STRUCTURE, ROOT SYSTEMS AND PERIODICITY OF SAVANNA PLANTS AND VEGETATIONS IN NORTHERN SURINAM

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CHAPTER I

INTRODUCTION

I. 1. PREMISES

Every species has ecological requirements which determine its possible habitats. A habitat with a particular set of properties will therefore accommodate a limited number of plant species, which together form the vegetation of that habitat. A unit of vegetation defined on the basis of species composition is therefore correlated with a very definite environment.

Starting from these premises, Braun-Blanquet has produced a system of classification of vegetation types based on similarities in floristic composition.

During several decennia many workers in Europe have described and classified vegetation according to the method of BRAUN-BLANQUET (1946). It has been shown that his premises are correct. Classification based on similarities in floristic composition reflects natural relationships; and correlations between the units and the environment are always evident. The basic unit, the association, has proved to be a useful and homogeneous unit.

A system based on floristic composition is by its nature limited to one floristic region.

Another limitation is that one can only point out the correlation between a habitat and a vegetation type, without increasing the insight into causal or functional relationships.

A vegetation unit, distinguished by floristic composition in general, also presents a definite physiognomy. This is true for subassociations, if not also for associations. Physiognomy, which includes structure, should never become involved in the classification, if one wishes to preserve the premises of the floristic system.

Physiognomic descriptions of species and vegetation types have been made since the distant past: one needs only remind oneself of the names of Grisebach, Drude, Warming, Schimper, Raunkiaer and Rübel. DU RIETZ (1931) gives an as yet unparalleled synopsis of this aspect of botany. The interested reader is referred to this review.

Many physiognomic characteristics occur in species that are totally unrelated taxonomically, and appear to be correlated with certain environmental factors. But this correlation is not unequivocal. On the one hand, plants have more than one response to a certain condition of the environment; on the other hand, a particular physiognomic feature may be correlated with more than one environmental factor. As CAIN (1950) says: "Since there is no life-form exclusiveness, since the harmony between structure and environment is not complete, the problem is a complex one."

In many cases an explanation of cause or function is apparent. However, the establishment of correlation does not prove a cause or function relationship. This proof must come from experimentation. Cain expresses this as follows: "Whether any causality is involved may be left to more refined studies, and to the weight of gradually accumulated circumstantial evidence from numerous similar studies."

From the foregoing it is clear that it is possible to compare vegetation units with those of other floristic regions, and to increase our understanding of vegetation-environment relationships, through the objective description of physiognomic attributes of floristic associations, and their correlation with the environment.

The present study is designed to extend the knowledge of relationships between some vegetational units of savannas and their environment, through a quantitative description of aspects other than floristic composition, and through the establishment of environmental correlations.

I. 2. THE CHARACTERISTICS UNDER CONSIDERATION

The physiognomy of vegetation is determined by the physiognomy of the constituent species. By describing the latter, with an indication of their share in the vegetation one describes the physiognomy of the vegetation. Only the arrangement in space, the vegetation structure, requires separate description.

In view of the complexity of habitat—physiognomy relationships, it is preferable to describe the various physiognomic features separately, and to correlate them individually with environmental factors.

In distinguishing life forms, and in adopting a system of life forms based on a combination of these features, it is inevitable that subjective judgements be made as to the relative importance of the physiognomic features. Moreover studies of increasing refinement will necessitate the recognition of new life form categories.

With the help of spectra of various characteristics of the component species, vegetation units may be characterized so that the comparisons with respect to these characteristics may be made with other vegetation units (Ch. I. 3).

DANSEREAU (1958, 1959) devised a system of recording vegetation structure and physiognomy. For purposes of the present study of correlations at the association level, his system has proved to be insufficiently detailed. But because of its visual representation it should be very useful in tracing structural and physiognomic affinities of floristically unrelated vegetation types, provided that one agrees with the choice of criteria incorporated in this system.

The criteria which together constitute physiognomy may be summed up in categories (cf. "life forms" sensu DU RIETZ, 1931).

Structure

Plants have long been classified according to habit as trees, shrubs, half shrubs and herbs (main life forms in Du Rietz). In due course, these forms were recognized to be associated with certain environmental conditions, so that now a vegetation description in these terms has some significance.

Nevertheless, important structural characteristics are left out of consideration in these categories, especially the "shoot architecture". Du Rietz treats the various possible shoot types as "growth forms". He combines different properties of the shoots, whereas in the present study it is necessary to consider these properties separately.

In this study the following are distinguished:

Posture of the shoots.

Degree of lignification of the stems.

Relation between shoots of one plant: single or multiple shoots, tussock forming or loose.

Level of ramification: simple, basally of distally ramified.

Position of leaves: scattered, basal, rosette, terminal.

Vegetation structure cannot be described by structural forms of the component species alone. A vegetation unit has its own characteristic spatial arrangement.

The vertical structural component is designated as a layer (stratum).

The horizontal structural component is described in terms of coverage and continuity of the layers.

Structural criteria are treated in Chapter IV.

Periodicity of vegetative parts

Du Rietz describes this concept with reference to species, as follows: "The differences between their physiognomy in the different seasons, and the seasonal distribution of their vegetation- and resting periods". In Chapter V these two facets of periodicity will be treated as seasonal aspects and seasonal rhythm, respectively.

Leaf characteristics

Leaf characteristics have long been included in all physiognomic descriptions of species as well as vegetation types. Consequently much is known about these features and their correlation with environment. The following are considered in this study:

Size (Ch. VI. 1); scleromorphy (Ch. VI. 2); indument (Ch. VI. 7); movements (Ch. VI. 8). A separate discussion of leaf shape appears to be superfluous. In Chapter VIII leaf shape is mentioned for every species, while under movements it is mentioned incidentally.

Protection of primordia

Through the work of Raunkiaer, the location of rejuvenation buds in relation to soil level has received much attention. Raunkiaer and many other authors were able to find good correlations between bud position and climate (Cain, 1950). The life forms of Raunkiaer are described in Chapter VI. 5.

Besides position of the rejuvenation buds, their covering and protection also merit attention (Ch. VI. 6).

Physiognomy of savanna species and vegetation units can be described satisfactorily using these categories of criteria. But correlation of characteristics with the environments is impossible without a consideration of root systems.

Root systems

Du Rietz (1931) notes the desirability of recognizing root life forms. Lacking adequate knowledge of root systems, he was unable to carry this out. Yet extensive publications by Cannon (1911), Shantz (1911) and Weaver (1920, 1925) were already available. Meanwhile the knowledge of root systems and soil—root relationships has been extended. A review of the literature is provided in Chapter III. 1.

The root systems of savanna plants are described according to total root morphology and distribution of roots within the soil. If the structure of the aerial part of the vegetation cannot be adequately described in terms of the structure of the constituent species alone, the same is true for its root system.

In the soil, layers can be distinguished with different densities of roots. The most important and most densily occupied layer is usually —and this is true for savanna vegetation—the upper soil layer, the sod layer. By describing the root distribution of each species in relation to this sod layer, it is possible to describe the root structure of a particular vegetation as a spectrum. Where a litter layer covers the mineral soil, root behavior in relation to such areas is described.

Hydrotypes

IVERSEN (1936) devised a system of hydrotypes, designed to express the adaptation of species to the water factor. He combines various criteria in the hydrotypes, all of which are related to water.

Using spectra of hydrotypes, he manages to characterize vegetation units. This provided a motive for the inclusion of hydrotypes in the present investigation (Ch. VI. 4).

Reproductive aspects, such as periodicity in flowering and fruiting, means of dispersal of the diaspores and properties of the seedlings, have been left out of consideration.

I. 3. UTILIZATION OF THE DATA

On the basis of the field data, spectra are established for the various groups of characteristics in each vegetation type. Using these spectra, one can compare the vegetation types with one another and in relation to the habitat.

A spectrum gives quantitative information as to the frequency of each category within a class of characteristics. But the question is which quantity should be considered. In any case the starting point is the species, the carrier of the characteristics.

RAUNKIAER (1916) uses the number of species in each category for the calculation of life-form spectra of a flora. For a spectrum of a vegetation type the numbers of species alone are not satisfactory, since a rare species would carry as much weight as a dominant one.

For vegetation spectra, Raunkiaer uses the number of shoots per unit area. This method is cumbersome, and has the disadvantage that shoots of different species are not equivalent.

The coverage of one species, expressed as a percentage of the total coverage of the stand, is a measure, however imperfect, of the share of the species in the stand. The mean degree of coverage of the species, expressed as a percentage of the mean total coverage of the vegetation type, indicates the share of the species in the vegetation type.

Coverage has the disadvantage of disregarding the number of individuals. One specimen with extensive coverage would carry more weight than very many individuals with slight coverage. BRAUN-BLANQUET (1951) proposes a combined estimate scale of coverage and abundance. His scale proves to be satisfactory for the description of sample plots. It is as follows:

+ sparsely present, coverage very slight
1 numerous but of slight coverage or rather sparce but with coverage up to 5 %
2 very numerous, or coverage 5–25 %
3 any number, coverage 25–50 %
4 any number, coverage 50–75 %
5 any number, coverage 75–100 %.

The numbers of this scale have no numerical value but are to be considered as symbols at most of associative significance. Even if they indicated only coverage, they would still not reflect the ratio between the various categories. Therefore it is not permissible to use them for mathematical computations. If Braun-Blanquet had used letters instead of numbers, no one would have conceived of using them mathematically.

For this reason, the method of SCHWICKERATH (1931) is incorrect because he expresses the importance of a species or group of species by using these numerical symbols as if they were mathematical numbers.

TÜXEN & ELLENBERG (1937) rightly convert the combined estimate scale to average cover percentages, and use these for further mathematical computation:

+ = 0.1 %	3 = 37.5 %
1 = 2.5 %	4 = 62.5 %
2 = 15 %	5 = 87.5 %

Cover percentages for 1 and 2 are higher than is theoretically correct, to allow for abundance. Opinions vary as to the right values for the symbols +, 1 and 2. For the sake of comparability the values of Tüxen & Ellenberg will be adopted in this study.

Spectra based on the combined estimate have the disadvantage that species of low coverage hardly count whereas their very presence may be of great indicator value from an ecological standpoint.

Besides the spectra compiled according to Tüxen & Ellenberg, we cannot do without those based on numbers of species. In the account of vegetation units both types of spectra will be given and used in comparisons.

The spectrum based on the combined estimate according to Tüxen & Ellenberg is computed as follows: of each species, the mean coverage is calculated by adding up all cover percentages (converted from the combined estimate data recorded from the sample plots) and dividing by the total number of sample plots. The sum of the mean coverages of all species of the vegetation unit represents the total mean coverage of this vegetation type. The sum of mean coverage figures of all species having a certain characteristic can be expressed as a percentage of the total mean coverage. From these percentages the spectrum is compiled. These percentages yields information about the relative importance of the species group with a particular characteristic in the vegetation type, but not about the coverage of this group.

Total mean coverage is not the same as the mean total coverage, the latter being the mean of field estimates of total coverage of sample plots. Mean total coverage is of course, never more than 100%, while total mean coverage may exceed 100% when several species overlap.

If more precise coverage data are available these would be preferable to deductions from the combined estimate. Abundant species of low coverage would have to be accounted for in a manner similar to the Tüxen & Ellenberg method.

Finally another disadvantage of percentages should be noted in vegetation of low total mean coverage, a slight shift in species coverage results in a very different percentage. This is all the more serious because values of mean coverage are based on rough estimates, and therefore inaccurate. Possible mistakes are magnified in this case. This source of error was inevitable in view of the original data. In Chapter IV. 3.1 the sum of the mean coverages of all species of a vegetation type are indicated, so that the reader can judge the value of the percentages.

In multi-stratal vegetation the environment varies with the layers. In order to compare corresponding layers, the sum of mean coverages of a category of plants must be expressed as a percentage of the total of the particular layer.

In the discussion of the *Polycarpaeo-Trachypogonetum* two sub-associations are mentioned, *P-T cyperetosum* and *P-T curatelletosum*. The former is a vegetation without tree layer, while the latter has a tree stratum of *Curatella americana* with a 40% coverage. There is a clear quantitative difference between the herb layers of both sub-associations, due to the presence of a tree layer in the *P-T curatelletosum*. When we wish to study the influence of the tree layer, we should relate the percentages of the species only to the herb layer, not to the vegetation as a whole. On the other hand, for comparison of the characteristics of this vegetation type as a whole with those of any other vegetation type, we should start from the total vegetation, rather than single layers.

The major part of this study deals with structure of species and vegetation both above and below the surface. Although an attempt was made to describe essential structural features in a quantitative manner, the resulting image remains fragmentary.

To provide a more complete picture, a structure diagram of each vegetation unit was drawn to scale. Source materials for these were drawings of root systems made in the field, drawings of the peg boards, and drawings of the habit of aerial parts, made mostly from dried material. In the compilation of diagrams, the mean coverage figures of the species according to Tüxen & Ellenberg were applied, as well as field estimates of coverage of the vegetation.

A transect of 10 m proved sufficient to represent the characteristic array of forms in their natural proportions. The figures are 1/25 natural size, only the diagram of *Ternstroemia-Matayba* scrub, *Humiria* variant is drawn at 1/50 natural size.

CHAPTER II

THE VEGETATION TYPES AND THEIR HABITATS

II. 1. TIME AND PLACE

The field work was carried out from July 1958 to May 1959. The basic data were worked out with some interruptions during the years

1960, 1961, 1962 and 1963 at Utrecht. The library and the herbarium of the Institute for Systematic Botany, Utrecht, were consulted frequently.

The investigations took place in the surroundings of the airfield "Zanderij", 45 km S. of Paramaribo. The majority of the vegetation types were studied on the Lobin savanna, located 3 km N.E. of the airfield. In addition, vegetation types on wet white sands were investigated S. of the Lobin savanna and scrub on dry white sand 2 to 3 km W. of the airfield.

