocharis*-swamp of the Coesewijne river. It is characterized by the presence of some species which occur also outside the savannas in similar localities (group 1c). The soil consists of a layer of 25 cm of very humic silty loam, with kawfoetoes, on heavy clay.

Dalbergia glauca is found under more or less the same conditions along the border of a savanna near Kopi, adjoining the swamp of the Kasiwinika river (LINDEMAN, unpubl.).

3.2.5. Community of Lagenocarpus guianensis

This community (see Table 8) was found in a rivulet along the loamy part of the Lobin savanna. This rivulet was deeper than the one with a vegetation of the *Ischaemetum guianensis*. Water table: Fig. 8.

On a savanna near Kopi LINDEMAN (unpubl.) found a similar vegetation type in a small marshy depression surrounded by an *Ischaemetum guianensis* vegetation.

The community is intermediate between a savanna and a swamp vegetation. It resembles e.g. the swamp type with *Lagenocarpus guianensis* and other Cyperaceae, described by LINDEMAN (1953).

CHAPTER VI

THE SAVANNA BUSHES (Table 10*)

VI. 1. INTRODUCTION

The majority of the constituent species of the savanna bushes occurs also in one or several types of scrub, wood or forest (see LINDEMAN & MOOLENAAR, 1959; HEYLIGERS, 1963). Therefore a classification of the bushes on a floristic basis would be meaningful only if all these vegetation types were taken into account. As the latter are not comprised in this study such a classification will not be undertaken here. HEYLIGERS (1963) deals with floristic and ecological relations between the different types as far as they are found on white and red sandy soils.

The following types are distinguished (see Fig. 15):

B 1. *Ternstroemia* (*punctata*) — *Matayba* (*opaca*) bushes, on dry and moist white sand
B 2. *Rapanea* (*guianensis*) bushes, on dry loamy sand and sandy loam
B 3. *Cupania* (*scrobiculata*) bushes, on moist loamy sand and sandy loam
B 4. *Clusia* (*fockeana*) — *Scleria* (*pyramidalis*) bushes, on wet white sand
B 5. *Marlierea* (*montana*) bushes, on wet loamy sand
B 6. *Roupala* (*montana*) — *Antonia* (*ovata*) bushes, on wet sandy loam.

	White sand	Loamy sand	Sandy loam
Dry	Ternstroemia-Matayba bushes	Rapanea bushes	
Moist		Cupania bushes	
Wet	Clusia-Scleria bushes	Marlierea bushes	Roupala-Antonia bushes

Fig. 15. Ecological range of the savanna bushes

A comparison between the flora of the bushes as a whole and that of the open-savanna communities as a whole may be obtained from the sections IV.3–7.

It is striking that the bushes in general have a high percentage of their species in common with several types of secondary forest. Obviously these species are heliophilous, or at least not harmed by much light.

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* Table 10 has been enclosed separately at the back of this issue.

The presence of bushes may be significant for the interpretation of the existence of a certain savanna or type of savanna. Data concerning their floristic composition, the occurrence outside the savannas and the ecology of the constituent species are of particular importance. This point will be dealt with here only superficially. However, the following correlation may be stated: The bushes of the *Rapanea-* and of the *Cupania*-type have relatively more species that occur also in rain forest (groups 2e–g, 3). This may support the view that the savannas of the Coesewijne-type, on which these types of bushes occur, owe their present existence to the annual burning of the vegetation and that they gradually would be overgrown by the surrounding (rain) forest as soon as the fires would cease.

Few data are available about bushes in other parts of tropical America. DUCKE & BLACK (1953) report many species from the so-called campinas of the Amazon region. It appears that many of the genera are the same as in northern Surinam but this does not apply to the species.

Chorologic spectra, the percentage of the Roraima element and dispersal spectra (applying to the species of the shrub layer only): see Table 9.

VI. 2. TERNSTROEMIA—MATAYBA BUSHES (HEYLIGERS, 1963)

Vegetation, habitat and subdivision: see HEYLIGERS (1963); section III.3.3.2; Table 10: type B 1 (Lobin savanna, white-sandy part, Photo 6).

The bushes of this type, in Guiana known as muri (= *Humiria*) bushes, are mere fragments of the *Ternstroemia—Matayba* scrub. They have, however, a very peculiar shape, and form a separate and characteristic formation which is called "evergreen bushland" by BEARD (1955). They are intermingled with open patches occupied by vegetation types classified with the open-savanna communities (ass. 1.1.2 and 1.1.3). Actually this formation does not fit into the savanna concept in whatever way it may be defined. (See also section VII.2: Kasipora-type.)

The majority of the species occurs also in savanna wood and/or forest (2d–f) and a number also in rain forest (2e–f), but all are able to complete their life-cycle in the bushes.

Distribution: Savannas of the Kasipora-type. In British Guiana the type occurs e.g. on the Wiruni-Ituni savannas (MARTYN, 1931). Probably the "*Humiria floribunda* community", reported from the Pakaraima range by FANSHAWE (1952), is related to this type.

Chorologic spectrum: The northern South-American element is relatively frequent, the American element is scarce.

VI. 3. CLUSIA-SCLERIA BUSHES (HEYLIGERS, 1963)

Vegetation, habitat and subdivision: see HEYLIGERS (1963); section III.3.3.2; Table 10: type B 4 (Lobin savanna, white-sandy part).

The bushes of this type occur among the open-savanna communities

TABLE 9

Chorologic spectra and dispersal spectra of the savanna bushes in percentages and the percentage of the Roraima element in a separate column R.

Vegetation type	Number of species	Geographical elements						R	Dispersal types					
		G	N	NE	MNE	S	A		1	2	8	9	11	14
Total of all types	91	26	18	13	3	18	22	35	2	36	3	2	7	50
Ternstroemia—Matayba bushes	30	27	27	16	–	20	10	53	3	33	3	–	3	58
Rapanea bushes	33	9	15	12	3	21	40	46	–	39	–	–	3	58
Cupania bushes	43	12	12	9	2	25	40	40	3	42	3	7	3	47
Clusia-Scleria bushes	19	49	20	16	–	5	10	54	–	42	–	–	–	58
Marlierea bushes	19	33	16	16	–	10	25	69	–	25	–	–	–	75
Roupala—Antonia bushes	33	18	18	28	–	12	24	51	–	45	–	–	–	55

on wet white sand, in particular the associations 2.1.2 and 2.1.3. The vegetation of the latter association may be locally shrubby and therefore transitional to the bushes (subass. b).

Nearly all species are also found in savanna wood and forest (2c–e). Only two species occur in rain forest (2e).

Distribution: Zanderij-type. Further ?

Chorologic spectrum: The percentage of the Guianan element is very high, that of the South-American and the American element low.

VI. 4. RAPANEA BUSHES

Vegetation and habitat: see section III.2.4.3.2; Table 10: type B 2 (Coesewijne savanna, see Photo 10).

These bushes are found scattered on the Coesewijne savanna. Probably they indicate the tendency of the surrounding forest to start the occupation of the savannas as soon as the annual fires would be stopped. The number of species typical for bushes (2a) is high and also the number of species that occur in savanna wood and forest (2c–f) and rain forest (2e–g, 3). (See also section VII.2: Coesewijne-type.)

Chorologic spectrum: The percentage of the Guianan element is relatively low, that of the American element relatively high.

VI. 5. CUPANIA BUSHES

Vegetation and habitat: see section III.2.1.3.2; Table 10: type B 3 (Lobin savanna, loamy part).

These bushes are found on the Lobin savanna and occupy the same position there as the bushes of the preceding type on the Coesewijne savanna. The number of constituent species is high (41) and about a fourth of them is typical for savanna bushes (2a). Half of the species may be found in savanna wood and/or forest (2c–f) and half of them also in rain forest (2e–g, 3). Chorologic spectrum: as in the former type.

VI. 6. MARLIEREA BUSHES

Vegetation and habitat: see section III.4.1.3.2; Table 10: type B 5 (1 record from the Gros savanna, 2 records from the De Jong Noord savanna).

Bushes dominated by *Marlierea montana* are found in an open vegetation with much *Rhynchospora curvula* (ass. 2.2.3) on the Gros and the De Jong Noord savanna. They consist of relatively few species only two of which are found also in rain forest (2e). It has to be remarked that *Marlierea* itself may occur in marsh forest.

VI. 7. ROUPALA—ANTONIA BUSHES

Vegetation and habitat: see section III.4.1.3.2; Photo 14; Table 10: type B 6 (3 records from the Gros savanna, 1 record from the De Jong Noord savanna).

The bushes on the pebble-knolls of the investigated savannas of the Saban-pasi-type have many species typical for savanna bushes (2a). The other species may occur in savanna wood and forest (2c–f), and some of them also in rain forest (2e–f), but typical rain-forest species are absent (2g and 3).

The list of species collected by LANJOUW (1936) on the Patrick savanna contains *Roupala montana*, *Antonia ovata* and *Tetrapteris squarrosa*. This suggests the presence of *Roupala—Antonia* bushes on this savanna which also belongs to the Saban-pasi-type.

The species found by LANJOUW and LINDEMAN on the savannas of the Welgelegen-type N. of the Wane-creek in 1953 (unpubl.) indicate that the bushes there are related to the *Roupala—Antonia* type.

CHAPTER VII

EXISTENCE, ORIGIN AND MAINTENANCE OF THE SAVANNAS

VII. 1. SAVANNAS IN GENERAL

VII. 1.1. **The part played by the climate**

A climate may be called a "savanna climate" whenever it (1) causes or (2) permits the development of a savanna vegetation.