For the location of the Lobin savanna the reader is referred to an outline map of N. Surinam in VAN DONSELAAR (1965). This publication also presents a vegetation map of this savanna.

II. 2. GENERAL DESCRIPTION OF THE VEGETATION TYPES

For further investigation, nine vegetation types were chosen on the basis of a rough survey of the Lobin savanna and data of HEYLIGERS (1963). Complete floristic descriptions of these types are presented by VAN DONSELAAR (1965).

The lists of the species and their coverages calculated after Tüxen & Ellenberg (Ch. I. 3) of the *Panicetum stenodoidis*, both sub-associations of the *Schizachyrio-Rhynchosporetum*, both sub-associations of the *Polycarpaeo-Trachypogonetum*, and the *Mesoseto-Trachypogonetum* were compiled from records which the author made together with J. van Donselaar. The trees scattered in these vegetation types, were plotted on a vegetation map. From this map their mean coverage values were estimated.

The lists of species of the *Xyrido-Paspaletum*, *Clusia-Scleria* scrub (*Comolia* variant) and the *Ternstroemia-Matayba* scrub (*Humiria* variant) are taken from HEYLIGERS (1963). However it is not possible to derive reliable mean coverage values of the species from the tables of this author. Personal observations compensated this deficiency with regard to the *Xyrido-Paspaletum*. Species of the two shrub-communities with high mean coverage had to be indicated simply with +.

Panicetum stenodoidis (Fig. 5)

For complete floristic description see VAN DONSELAAR (1965).

The *Panicetum stenodoidis* occurs on the lowest part of the Lobin savanna. At its lower side it is bordered by the *Arundinello-Panicetum stenodis* or the forest border, on its higher side by the *Schizachyrio-Rhynchosporetum mesosetosum*. The soil consists of silty clay loam. See further Ch. II. 3. 2. 3.

The vegetation, on the average covering nearly 100%, is made up completely of grasses and sedges, forming closely crowded tussocks. The highest tussocks, that determine the aspect of the vegetation type, reach a height of 60 cm. The majority of the tussocks, however, is about 20 cm high. Half-shrubs, and shrubby specimens of *Curatella americana* occur sporadically not exceeding a height of 1 m. Only one tree of *Curatella* was observed. During the growing season the aspect of the vegetation is green and fresh because it is determined by *Leptocoryphium lanatum* and *Rhynchospora globosa,* which are not hairy. This is in contrast to the other vegetation types that are dominated by pubescent species like *Trachypogon plumosus* and *Mesosetum cayennense.* The entire vegetation dries up in the long dry season and succumbs to fires.

List of species with their mean coverages calculated after Tüxen & Ellenberg

Emergent layer (1 m)

Curatella americana	0.01

High herb layer (60 cm)

Aristida tincta	1.50
Axonopus purpusii, narrow leaves	4.41
Leptocoryphium lanatum	5.40
Panicum nervosum	0.20
Rhynchospora globosa	37.3
Schizachyrium riedelii	0.40
Scleria bracteata	0.02
Trachypogon plumosus	0.40
Coutoubia spicata	0.02
Phaseolus peduncularis var. clitoroides	0.01
Turnera ulmifolia	0.03

Low herb layer (20 cm)

Andropogon leucostachyus	1.90
Axonopus pulcher	4.00
Axonopus purpusii	0.01
Bulbostylis junciformis	0.01
Mesosetum cayennense	37.3
Panicum stenodoides	21.5
Rhynchospora barbata var. barbata	21.2
Buchnera palustris	0.04
Cassia cultrifolia	0.01
Habenaria spec.	?
Hyptis atrorubens	0.01
Polygala adenophora	0.07
Sipanea pratensis	1.90
Tibouchina aspera	0.90

Schizachyrio-Rhynchosporetum mesosetosum (Fig. 7)

For complete floristic description see Van Donselaar (1965).

The vegetation occurs on the Lobin Savanna, bordering at its lower edge upon the *Panicetum stenodoidis* and at its upper edge upon the *Schizachyrio-Rhynchosporetum mitracarpetosum.* The soil consists of sandy clay loam. See further Ch. II. 3. 2. 3.

The vegetation is made up mainly of small tussocks, up to 20 cm high, mixed with higher ones up to 50 cm and lower ones up to 10 cm. The vegetation is not closed so that the bare soil surface appears in many places.

The mean coverage is 80%. Shrubs and half-shrubs are scarce, but more frequent on small earthen termitaries, which for this reason are a conspicuous feature of this vegetation type. On aerial photographs this vegetation therefore presents a spotted image. Trees and higher shrubs of several species are rare. The vegetation dries up almost completely and is burnt annually in the long dry season.

List of species with their mean coverage, calculated according to Tüxen & Ellenberg

Scattered trees (ca 7 m)

Astrocaryum segregatum	0.01
Byrsonima crassifolia	0.10
Licania divaricata	0.03
Rollinia exsucca	0.01
Trattinickia burserifolia	0.01

High herb layer (ca 50 cm)

Leptocoryphium lanatum	0.55
Schizachyrium riedelii	2.80
Trachypogon plumosus	11.8

Medium herb layer

Axonopus pulcher	8.5
Axonopus purpusii	2.0
Aristida tincta	4.8
Mesosetum cayennense	38.5
Rhynchospora barbata var. barbata	28.5
Buchnera palustris	0.10
Cassia cultrifolia	0.10
Hyptis atrorubens	0.05
Mitracarpus discolor	0.01
Polygala adenophora	0.30
Sipanea pratensis	1.50

Low herb layer

Aristida capillacea	0.30
Bulbostylis junciformis	0.50
Scleria hirtella	0.01
Scleria micrococca	0.04

Mainly on termitaries

Curatella americana	0.01
Eriosema crinitum	0.01
Eugenia punicifolia	0.03
Eupatorium amygdalinum	0.01
Riencourtia glomerata	0.02
Scleria bracteata	0.01
Tibouchina aspera	0.80

Schizachyrio-Rhynchosporetum mitracarpetosum (Fig. 8)

For a complete floristic description see Van Donselaar (1965).

On the Lobin Savanna the *Schizachyrio-Rhynchosporetum mitracarpetosum* borders at its lower edge on the subassociation mesosetosum, at its higher edge on the *Sclerio-Trachypogonetum*, which is related to the *Polycarpaeo-Trachypogonetum*. The soil consists of sandy loam to sandy clay loam. See further Ch. II. 3. 2. 3.

Just as in the other subassociation, the vegetation is composed mainly of low tussocks (20 cm). However, higher *Trachypogon plumosus* tussocks play a more important part and this has a profound effect on the aspect of the vegetation. The appearance of this type is more luxuriant than that of the previous one, particularly when *Axonopus pulcher* bears its golden spikes. Some common species attain their highest coverage here, e.g. *Tibouchina aspera* and *Sipanea pratensis*. The number of tree and shrub species is rather high. Termitaries are present here and there but their vegetation is not conspicuously different. All grasses and sedges dry out and are burnt in the dry season, but *Sipanea pratensis*, *Tibouchina aspera* and all woody species retain some green leaves throughout the year.

Among the vegetation of this subassociation bushes are found, with an area of some tens of square meters and a height of about 7 m. These are not considered here.

List of species with their mean coverages, calculated according to Tüxen & Ellenberg

Scattered trees (ca. 7 m)

Araliaceae spec.	0.05
Astrocaryum segregatum	0.05
Byrsonima crassifolia	0.50
Casearia spec.	0.01
Curatella americana	+
Himatanthus articulata	0.05
Licania divaricata	0.05
Maprounea guianensis	0.05
Pithecellobium jupunba	0.03
Tapirira guianensis	0.05

Emergent layer (up to 2 m)

Aeschynomene paniculata	0.01
Davilla aspera	0.01
Symplocos guianensis	0.01
Tibouchina aspera	6.4

High herb layer (60 cm)

Andropogon leucostachyus	0.20
Imperata brasiliensis	0.01
Schizachyrium riedelii	5.7
Scleria bracteata	1.10
Trachypogon plumosus	25.2
Elephantopus angustifolius	0.01
Eupatorium amygdalinum	0.20
Riencourtia glomerata	0.01
Tibouchina aspera	6.4

Medium herb layer (40 cm)

Aristida tincta	0.60
Axonopus pulcher	38.2
Axonopus purpusii	4.1
Aeschynomene brasiliana	0.01
Buchnera palustris	0.01
Cassia cultrifolia	0.40
Cassia hispidula	0.01
Coutoubia spicata	0.01
Eriosema crinitum	0.01
Eugenia punicifolia	0.05
Hyptis atrorubens	0.40
Mitracarpus discolor	0.01
Phaseolus longaepedunculatus	0.01
Polygala adenophora	0.05
Polygala longicaulis	0.25
Sipanea pratensis	3.1
Zornia diphylla	0.01

Low herb layer (15 cm)

Aristida capillacea	0.20
Bulbostylis capillaris	0.01
Bulbostylis junciformis	8.4
Rhynchospora barbata var. barbata	10.5
Scleria micrococca	0.20
Mitracarpus microspermus	0.40

Polycarpaeo-Trachypogonetum cyperetosum (Fig. 9)

For complete floristic description see Van Donselaar (1965).

The highest parts of the Lobin savanna are occupied by the *Polycarpaeo-Trachypogonetum.* The two subassociations form a mosaic, but the subassociation *curatelletosum* is more common on the highest spots. The soil consists of loamy sand. See Ch. II. 3.2.3.

Trachypogon plumosus, with its large spreading tussocks 60 cm high, is the dominant species. Because of the spread of the shoots and the leaves the coverage is high, though the tussocks are standing far apart at their base. Between the tussocks herbs and half-shrubs of many species are found, but together they cover only a small part of the surface and contribute little to the aspect of the vegetation. The coverage of the lower herb layers is scant. Especially the tussocks dry up in the dry season and burn violently.

Polycarpaeo-Trachypogonetum curatelletosum (Fig. 11)

For complete floristic description see Van Donselaar (1965).

Among vegetation belonging to the previous subassociation trees of *Curatella americana* are found. They have the gnarled form of orchard trees, which is described by many authors. Underneath the *Curatellas* the vegetation is different, though nearly all the species are the same. The share of grasses is clearly smaller, that of the other herbs, half-shrubs and shrubs larger. The evergreen *Heliconia psittacorum* is a particularly conspicuous species. High shrubs also grow with greater frequency under the *Curatellas.* This undergrowth is continuous in places where the open trees touch one another. Except for the shrubs and *Heliconia* the whole vegetation is usually desiccated in the dry season and the annual fires are violent. After the fire *Curatella* sheds its large, stiff and rough leaves.

List of species with their mean coverages, calculated according to Tüxen & Ellenberg

Tree layer (8 to 10 m)

	cyp.	cur.
Astrocaryum segregatum	+	0.01
Byrsonima crassifolia	0.03	0.03
Curatella americana	+	41.—
Himatanthus articulata	0.01	0.01
Licania divaricata	0.01	0.01
Maprounea guianensis	0.01	0.01
Pithecellobium jupunba	0.01	0.01
Tapirira guianensis	0.01	0.01
Trattinickia burserifolia	0.01	0.01

Emergent layer (to 2 m)

	cyp.	cur.
Aeschynomene paniculata	0.05	0.10
Curatella americana, shrub	0.29	–
Davilla aspera	–	0.01
Desmodium asperum	0.01	0.05
Psidium guineense	0.01	0.04
Symplocos guianensis	–	0.01

High herb layer (ca. 80 cm)

	cyp.	cur.
Cyperus flavus	0.28	0.04
Panicum rudgei	0.01	2.50
Paspalum plicatulum	–	2.10
Schizachyrium riedelii	7.5	2.10
Scleria bracteata	–	0.40
Trachypogon plumosus	65.2	55.7
Amazonia campestris	0.01	0.37
Ayenia tomentosa	–	0.37
Borreria latifolia	0.01	0.03
Cassia cultrifolia	0.09	0.07
Cassia flexuosa	0.01	0.03
Cassia patellaria	0.02	0.43
Centrosema brasiliensis	0.01	0.03
Crotalaria stipularia	0.04	0.07
Croton hirtus	0.01	0.06
Elephantopus angustifolius	0.05	0.10
Eriosema violaceum	0.53	0.74
Eupatorium amygdalinum	0.04	0.03
Eupatorium odoratum	0.02	0.01
Galactia jussieuana	0.26	4.40
Heliconia psittacorum	0.01	6.40
Hybanthus ipecacuanha	0.01	0.06
Oxypetalum capitatum	0.03	0.04
Pavonia speciosa	0.01	–
Phaseolus longaepedunculatus	0.03	0.03
Phaseolus peduncularis var. clitoroides	0.05	0.43
Pterolepis trichotoma	–	2.10
Riencourtia glomerata	0.30	5.70
Stylosanthes guianensis	0.04	0.10
Tephrosia sessiliflora	2.54	2.20
Tibouchina aspera	0.04	–
Turnera ulmifolia	0.01	0.03

Medium herb layer (40 cm)

	cyp.	cur.
Andropogon leucostachys	–	0.01
Axonopus pulcher	17.8	0.43
Axonopus purpusii	0.01	0.01
Aeschynomene brasiliana	0.05	0.74
Aeschynomene hystrix	0.02	0.01
Cassia faginoides	0.01	–
Cassia hispidula	0.09	0.44
Conyza chilensis	0.02	2.20
Desmodium barbatum	0.08	0.43
Eriosema crinitum	0.05	0.07
Eugenia punicifolia	0.01	0.04
Euphorbia brasiliensis	0.04	0.07
Hyptis atrorubens	0.29	0.40
Mitracarpus discolor	0.06	0.41
Myrosma cannifolia	–	0.36
Pectis elongata	0.01	–
Piriqueta cistoides	0.03	0.03
Richardia scabra	0.02	0.04
Sebastiana corniculata	0.01	0.03
Sipanea pratensis	0.03	0.01
Tephrosia purpurea	0.05	0.40
Zornia diphylla	0.08	0.40

Lowest herb layer (15 cm)

	cyp.	cur.
Bulbostylis capillaris	7.05	7.18
Bulbostylis fasciculata	0.27	0.37
Bulbostylis junciformis	2.30	0.04
Cyperus amabilis	0.06	–
Dichromena ciliata	0.02	0.40
Rhynchospora barbata var. barbata	0.01	–
Scleria micrococca	0.02	0.01
Mitracarpus microspermus	0.05	0.75
Paepalanthus subtilis	0.02	–
Phyllanthus diffusus	0.04	0.03
Polycarpaea corymbosa	2.06	0.06
Polygala longicaulis	0.54	0.03

Epiphytes on *Curatella*

	cyp.	cur.
Polystachya luteola		+
Anthurium gracile		+

Mesoseto-Trachypogonetum (Fig. 10)

For complete floristic description see VAN DONSELAAR (1965).