Nearly all investigators who recently have dealt with the origin of savannas, are of the opinion that savanna climate in the former sense does not exist. BEARD (1953) treats this subject at length and, after presenting many examples, comes to the following conclusion: "We merely have to inquire whether there is any climate which will cause the appearance of savanna in the absence of fire or any adverse edaphic condition. We are bound to conclude that there is not."; and: "There is no climate on record under which there is savanna on optimum sites."

Some German students are of opinion that a savanna climate does exist in the latter sense, that is to say as a precondition for the existence of savannas. C. TROLL (1952) formulates their starting-point in this way (translated): "There is a climatic main division of the vegetation and a local-edaphic subdivision of equal importance. On the one hand there are climatic vegetations zones, on the other edaphic variants". Further this author mentions that every natural vegetation type has several secondary types caused by human interference, but that the character of the original type always may be deduced from the secondary ones.

With regard to the savannas this is illustrated as follows (translated): "It is possible from case to case, and in many instances it has even been proved, that the open grass plains with scattered trees, single or in small groups, and also the half open savanna formations originally were covered more densely with forest. Under the savanna climate, however, these were no rain forests but several types of savanna forest." It is clear that here a "savanna climate" is considered to be a climate that permits the existence of savannas, and "savanna forest" any type of forest that may be turned into savanna.

LAUER (1952), presents some general ideas concerning the relation between the main division and the subdivisions of the vegetation. He mentions local climate (!), soil, animals and men as the factors determining variations within the climatic vegetation zones.

Against this background JAEGER (1945) distinguished in the tropics three main vegetation zones, that would be correlated with a definite climate, viz.:

Tropical rain-forest zone – always wet
Grassland zone – alternately wet and dry
Desert zone – always dry

The grassland zone is covered with "savanna forest", with treeless savanna vegetations and with types intermediary between these two. What type will be present in a certain locality, depends upon edaphic and biotic factors. The grassland zone is divided into three subzones, viz. a "wet savanna-", a "dry savanna-", and a "thorny savanna-zone". These subzones are covered with physiognomically different types of savanna (as far as genuine savanna is involved!) and corresponding forest types. The subzones are subject to types of climate that differ in the total precipitation and in the number of dry months per annum. A month is considered to be dry when its mean precipitation is less than 30 mm.

LAUER (1952) adopts in the main the division of the vegetation proposed by JAEGER, but he corrects and refines it in his own way. The climatic types which he tries to correlate with the vegetation units, are defined differently. Not only the total precipitation and its distribution in the course of the year, but also the temperature is taken into account. This is in principle correct and important, but in the following no attention will be paid to it, as the differences in temperature within the area under consideration are of relatively minor importance.

Wet and dry months are distinguished by the aid of an index based on a formula by DE MARTONNE (1926)

$$I = \frac{12\,n}{t + 10}$$

t = mean temperature of the month in degrees centigrade
n = mean precipitation of the month in mm

dry month: $I < 20$, wet month: $I > 20$.

Localities with the same number of wet months according to this index may be linked up by lines, so-called "isohygromenes". In South America the relation between climate and vegetation zone can be expressed as follows:

Rain-forest zone – isohygromene 10–12
Wet savanna zone – isohygromene 7–10
Dry savanna zone – isohygromene 5–7
Thorny savanna zone – isohygromene 1–5
Half desert and desert zone – isohygromene 0–1

This relation has been mapped and it is likely to be correct in so far as the larger savanna, campo and llano areas are concerned. Lauer's argumentation, however, does not satisfy in all respects. It does not stand out clearly that his delimitation of the vegetation zones was unbiassed.

The application of these ideas to the savannas of northern Surinam does not meet with success (see Bakker, 1954). Though many savannas are found here the whole area has at least ten wet months per annum. Lauer maps the country as if it were completely covered with rain forest! It may be asked whether this has to be regarded as a minor deviation that does not affect the main lines of his scheme, or whether it is due to a fundamental mistake in the argumentation, which might reveal itself also in other cases.

It is true that the three authors under consideration nowhere refer to the *ecosystem* concept or to its German equivalent "Holozön". They only mention the influence which the habitat factors exercise on the vegetation, but neglect the effect of the latter on the habitat.

Climate, soil, animal communities and vegetation may make up a relatively stable system. If one of the components changes, this must have consequences for the others. If e.g. a wood vegetation would change into a savanna vegetation under the influence of shifting cultivation and burning, the micro-climate, the soil and the animal communities would change too. If such a process would spread over large areas, even the macro-climate would be affected.

Two different ecosystems may be characterized by vegetations that are similar in structure, physiognomy and even in floristic composition. This may be the result of a single dominating factor which is present in both cases, but it may also be that in both cases the result of the interplay between the other three components is felt by the vegetation as identical. This means that a certain vegetation type may be found under quite different types of climate if this difference is counterbalanced by differences e.g. in topography and/or soil type. In that case it is not possible to correlate the type of vegetation with a definite type of climate.

It appears that this postulated situation in fact is of frequent occurrence, as many investigators (e.g. Beard, 1944, 1955; Fanshawe, 1952; Richards, 1952) state that in the tropics the vegetation type depends in the first place upon the water economy of the soil. This water economy is determined partly by the climate and partly by the topography and the properties of the soil. If this is conceded, we can not expect to find vegetation zones in the tropics correlated with types of climate.

Rawitscher (1948, 1950, 1952) who deals among other things with these relations, says (translated): "Things like this of course are not influenced by general climatic formulae, and the impossibility to handle the problem mathematically is so evident, that it would be sensible and justified for a botanist to reject such formulae."

In spite of all these theoretical objections the fact remains that the large savanna areas of South America are situated within the isohygromenes of Lauer's "wet savanna zone". Therefore it would be good, in anticipation of the exposition given in the next section, to examine the probability of a rather simple relation between the climate and the water economy of the savanna soils.

Already in 1944 Beard arrived at the conclusion that the rooting zone in the soil of natural savannas is characterized by the alternation of a period in which it is saturated with water and a period in which it dries up. Even in case the different soil types would be distributed haphazardly with regard to the types of climate, it is to be expected that such an alternation would occur more frequently in regions where there is a pronounced contrast between the dry and the wet season. However, there might even be a stronger bond between the water economy and the climate. Often the alternation of saturation and desiccation is caused by the presence of an impermeable layer in the subsoil. The formation of such a layer is stimulated by a widely fluctuating water table, and this fluctuation again is the more pronounced the stronger the contrast is between the precipitation in the wet and in the dry season. In this way it seems possible to interpret the relation found between the situation of the large savanna complexes in South America and the climate of Lauer's "wet savanna zone".

However, in this respect the decisive feature of the climate is the presence of a difference between the precipitation of the successive seasons, not the absolute values. Beard very properly remarked that a savanna must have a climate with periodically rainfall, without further specification. This means that even under a climate without a single "wet" or "dry" month in the sense of Lauer, and in the absence of dominant biotic factors, a savanna vegetation may occur, provided that periodocity in the rainfall results in the alternation of periods of saturation and of desiccation in an upper soil layer of sufficient thickness. This, however, will occur less frequently under circumstances differing from those prevailing under the "savanna climate" of Lauer.

We may say therefore that a savanna climate does exist so long as it is defined as a climate that is a necessary condition for the occurrence of a savanna vegetation. Essential is a certain difference between the precipitation of the different seasons. The index applied by Lauer is theoretically incorrect, because it is based on absolute values, but in general it suffices for the delimitation of the climate of the so-called "wet savanna zone".

VII. 1.2. Other factors in combination with climate

As said before it appears that in many cases the alternation between a saturation with stagnant water and a desiccation of the soil is responsable for the existence of a savanna vegetation. BEARD (1953), who deals with this subject in detail, states: "It seems that there are two classes of trees adapted to severe habitats at low elevations in the tropics: those adapted to withstand desiccation of the soil, which cannot tolerate flooding, and those adapted to flooding, which cannot tolerate desiccation. The impermeable subsoils of savanna lands create perched water tables which come and go with the rains. The layers of the soil which are above this obstruction and to which the roots are confined are waterlogged in wet weather and dried out completely at other times, so that a constant alternation of the two extremes is set up. The only trees which seem able to tolerate such conditions are the few oddly gnarled species found in savannas, whereas the xeromorphic herbs, particularly the bunch grasses, seem to be well adapted to the site." According to AUBRÉVILLE (1962), in particular the seedlings of normal trees are not able to withstand the alternation of desiccation and flooding.

The conditions under which savannas occur, in combination with a periodic rainfall, may be summarized as follows (in general see BEARD, 1953):

A. The savanna vegetation is seral.

1. A very thin layer of soil overlies unweathered parent rock, or there are small amounts of soil in fissures. Examples: the small savannas of the Tafelberg (MAGUIRE, 1945 a), the Kaieteur savanna (JENMAN, 1882).
2. A thicker soil layer overlies parent rock. Examples: savannas on Barbuda (BEARD, 1949) and on Cuba (BENNET & ALLISON, 1928). The same effect is achieved if freshly weathered parent material is (still) impermeable.
3. The savanna presents a stage in the process of the heightening of a river bank or the silting up of a former river bed. The fluctuating water level of the river itself causes an alternation of deep groundwater levels and flooding. HUBER (1900, 1902) interpretes in this way the existence of savannas along and in the immediate environment of the lower Amazon river. DUCKE & BLACK (1953) consider this interpretation as possibly correct.