The *Mesoseto-Trachypogonetum* is found in the southern part of the Lobin savanna on white sand (Ch. II. 3.2.3.).

Just like in the *Polycarpaeo-Trachypogonetum* the aspect is determined by the large, widely spreading tussocks of *Trachypogon plumosus*. However, they do not touch one another. Low grasses and sedges are found between the tussocks. Particularly *Mesosetum loliiforme* with its long runners, and the small tufts of *Bulbostylis conifera* may be abundant. The mean coverage is 50%. Small shrubs are more frequent here than in the other types, but their combined coverage is small. Even in the dry season they retain some leaves, but the remainder of the vegetation dries up completely. Here and there a high shrub is present. The vegetation burns every year.

List of species with their mean coverage, calculated according to Tüxen & Ellenberg

Emergent layer (up to 2 m)

Cassia ramosa var. ramosa	6.13
Curatella americana	0.02
Tetracera asperula	0.02
Tibouchina aspera	1.94

High herb layer (60 cm)

Trachypogon plumosus	18.3
Byrsonima crassifolia	0.59
Waltheria americana	0.01

Medium herb layer (40 cm)

Axonopus pulcher	6.9
Cyperus flavus	0.01
Aeschynomene hystrix	0.07
Buchnera palustris	0.04
Cassia flexuosa	0.02
Cassia hispidula	0.88
Cassytha filiformis	0.02
Comolia lythrarioides	0.02
Desmodium barbatum	0.02
Eugenia punicifolia	0.04
Mitracarpus discolor	0.61
Phaseolus peduncularis var. clitoroides	0.01
Polygala variabilis	0.02
Schwenckia americana	0.02
Sebastiana corniculata	0.01
Stylosanthes viscosa	0.34
Zornia diphylla	0.04

Low herb layer (15 cm)

Bulbostylis conifera	16.1
Bulbostylis capillaris	0.28
Bulbostylis fasciculata	0.58
Bulbostylis junciformis	1.43
Mesosetum loliiforme	23.6
Rhynchospora barbata var. glabra	0.28
Scleria micrococca	0.29
Paepalanthus subtilis	1.13
Phyllanthus diffusus	0.02
Polycarpaea corymbosa	0.02
Polygala adenophora	0.06
Polygala longicaulis	0.33

Xyrido-Paspaletum (Fig. 12a)

For complete floristic description see Heyligers (1963), and Van Donselaar (1965).

On white sand with ground water reaching the surface during the greater part of the year a sparse vegetation is found, consisting of low, small tussocks (15 cm at most) and many small, slender therophytes. Part of the species have rosettes of flat-lying leaves. Low shrubs are scattered. A rather common species is *Lagenocarpus tremulus*, a sedge (40 cm high) with a rhizome just at the surface. There are quite a number of *Xyridaceae* and *Lentibulariaceae*.

According to Heyligers, the maximum coverage is 40%, the mean coverage 25%. The present investigation was carried out, however, in a vegetation covering 60%. An algal layer, mentioned by Heyligers, was not observed here.

There is not much material for burning in this low and open vegetation and therefore fires do not occur every year.

List of species with their mean coverage, calculated according to Tüxen & Ellenberg

High layer (up to ca. 1 m)

Comolia vernicosa	0.02
Clusia fockeana	0.10
Humiria balsamifera	0.02
Licania incana	0.10
Ternstroemia punctata	0.02
Tetracera asperula	0.03
Tibouchina aspera	0.02
Hypolytrum pulchrum	0.02
Lagenocarpus tremulus	0.10
Leptocoryphium lanatum	0.06

Low layer (up to 15 cm)

Mesosetum loliiforme	1.80
Panicum micranthum	8.2
Paspalum polychaetum	0.70
Paspalum pulchellum	1.30
Rhynchospora arenicola	0.05
Rhynchospora barbata var. glabra	0.06
Rhynchospora curvula	0.04
Rhynchospora graminea	2.30
Rhynchospora tenuis	0.05
Abolboda americana	1.30
Burmannia bicolor	0.03
Cassytha filiformis	0.06
Comolia lythrarioides	0.10
Comolia veronicaefolia	0.02
Drosera capillaris	2.30
Genlisea spec.	0.05
Lisianthus coerulescens	0.02
Paepalanthus polytrichoides	2.50
Perama hirsuta	1.30
Polygala appressa	0.07
Polygala adenophora	0.07
Sauvagesia sprengelii	1.10
Syngonanthus umbellatus	0.07
Syngonanthus gracilis	0.04
Utricularia fimbriata	2.30
Utricularia guianensis	0.02
Utricularia spec.	0.02
Xyris glabrata	0.02
Xyris guianensis	9.00
Xyris longiceps	0.02
Xyris subuniflora	0.07
Xyris surinamensis	1.30

Clusia fockeana-Scleria pyramidalis scrub, variant of *Comolia vernicosa* (Fig. 12b)

For complete floristic description see HEYLIGERS (1963).

Among the low and open vegetation of the *Xyrido-Paspaletum*, bushes are found covering an area of some tens of square meters at most, their height usually not exceeding 1½ m. Exceptionally a single shrub may reach up to 3 m. A conspicuous species is the little palm *Bactris campestris* that often grows in the centre above the shrubs. The sandy surface in the bushes is covered with a layer of litter. In bushes with a closed shrub layer the undergrowth is sparse; grasses and sedges are practically absent. The shrubs are evergreen. It is striking that in many species the leaves are concentrated at the end of the twigs. The bushes are burnt now and then, not annually.

List of species

High shrub layer

Bactris campestris	
Clusia fockeana	+
Conomorpha magnoliifolia	
Licania incana	+
Marlierea montana	
Pagamea capitata	
Scleria pyramidalis	
Ternstroemia punctata	+

Layer of low shrubs and high herbs (medium layer)

Comolia vernicosa	+
Croton hostmanni	
Doliocarpus calinea	
Humiria balsamifera	+
Hypolytrum pulchrum	
Lagenocarpus tremulus	
Lisianthus uliginosus	

Miconia ciliata
Panicum nervosum
Retiniphyllum schomburgkii
Tetracera asperula
Cassytha filiformis

Low herb layer

Actinostachys pennula
Lagenocarpus amazonicus +

There may be a moss layer with *Cladonia* spec. and *Spaghnum kegelianum*, but it is not considered here.

Ternstroemia punctata-Matayba opaca scrub, variant of *Humiria balsamifera* (Figs. 13 and 14)

For complete floristic description see HEYLIGERS (1963).

The typical form of this vegetation type consists of dome-shaped bushes surrounded by nearly bare, white sandy soil. The area covered by the bushes varies from a few to some hundreds of square meters. The shrubs attain a height of about 5 m; in the centre, trees may reach a height of 7 m. The canopy is closed and touches the ground near the edges, where *Humiria balsamifera* always forms its lowest part. The light intensity in the bushes is low and there is no herbaceous undergrowth except for some terrestrial orchids. The surface is covered with a layer of litter that in the centre may be several dm thick. Along the edges some typical species are found: *Lagenocarpus weigelti*, *Axonopus attenuatus*, *Actinostachys pennula* and *Schizaea incurvata*. The shrubs are evergreen.

Fires may spread from the adjoining open vegetation to the bushes and in that case the dry litter may keep smouldering for a long time.

List of species

Layer of emergents

Bombax flaviflorum
Matayba opaca
Ormosia costulata
Pagamea guianensis
Trattinickia burserifolia
Conomorpha magnoliifolia

Closed canopy

Clusia fockeana +
Clusia nemorosa
Humiria balsamifera +
Ilex jenmani
Licania incana +
Maprounea chlorantha
Pagamea capitata
Torrubia spec.
Protium heptaphyllum
Swartzia bannia
Ternstroemia punctata

Undergrowth

Calycolpus revolutus
Myrcia silvatica
Retiniphyllum schomburgkii
Bredemeyera densiflora
var. glabra
Doliocarpus calinea
Tetracera asperula

Herb layer at the edge of the bush

Actinostachys pennula +
Schizaea incurvata
Axonopus attenuatus
Lagenocarpus weigelti
Borreria suaveolens
Trachypogon plumosus

Herbs in the bush

Catasetum spec.
Epidendrum nocturnum

II. 3. THE ENVIRONMENT

II. 3.1. The climate

The climate of Surinam was described by BRAAK (1935); and

OSTENDORF (1953–1957) provided supplementary data. SCHULZ (1960) presents a review in connection with his ecological investigations, that is generally sufficient for the present. The following data are derived from it.

The temperature varies only slightly in the course of the year. The mean value is 27.1° C.

The humidity and the number of hours with sunshine are related to rainfall.

The main climatic factor that varies strongly in the course of the year is the rainfall. The annual precipitation of the stations in northern Surinam is between 2000 and 2400 mm. Four periods are distinguished (see Fig. 1): A long rainy season from April to August, a long dry season from August to December, a short rainy season from December to February, a short dry season from February to April.

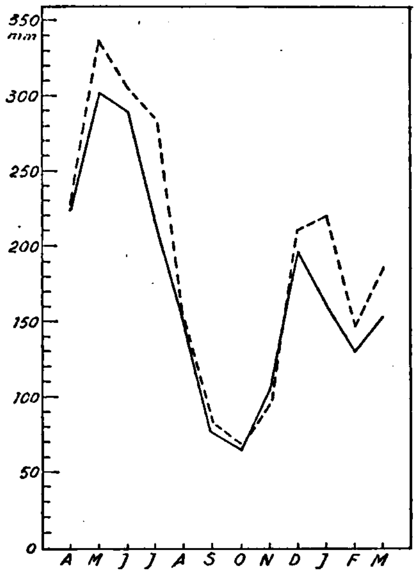

Fig. 1. Monthly rainfall at two stations (beginning with April).
——— Republiek (after VOETS, 1959b)
- - - - - - - Kabel (after OSTENDORF, 1957)

The short dry season does not occur every year so that the short rainy season sometimes passes directly into the long rainy season. Periods of 30 days with a total precipitation of less than 60 mm occur nearly annually during the long dry season and occasionally during the short dry season. In most months considered as dry the rainfall varies between 60 and 100 mm.

For the vegetation not only the absolute monthly values are of importance, but also the variations from month to month. Of prime importance is the fact that now and then a year occurs with an extremely prolonged long and or short dry season.

The two years preceding the investigation (1957 and 1958) were drier than normal.

II. 3.2. **The soil**

II. 3.2.1. Introduction

The soil influences the vegetation in many different ways, but the most decisive factor is the hydrology. The hydrology of the layers with roots depends on two water sources: ground water and rain water.

With regard to the wetting of these layers by the ground water the height of the water table and of the ascending capillary water are of importance. The latter is determined by the diameter of the soil capillaries and this in turn depends on the texture and the structure of the soil. In the zone that is alternately dry and saturated with water poor in oxygen, spots caused by oxydation and reduction occur: the gley horizon. This horizon can be used for tracing the height that has been reached by the ascending capillary water.

The wetting with rain water depends on several factors. If a shower falls on a desiccated topsoil, this layer takes in as much water as can be stored in the pores. The excess water stagnates on the surface or runs off. The topsoil retains a part of the water (field capacity), whereas another part sinks down to deeper layers. This process is repeated during and after every shower. The thickness of the wetted layer depends among other things on the duration and the amount of the precipitation.

The speed with which water is taken in is determined by the size of the pores at the surface. A soil may be blocked, i.e. the structure of the topsoil is so compact that hardly any water is taken up. The field capacity and the amount of percolating rain water is determined by the diameter of the pores.

Desiccation of the soil is caused by evaporation as well as by transpiration. The evaporation is correlated, just like wetting, to the size of the pores (aeration). The transpiration depends among other things on the type of vegetation and the depth and the density of the root systems. Through transpiration the soil dries to the "wilting point".

So the pore-size is of great importance for the hydrology of the soil. It is determined by the texture and the structure. The savanna soils hardly have any structure so that the texture is the decisive factor.

Other features that play a role in the wetting of the deeper soil layers are channels of old roots and animal burrows.

The height of the water table and the amount of rain water taken up determine whether there is contact between these two water sources or whether a permanently dry layer remains between the ground water and the water in the topsoil.

An impermeable layer at some depth of course influences strongly the hydrology of the layers with roots. In the rainy season it causes a quick saturation, in the dry season it causes desiccation, for it blocks the supply from below.

It is known from data by FOLLET-SMITH (1930), MÜLLER (1945) and HEYLIGERS (1963) that savanna soils are poor in nutrients. Heyligers shows in addition that the nutrient content of bleached sand soils and that of soils with a heavier texture do not differ nearly as much as might be expected. This author remarks further: "In the savanna too the physical soil factors will be more important for the vegetation than the chemical factors." Because of the findings by Heyligers no chemical analyses of the soils were carried out.

The air content of the soil is directly related to the water content. Together, air and water occupy the total pore space. O_2 and CO_2 are of importance for the vegetation, the former being taken up, the latter given of by the roots. In a layer with roots the O_2-content is lower, the CO_2 content higher than in the adjoining soil. Good aeration may maintain the proper equilibrium.

A soil saturated with water contains little O_2. Rainwater is saturated with O_2. The longer it has been in contact with roots, the less O_2 and the more CO_2 is dissolved in the water.

An increase of the temperature causes a decrease of the amount of O_2 dissolved in the soil water. The temperature of the soil depends on the insolation during the daytime and the radiation at night. A difference between the temperature may cause distillation of water from a warm to a cold layer.

The presence of organic matter in the soil has many consequences. It improves the structure, i.e. wider pores and larger soil aggregates are formed and the water-holding capacity is better. The organic material increases the mineral content and it entails increase of organisms in the soil, so that more O_2 is consumed and more CO_2 produced.

II. 3.2.2. Methods

The soil was investigated in several spots in every vegetation type. In general samples were taken to a depth of 1.20 m, sometimes deeper if the roots penetrated deeper. Members of the "Dienst Bodemkartering" (Department of Soil Survey) in Surinam described the majority of the profiles.

The depth of the ground-water table was measured every week in vertical tubes sunk in several spots in each vegetation type.

The samples of one representative profile of every type were analysed in the pedological laboratory of the "Koninklijk Instituut voor de Tropen" (Royal Institute for Research in the Tropics) at Amsterdam.

The following factors were taken into account:

Texture

In conformity with the Dept. of Soil Survey the "Soil Survey Manual of the U.S. Department of Agriculture" was used for the distinction of fractions and texture classes.

The fractions are:

gravel	>2 mm
very coarse and coarse sand	2 mm–200 μ
fine and very fine sand	200–50 μ
silt	50– 2 μ
clay	<2 μ

The exact limit between coarse and fine sand is 297 μ, the one between sand and silt 53 μ.

For the texture classes see Fig. 2. The division of the class "clay" into "clay" and "heavy clay" is derived from Van der Voorde (1957).

Method of analysis: 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 weight of particles ranging from 0–2 mm.

Percolation rate

Method: Gentle shaking of the soil during at least 1 hour in tubes 2.1 cm in diameter until a standard 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.

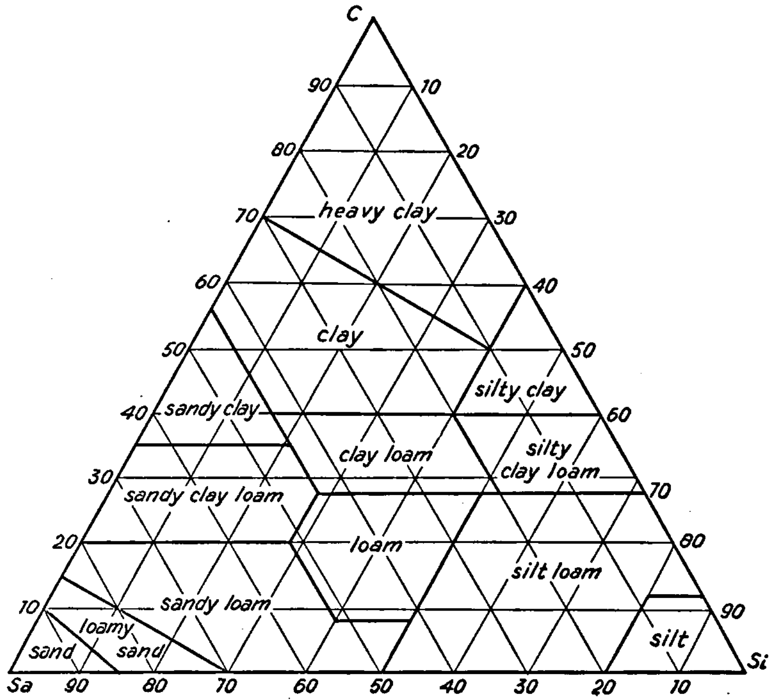

Fig. 2. Texture classes.

Measuring the percolated water at fixed times. The amount is expressed in ml/h.

Since with this method the structure is disturbed, the measured percolation rate is not in agreement with the value of this factor in the field. The values only provide a rough comparison between soils, in this respect.

Moisture content

The moisture content is the % difference in weight between air dried soil and soil dried for 3 hours at 105° C. This value appears to be directly related to the clay content of the soil.

C-content

Method: Normal analysis (Walkley-Black). Oxydation with bichromate + conc. sulphuric acid. Retitrating of the surplus bichromate with ferrosulphate. The C-content is given as a percentage of the soil dried at 105° C. It appears to be related to the density of the root systems in the layer.

N-content

Method: Destruction with "selenium mixture after Kjeldahl" and conc. sulphuric acid. Micro-kjeldahl analysis (steam distillation, titration of accumulated ammonia). The N-content is given as a percentage of the soil dried to 105° C. It is added only for the sake of completeness. The same holds for the C/N ratio.

A picture of the hydrology was gleaned from the following data:

Measurements of the water table in vertical tubes

Texture

Gley-horizon. It has to be noted that no gley-horizon is present in bleached sand. HEYLIGERS (1963) observed that the capillary water ascends to about 40 cm above the ground-water table.

Percolation rate. The method described above may be justified in view of the fact that the savanna soils present hardly any structure.

Observations concerning runoff and drainage channels.

II. 3.2.3. Description of the soil

Panicetum stenodoidis

Description of a representative profile:

0–13 cm silty clay loam; brown-grey
13–25 cm silty clay; brown-grey passing into orange
25–54 cm heavy clay; orange with brown and grey spots
54–97 cm silty clay; light grey, purple and orange spotted
deeper heavy clay;
Many hard concretions at about 90 cm.

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	⩽ 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 13	–	9	52	39	2.59	0.18	14	3.2	1
13– 25	–	12	44	44	1.56	0.13	12	3.1	3
25– 54	–	5	33	62	0.77	0.09	9	3.4	1
54– 97	–	4	44	52	0.30	0.05	6	2.9	1
100–120	–	7	35	58	0.26	–		2.8	1

Hydrology

Water-table measurements: see Fig. 3, A. During the dry season the ground water is at least at a depth of 2.50 m, during the rainy season it rises to the surface.

Gley-phenomena are found already at a depth of 10 to 30 cm.

The percolation velocity is very low; this is related to the texture.

Every shower results in a strong run-off, even in the long dry season. In the long dry season the soil dries up and cracks appear with a depth of 70 cm and a width of 10 cm.

In the long dry season the bone-dry soil contains no water available to the vegetation. Owing to the heavy texture little rain water is taken up at the surface, so that the soil is wetted only slowly from above. There is much water running off, partly coming from the higher parts of the savanna, and this water disappears mostly into

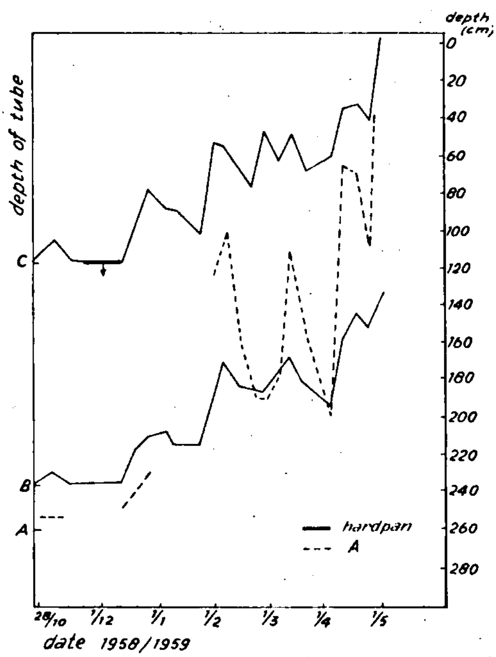

Fig. 3. Water-table fluctuations.

the deep cracks. Therefore, the soil becomes wetted rapidly down to a depth of several decimeters, the ground water rises quickly and saturates the soil up to the surface. Another result of the heavy texture and the poor structure, i.e. the small pore-size, is the low rate of evaporation, so that the soil dries relatively slowly.

Comparatively short periods of drought alternate with periods of water saturation.

Schizachyrio-Rhynchosporetum mesosetosum

Description of a representative profile:

0– 30 cm	coarse-sandy clay loam; grey to brown-grey
30– 47 cm	coarse-sandy clay; orange
47– 75 cm	clay; orange, with dark grey and purple concretions
100–120 cm	sandy clay

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 15	–	58	11	31	1.00	0.11	9	2.0	42
15– 29	–	58	11	31	1.00	0.07	14	2.0	45
29– 47	–	47	15	38	0.63	0.06	11	2.2	10
47– 75	–	21	21	58	0.33	0.04	8	3.2	4
100–120	–	48	6	46	0.12	0.03	4	2.2	6

Hydrology

During the period of the observation, which did not include the optimum of the long rainy season, no ground water was found in the tube down to a depth of 2 m.

Gley-phenomena occur below a depth of 30 to 50 cm.

The percolation velocity is related to texture: in sandy loam it is higher than in the clay that is found on a depth of about 45 cm. The values are higher than in the *Panicetum* but markedly lower than in lighter soils.

Run-off is considerable. On some slightly sloping parts of the Lobin savanna the run-off currents leaves narrow drift lines against the tussocks.

During the long dry season the soil is completely dry at least down to the limit of the gley-phenomena. The clay fraction is not large enough to cause shrinkage cracks. The wetting of the upper decimeters results exclusively from intake of rain water. As a consequence of the texture and run-off only a little water is taken up slowly. From the available data it can not be concluded whether the rain water and the ground water reach one another. The same is true for the fluctuations of the water table.

Earthen termitaries are strikingly abundant among this sub-association of the *Schizachyrio-Rhynchosporetum*. The texture in their profiles does not differ markedly:

+30–0 cm sandy clay loam; light grey
0–35 cm sandy clay loam; dark grey
35–60 cm clay; orange

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
+ 25–20	–	69	2	29	1.66	0.12	14	2.0	24
+ 5– 0	–	51	21	28	1.38	0.16	9	2.1	18
12–17	–	49	24	27	1.37	0.10	14	2.1	17
35–40	–	42	14	45	0.72	0.08	9	2.5	11

In the termitaries the humus content is higher, while the percolation rate is lower.

The system of channels in the termitaries may function as a drainage system. Therefore the soil is wetted quicker down to the depth reached by the channels. On Photo 1 channels are seen to reach down to a depth of 60 cm below the level of the original surface. At the lower right one sees a wide but now filled-up burrow of an armadillo.

Schizachyrio-Rhynchosporetum mitracarpetosum

Description of a representative profile:
0– 30 cm coarse-sandy loam; brown-grey
30– 60 cm idem; grey-brown
60– 90 cm idem; grey-brown with small grey spots
90–120 cm idem; yellow-brown with orange and yellow spots
In some places the soil below 90 cm consists of sandy clay.

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 30	–	78	52	20	0.91	0.06	15	1.1	26
30– 60	–	76	3	21	0.40	0.03	14	1.0	56
60– 90	–	61	9	30	0.24	–	–	1.2	33
90–120	–	41	12	47	0.24	0.03	8	1.7	21

Hydrology

During the period of the observations, which were stopped before the height of the long rainy season, no water was noticed in a tube with a depth of 4.40 m.

Gley-phenomena are found from 40 to 80 cm downwards.

The percolation rates are lower than in the lighter soil of the *Polycarpaeo-Trachypogonetum*, but higher than in the heavier soil of the *Panicetum*.

There is a strong run-off.

During the long dry season the soil is dry at least down to the upper limit of the gley-phenomena. The upper layers are wetted only by rain water. The texture, the percolation velocities and the run-off suggest that only little rain water is taken up slowly. From the available data it can not be deduced how deep the wetting penetrates nor if rain water and ground water make contact.

Polycarpaeo-Trachypogonetum

The soil of the two subassociations is identical.

Description of a representative profile:

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

The depth at which the loamy sand passes into sandy loam varies according to elevation.

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0–12	2.1	87	2	11	1.26	0.06	21	1.0	60
12– 51	1.3	83	6	11	0.72	0.05	14	1.1	70
51– 84	1.9	79	2	19	0.75	0.03	25	1.0	65
84–120	1.9	70	2	28	0.60	–		1.4	16

Hydrology

In a tube with a depth of 4.40 m no water was found during the period of the measurements, which were stopped before the height of the long rainy season.

As a rule, gley-phenomena do not occur above a depth of 1 m. Their depth depends on the elevation of the surface level.

Percolation rates are high compared with those of heavier soils, but lower than in pure sand soils. The values are much higher in the loamy sand than in the sandy loam at a greater depth.

No run-off is observed.

Since all rain water is taken up, and percolation rates suggest that it sinks down easily to the depth of the gley-phenomena, it may be concluded that the rain water and the ground water come into contact. The heavy texture of the deeper layers and the related low percolation velocities will impede the drainage during the long rainy season, so that not all rain water sinks out of the layers with roots.

During the long dry season the soil dries up at least to the depth of the gley-phenomena. However, every shower, also the scarce ones during the long dry season, penetrates and wets the soils, though temporarily.