B. The savanna vegetation is the natural, "edaphic" climax.

1. There is a true groundwater table that fluctuates widely. Example: wet white-sand savannas near Jodensavanne (HEYLIGERS, 1963).
2. There is an impermeable layer at a certain depth (for many examples see BEARD, 1953) resulting from
   a) normal deposition, or
   b) the formation of a bank, mostly an iron pan or a clay bank.

Whenever the distance from the surface of the soil to the lowest groundwater level or to the impermeable layer is either too small or too large to allow the development of a savanna vegetation, the "correct" situation may develop as a result of sedimentation or sheet-wash respectively. The former case may be illustrated by the savannas along the Amazon river (see A. 3). Another example is mentioned by LASSER (1955), who is of the opinion that in some localities in the Venezuelan llanos forests changed into savannas in consequence of the heightening of the soil by sedimentation. BAKKER (1951, 1954) treated the occurrence of the latter case on Surinam savannas. However, it is likely that sheet-erosion takes place only after other factors already have caused the disappearance of the tree layer.

C. Anthropogenic savannas in general originate from abandoned clearings that are subject to a rigorous regime of burning. This process is effective particularly along the borders of existing savannas, whether natural or not. Just like the existence of natural savannas it is not entirely independent of the climate and water economy of the soil related to the latter. The vegetation arising on the abandoned clearings has to be periodically inflammable i.e. dry.

It is very well possible that in particular during very dry years the dry woods bordering the savannas may catch fire, so that in the long run a lasting extension of a savanna may result (see HEYLIGERS, 1963, p. 124; LINDEMAN, 1953, p. 91; AUBRÉVILLE, 1959).

Unlike "edaphic" savannas, which always have a more or less flat topography, anthropogenic savannas may be hilly. Many examples of such anthropogenic savannas can be given: French Guiana (AUBRÉVILLE, 1961 b), Dominica (BEARD, 1949), locally in central and S. Brazil (CHEVALIER, 1928, 1929), E. Brazil (RAWITSCHER, 1948, 1950, 1952), Petén in Guatemala (LUNDELL, 1937), central Africa (a.o. LEBRUN, 1937; DUVIGNEAUD, 1949, 1953; SILLAN, 1958), etc. Surinam is dealt with in the next section.

Finally it has to be mentioned that BEARD (1953) discarded the infertility of the soil as a possible cause for the existence of savannas. He showed clearly that there is no relation between the distribution of the savannas and that of infertile soil types.

The factors which gave rise to the development of a savanna and those which maintain it, are not necessarily the same. E.g. a savanna vegetation may originate as a stage in a succession, the heightening of the soil by sedimentation being the responsible change in the habitat. Such a savanna vegetation may be maintained, though continually changing in composition, in spite of the continued heightening of the soil, if other factors prevent the development of trees. These factors may be grazing of animals and fires, the latter caused by natural agents or lighted by man.

A prevention of tree-growth by wild grazing animals is not likely in the South American of today. Large herds of herbivores are not reported from the savannas. Maybe that this was formerly different.

SCHOMBURGK (1848) observed many roes on the Rupununi savannas, usually grazing alone, sometimes in groups of at most five.

There are many savannas, campos and llanos on which today cattle is raised. However, the animals may suffer from diseases because the vegetation is deficient in some essential nutrients. Therefore these nutrients either have to be provided directly or the soil has to be fertilized (see e.g. FOLLET–SMITH, 1930; HOOCK, 1960). This, however, supports the view that the savannas never may have been rich in wild animals.

Natural fires may originate from lightning, as on the plain of Rwindi Rutshuru, Congo (LEBRUN, 1937), and from heating in a thick layer of inflammable litter (LINDEMAN, 1953, p. 92). However, in general intentional setting afire has been from long-ago and still is of much more importance.

As far as South America is concerned, no author assumes that the scarce indian population could be responsable for the existence of the extensive savanna areas, but it is on the other hand generally accepted that the present savannas, both the natural and the anthropogenic ones, are strongly influenced by repeated burning (see e.g. PILGER, 1902; MYERS, 1933, 1936; BEARD, 1953; HUECK, 1957, 1961; PAFFEN, 1957). Students of the indian way of living also mention again and again the setting afire of the vegetation as a hunting method (LOWIE, METRAUX, GILLIN, KIRCHOFF, all in STEWARD, 1948; SAUER, 1944). In this way a relatively thin population, in particular when leading a nomadic life, is able to keep enormous areas under a fire regime.

A savanna area, interesting in this respect, has been described by LEBRUN (1937). The plain of Rwindi Rutshuru in Congo owes its recent origin (from a geologic point of view) to the silting up of a large lake. There obviously has been a stage in the succession represented by a savanna vegetation. Since this stage was reached, the savanna vegetation has maintained itself as a result of fires, which in this region originate from lightning as well as from intentional setting afire. The former alone would not be sufficient. It seems possible that the whole transformation from lake into plain took place in the presence, and consequently also under the influence, of a fire raising population.

The opposite might occur too. As a result of the deforestation the soil of an anthropogenic savanna might change in such a way that the savanna vegetation would persist even after grazing and burning were stopped. The poorly or not at all permeable hardpan often found in the subsoil of clay savannas, might just be a facet of the decline in structure, which takes place in these clay soils after the disappearance of a protecting canopy and of an extensive root system traversing the soil. The description given by BEARD (1949) of the savannas on Dominica suggests that there such a situation may be present. The phenomenon will be dealt with in more detail in the next section in the discussion of the Welgelegen-savannas.

Another agent that might come into play after deforestation and might create at least temporarily the fitting conditions for a savanna vegetation, is sheet-erosion.

If in a large savanna area the conditions for the maintenance of a savanna vegetation would deteriorate for some reason or another, the evolution to forest would probably take a very long time. In the first place there is the question of accessibility. It might take a long time before an appreciable amount of diaspores of the appropriate tree species reach the area. However, a factor of even greater importance might be that the seeds of the trees fail to germinate or that the seedlings fail to grow up, because the microclimate is unfavourable to them, or the surface layer too hard, or the competition to the grasses too severe, etc. There are indications that in such a case a savanna would be afforested starting from the edges and eventually from already existing bushes. Young trees may arise also under "trees" like *Curatella americana.* (See the description of the Lobin and the Coesewijne savanna, III.2.) If, however, the savanna is quite open, it would only be invaded by the forest along its borders, and the centre would stay open for a very long time.

Finally the possibility has to be mentioned that a savanna may have originated during an earlier geologic period, under other ecological conditions, and that it is maintained now owing to one of the influences already mentioned. Authors dealing with this possibility came to be conclusion that there must have been a period during which the savannas of South America had a much larger extension than they have at present. Some of them did not enter into any further details (WEBERBAUER, 1936; PAFFEN, 1957; HUECK, 1958, 1959, 1961), others assumed that this period must have covered the last glacial age (SAUER, 1944; WILHELMY, 1952; AUBRÉVILLE, 1962), but only one of them could prove that, at least in northern South America, it has been indeed the last glacial age (VAN DER HAMMEN, 1961).

Most authors are of opinion that the still existing large savanna areas and also some smaller ones, e.g. those of the Amazon region, are on the one hand remnants of much more extensive and cohering savanna areas, but that their present vegetation on the other hand is in conformity with their present ecological conditions. If the fires would cease, only their marginal zones would become covered by the forward pushing forest. Only AUBRÉVILLE (1962) supposes that there is hardly any place on the large savannas where a relation can be proved between the present vegetation and the natural habitat. The hypothetical contemplations on this matter, as a rule, are based on a too small amount of factual data and therefore have a too speculative character. The views of VAN DER HAMMEN and his cooperators are an exception, but unfortunately the latter have been worked out and published but partly as yet.

With regard to the foregoing it is of importance to know at what time man entered South America. SAUER (1944) remarks in this respect: "..., if we are permitted to contemplate a first peopling of the continent while glacial and pluvial conditions still prevailed in the midlatitudes, a different climatic situation may have existed about the Gulf of Darien...". In that case the first indians would have entered a land of savanna instead of virgin forest. This would have had far-reaching consequences for the evolution of the vegetation. The investigations aiming at a solution of this problem are continued (WILLEY, COLLIER, STEWARD, all in STEWARD, 1948/49). In North America the presence of man during the Würm glacial age has been proved with certainty, but not (yet) in South America.

VII. 2. THE SAVANNAS OF NORTHERN SURINAM IN PARTICULAR

After what has been said in the foregoing section the treatment of the northern Surinam savannas may be relatively short.

The climate itself nowhere plays a decisive part, but it is such that it enables the existence of savannas, "edaphic" as well as anthropogenic ones.

There are no indications that any savanna vegetation would represent a stage in a succession, at least not in a progressive one.

The vegetation of nearly all savannas is set periodically on fire, of many of them once or even more than once a year. This observation led GONGGRIJP & BURGER (1948) to believe that all Surinam savannas would be anthropogenic fire-savannas. This conception, however, is too simple, as may appear from some earlier and many later publications including the present one.

The existence of the savanna of the Watamalejo-, the Zanderij-, the Bosland- and the Saban-pasi-type are to be ascribed to natural, edaphic conditions.

The savannas of the *Watamalejo-type*, on the offshore bars of the old coastal plain, have in their subsoil at a depth of 70 to 90 cm an iron pan. This bank originated in the course of normal soil-developing processes. The type matches LANJOUW's (1954) "leached-soil-and-impermeable-ironpan-type". The vegetation is not burnt. See further LINDEMAN (1953), BAKKER & LANJOUW (1949) and BAKKER (1951, 1954).

The savannas of the *Zanderij-type* have a widely fluctuating ground-water-table which may simply be the result of a flat, relatively shallow soil overlying flat-bedded rock, so that drainage is impeded (HEYLIGERS, 1963). It is also possible that in some cases the iron pan, which is often present, causes in the wet season a perched, not genuine ground-water-table, which exerts the same influence on the vegetation as a genuine one. This iron pan is the result of a normal profile development, but this took place long ago. The present upper layers have been deposited on the old profile. Undoubtedly sheet-erosion lowered in many localities the surface to the height which is proper for the existence of this savanna type (BAKKER, 1951, 1954). The infertility of the soil is in this respect of no importance.

The savannas of the *Bosland-type* have a soil with a genuine savanna water-economy, for it consists of a thin colluvial upper layer overlying either an iron pan or the weathered, residual, but impermeable parent material. These savannas are not burnt. See COHEN & VAN DER EYK (1953) and VAN DER EYK (1957).

The soil conditions of the savannas belonging to the *Saban-pasi-type* differ considerably from place to place. In all cases observations concerning the water economy indicate a natural savanna habitat. This is in agreement with the impermeability of the subsoil, whether it consists of weathered or unweathered rock. In the valleys of the rivulets it is the low position that makes possible a fluctuating water level. See VAN DER EYK (1954), COHEN & VAN DER EYK (1953) and VAN KOOTEN (1953, 1954). Only where drainage conditions are better, bushes occur; so on the knolls consisting of residual pebbles, on the tops covered by a sand layer and in other localities with a thick layer of leached and well-permeable sand.

The vegetation of these savannas is burnt regularly, in spite of the diminuation of the population after the fall in the gold-mining. There are now no indians living even at a far distance, but that they formerly inhabited these savannas is proved by potsherds found deep in the soil (VAN KOOTEN, 1954).

The savannas of the *Welgelegen-type* are no uniform group from the present point of view. The occurrence of the *wet variation* N. of the Wane-creek is ascribed by BAKKER & LANJOUW (1949) and BAKKER (1951, 1954) to the impermeability of the clay at a depth of 50 to 60 cm or less. The type is called by LANJOUW (1954) "impermeable-clay-layer-type". BAKKER supposes that originally swamps were found here, and afterwards forests, the layer above the impermeable subsoil being thicker at that time. Sheet-erosion would have lowered the surface to such a level that a water economy favourable to the development of a savanna vegetation came into existence. This does not seem probable. Sheet-wash in a forest with a flat soil-surface seems unlikely and has to be proved before it can be accepted.

The occurrence of savannas of the wet variation in the Para region may be interpreted in another way. The "schol"-soils here are covered mainly with forest. The subsoil consists of very sticky clay and the surface is set with many kawfoetoes in agreement with the high water table in the wet season (VAN DER EYK, 1957).

In general the topography of the savannas is not different from that of their surroundings. The savanna soil clearly shows the alternation of saturation with water and desiccation. This becomes comprehensible if it is assumed that the origin of these savannas is anthropogenic (see III.1). The flooding is in agreement with the situation in the adjoining forests and is caused by the poor permeability of the subsoil and the poor drainage of the flat "schols". The difference in micro-climate, however, is responsible for the fact that in the dry season the soil of the savannas dries out completely, whereas the soil of the forests does not. It does not appear impossible that some of these savannas, viz. those without *Curatellas* and bushes, would disappear very slowly if the burning would be stopped, on account of the inward moving forest border. Moreover, it is possible that the surface erosion after the clearing has diminished the distance between the surface and the poorly permeable clay-subsoil, so that a water economy was established still more in conformity with the one of natural savannas. In addition the clay-subsoil may dry up irreversibly, as a result of the unhindered solar radiation, and in consequence it may become still less permeable.

The *dry variation* of the Welgelegen-type includes one or more savannas that by COHEN & VAN DER EYK (1953) are considered to be of anthropogenic origin. The maintenance of their vegetation depends in the first place upon the fires but in sofar as these savannas may have wetter parts, the latter offer the same conditions as the savannas of the wet variation in the Para region.

In general the soil conditions and the vegetation of these savannas are in fairly good agreement with those found in the savannas of the Coesewijne-type.

According to COHEN & VAN DER EYK (1953) the savannas of the *Coesewijne-type* are anthropogenic.

BAKKER & LANJOUW (1949) and LINDEMAN (1953) call the savanna of this type near Tibiti-sabana a fire-savanna, and the observations on the Lobin and the Coesewijne savanna too indicate that spontaneous afforestation would take place as soon as the fires were stopped. Wherever the fire has given delay, in particular near the eastern (= under the lee) forest borders, treelets make their appearance and bushes are formed that give the impression of being capable of further extension. The presence of a more or less drooping *Curatella* in many of the bushes also indicates that these bushes are outposts of the forest that wants to expand, and not relics of forest that is forced to retreat.

The lowest parts of these savannas, having the heaviest and wettest soils, do in some cases not even belong to the Zanderij but to the Coropina formation and are completely comparable with the Welgelegen-savannas in the Para region. The supposition of BAKKER (1954) that on these parts a tendency to the formation of a natural savanna might beforehand have been present, is not taken over here. That the present water economy resembles more or less the one of a natural edaphic savanna, is probably not the cause, but the result of the disappearance of the trees.

The savannas of the *Kasipora-type* are occupied partly by a closed and partly by a discontinuous shrub vegetation (*Ternstroemia-Matayba* type B 1) and besides in some places by a one-layered vegetation of *Trachypogon plumosus* (*Mesoseto—Trachypogonetum*, 1.1.1). Only the last one is a true savanna vegetation.

Opinions differ with regard to the ecological background of the discontinuous shrub vegetation (muri scrub), but they need not exclude one another. LINDEMAN & MOOLENAAR (1955, 1959) place it at the end of the edaphic series: savanna forest – savanna wood – scrub savanna – dry open savanna, in which the principal change in the habitat is the lengthening of the period of water-shortage. BEARD (1955) too mentions this series, although he applies other names to the various types. HEYLIGERS (1963) assumes that this opinion may be correct in certain cases, but not in all. VAN DONSELAAR–TEN BOKKEL HUININK (1966) accepts the view that the habitat of the discontinuous muri scrub presents the ultimate possibilities for the development of shrubs. She is of opinion that this habitat might be occupied by closed savanna scrub if the influence of the drought was uniform from year to year. However, a very dry year occurs now and then and in this habitat the extreme drought may kill all or many shrubs completely, even their root systems. In that case a quick regeneration of the vegetation as a whole is impossible. Regeneration will take place gradually, starting with the shrubs that survived the drought and with new seedlings of shrubs. VAN DONSELAAR–TEN B. H. actually observed that bushes may arise on bare sand and that they may fuse afterwards.

The scrub and the bushes are subject to burning, but probably this is not the decisive factor for the existence of the latter, for the fire does not kill the underground parts of the shrubs.

So according to VAN DONSELAAR–TEN B. H. the muri scrub has to be regarded as a more or less permanent state of regeneration of the closed savanna scrub in the most extreme part of the habitat of the latter.

According to HEYLIGERS (1963) the *Trachypogon* vegetations on the dry white sands are found probably in localities where dry savanna wood or even savanna forest has been burnt down radically. This vegetation can maintain itself only if it is burnt frequently. If the fires fail to come, it passes into a vegetation of *Bulbostylis conifera*, identical with the one on the open patches among the bushes (ass. 1.1.3), and then the regeneration may start.

LANJOUW's opinion (1936) that open savanna may originate from the burning of savanna wood, appears to be appropriate to the Kasipora-type.

In the foregoing it has been tried in the first place to interpret the *present existence* of the savanna vegetations with the aid of the present ecological conditions to which they are subjected. This appears to be possible. The existence of part of the savannas is due to edaphic, particularly "water economic" factors: the savannas of the types Watamalejo, Welgelegen N. of the Wane-creek, Bosland, Zanderij and Saban-pasi. The vegetation of the three first mentioned types is not burnt, that of the two last mentioned ones is, but this is not essential for their continuance. The savannas of the dry variation of the Welgelegen-type and of the Coesewijne-type are maintained only if their vegetation is regularly set afire. Probably this is true also in the case of the savannas of the Kasipora-type, for the parts with a genuine savanna vegetation as well as for those with a muri vegetation. The vegetation of the Welgelegen-savannas in the Para region is burnt too; their origin is probably anthropogenic. However, in view of the present structure of their soil it does not seen impossible that some of them would maintain themselves for a long time if the fires were stopped.

It is likely that the savannas which are open to-day only as a result of repeated burning, owe their *origin* to the action of man too.

It is much more difficult to say something sound concerning the origin of the present edaphic savannas. A single attempt will be made. It may perhaps be assumed that savannas on wet white sand (Zanderij-type) developed out of those on dry white sand (Kasipora-type) as a result of sheet-erosion.

The more open Kasipora-savannas in turn might have originated from the burning of savanna woods and scrubs, as assumed by LANJOUW (1936). The latter assumption links up with an idea of SCHULZ (1960, p. 126 and 143) according to which the white sands might have developed by leaching after the indians had destroyed the forests on the not-leached soils.

With regard to the foregoing problems it is of importance to know how old the different savannas may be. As far as the present flora may provide information, the following may be remarked.