Mesoseto-Trachypogonetum

Description of a representative profile:

0– 22 cm sand with some gravel; light grey
22– 72 cm idem; light brown and grey spotted
72–120 cm idem; white

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0–22	0.5	96	2	2	0.33	0.02	17	0.1	304
22– 72	–	96	3	1	0.07	0.01	7	0.2	168
72–120	–	97	2	1	0.03	0.01	3	0.2	150

Hydrology

The results of the water-table measurements are presented in Fig. 3, B. During the long dry season no ground water appeared in a tube of 2.20 m, but during the short rainy season this level was reached occasionally. When the rains continued, the water table rose. The maximum level was not observed, for the measurements had to be stopped before the peak of the long rainy season. The highest level registered was 1.30 m below the surface, when the long rainy season had been in progress for one month.

Under the same vegetation type HEYLIGERS (1963) observed a fluctuation of the water table between 5.40 and 4.40 m. According to this author the capillary water rises 40 cm above the water table.

The percolation rates are high and probably in accordance with the situation in the field, for this sandy soil is unstructured.

All rain water is taken up, during the rainy as well as the dry seasons. The field capacity of a sand soil is small and therefore the water will sink down quickly to a depth beyond the reach of the plants. In the habitat under consideration it reaches the ground water rapidly, and in consequence the water table rises quickly when the rains continue, at least up to a depth of 1.30 m below the surface, while the capillary water goes still 40 cm higher. However, due to the wide pores the evaporation is high and the soil dries quickly to a great depth when the rainfall ceases.

Xyrido-Paspaletum

Description of a representative profile:

0–30 cm sand; dark grey
30–60 cm idem; light grey to white

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 20	–	94	5	1	0.24	0.02	12	0.1	110
20– 30	–	96	2	2	0.15	0.02	8	0.0	160
30–100	–	93	6	1	0.85	0.08	11	0.5	10

Hydrology

From personal observations and the data of Heyligers it appears that the ground water reaches to the surface during the greater part of the year, sometimes even above it. According to Heyligers the ground water sinks down to a depth of 70 cm in the dry season. This means that, at that time, at least the upper 30 cm are desiccated completely. On a part of the savanna with a hardpan at a depth of 1.10 m the soil above this level appeared to dry up, Fig. 3, C. It is clear that in every instance the upper decimeters have no water available for the vegetation during the dry season. Since rain water is taken up easily, the water table rises quickly during periods of continued rain.

Clusia-Scleria scrub, *Comolia* variant

Description of a representative profile:

+5– 0 cm	litter
0–20 cm	humic sand; grey
20–40 cm	humic sand; grey-brown
40–70 cm	light humic sand; light grey-brown
70– cm	sand; light grey to white

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0–20	–	96	2	2	1.46	0.05	29	0.7	100
20–40	–	95	2	3	0.78	0.04	20	0.4	110
40–70	–	96	3	1	0.12	0.06	2	0.1	125

Heyligers remarks that the soil surface in the bushes is often a little elevated. This was not observed in the bushes studied during this investigation. The hydrology is the same as in the soil of the *Xyrido-Paspaletum.*

The prominent difference between the two soils is the presence of a layer of litter in the bushes. This layer causes a higher humus content and a higher moisture content. It tends to diminish both the evaporation from the soil and the insolation.

Ternstroemia-Matayba scrub, *Humiria* variant

Description of a representative profile:

+10– 0 cm	litter
0– 60 cm	sand; brown-grey
60–155 cm	idem; lighter, passing into white
155–266 cm	idem; white
266–290 cm	and deeper iron pan: brown

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 10	–	97	2	1	1.20	0.05	24	0.3	220
ca 40	–	95	4	1	0.44	0.02	22	0.2	370
ca 110	–	97	2	1	0.08	–		0.1	290
ca 170	–	97	2	1	0.03	0.01	3	0.02	122
ca 240	–	97	2	1	0.03	0.01	3	0.04	176
ca 280	–	86	5	9	1.58	0.04	40	0.9	1

For comparison a white sand profile is described from a spot almost without vegetation, occurring between the bushes:

0– 20 cm sand; white-grey
20– 90 cm idem; light brown-grey
90–120 cm idem; white

depth	> 2 mm (%)	2 mm–50 μ (%)	50–2 μ (%)	< 2 μ (%)	C	N	C/N	moisture (%)	percolation rate (ml/h)
0– 20	–	97	2	1	0.05	0.01	5	0.1	> 400
50– 70	–	96	3	1	0.08	0.03	3	0.1	180
100–120	–	97	2	1	0.02	–		0.0	192

This soil differs from those of the *Clusia-Scleria* scrub and the *Xyrido-Paspaletum* mainly by the depth of the water table. According to Heyligers the water table below the *Ternstroemia-Matayba* scrub does not reach higher than 2 m below the surface, whereas in the dry season it sinks much deeper. In the bushes studied here a hardpan was present at a depth of about 2.75 m. During the dry season the soil dries out to this level, whereas in the rainy season drainage is impeded. From the available data it can not be concluded to which level the water may rise.

The influence of the litter layer is the same as on the wet white sand. The upper decimeters have a higher humus content, their percolation rate is lower though nevertheless high.

CHAPTER III

ROOT SYSTEMS

III. 1. Review of the literature

III. 1.1. **Anatomy**

The functions of the roots are the anchoring of the plant in the soil and the taking up of water and nutrients from the substrate.

At the germination of the seed the radicle emerges; in the dicotyledons this usually develops into the primary process. A primary root growing straight down, decreasing in thickness, is called a tap root. In the monocotyledons the radicle has no permanent function and often disappears. The roots formed later on are cladogenous, i.e. they originate from the bases of the shoots (Troll, 1949). The lateral roots are formed acropetally, i.e. the youngest is nearest to the root tip. Under the stress of special conditions new roots may grow from dormant primordia, present along the shoots as well as the roots. Secondary roots and sprouts may originate also from old roots. Even fibrous roots may develop along old roots and disappear quickly according to the circumstances (Kutschera, 1960). Troll (1949) calls all roots formed during the later life of the plant "adventitious" roots. According to Kutschera the ability to form such adventitious roots is unlimited.

The underground part of the herbaceous shoot, that survives the unfavourable season, is called caudex (Pulle, 1950).

At some distance from the root tip, where the longitudinal growth has ceased, root hairs are present, i.e. proliferations of the epidermal cells. The slimy outer layer of the hairs establishes close contact with the soil particles. In general the root hairs take up water and nutrients, but in some species this function is taken over by the non-corky root epidermis (water plants), or by mycorrhiza (METSÄVAINIO, 1931). The life of the root hairs is limited. The formation of a cork layer stops further absorption. The hairs degenerate and are decomposed by soil organisms. Some species have root hairs along the entire length of the roots. In this case secondary thickening does not occur.

In most dicotyledons secondary thickening occurs in older parts of the root; not, however, in the monocotyledons. In palms and grasses the outer wall of the epidermis is cutinised. The endodermis also forms an impermeable layer. Finally the endodermis or a pericambial cork layer isolates the bark from the inner parts of the root. As a rule only the young part of the root just behind the tip participates in the absorption of water and nutrients.

KUTSCHERA (1960) remarks that even dead roots may function as water channels. Kramer (cited by Kutschera) also is of opinion that even a root system with a cork layer may take up enough water to compensate a minor loss of water by transpiration.

III. 1.2. **Root hairs**

Root hairs do not tolerate desiccation. They die off and are decomposed by soil organisms (CANNON, 1911; WEAVER & CLEMENTS, 1938; SPECHT & RAYSON, 1957). When the soil is wetted again, new root hairs are formed.

The development of root hairs is optimal in moist, well aerated soils. In wet as well as in dry soils the number of root hairs per area is smaller but often they are longer (METSÄVAINIO, 1931; WEAVER & CLEMENTS, 1938).

Metsävainio found that the number and the length of root hairs in a peat soil is dependent on the nutrient content. In oligotrophic peat the root hairs are less numerous but longer than in eutrophic peat.

DEAN (1933) showed that Calcium influences the development of root hairs in *Typha latifolia*.

Aeration and oxygen supply play an important role. It appears in all cases that a good aeration stimulates development (METSÄVAINIO, 1931; DEAN, 1933; LOEHWING, 1934; WEAVER & CLEMENTS, 1938).

III. 1.3. **Mycorrhiza**

Mycorrhiza is frequently associated with trees. The cover of fungi prevents further longitudinal growth, resulting in a strong ramification. WEAVER & CLEMENTS (1938) say: "Plants showing a good development of mycorrhiza have roots that are short and thick and present a coral-like appearance".

Mycorrhiza is found especially associated with roots in a humus layer and in peat soils (METSÄVAINIO, 1931; WEAVER & CLEMENTS, 1938).

Metsävainio mentions that many species with mycorrhiza lack root hairs.

III. 1.4. Intercellular spaces and aerenchyma

Intercellular spaces in the stem and the root play a role in the gas exchange of the plant, consequently also in the oxygen supply of the roots.

METSÄVAINIO (1931) and OSVALD (1919) found in peat that the intercellular spaces are larger if the oxygen content of the soil is lower. *Ranunculus acer* and *R. repens*, both occurring on soils differing in oxygen content, show larger intercellular spaces in an environment poor in oxygen. CANNON (1925) even found indications that roots give off oxygen to a soil very poor in oxygen.

Only species with large intercellular spaces are able to exist in the ground water. All genuine hydrophytes have air channels. According to EAMES & MCDANIELS (1925) the term aerenchyma physiologically applies to "any loose aerating tissue ... Structurally aerenchyma is a very delicate tissue in which thin partitions enclose air spaces entending parallel with the plant axis. This tissue is formed by a phellogen layer, either cortical or epidermal in origin".

KUTSCHERA (1960) observed that drought may be the cause of spaces in the bark of the root, so large that the connection between exodermis and endodermis is maintained only by a few rows of cells. She assumes that these spaces are at once filled with water when a shower occurs, so that the water is immediately at the disposal of the plant. So in this case the spaces serve the water supply.

In the bark of monocotyledon roots, "large, radial air spaces may arise, because all cells of one or more adjacent radial rows diverge, die off and shrink into thin membranes" (REINDERS, 1943, translated). "These spaces may be in open connection with the intercellular spaces of stem and leaves and therefore perhaps contribute to the oxygen supply of the root; they occur, however, also in steppe grasses and here they are sometimes considered as water containers, though without much evidence."

III. 1.5. Attachment of the plant

Especially the central part of the root system has the function of supporting and to anchoring the plant. Here secondary thickening takes place (LIESE, 1926; LAITAKARI, 1927; MCQUILKIN, 1935; RIEDEL, 1937). Pressure particularly influences the secondary thickening of the root. This can be observed on the leeward side of wind-trees (McQuilkin, Riedel). In this connection we may also mention the buttresses in tropical rain forest that occur only in trees with superficial root systems (RICHARDS, 1952), and the vertical flattening close to the stem of horizontal roots of *Pinus sylvestris* without tap root (LAITAKARI, 1927).

Riedel deduces the anchoring function from the structure of the tap root.

PINKERTON (1936) attributes the function of attachment to secondarily cutinised root hairs in *Commelinaceae*.

III. 1.6. **Shape of the root system**

The question of how far the shape of the root system is determined genetically or ecologically has been the subject of many investigations (CANNON, 1915, 1918; HELLRIEGEL, in OSVALD, 1919; WEAVER, 1919; WEAVER & CLEMENTS, 1938; BISWELL, 1934; KRAUS, WOBST & GÄRTNER, 1934; DITTMER, 1959). Different conclusions were drawn, depending on the species and the type of habitat under consideration.

It appears that the depth reached by the roots, the frequency of ramification and the degree of spreading are to a large extent determined by the environment, though there are species that present similar root systems in different habitats (WEAVER, 1919; DITTMER, 1959).

Hellriegel (cited by OSVALD, 1919) says that plants tend to realize a genetically fixed root system, but that habitat factors modify it.

WEAVER & CLEMENTS (1938) say, on the basis of experiments by Howard with *Phlox* in India: "There is evidence that after long periods of time, during which the soil conditions have had time to impress themselves upon the variety of plants, by a process of natural selection a condition of equilibrium between the type of plant and the soil may be attained".

A species is not able to exceed its genetic potential even if the habitat might demand so. It appears e.g. that *Prosopis velutina*, a species rooting in natural habitats with a deep tap root, cannot maintain itself if the development of this tap root is impeded (CANNON, 1918). Some genetic types are more plastic than others. A species with a tap root and laterals is adapted to more different conditions than a species with its primary root and laterals running superficially.

The habitat selects an assortment of species of appropriate potential. Those which do not fit are unable to live there. The habitat may modify root systems that in principle fit into it already.

III. 1.7. **Water**

> "*Since root position so clearly reflects the moisture conditions of the soil, especially when interpreted in its community relations*..." (WEAVER, 1919, 1920).

Many workers have made field studies of the method of rooting of species and vegetation types. Properties of the soil were determined in connection with the study of roots. Time and again it was shown that the roots are influenced primarily by the hydrology of the soil.

Therefore, the mode of rooting will now be considered in relation to different hydrologic regimes in the soil.

Photo 1

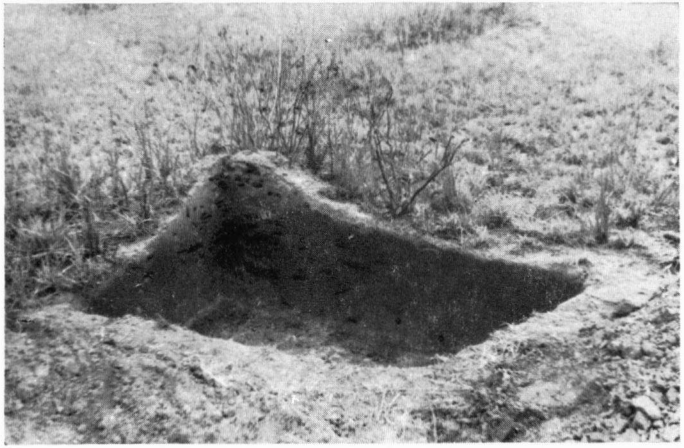

Photo 2

Photo 3

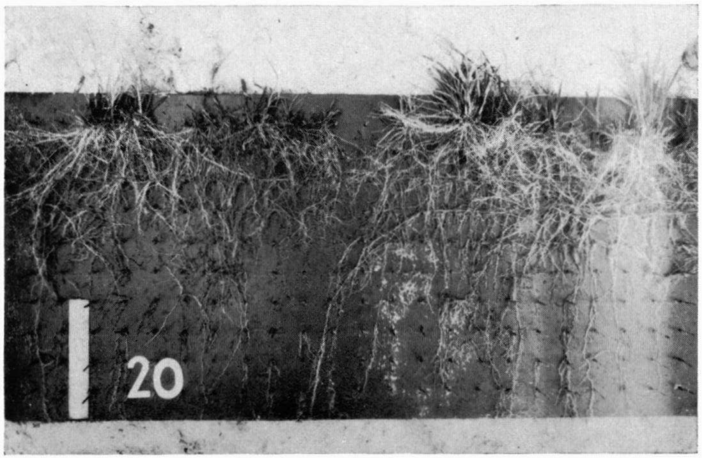

Photo 1. Termitary in *Schizachyrio-Rhynchosporetum mesosetosum*. Bottom right a filled up borrow of an armadillo. The other burrows are of termites. On the hill *Tibouchina aspera* and a small *Curatella americana*. (Ch. II. 3.2.1).

Photo 2. The placing of a board of nails. Two men are cutting of a slice of soil by means of a wire. The shrub at the left is *Symplocos guianensis*. (Ch. III. 2.1)

Photo 3. Board of nails with root systems dug out in *Schyzachyrio-Rhynchosporetum mesosetosum*. From left to right: *Axonopus purpusii*, *Axonopus pulcher*, *Schizachyrium riedelii* and *Mesosetum cayennense*. (Ch. III. 2.1)

Photo 5

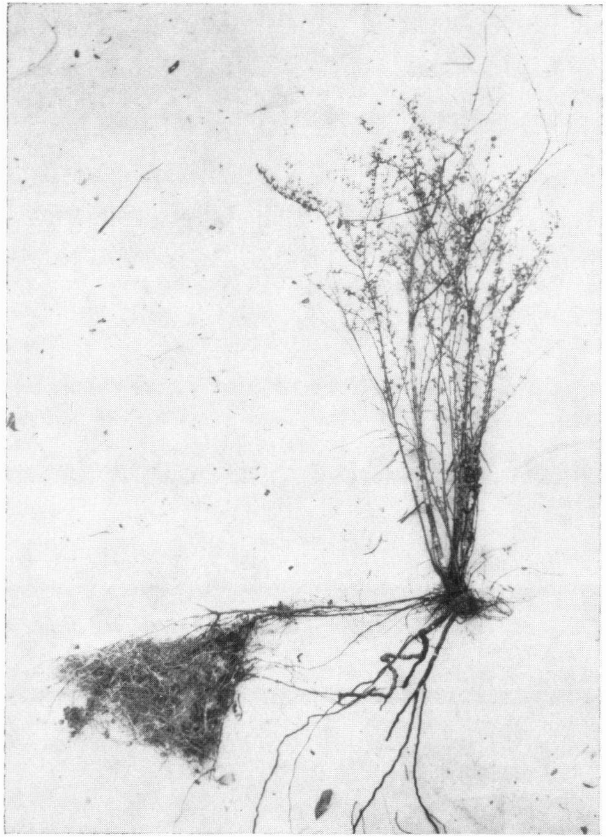

Photo 4

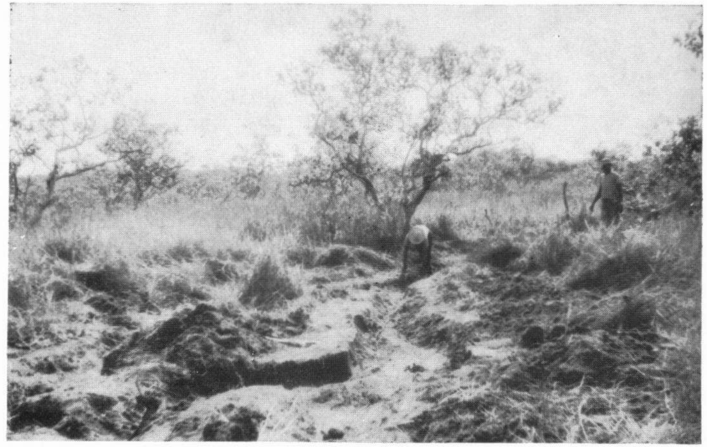

Photo 4. The digging out of the root system of *Curatella americana* in *Polycarpaeo-Trachypogonetum*. Note the rope-like roots in the excavation. (Ch. III. 2.1)

Photo 5. *Cassia ramosa* var. *ramosa*. The root criss-cross was situated under a sugar-loaf shaped termitary. (Ch. III. 4.7)

A. Soils with alternating dry and wet periods (CANNON, 1911; MARKLE, 1917; WEAVER, 1919, 1920; HOLCH, 1931; SPECHT & RAYSON, 1957; DITTMER, 1959).

1. During the dry season the soil desiccates beyond the wilting point, down to a greater depth than is reached by the roots. The field capacity of the soil also influences the rate of desiccation.

a. Soil with a small field capacity, therefore drying rapidly: the root systems are superficial and extensive. Some species have small, rudimentary roots that grow in response to out-of-season rains; others are able to form secondary fibrous roots at a moment's notice, so that advantage is taken of every shower. During droughts the fibrous roots die off.

b. Soil with a large field capacity, still containing some water at a certain depth during the early part of the dry season. In the course of the dry season, however, the soil dries completely down to the ultimate depth of the roots. The root systems reach deeper than those under (a).

KUTSCHERA (1960) remarks about the influence of drought among other things (translated): "It is . . . an indication of dry habitats that the root systems of many species are progressively reduced to less strong and often widely extending roots which produce numerous, more or less long and thin fibrous roots. These fibrous roots may die off during dry periods without much harm to the plants, so that a small amount of root-surface remains exposed to the stronger suction force of the soil. At the start of the wet season they are replaced quickly and then can serve the water supply best in non-suberized or slightly corky state."

2. During the dry season water remains available for the roots at a considerable depth: both species with only a superficial root system and species with one or more long, deeply penetrating roots, reaching the water reservoir, are found here. In the dry season only the deeply penetrating roots function. The long tap root often has superficial laterals (CANNON, 1911; BISWELL, 1934).

NEDROV (1937) wrapped the upper part of tap roots in an impermeable cover. The experiment showed that the plants were able to get enough water and nutrients from the deeper layers alone.

B. Soils with water permanently available

In habitats with a permanently moist soil, other factors modify the shape of the root systems, such as structure and nutrient content of the soil. When at a certain depth a layer occurs with a greater field capacity, caused by a different structure and humus content, the roots ramify more intensively in that layer (WEAVER, 1919; YEAGER, 1935; KEIL, 1940).

Roots do not penetrate from a moist layer into a dry layer. Therefore, the boundary between a wet and a dry layer in a profile means a barrier to the roots (ROTMISTROF, 1926).

The topsoil often is more moist than the deeper layers. This may have several causes, such as higher humus content, better structure, direct wetting by rain water. In this layer there is an accumulation of roots; it is called the sod-layer (KRAUS, WOBST & GÄRTNER, 1934; WEAVER; JONKER, 1958).

Experiments by HENDRICKSON & VEIHMEYER (1931) also show that roots do not penetrate from a moist environment into a dry one. They cultivated plants in baskets of wire netting filled with soil and covered with a layer of wax. These baskets were put in bigger pots also filled with soil. The wax layer was impermeable to water, but roots could penetrate it. The experiments involved the creation of differences in the moisture content inside and outside the wax layer and led to the result mentioned above.

The root system of a species is the more extended the lower the moisture content of the soil, as long as the latter is not too dry (OSVALD, 1919; SPERRY, 1935; WEAVER & CLEMENTS, 1938; KEIL, 1940). Comparable vegetation types tend to have more extensive root systems under conditions of lower moisture (WEAVER, 1920). Species occurring on several soil types with different hydrologic conditions generally adapt their way of rooting to the prevailing type, fitting into the hydrology of their habitat.

C. Soils saturated with water during part of the year

In soils with a high water table, at least during part of the year, the root systems are pushed upwards, as it were, by the ground water. The depth to which the roots penetrate is determined by the ground water (ELLIOTT, 1924; LAITAKARI, 1927; METSÄVAINIO, 1931; KRAUS, WOBST & GÄRTNER, 1934).

OSVALD (1919) cultivated peat vegetations in concrete basins under controlled hydrologic conditions. His experiments showed the same picture.

Roots developed during a dry season with a deep water table die off when the water table rises again and the soil becomes waterlogged (METSÄVAINIO, 1931; HEYWARD, 1933; ROGERS, 1935; WEAVER & CLEMENTS, 1938). The influence of the ground water generally is attributed to lack of oxygen. Only species with special adaptations can root in the ground water.

KRAMER & COILE (1940) and ROGERS (1935) calculate that the water does not move through the pores towards the roots, as was assumed formerly, but that the roots provide themselves with water by penetrating fresh soil again and again, i.e. by growing towards the water. As the old root parts do not take up water any more, the soil occupied by them is available again as a water source for young roots.

III. 1.8. **Soil structure**

Soil structure determines the resistance encountered by a growing root. A friable, loose soil is more easily penetrated by roots than a hard, compact one (KEIL, 1940; GOEDEWAGEN *et al.*, 1955; JONKER, 1958). Sometimes the roots will avoid a compact soil layer, even if it offers more moisture and nutrients than adjacent layers (MARKLE, 1917). When roots do invade a layer of poor penetrability, they take on a shorter, thicker, often contorted appearance (MARKLE, 1917; WEAVER, 1919, 1920; KUTSCHERA, 1920; MCQUILKIN, 1935; KRAUS, WOBST & GÄRTNER, 1939). In a comparison of soil types WEAVER (1919) notes that roots produce more laterals in less compact soils.

The effect of hardpan layers upon root systems has been studied by various authors. Usually, roots do not penetrate into this hard layer, but turn sideways. Through breaks and any old root channels or worm burrows a few roots may penetrate below the hardpan. If the layer below it is moist and rich in nutrients, the roots will ramify (YEATMAN, 1955). Some hardpan layers are soft when damp, and offer no resistance to roots. Such moist hardpan accommodates the root system, that also reaches the deeper layers. To what extent the roots remain alive during the subsequent dry season is unknown (WEAVER & CHRIST, 1922; MARKLE, 1917).

The well known phenomenon of roots growing through decayed roots or root channels may be explained by greater moisture and nutrient content, but also by the lower mechanical resistance of such channels (LAITAKARI, 1927; WEAVER & CLEMENTS, 1938; KEIL, 1940; YEATMAN, 1955).

III. 1.9. **Nutrient supply, organic material**

"In every case where roots came in contact with a fertilized layer they not only developed much more abundantly and branched more profusing, but such a layer apparently retarded normal penetration into the soil below" (WEAVER, JEAN & CHRIST, 1922). Field observations by LAITAKARI (1917), KRAUS, WOBST & GÄRTNER (1934), WOODS (1937), KEIL (1940) and YEATMAN (1955) confirm this report. Experiments with alternating layers rich and poor in nutrients, and with experimental soils of different humus content (MOORE, 1922; WEAVER, 1925; WAHLENBERG, 1929) provide similar evidence. It appears, moreover, that the shape of the roots changes with the nutrient content. In soil rich in nutrients roots tend to be shorter and more ramified than in poor soil (e.g. LAITAKARI, 1917; METSÄVAINIO, 1931; TURNER, 1936; KUTSCHERA, 1960).

Phosphates promote longitudinal growth and branching (WEAVER & CLEMENTS, 1938). Nitrates retard longitudinal growth but enhance ramification (WEAVER, 1925).

Plentiful Ca results in strong roots with many root hairs. Ca deficiency causes short roots.

Plentiful K is correlated with roots of similar appearance to those of moist habitats (KUTSCHERA, 1960).

ROGERS (1935) determined the ratio of the mass of aerial parts to that of the roots of fruit trees. He concludes that in poor soil a greater mass of roots is necessary to support a given mass of aerial parts than in soils rich in minerals.

Kutschera reaches the same conclusion. Poor mineral content does not prohibit growth, however, since even in poor soil roots are found (JONKER, 1958).

Unfavourable moisture content (KRAUS, WOBST & GÄRTNER, 1934) or structure (MARKLE, 1917) may be more decisive, so that under such circumstances roots are limited to layers of better structure and moisture content, but low in nutrients.

III. 1.10. **Oxygen and carbon dioxide**

Oxygen is required by the processes in the roots. This is absorbed by roots from the soil, unless there are special adaptations such as aerenchyma, large intercellular spaces, and aerial roots. For proper functioning of the roots, aeration of the soil is important. The air occurs in pores among the soil particles.

Water/air ratio in the soil

The wetter the soil, the less pore volume is available for soil air. The oxygen dissolved in soil water is not sufficient for most species. During periods of oxygen deficiency absorption stops, while transpiration continues. The plants, though rooted in wet soil, develop a water shortage. They wilt, leaves drop off, and eventually they die (LIVINGSTONE & FREE, 1917; BERGMAN, 1920; WEAVER & CLEMENTS, 1938).

CANNON (1925) found in *Pisum* a "shrinking of the meristematic tissue of the root tip" in the absence of oxygen. After prolonged shortage, the root will not recover, although an entirely new root system may be formed (LIVINGSTON & FREE, 1917; KNIGHT, 1921).