The relative age of savannas with regard to one another might possibly be estimated by comparing their number of species. Of course only vegetations belonging to the same type and subject to the same conditions may be compared. More species in a vegetation might indicate a longer existence of the vegetation at that locality. However, such a comparison is very difficult, particularly if isolated savannas are considered. Not only time, but other factors of accessibility too play a role and may disturb the picture completely. Another difficulty is that in the literature concerning savannas outside Surinam complete lists of species occurring in any concrete vegetation found in a definite locality, or even in a vegetation type are almost completely absent. Therefore one has to be content with the impression that in general the vegetations of the northern Surinam savannas, also those of the apparently anthropogenic ones, are not at all poor in species if compared with similar vegetations in other parts of tropical America. However, it appears that the campos cerrados in E. Brazil, at least those of Lagoa Santa described by WARMING (1892), are much richer in species than the orchard savannas of northern Surinam (see V. 8.1.2). So in general the northern Surinam savannas have not to be considered on these grounds as relatively young. This is also indicated by the presence of some endemic and other remarkable species in this respect, found also on apparently anthropogenic savannas (see IV.5.2).

However, these undifferentiated statements contribute next to nothing to the solution of the problems under consideration. See further Chapter VIII.

Finally it has to be seen whether in northern Surinam too the savannas formerly may have had a larger extension, and whether there are indications that certain savannas may be remnants of originally larger complexes. With regard to the former question: VAN DER HAMMEN (1961, and verbal information) showed on the ground of palynological investigations that the savannas in northern British Guiana occupied extensive areas during the Würm glacial period. Before and after that period mangrove-vegetations were prevailing, but since 1200 B.C. the savannas are extending again. This alternation is correlated with marine trans- and regressions that took place in Surinam in the same way. It is possible that the decrease in extent of the savannas, set in after the glacial age, was mainly due to gradual flooding of savanna areas in the low lying coastal zone. Undoubtedly the rising of the sea-level also influenced the habitat of the savannas (if present already) of the more elevated Zanderij formation, but it is hard to say whether this meant an extension or a reduction of their total area. Mutatis mutandis the same holds for the extension of the savannas after 1200 B.C. And which was the part of the climate and which that of men? Further contemplation of these matters is not justified because too much is uncertain. However, the possibility that some of the savanna areas or types in northern Surinam, also among the apparently anthropogenic ones, may have existed already during the Würm glacial age, can not be excluded.

CHAPTER VIII

GENERAL DISCUSSION AND FINAL CONCLUSIONS

DANSEREAU (1951, p. 174): "The flora of a locality or a region is the residue of all the plant species which in the course of geological time, have occupied that territory and have successfully withstood the subsequent climatic and other vicissitudes or have taken refuge elsewhere and more or less recently reinvaded." "On the other hand, the vegetation consists of a definite quantitative representation of the species available in the local flora." "A knowledge of the *flora* will allow a classification of its species into floristic elements of common origin; a knowledge of the *vegetation* will permit an entirely different classification based on ecological requirements and usual rôle of the plant individuals in the landscape. *The former are historical indicators, the latter ecological indicators.*"

From this point of view the treatment of the savanna flora in Chapter IV and of the vegetation in Chapters V and VI may be regarded. However, if one wants to obtain an all-over picture of the plant-life of a region or a type of landscape, one should not disregard that the species composing the flora have ecological requirements of their own, and that a vegetation type has a distribution and a history just as well. Nevertheless this quotation of DANSEREAU is a good background for an attempt to present a synthesis of all available data concerning some of the northern Surinam savannas. The origin of the flora will have a central position in this discussion.

The savannas of northern Surinam are situated partly close to the northern edge on the exposed part of the Guiana shield, partly on relatively young sediments north of this edge.

During the Mesozoic, before the deposition of the sediments north of it, the shield was partly covered by a thick, level layer of sandstone, the Roraima formation. At that time the Angiosperms did not yet exist or they were in the prime of their development.

Next the shield started to rise. What happened with the flora during this process? A number of species may have survived the changing of the climate caused by the uplift itself and by other factors as well. New species may have developed. Other species may have become extinct, or may have descended to lower altitudes, on the shield or even outside the shield, meeting their ecological requirements. New species may also have immigrated, finding a suitable habitat under the changed conditions.

With regard to the Roraima plateau the situation is still more complicated. During the uplift the plateau was broken down and the weathered sandstone was gradually removed to the edges of the shield. At present the surface of the former plateau is represented only by the flat tops of a number of isolated table-mountains. These tops are covered with scrub and open savanna vegetation, composed of species partly identical or related with those of the pure white and (wet) loamy sand-savannas of northern Surinam.

The present properties of the tops, their flora and the knowledge with regard to the conditions under which natural savannas now exist, suggest that the former plateau may have been covered over large areas by savanna vegetation. Since a relatively high percentage of the savanna species of the table-mountains have areas of distribution reaching now far beyond the limits of Guiana or even of northern South America, it may be presumed that already in an early stage of the rising there were ample possibilities for savanna plants to migrate to and from the plateau. This exchange must have become more and more impeded as the break-down continued and the distance between the isolated parts increased. The different stages of this process are illustrated by the many species endemic to greater and smaller groups of table-mountains or even to a single one.

One may imagine that during the break-down here and there, on a lower level than the original plateau, smaller sandstone flats originated and existed for some time. [1]) It also may have happened that the sand produced by the weathering accumulated here and there temporarily on parts of the shield formerly not overlain by Roraima sandstone. It is quite possible that in both cases savanna conditions developed locally. Moreover, savannas with similar soil properties may have existed on different parts of the basic shield as e.g. the savannas of the Saban-pasi-type do now.

All these supposed savannas may have functioned as an inconstant

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[1]) An example is known in Surinam: the Kappel savanna.

bridge or chain of stepping stones from the original Roraima plateau to the sands of the Zanderij formation. This bridge may have been used i.e. by those species that at present are found only on the table-mountains and on the savannas of the Zanderij formation and other ecologically comparable white-sandy sites on and around the Guiana shield (e.g. most characteristic species of the *Syngonantho—Xyridion*; *Schizaea incurvata*, *Axonopus attenuatus*).

Other roads for migration may have been formed by the rivers that at that time, more than at present, may have had sandy banks suitable for savanna plants.

Nevertheless it is possible that such bridges did never exist or existed only before the Zanderij formation was definitely exposed as dry land, or only outside of Surinam. In that case the species may have reached the Zanderij sands indirectly from other regions, e.g. by the way of northern British Guiana.

The species that are endemic on one or several of the table-mountains either may have developed after the contact with the younger sediments was broken up and/or they require the special climate of the high tops. The species restricted to the younger sandy savanna areas of northern South America i.e. not known from the table-mountains (e.g. *Bulbostylis fasciculata*, *Lagenocarpus weigeltii* and *Xyris surinamensis*) either may not yet have been found there or may have originated on the shield but become extinct there as a result of the changed conditions or they have developed later outside the shield whether or not from original "shield species".

Altogether it appears that the savannas of the Zanderij- and the Kasipora-type, in particular the vegetation types of the *Syngonantho—Xyridion*, derived the greater part of their species directly or indirectly from the Roraima plateau. There are many uncertainties with regard to the migration routes, but the success of the species after their arrival on the Zanderij sands must be ascribed to the ecological similarity of their original site with the one largely present or developing here.

It has to be remarked that this theory partly is in agreement with the ideas of FANSHAWE (1952) concerning the division of the flora of British Guiana (see IV.5.4). However, FANSHAWE takes the line that the whole of the interior of B.G. was covered by the Roraima formation. Therefore he regards the so-called Pakaraima flora as the original one and the ancestor of the Upland flora of the uncovered basement rock by which it was followed. Next the Lowland flora of the White Sand Series was directly derived from the Upland flora. FANSHAWE stresses also the ecological relationship between the habitat of the first and the last flora, whereas the second occupies rather different sites.

On the other hand the theory is in contradiction with the concepts of DUCKE & BLACK (1953) on this subject. In the lower Amazon basin here and there white-sandy savannas are found, called "campinas". at least by these authors. All available data point to a close relation between their flora and that of the white sands in N. Surinam and of the tops of the table-mountains as well. The authors consider this flora as a "genuine, although highly specialized, part of the hylaea flora, closely allied to the catinga of the Rio Negro basin". The hylaea comprises, according to their circumscription, also the Guianas, with exclusion, however, of "the arenitic plateaus and table-mountains".

The vegetation types of the Saban-pasi-type, in particular of the *Bulbostylidion lanatae*, have a composition resembling that of the *Syngonantho—Xyridion* communities. The theory expounded above may be helpful in the interpretation of this fact. In the first place there may have been from the beginning a certain similarity between the savanna flora on and that outside the sandstone cover. The wet loamy sands of the subgraywacke landscape present savanna sites that are ecologically related to the tops of the table-mountains. On the other hand, if at the time of the undisturbed plateau no links existed between the presumed Roraima savannas and those on the subgraywacke, the connection may have come into being during the break-down of the plateau. It is possible that many species, on their way down, settled here, finding suitable conditions. It is very well possible too, that in that case many species connecting the *Syngonantho—Xyridion* and the *Bulbostylidion lanatae* now (e.g. *Panicum micranthum*, *Rhynchospora graminea*, *Sauvagesia sprengelii*), have spread directly from the Saban-pasi savannas over the savannas of the Zanderij formation, in particular as the sediments of this formation formerly may have reached farther into the interior (see III.4). The few species of this group that do not occur on the table-mountains either may be original species of the shield-outside-the-cover, or may have developed later on the shield or on the Zanderij sand, whether or not from Roraima species (e.g. *Bulbostylis circinata* and *Scleria pyramidalis*). Quite another possibility is immigration (*Paspalum pulchellum* ?).

The species of the Saban-pasi savannas that do not occur on the table-mountains and not on the white Zanderij sands may have developed on the shield (*Rhynchospora rhizomatosa*) or immigrated from elsewhere (*Mesosetum tenuifolium* and *Prestonia perplexa* ?).