O_2/CO_2 ratio

Soil organisms utilize oxygen and produce CO_2. Since gas exchange with the atmosphere is chiefly by diffusion, the O_2/CO_2 ratio deteriorates with increasing depth. Structure has a profound effect upon aeration and O_2 content of the soil. In poorly aerated soils we always find superficial root systems, since this layer offers the best gas exchange rates with the atmosphere (OSVALD, 1919; WEAVER & HIMMEL, 1930; METSÄVAINIO, 1931; DEAN, 1933). When aeration is improved experimentally or increased by flushing with air, the result is a more homogeneously distributed root pattern. Roots become more branched (CANNON, 1925; DEAN, 1933; LOEHWING, 1934) and the number of root hairs increases. However LOEHWING (1934) observes that with increased aeration the number of root hairs per unit area increases, but that the area of each root that bears root hairs will decrease, as well as the life span of the root hairs. The same author shows that in sunflowers and soybeans the nutrient absorption is greater under conditions of improved oxygen supply.

The connection between soil air and the atmosphere

Exchange between soil air and atmosphere is evidently very important. When the surface is covered by a poorly aerated layer, e.g. a peat layer (heath peat in YEATMAN, 1918), the lower layers will have poor aeration, resulting in an absence of deep roots. Where this layer is interrupted, roots penetrate at once to the subjacent layer. A dense sod layer may also be an obstacle to deep rooting, because all oxygen introduced in rain water is used up by the sod. Only de-oxygenated water reaches the deeper soil layers. Furthermore, the CO_2 produced by the sod may become harmful to the roots (WEAVER & CLEMENTS, 1938).

The reaction to oxygen deficiency depends upon the species. Some have low oxygen requirements and develop roots without special adaptations in oxygen-poor habitats, such as the deeply rooted *Prosopis velutina* (CANNON, 1915) and *Salix nigra*, which roots under water (LIVINGSTON & FREE, 1917); others, such as *Cactaceae*, are very susceptible to oxygen deficiency (CANNON, 1915). In general, plants of well-aerated habitats are more sensitive than those of poorly aerated environments, according to WEAVER & CLEMENTS (1938); and according to LIVINGSTON & FREE (1917) individuals with small root systems are less sensitive than extensively rooted members of the same species.

CANNON (1925) considers oxygen deficiency in relation to temperature, on the basis of experiments "The water saturated walls of the root hairs are intimately related to the water films of the soil, with a cell wall-water boundary, but with a continuity of water. A gas-water boundary delimits the water film on the opposite side."

The amount of dissolved oxygen depends on the temperature; it increases with decreasing temperature. Using root growth as a criterion, CANNON distinguishes an "upper critical partial pressure", i.e. an oxygen concentration allowing for normal growth, and a "lower critical partial pressure", under which root growth is rendered impossible. The interval between these points is that of oxygen shortage. The lower critical concentration is for all species about 1%. The upper critical concentration differs, and determines the oxygen sensitivity of the species. It also varies with temperature in such a way that at lower temperatures the oxygen concentration may be lower, between 2% and 8% depending on the species.

Finally, some species are adapted to low oxygen content of the soil by means of aerenchym, large intercellular spaces, or aerial roots (OSVALD, 1919; METSÄVAINIO, 1931; WEAVER & CLEMENTS, 1938).

Carbon dioxide

CLEMENTS (1921) reports that carbon dioxide concentrations of 2–10% in soil air is harmful to roots, depending on the species. Such percentages occur regularly.

HOLE (1918) says that carbon dioxide is especially injurious in combination with low oxygen content.

III. 1.11. **Temperature**

Experiments of many workers have shown that root growth is temperature-dependent. There are maximum and minimum temperatures beyond which growth ceases. The absolute values are different according to species.

In the soil a gradient of temperature prevails. In temperate regions the deeper layers are usually cooler during the growing season than the top layer. This difference may be responsible for superficial root systems (CANNON, 1915; WOODS, 1957). Cannon reports for two superficially rooted species that they will develop deep roots, provided the subsoil temperature is raised sufficiently. For species which must obtain water from deeper soil layers in the dry season, temperature may thus be quite important. According to KUTSCHERA (1960) this applies especially to winter-annuals. This author also reports a correlation between temperature and root colour. At low temperatures roots are pale, at high temperature yellow to brown, owing to cork formation.

Temperature affects the requirement for oxygen concentration (Ch. III. 1.10).

Temperature differences between layers can also cause displacement and condensation of water vapour.

III. 1.12. **Light**

Light influences assimilation and through the quantity of assimilates also root growth.

HOLCH (1931), BISWELL (1934), NEDROV (1937) and WEAVER & CLEMENTS (1938) all found experimentally that plants in the shade have smaller root systems than similar plants in the sun. Teleologically speaking we may say that sun plants need a larger root system in order to meet the increased demand of transpiration.

III. 1.13. **Competition**

Competition for space for the roots occurs among the individuals of the same locality. The picture of the roots of the vegetation type is one of layers, so that the soil and available water are used in the most economical way (CANNON, 1911; MARKLE, 1917; WEAVER, 1919, 1920). Especially among individuals of one species, which are rooted in the same layer and are moreover active during the same period, root competition is intensive. As a result of this KEIL (1940) finds in *Taraxacum* a distribution of the lateral roots from the tap root in stories. He concludes that lateral roots are found only where there is room.

ADAMS (1929) noted the downward growth of superficial lateral roots of *Pinus banksiana*, when competition for water arises with members of the same species.

MARKLE (1917) says that when there are two dominants in a vegetation, they are rooted in different layers. In a "pure stand" the root competition will therefore be intensive (WEAVER & KRAMER, 1933).

In some cases competition for space and water may prevent further development of the vegetation, although the space above ground is not completely utilized. "The composition of an association is probably determined largely by root competition" (MARKLE, 1917).

III. 1.14. **Mowing and grazing**

"An abrupt decrease in the photosynthetic activity causes a corresponding decrease in the growth of roots." (BISWELL & WEAVER, 1933). Mowing and grazing are both the cause of sudden decrease as indicated above. BISWELL & WEAVER (1933), NEDROV (1937), WEAVER & CLEMENTS (1938) noted a reduction in root systems by repeated grazing and mowing. OSVALD (1919) notes that root systems become superficial under the influence of mowing in bogs.

The same may result from a rapid succession of fires.

III. 1.15. **Periodicity**

Two kinds of periodicity may be distinguished: 1) an annual periodicity, induced by external factors, 2) a life cycle, induced by internal factors.

Annual periodicity

CANNON (1911), McDOUGALL (1916), SCOTT (1928), McQUILKIN (1935) and SPECHT & RAYSON (1957) all describe a period of quiescence in root growth, caused by the deterioration of the environment, such as drought or cold. Growth always resumes when conditions permit. Only LAITAKARI (1927) reports for *Pinus sylvestris* a constant number of dormant and active root tips during the entire year.

Life cycle

LIESE (1926) and LAITAKARI (1927) describe for *Pinus sylvestris* the growth of roots from germination until death. In the juvenile stage there is an annual increase in growth. After this a period of constant annual increase in length occurs and finally they note a annual decline. Liese attributes this phenomenon, apart from aging, also to a logistic cause, i.e. the ever increasing distance which must be traveled by the building materials on the one hand and water and nutrients on the other hand.

KUTSCHERA (1960) states that the root mass is smallest during the flowering period, since all assimilates are used in flowering and fruit development. The destruction of roots is not compensated by the construction of new roots.

III. 2. METHODS

III. 2.1. **Field procedure**

For the exposure of root systems of the "fibrous" type, the "nail bed" method of Rotmistroff was used (METSÄVAINIO, 1931; GOEDEWAGEN, cited by JONKER, 1958).

In a board measuring 115 by 50 cm, nails are placed at intervals of 5 cm in such a way that the pointed ends protrude 8 cm. The result resembles the nail bed of a fakir. A pit is now dug beside the plant or row of plants whose root systems are to be studied. The wall on the side of these plants is made vertical and smoothed out. The board of nails is placed against this wall, with the nails into the wall. A groove is then made along the sides and bottom of the board so that a wire may be pulled through the soil, past the points of the nails (Photo 2). In this way a slice of soil is cut off which will be attached to the board of nails, containing a cross section of the root system of the plant that is to be studied. The board with soil can be transported. By washing away the soil from between the nails (with a garden hose or with buckets when no running water is available) the roots are exposed, kept in place by the nails.

After experimenting with soaking of the soil in synthetic baths, or soda, it turned out that the soils involved in this study can be washed out best without prior soaking.

The roots were drawn to scale and photographed. The drawings give a better picture than the photographs.

In dense vegetation of monocotyledons a nail board does not only give a picture of individual root systems, but also of the vegetation (Photo 3).

The root systems having a main root cannot be exposed in this way. In these species the roots must be dug out. Indian helpers became very adept at this and developed a great patience. Even in a soil where a pit had to be dug with a pick axe, they exposed the roots down to the last root tip using homemade wooden tools (Photo 4). Drawings of the root system were made in situ.

III. 2.2. **Notation**

In order to compare root systems and make correlations with environmental factors, it is necessary to describe root systems in such a way that these comparisons are made quantitatively possible (see Ch. I.2.).

For this purpose a number of root forms were distinguished, and a number of possibilities of root distribution through the soil layers.

For those habitats where a litter layer covers the surface, it appeared desirable to determine whether the roots were limited to the litter area.

Forms of root systems

The root systems were first classified as a) systems with a well developed main root and laterals: the primary root type. b) systems lacking a main root with many equivalent roots: the "fibrous" type. In many cases this division coincides with that between dicotyledons and monocotyledons. There were a few dicotyledons, always Compositae, with fibrous root systems.

Names were selected in such a way that the intended form would be self-explanatory. Names already available in the literature were adopted.

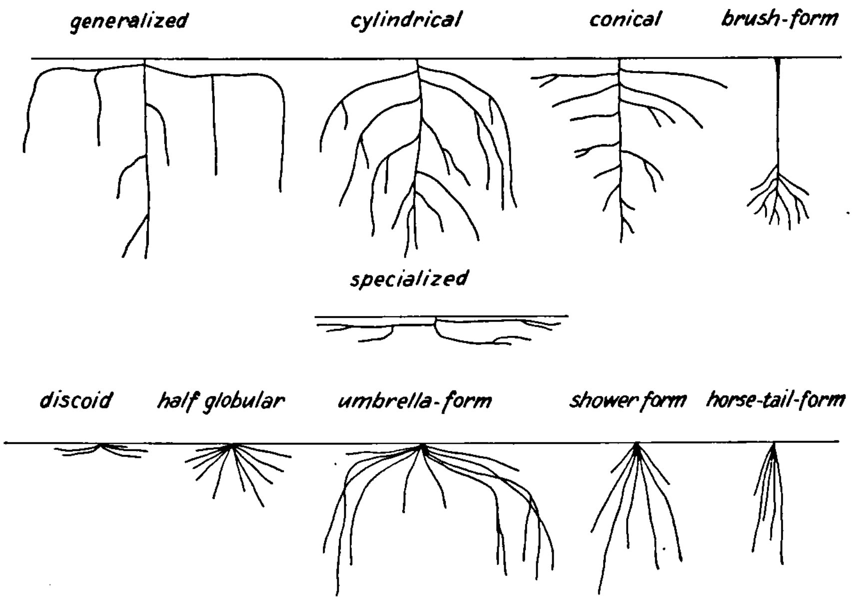

Fig. 4. Root-system forms.

Primary root type (see Fig. 4)

- specialized form
- generalized form
  - mushroom shape
  - cylinder shape
  - cone shape
  - brush shape
  - R. generalized

Fibrous type

- disc shape
- hemispherical shape (in fig.: half globular)
- umbrella shape
- shower shape
- horsetail shape

CANNON (1911) uses the terms generalized and specialized, which are found in much American literature. Root systems are distinguished as specialized when the primary root does not grow down but bends sideways in the superficial layers.

Generalized refers to all root systems with normal primary root and laterals along the entire length. This group needed further subdivision for the present study. KUTSCHERA (1960) described the cylinder and cone shape.

The mushroom shape is not necessarily a spatial form but mostly a cross section in the diagram. In most dicotyledons the number of roots is too small to result in a three dimensional mushroom shape.

Not all root systems of the generalized form belong to the four shapes: cylinder, cone, mushroom and brush. In the present study only few species are involved. They are lumped as "rest generalized" and indicated in future paragraphs as R. generalized.

The shapes of the fibrous types are self explanatory.

Distribution through the soil layers

The distribution of root systems through the soil will henceforth be called "distribution type".

The densely rooted superficial layer will be referred to as the sod layer. The following types are distinguished:

A. rooted exclusively in the sod layer
B. primarily in the sod layer, a few roots penetrate to layers below
C. roots 50% in and 50% below the sod layer
D. roots mostly below the sod layer
E. roots exclusively in the litter layer
F. roots at the boundary of litter layer and mineral soil.

III. 2.3. **Utilization of data**

Root systems of all species in all units of vegetation were completely or partly exposed as much as possible and desirable. In each unit there are a few species, however, which were not dug up. In most cases a prediction is possible of their root system on the basis of their behaviour elsewhere and of the general root picture of the association. In the discussion of the root system of these units such species are indicated in parenthesis.

For each vegetation unit, the root-form spectrum and the root-distribution spectrum are given, both on the bases of the number of species and of the combined estimate according to TÜXEN & ELLENBERG (Ch. I. 3).

The sum of the mean coverages does not indicate the coverage of the roots but the coverage of aerial portions of the species possessing a certain root system.

For the structural diagrams maximum use was made of the results of the nail boards.