The savannas N. of the Wane-creek, belonging to the old coastal plain, are probably younger than the preceding types, and the available data suggest that their flora is a selection from the floras of the latter. The vegetation of the Watamalejo savannas on the bleached sands of the old offshore bars may be included in the *Syngonantho—Xyridion*, but some of the most common and characteristic species of this alliance were not found, e.g. *Rhynchospora tenuis*, *Paspalum polychaetum*, *Paepalanthus polytrichoides* and *Xyris surinamensis*. Similarly the wet Welgelegen savannas, as far as they have sandy topsoils, are covered by vegetations of the *Bulbostylidion lanatae*, but without such species as *Bulbostylis spadicea*, *Rhynchospora rhizomatosa* and *Mesosetum tenuifolium*. Other common species occurring in both alliances and whether or not in other vegetation types too, but lacking here, are *Bulbostylis circinata*, *Rhynchospora graminea*, *Leptocoryphium lanatum*, *Axonopus pulcher*, *Trachypogon plumosus* and *Tibouchina aspera* (LANJOUW & LINDEMAN, unpubl.).

It may be assumed that the savannas and vegetation types not yet mentioned owe their existence to anthropogenic influences, and that they are in general younger than the preceding ones. If this is true they must have derived a part of their species from the already existing types, whereas another part may have immigrated from elsewhere.

The wet and very wet sites of the probably anthropogenic savannas have relatively few species in common with similar sites on natural savannas. This emerges if one compares the *Syngonantho—Xyridion* and the *Bulbostylidion lanatae* with the *Imperato—Mesosetion* and the *Axonopodion chrysitis*. Most characteristic species of the *Paspaletalia pulchelli* are more or less restricted to the first two alliances. Most species connecting all four alliances or only the last three are common savanna species with a wide ecological range and a relatively wide distribution. Another number of species common to the last three or two alliances (e.g. *Panicum stenodoïdes*, *Hypolytrum pulchrum* and *Rhynchospora globosa*) or restricted to the last one only, also have relatively wide areas. So it appears that the texture of the soil and probably also differences in the water economy impede the penetration of many species from the savannas of the Zanderij- and the Saban-pasi-type into the anthropogenic wet and very wet savanna sites on the Coesewijne- and the Welgelegen-type. Their place is taken by other species of wet soils with generally a wider distribution and, as a whole, a smaller percentage of the Roraima element.

Though the *Mauritio—Hypogynion* has a small group of characteristic species of its own, the flora of the savanna rivulets is essentially a mixture of savanna species and swamp species.

The orchard-savanna vegetations belonging to the *Curatello—Trachypogonion* and occurring on dry and moist, red, pure and loamy sands of the Coesewijne- and the dry variety of the Welgelegen-type, have a strikingly high percentage of their species in common with the campos cerrados of central and eastern Brazil. Only a small percentage of these species belongs to the Roraima element. These campos are far richer in species than the orchard savannas of N. Surinam and probably older too. Therefore it seems possible that many of these species came to Surinam from the Brazilian campos. However, it is hard to imagine how they could traverse the Amazon river and the extensive forest areas to the north and south of it. This brings to the fore again the probability that the present wide distribution of many American savanna species can be interpreted only in terms of formerly much more extensive savannas. The author does not feel competent at present to deal with this highly complex problem.

Very little may be said of the flora of the dry *Rhynchosporo—Trachypogonion* and its origin. It is striking that this alliance, like the other alliances on the heavier soil types (*Imperato-Mesosetion* and *Axonopodion chrysitis*), seems to be related only to vegetation types occurring in the western part of Guiana and far more to the west. However, the chorologic spectra of the different associations do not reflect this phenomenon.

A final question may be put forward: what is the natural habitat of the species characteristic for dry savanna vegetations (order *Trachypogonetalia*)? Probably some of the associations on dry white sand, viz. those on the open patches between the muri bushes, are natural. However, many species occur only on other dry soil types, in vegetation types that in N. Surinam owe their present existence to human influences, e.g. all characteristic species of the *Curatello-Trachypogonion.* In view of the concept that at present natural savanna vegetations depend on the alternation of desiccation and saturation with water of the topsoil, there is no place for natural dry savannas.

Is it possible that the dry savanna species developed after the human influence had started, or that they developed longer ago on savannas that were subject to natural fires? Or are they at home in drier existing vegetation types like the catinga of N.E. Brazil? A cognate question is what the exact ecological conditions in the heart of the Brazilian campos are. The available literature does not give sufficient and clear information on these points.

SUMMARY

Geology and soils in general

Surinam is situated at the northern edge of the very old and stable Guiana shield. Six-sevenths of the country's surface are occupied by formations belonging to the shield and designated together as the *basal complex.* However, the *Roraima formation* does not belong to the complex. It was deposited during the Mesozoic (probably the Cretaceous) as a thick layer mainly consisting of sandstone that covered the greater part of the shield. Later on the original sandstone plateau was dissected, a process accelerated by the uplifting of the shield, and finally it disappeared almost completely by erosion. The former surface is now only represented by the flat tops of some table-mountains one of which is found in the interior of Surinam: Tafelberg. See SCHOLS & COHEN (1953).

The surface of the northern seventh part of the country is occupied by deposits of Quaternary age. In general may be distinguished (from the south to the north): 1) The *Zanderij formation,* consisting mainly of sands of continental origin; 2) the *Coropina formation,* comprising the "old coastal plain"; the main parts are (a) the so-called "schols", i.e. the remnants of an old sea-clay plain, separated by filled-up tidal gullies, and (b) the remnants of the offshore bars that formerly separated the plain from the sea; 3) the *Demerara formation,* comprising the "young coastal plain". See VAN DER EYK (1954, 1957).

Geological-pedological classification of the savannas

Savannas are found on the basal complex, the Roraima, the Zanderij and the Coropina formation. COHEN & VAN DER EYK (1953) classify them as follows:

I Savannas of the Coropina formation
  1. Watamalejo-type – on the offshore bars

2. Welgelegen-type – on the "schols"

II Savannas of the Zanderij formation
- a. Kasipora-type – on dry bleached sand soils
- b. Zanderij-type – on wet bleached sand soils
- c. Coesewijne-type – on non-bleached soils

III Savannas of the Roraima formation: *Tafelberg-type*

IV Savannas of the basal complex
1. Paroe-type – on granitic soils
2. Bosland-type – on schist hills
3. Saban-pasi-type – on subgraywacke hills

Savanna soils

The climate is characterized by the sequence of a long rainy season (April–July), a long dry season (August–November), a short rainy season (December–January) and a short dry season (February–March).

In connection with this periodicity the water-table in many places fluctuates strongly in the course of the year. During the dry seasons the upper layers of the savanna soils are always completely dry, except just after a shower. A soil is called very dry if even during the rainy seasons the upper layers are not influenced by the ground water. A very wet soil, however, at this period is covered by some cm of water; in addition it is characterized by many small hummocks, in Surinam called "kawfoetoes", which are built up by worms and in which these animals are able to keep their heads above the water. Certain soils occur that in spite of deep water-tables are wet, because an impermeable layer in the subsoil impedes drainage of the topsoil. Of course there is a scala between the extremes "very dry" and "very wet".

The texture of the upper layers ranges from bleached and slightly red sand to sandy and silty clay.

Object of the investigation

The flora and the vegetation of the northern Surinam savannas are the object of this investigation. These savannas do not only represent the types of the Zanderij- and the Coropina-formation, but also the Bosland- and the Saban-pasi-type, for these two types are present on the basal complex only near its northern border.

The *following savannas have been studied.* Welgelegen-type: the savannas of Bersaba and Vierkinderen, the Bigi-olo savanna near Hanover and the Fransina savanna near Welgelegen; Kasipora- and Zanderij-type: the white-sandy part of the Lobin savanna near Zanderij; Coesewijne-type: the loamy part of the Lobin savanna, the savanna Mimili Okili near Powaka, the Doti savanna near Wisawini and the Coesewijne savanna near Bigipoika; Saban-pasi-type: the Gros savanna and the De Jong Noord savanna.

Data of some other authors pertaining to these and the other types have also been taken into account, some published (LANJOUW, 1936; MAGUIRE c.s., 1948; HEYLIGERS, 1963), some unpublished.

The savannas present a marked diversity, among other things with regard to the structure of their vegetation. However, nearly all satisfy this *definition*: "A savanna (or a campo) is an area with a xeromorphic vegetation comprising an ecologically dominant ground layer consisting mainly of grasses, sometimes together with sedges, and with or without trees and/or shrubs either forming a more or less continuous layer, or in groups, or isolated."

The species have been studied with respect to the relation with the habitat, the means of dispersal and the area of distribution, all in mutual correlation. Vegetation-units have been distinguished and classified; ecological and chorologic aspects have been taken into account.

A combination of all data, obtained during this as well as former investigations by others, permits the drawing of a provisional and general picture of the flora and the vegetation of the northern Surinam savannas as far as the present aspects are concerned.

The following statements all apply to N. Surinam only, unless mentioned otherwise.

Flora

Habitat in general. Nearly all plants occurring on the savannas are heliophilous and are able to survive repeated burning.

The flora of the open vegetation types consists of about 270 species the majority of which (72 %) is restricted to the open savannas. However, there are species occurring either in other open situations too, partly as weeds (8 %), or on wet savannas and other wet places (3 %), or in savanna rivulets and in swamps (7 %), or in savanna bushes (8 %). Out of ca. 100 species of the savanna bushes only 15 % are restricted to this vegetation type. The other species occur either also in the open savanna (20 %), or along forest borders (8 %), or in savanna wood and forest (23 %) and/or even in rain forest (31 %). A group of 12 % belonging to the last category does not flower or even not grow high in the bushes. Quite apart from this division other groups may be distinguished among the species of the bushes in the following way: occurring also in secondary forest (31 %) in marsh forest (9 %), in swamps (3 %).

The trees and shrubs of the savannas support only few epiphytes and (half-) parasites; these belong to 19 different species.

In the field nearly all species show some (factual) *range with regard to the degree of moistness and the texture of the soil.* The texture itself is not necessarily the decisive factor as there is a relation between the texture and some other properties of the soil, e.g. the consistency and the mineral content. This has not been further investigated. The same holds for the species preferring slightly shaded localities. These spots have a microclimate that differs more from that of its surroundings than in light intensity only.

The majority of the open-savanna species have *diaspores* that are not obviously adapted to any agent of dispersal (71 %). The remaining 29 % are distributed over 6 different categories. The diaspores of the species of the bushes belong partly to the non-adapted forms too (35 %), but 50 % of them are fleshy.

Generally speaking, the savanna species have a wider *geographic distribution* than the spieces of the flora of Surinam as a whole. This is particularly true for the open-savanna species.

On the basis of similar areas of distribution the species are classed under 6 *geographic elements*, viz. the Guianan (G), the northern South-American (N), the northern + eastern South-American (NE), the Middle- and northern + eastern South-American (MNE), the South-American (S) and the American element (A). The distribution of the species of the open-savanna vegetations and of the bushes, respectively, among the geographic elements is as follows (percentages): G 12 : 26; N 11 : 18; NE 16 : 13; MNE 10 : 3; S 9 : 18; A 42 : 22. It appears from a comparison of these figures too, that the species of the first group in general have a wider distribution.

Apart from the geographic elements the *Roraima element* has been distinguished. It comprises all species collected on one or several of the table-mountains in the Guianan interior. The distribution of these species among the geographic elements does not differ considerably from the one of the savanna flora as a whole.

It may have appeared already from the foregoing that the species of the bushes, though presenting a higher percentage of adapted diaspores, nevertheless do not have areas of distribution wider than those of the open-savanna species. The expected correlation is, however, apparent if the two groups are considered separately: the mean area of distribution of the species with adapted diaspores is wider than the one of those with non-adapted diaspores.

A comparison of the ecological and the chorologic aspects brings to the fore two focal points within the savanna flora: The elements with a small distribution (G and N) are most numerously represented on wet to very wet sandy (in particular white-sandy) soils, whereas the elements with a wide distribution (MNE, S and A) are concentrated on dry and moist non-bleached sands and loams and on very wet soils and present a preference-top on dry and moist loamy sand.

The Roraima species are by far the most numerous on the wet white sand, in general they are more numerous on wet than on dry soils.

Vegetation

Vegetation-units have been distinguished and classified according to the *Braun-*

Blanquet school. It has been attempted to make the groups of so-called characteristic and differential species correspond with ecological groups in the sense of DUVIGNEAUD (1946, 1949). The latter consist of species with clear, sociological affinities between them because of similar habitat requirements.

The open-savanna (and orchard-savanna) vegetation-types have been united into a single class which is defined and divided as follows: Class *Leptocoryphio-Trachypogonetea.* Principal species: *Trachypogon plumosus, Leptocoryphium lanatum, Axonopus pulcher* and *Rhynchospora barbata.* It seems likely that this class and its subdivision up to and including the alliances may be applied to the whole of Guiana.

1. Order *Trachypogonetalia plumosi.* Principal species: *Trachypogon plumosus, Axonopus pulcher* and *Bulbostylis junciformis.* On very dry to moist soils.

1.1. Alliance *Cassio* (*ramosae*)-*Trachypogonion.* Principal species: *Trachypogon plumosus, Axonopus pulcher* and *Bulbostylis conifera.* On white sands. There are 3 or 4 associations two of which occur on open patches between so-called muri-bushes (see B1). Distribution: Kasipora-type; Guiana and adjoining parts of Brazil.

1.2. Alliance *Curatello-Trachypogonion.* Among the many tens of species the most common ones are *Trachypogon plumosus, Axonopus pulcher, Schizachyrium riedelii* and *Heliconia psittacorum.* Usually there is a thin layer of trees mainly consisting of *Curatella americana,* giving the vegetation the aspect of a type of so-called orchard savanna. A rather large part of the species occurs outside the savannas on other open spots too. The alliance occurs on pure reddish and on loamy sands. On the savannas of the Coesewijne- and the Welgelegen-type 5 associations are present. Similar vegetation types are found throughout Guiana, on the central Venezuelan llanos and far into E. Brazil.

1.3. Alliance *Rhynchosporo* (*barbatae*)-*Trachvpogonion.* Principal species: *Axonopus pulcher, Leptocoryphium lanatum, Mesosetum cayennense, Bulbostylis conifera* and *Rhynchospora barbata* var. *barbata.* On sandy (clay) loam. Two associations on savannas of the Coesewijne-type; they are related to vegetation types in French Guiana and in regions farther to the west, up to the Venezuelan llanos and some of the West Indian Islands.

2. Order *Paspaletalia pulchelli. Leptocoryphium lanatum* is the only species which is common in all communities of this order. In general the vegetations are not closed. On wet (or even very wet) soils.

2.1. Alliance *Syngonantho-Xyridion.* Principal species: *Paspalum pulchellum, Panicum micranthum, Rhynchospora barbata* var. *glabra, R. graminea, Xyris guianensis* and *Abolboda americana.* On white sands, wet and very wet. Three associations are found on the savannas of the Zanderij- and the Watamalejo-type. Distribution: Guiana and adjoining parts of Brazil, also on the table-mountains of the Guianan highlands.

2.2. Alliance *Bulbostylidion lanatae.* Principal species: *Trachvpogon plumosus, Paspalum pulchellum, Panicum micranthum, Mesosetum tenuifolium, Rhynchospora barbata* var. *barbata* and *R. rhizomatosa.* On loamy sand and sandy loam; wet. In northern Surinam 5 associations occur on savannas of the Saban-pasi- and the Watamalejo-type. Distribution: Guiana, probably also on the table-mountains.

2.3. Alliance *Imperato* (*brasiliensis*)-*Mesosetion* (*cayennensis*). Principal species: *Leptocoryphium lanatum, Mesosetum cayennense, Imperata brasiliensis, Rhynchospora barbata* var. *barbata* and *R. globosa.* On wet sandy loam and heavier soil types. Four associations on savannas of the Coesewijne-, Welgelegen- and Saban-pasi-type. Related vegetation types occur, as far as known, only in regions more to the west, up to the llanos and Guatemala.

3. Order *Panicetalia stenodis.* Principal species: *Leptocoryphium lanatum, Panicum nervosum, Hvpogynium virgatum, Heliconia psittacorum* and *Tibouchina aspera.* On very wet soils, in savanna rivulets and small depressions. There are 2 alliances, both showing relationship with vegetation types occurring in regions more to the west, up to the llanos and some West Indian Islands.

3.1. Alliance *Axonopodion chrysitis.* Principal species: *Leptocorvphium lanatum, Panicum nervosum, Rhynchospora globosa* and *Tibouchina aspera.* On very wet soils of sandy loam and heavier. In N. Surinam 3 associations are found on savannas of the same types as alliance 2.3.

3.2. Alliance *Mauritio-Hypogynion* (*virgati*). Principal species: *Hypogynium virgatum,* *Leptocoryphium lanatum, Panicum nervosum, Rhynchospora glauca, Heliconia psittacorum* and *Tibouchina aspera.* Typical are the tall palms of *Mauritia flexuosa.* The alliance has rather many species in common with the communities of swamps, e.g. *Blechnum indicum* and *Rhynchospora cyperoides.* There are 3 associations, found in rivulets and depressions on savannas of all types.

The different types of savanna-bushes are merely described. A classification or floristic grounds would be justified only if the savanna woods and forests were included in it too.

B1. *Ternstroemia-Matayba bushes.* See HEYLIGERS (1963). Principal species: *Ternstroemia punctata, Clusia fockeana, Licania incana, Humiria balsamifera* var. *guianensis* ("muri"), *Pagamea capitata, Matayba opaca* and *Conomorpha magnoliifolia.* On dry white sand.

B2. *Rapanea bushes.* Principal species: *Rapanea guianensis, Davilla aspera, Tapirira guianensis, Symplocos guianensis, Miconia rubiginosa, Byrsonima crassifolia, B. coccolobifolia* and *Curatella americana.* On dry loamy sand and dry sandy loam.

B3. *Cupania bushes.* Principal species: *Cupania scrobiculata* var. *frondosa, Davilla aspera, Byrsonima crassifolia, Miconia ciliata, Maprounea guianensis, Protium heptaphyllum, Symplocos guianensis* and *Curatella americana.* On moist loamy sand and moist sandy loam.

B4. *Clusia-Scleria bushes.* See HEYLIGERS (1963). Principal species: *Clusia fockeana, Licania incana, Bactris campestris* and *Scleria pyramidalis.* On wet white sand.

B5. *Marlierea bushes.* Principal species: *Marlierea montana, Bactris campestris* and *Licania incana.* On wet loamy sand.

B6. *Roupala-Antonia bushes.* Principal species: *Roupala montana, Antonia ovata, Davilla aspera, Miconia ciliata, Bactris campestris, Licania incana, Humiria balsamifera* div. var., *Pagamea guianensis* and *Marlierea montana.* On knolls of pebbles embedded in sandy loam; wet.

Existence, origin and maintenance of the savannas

There is no type of climate that accounts for a savanna vegetation irrespective of other conditions. However, a climate that permits the existence of savanna vegetations may be called a "*savanna climate*". The latter is characterized by a certain difference between the precipitation in dry and wet seasons, independent of absolute values.

The climate of northern Surinam is a savanna climate in this sense.

A savanna vegetation is *natural*, i.e. *determined edaphically*, if the upper layer of the soil is alternately desiccated and saturated with water, thus in general in wet and very wet localities and in rivulets. As far as known the following savanna types and vegetation types are involved in this situation (the rivulets left out of consideration): Watamalejo (2.1) Welgelegen, partly (2.2), Zanderij (2.1 and B4), Saban-pasi (2.1 and B5, 2.2. and B6) and Bosland (?).

A savanna vegetation occurs in dry localities only if *fires* prevent the formation of a closed layer of trees or shrubs. This is found among the following types: Welgelegen, partly (1.2 and 1.3), Coesewijne (1.2 and B2, 1.3 and B3) and Kasipora (1.1 and B1).

Parts of the savannas of the Welgelegen-, Coesewijne- and Saban-pasi-type occupied now by vegetations of the *Imperato-Mesosetion* (2.3) and the *Axonopodion chrysitis* (3.1) would probably be overgrown very slowly by the surrounding forest and only starting from its edges if the fires were stopped.

It might be easily assumed that savannas owing their maintenance at present only to deliberate burning, originated from forests as a result of human interference as well. However, the possibility may not be excluded that they came into existence very long ago, either caused by natural fires or in consequence of a water economy of the soil differing from the present one.

Final conclusions

All available data concerning the flora and the vegetation of the northern Surinam savannas justify the following theories:

The wet white-sand savannas of the Zanderij-type have vegetation types (2.1) consisting of species that mainly stem from formerly or still existing savannas on the basal complex and on the Roraima formation, probably chiefly on the latter. These species may have reached the Zanderij formation either directly by means of series of savannas in the interior that still may have been present during the break-down of the Roraima plateau, or indirectly by the way of other sandy regions bordering the edges of the Guiana shield.

The vegetations of the savannas belonging to the Saban-pasi-type on wet loamy sand and sandy loam (2.2) consist of species which already for a long time were common to the basal complex and the Roraima plateau or/and which originated from the plateau, and besides of species that developed on the basal complex or migrated from elsewhere to the subgraywacke-area.

The savannas of the Watamalejo-type and of the Welgelegen-type N. of the Wane-creek have a flora that may be regarded as a selection from that of the two preceding types.

The vegetation types on dry and moist, red, pure and loamy sands belonging to the Coesewijne- and the Welgelegen-type (1.2) have a high percentage of their species in common with the campos of central and eastern Brazil. It seems possible that these species came to N. Surinam from the campos.

The species combination of the savanna vegetations from other habitats does not permit a conclusion with regard to their possible origin.

APPENDAGES

1. ADDITIONS TO TABLES 6*, 7*, 8* AND 10*

Every species occurred in the association indicated in the first column in one record only, except where the number of times is added.

Table 6:

1.1.1.a.a.	*Pouteria trigonosperma*	+
	Pagamea guianensis	+
1.1.1.a.c.	*Borreria capitata*	+
1.1.2.a.	See HEYLIGERS	
1.2.1.	*Gonolobus ligustrinus*	+
	Clitoria guianensis	1
	Cassia glandulifera	2
	Siparuna guianensis	+
1.2.2.a.	*Phyllanthus orbiculatus*	+
	Pterolepis trichotoma	2
	Tapirira guianensis	+
1.2.3.	*Borreria capitata*	+
	Miconia albicans	+
	Astrocaryum segregatum	1
1.2.4.	*Lisianthus uliginosus*	+
	Miconia ciliata	+
	Protium heptaphyllum	+
1.3.1.c.	*Hyptis lantanifolia*	+
	Triphora surinamensis	+
1.3.2.a.	*Himatanthus articulatus* (juv.)	+
	Dioclea guianensis	+

Table 7:

2.1.1.a.	*Utricularia* spec.	+ (2 ×)
	Mauritia flexuosa (juv.)	+
2.1.2.a.	*Utricularia* spec.	+ (2 ×)
2.1.3.a.	*Utricularia* spec.	+ (2 ×)
2.2.1.	*Catasetum* spec.	+

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* Tables 6, 7, 8 and 10 have been enclosed separately at the back of this issue.

	Drosera cayennensis	+	
2.2.3.a.	*Catasetum* spec. nr. 721	+	
2.2.4.b.	*Catasetum* spec. = nr. 721	+	
	Licania incana	+	
	Clusia fockeana (juv.)	+	
2.3.1.	*Catasetum* spec. = nr. 721	+	
	Bulbostylis vestita	+	
2.3.2.	*Paspalum carinatum*	+	
	Bulbostylis surinamensis	+	
	Habenaria spec. nr. 591	+	
	Cassia tetraphylla var. *brevipes* (seedling)	+	(2 ×)
2.3.3.	*Eugenia punicifolia*	+	
2.3.4.	*Elephantopus angustifolius*	+	
	Dipteracanthus angustifolius	+	(2 ×)
	Triphora surinamensis	+	
	Habenaria spec. nr. 663	+	(2 ×)

Table **8**:

3.1.1.	*Bulbolstylis junciformis*	+	
	Cassia cultrifolia	+	
	Phaseolus peduncularis var. *clitorioides*	+	
	Phaseolus longipedunculatus	+	
	Elephantopus angustifolius	+	(2 ×)
	Eriosema violaceum	+	
	Curatella americana (juv.)	+	
	Coccoloba latifolia	+	
	Stenorrhynchus spec. nr. 229	+	
3.1.2.	*Platonia insignis* (juv.)	+	
3.1.3.	*Symplocos guianensis*	+	(2 ×)
	Thrasya petrosa	+	
	Schizachyrium riedelii	+	
	Bulbostylis junciformis	+	
	Ravenala guianensis	+	
	Geissopappus caleoides	+	
	Aeschynomene hystrix (juv.)	+	
	Mitracarpus discolor (seedling)	1	
	Mesosetum loliiforme	1	
	Lyroglossa euglossa	+	
3.2.1.	*Zornia tenuifolia*	+	
	Panicum errabundum	+	
	Bulbostylis surinamensis	+	
	Utricularia spec.	+	
3.2.2.	*Cleistes* spec. nr. 720	+	
	Hepaticae spec.	1	

Table **10**:

Every species occurred in one record of the type of bushes; in the first column the species group and additional habitat are indicated.

Rapanea bushes

2 d	*Hirtella paniculata*
2 g	*Eugenia compta*
3 b	*Hebepetalum humiriifolium*
1 a	*Ichthyothere terminalis*
	Bulbostylis capillaris var. *tenuifolia*

Cupania bushes

1/2b	*Centrosema brasilianum*
2 c K	*Humiria balsamifera* var. *balsamifera* fo. *acuminata*

3	*Licania divaricata*
3 b	*Vochysia densiflora*
	Guatteria schomburgkiana
3 c	*Vismia angusta*
K	*Simarouba amara*
	Miconia tomentosa
KS	*Myrcia fallax*
K	*Goupia glabra*
1 a	*Desmodium barbatum*
	Coutoubea spicata
	Hyptis atrorubens
	Adiantum serrato-dentatum
	Bulbostylis junciformis
	Galactia jussieuana
	Panicum rudgei

Clusia – Scleria bushes

2 d	*Bombax flaviflorum*
1 a	*Syngonanthus umbellatus*

Marlierea bushes

1 a	*Mesosetum loliiforme*
	Aristida tincta
	Polygala adenophora
	Panicum micranthum
	Mesosetum tenuifolium

Roupala – Antonia bushes

2 b	*Gonolobus ligustrinus*
2 e	*Miconia kappleri*
1 a	*Sporobolus cubensis*
	Axonopus purpusii (narrow leaves)
	Echinolaena inflexa
3	*Platonia insignis*

2. EXPLANATION TO TABLES 6*, 7*, 8*, AND 10*

Tables **6**, **7**, **8**, *and* **10**:

Ch = characteristic species
D = differential species
Geographic element – see IV.5.3
(Range with regard to) moistness of the soil: see II.3.2; ( ) few data available
(Range with regard to) texture of the soil: see II.3.2; ( ) few data available
Association etc. – see V.8 and VI
× = species present, quantity etc. unknown
(×) = species present in the vegetation-unit, but not found in the area under consideration.

Table **10**

Additional habitat – see IV.2
Habit: h = herb, cl = climbing, (cl) = climbing, but in bushes eventually as shrub, t = present eventually as tree
bold type – species eventually dominant

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* Tables 6, 7, 8 and 10 have been enclosed separately at the back of this issue.

3. Legend to the Annotated List of Species*

Column 1a Geographic element – see IV.5.3
1b Area of distribution – see IV.5.2
2 Roraima element (see IV.5.4):
  A Auyán-tepuí R Mount Roraima
  D Cerro Duida S Serro Sipapo
  K Kaieteur plateau T Tafelberg
  P Ptari-tepuí Y Cerro Yaví
3 Habitat in general – see IV.2
4 Range with regard to texture of the soil – see II.3.1; ( ) few data available
5 Range with regard to moistness of the soil – see II.3.2; ( ) few data available
6 Shadow-loving species (×)
7 Synsystematic position – see V.8 and VI: Cl = class, Ch = characteristic species, D = differential species
8 Dispersal type – see IV.4
9 Particularities

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