III. 3. RESULTS

III. 3.1. **Panicetum stenodoidis** (Fig. 5)*

The sod layer is dense and reaches down to 20 to 25 cm. The deepest roots go down to 90 cm. At this depth a hard layer of concretions occurs. For technical reasons it was not possible to excavate roots any deeper. Not many roots would have gone deeper, since only a few reached 90 cm. The majority of the roots below the sod layer ended at 50 or 60 cm.

Distribution type	Sum mean coverages (%)	Number species (%)
A	2.0 + (0.3)	11.5 + (15.3)
B	3.1 + (15.3)	7.7 + (15,3)
C	75.1	30.7
D	3.9	3.8

A major source of uncertainty under B type lies in the presence of *Rhynchospora barbata* var. *barbata*, with mean coverage of 15%. On

*) Figs. 5–14 have been enclosed separately at the back of this issue.

the basis of the rooting method in the adjacent unit, the *Schizachyrio-Rhynchosporetum mesosetosum*, its behaviour was predicted. The dicotyledons present are rooted, as far as known, exclusively in the sod layer (A). The species which are rooted only shallowly (A + B), are found primarily in the lowest herb layer. The dense root system underneath the sod layer to a depth of 50 to 60 cm, and the prevalence in coverage of type C, that is rooting with as many roots below as in the sod layer, may be correlated with the water economy of the soil (Ch. II. 3.2.3). Owing to the long periods of high water tables and the great field capacity of the clay soil the roots encounter sufficient moisture during a large part of the year in the deeper layers. Following the dry season these are again rapidly moistened by rain water which collects in the shrinkage crevices.

The restriction of the roots of the sparsely represented dicotyledons in the superficial layer can be explained by water surplus during the wet season and the attendant oxygen deficiency. Apparently, monocotyledonous roots are not severely affected by this water surplus.

Shape	Sum mean coverages (%)	Number species (%)
R. generalized	(+)	(7.7)
mushroom . . .	(+)	(7.7)
specialized . . .	2	11.5
hemispherical .	4.2 + (15.3)	11.5 + (11.5)
horsetail	49.5	15.3
disc	(+)	(7.7)
shower	28.4	11.5

The spreading shapes such as umbrella and disc are practically absent; horsetail and shower form, both narrow and deep, prevail in the coverage. We can correlate this with the lack of percolating rain water in the total water economy, due to the poor permeability and the "run-off", and also with the supply of water from below from the ground water and rain water collected in the shrinkage crevices. An extensive horizontal root system, suitable for the interception of percolating rain water, would not be useful, while a deeply developed system will be beneficial.

Correlations

Sufficient moisture in layers below the sod layer during long periods of time-prevalence of type C.

Water supply from below—narrow shapes such as horsetail and shower.

Ground water at the surface during part of the year—superficial rooting of dicotyledons.

Slow uptake of rain water—few spreading forms such as umbrella and disc.

III. 3.2. Schizachyrio-Rhynchosporetum mesosetosum (Fig. 7)

The sod layer reaches down to 15 cm. A few deeper roots go to 50 to 60 cm at most.

Distribution type	Sum mean coverages (%)	Number species (%)
A	+ + (0.7)	6.4 + (25.8)
B	95.0 + (+)	22.5 + (6.4)
C	2.7 + (0.1)	9.6 + (6.4)
D	0.5	3.2

The root system of 12 species, with a total percentage of the mean coverage of 0.94% has been established elsewhere. The root system of 4 tree species is not known.

The different layers have different rooting depths. The highest layer is composed of species with type B and a few of type C. The medium herb layer is rooted almost entirely according to B. The low herb layer is entirely composed of species of the A type. They are rooted in the upper half of the sod layer.

The vegetation is rooted mainly in the sod layer. B type is predominant. No root reaches the area of the ground water. Very occasionally one reaches the gley horizon.

We must conclude, that the vegetation is dependent upon rain water, although capillary ground water will reach a few dm below the surface at its highest level. The percolation velocity is slight and there is considerable run-off. It is not known how deeply the soil is penetrated by rain water. It has also not been ascertained whether rain water makes contact with ground water or whether a dry layer is present permanently between the two. A dry layer constitutes a barrier to root growth. The fact that roots do not penetrate down to the capillary ground water can only be explained by assuming such a dry layer. Water excess, another possible explanation for the limitation of roots to superficial layers, appears to be no obstacle in the *Panicetum* and therefore cannot be limiting in this association especially for species that occur in both units (see Ch. III. 3.1). Further confirmation of the presence of a dry layer is found in the behaviour of roots in termite hills, which occur in this vegetation (see below).

Shape	Sum mean coverages (%)	Number species (%)
R. generalized .	0.8 + 0.4	3.2 + (9.6)
mushroom . . .	+	3.2
cylinder	(+)	(3.2)
cone	+	3.2
specialized . . .	1.4 + (0.1)	6.4 + (3.2)
hemispheric . .	95.5 + (0.4)	22.5 + (3.2)
disc.	+ + (+)	3.2 + (12.9)
shower	0.4	3.2

The rooting method of 6 species (19.3%) is not known.

The preferred form is the hemispherical shape. The horizontal root is mostly somewhat longer than the radius of the projection of the aerial parts. Both extensive horizontal forms and deeply penetrating forms are lacking or scarcely represented. This is in accordance with the slow percolation and therefore slight uptake of rain water, and the supposed dry layer between ground water and rain water zones.

The limitation of roots to the sod layer could also be influenced by oxygen supply. In compacted soil with slow percolation and a well developed sod layer, the rain water which finally sinks through the sod layer will be poor in oxygen. The air circulation is also poor. However, oxygen deficiency did not appear to be a limitation for monocotyledon roots in the *Panicetum*.

Termite hills

In the *Schizachyrio-Rhynchosporetum mesosetosum* there are termite hills with distinctive vegetation. They have a diameter of 1.5 to 2 m and a height of about 60 to 80 cm. In the description of the soil (Ch. II.3) the differences with the unmodified soil were discussed. The most important is the presence of a system of burrows down to about 60 cm below the original surface; this will cause better drainage to this depth. Two termite hills were dug up to study the root systems of species found on them. It was shown that some of the species were already present before the termites began their work. These species (*Tibouchina aspera*, *Curatella americana* and *Eriosema crinitum*) kept pace with the growth of the termite hill. They produced secondary roots in the hill and their root systems go deeper than dicotyledons in the rest of the vegetation and also deeper than most grass roots, to 40 or 60 cm. The form of the root systems is R. generalized, cone, cylinder, and mushroom. The root behaviour is in good agreement with the supposed better drainage, which makes water available more rapidly, in greater quantity and to greater depth.

In addition to the species mentioned, a few others occur on termite hills with a superficial disc type root system (*Eupatorium amygdalinum*, *Scleria bracteata*).

Correlations

Rain water the important source in soil with poor percolation—superficial roots, type A and B.

Rain water absorbed into the soil only slowly—no extensive roots, hemispherical shape prevails.

Better drainage in termite hills—deeper root systems, type C and R. generalized form.

III. 3.3. **Schizachyrio-Rhynchosporetum mitracarpetosum** (Fig. 8)

The sod layer goes down to 15 cm, a few roots penetrate to 30 cm and the roots of a sporadic shrub reach to 1 or 1.50 m. One tree, *Himatanthus articulata*, had a main root down to at least 3 m.

Distribution type	Sum mean coverages (%)	Number species (%)
A	9.3 + (9.9)	6.6 + (33.3)
B	63.0 + (5.6)	13.3 + (13.3)
C	11.4 + (+)	11.1 + (8.8)
D	0.4	2.2
?	0.1	11.1

The deduced forms are, under type A: *Bulbostylis junciformis*, and under type B: *Schizachyrium riedelii*. The latter was dug up in two adjacent vegetation types so that a prediction is fairly safe. The roots of 5 species are unknown: 4 of these are trees. Of the remaining trees 3 are rooted according to C, one as A, B and D.

The layering of roots corresponds more or less to the aerial layering. In the emergent layer *Tibouchina aspera*, with the greatest coverage, is rooted according to type C. In the upper and middle herb layers type B is by far the most important as to coverage. In the low herb layer we encounter exclusively species of type A. In all layers a relatively large number of species with type A is found.

When this picture is matched with the water economy of the soil, we may conclude that rain water is the only water source for almost the entire vegetation. The gley horizon occurs at 40 to 80 cm, a depth which is reached only by the roots of a few trees and shrubs. The run-off is considerable due to the compaction of soil and the poor percolation. Rain water infiltrates into the soil only slowly. From the fact that roots are limited to the upper 20 cm we may deduce that the soil is not moistened deeper. A dry layer always froms a barrier to roots.

Most shrubs penetrate with a single root to a depth where they encounter ground water. Probably they are able to utilize this during the dry season while in the rainy season the superficial root system benefits from rainfall.

In part of the species the deepest roots were dead, in another group they bent sideways. Both phenomena are correlated with the lack of oxygen in ground water.

Shape	Sum mean coverages (%)	Number species (%)
R. generalized .	3.4	13.3
mushroom . . .	11.8 + (0.4)	15.5 + (6.6)
cone	(+)	(2.2)
specialized . . .	+ + (+)	4.4 + (2.2)
hemispherical .	47.2 + (5.5)	8.8 + (8.8)
disc.	23.2 + (7.6)	4.4 + (11.1)
?	0.4	20.0

The mushroom shape has a main root which reaches down below the sod layer, in some trees and shrubs down to ground water. The superficial laterals become very long especially in trees and shrubs. The remaining forms of the primary root type are limited to the sod layer. Only two types of fibrous root systems are represented: disc and hemispherical. Even in the hemispherical shape we find that the horizontal roots spread beyond the radius of the aerial portions.

From the root forms it is clear that the vegetation is dependent primarily on rain water. Even species which extend to ground water level still have an extensive system in the sod layer. Shapes which are primarily downward are lacking.

The root system of this unit can be divided into two types.

1) Superficial systems dependent exclusively on rain water.

2) Systems in which part of the root, usually the primary root, penetrates to the ground water while another part remains in the sod layer and benefits from rain water.

A possible explanation of the fact that dicotyledon roots are able to penetrate through the supposed dry layer between rain water and ground water, is discussed in Chapter III.3.11.2. Another factor may be the cork layer which is well developed and prevents desiccation in dicotyledons.

Correlations

Rain water the principal source of water in a soil with poor percolation—superficial systems, type A and B; hemispherical, disc, specialized, and mushroom shapes.

A dry layer—a barrier to most roots, except a few dicotyledons.

Ground water shallow but below the dry layer—a few dicotyledon roots penetrate to layers within reach of ground water.

Oxygen deficiency in layers within reach of the ground water—dicotyledonous roots die or bend sideways.

III. 3.4. **Polycarpaeo-Trachypogonetum, both subassociations** (Figs. 9 and 11)

For a discussion of the method of comparison of the two subassociations, see Ch. I.3.

The sod layer goes to 15 or 20 cm. Many roots penetrate to 40 or 50 cm. Some go down to 1.20 m.

Cyperetosum

Distribution type	Sum mean coverages (%)	Number species (%)
A	9.6 + (2.7)	17.8 + (16.2)
B	22.5 + (2.4)	9.5 + (8.2)
C	61.5 + (+)	19.1 + (2.7)
D	0.2 + (+)	2.7 + (1.3)
?	0.2	21.9

Curatelletosum

Distribution type	without *Curatella* Sum mean coverages (%)	Number species (%)	with *Curatella* Sum mean coverages (%)
A	17 + (8.0)	20.3 + (13.5)	11.1 + (5.7)
B	3 + (3)	8.1 + (9.4)	2.3 + (2.1)
C	58 + (+)	16.2 + (4.0)	69.2 + (+)
D	4 + (+)	2.7 + (1.3)	3.0 + (+)
?	8	24.3	5.5

There are many species whose root system was not excavated. Their coverage in the cyperetosum is slight, in the *curatelletosum* it is higher. Most are annual species.

Both subassociations are rooted mostly according to type C, with as many roots in the sod layer as below. Most species are rooted according to types A and B however.

As to the distribution among the layers, the lowest layer in both cases is rooted according to type A, while the tree layer and the emergent layer are dominated by type C. The herbaceous layers are rooted according to types A, B, and C, while in the high herb layer type C prevails. The root picture is in agreement with expectation on the basis of data concerning water economy and soil type. There are no demonstrable differences between the soils of the two subassociations. Capillary ground water reaches to about 100 cm below the surface. This depth is reached only by a few dicotyledon roots. At the level of the gley horizon the roots of some species are bent and branched. This includes *Curatella americana*, the shrubs *Eugenia punicifolia*, *Psidium guineense* and *Galactia jussieuana* and the half-shrub *Cassia hispidula*.

The majority of the vegetation is not so deeply rooted and is therefore limited to rain water. The soil has good percolation, there is no run-off, so that all rain water is absorbed. The deeper layers from 80 cm on are constructed of finer material and have therefore a less rapid percolation, so that rain water does not sink out of reach immediately.

The roots therefore will encounter moisture below the sod layer. Root type C prevails in both subassociations.

On the other hand the soil becomes completely dry down to ground water during the dry season. This is probably the reason why there are so few species especially among the monocotyledons, which reach ground water. The plants would have to have a protection for the root system along a considerable length. Dicotyledons with protective cork layers around the roots are probably better adapted than monocotyledons.

The difference between the two subassociations is first of all the presence of *Curatella americana*. For a discussion of the root system of *Curatella* see Ch. III.3.11.1.

The other differences are mainly quantitative. The species composition is almost identical. For a comparison of the subassociations, *Curatella* is not considered in the *curatelletosum*. In the *curatelletosum* there is an increase in dicotyledons at the expense of the grasses.

It appears that in the *curatelletosum* high coverage occurs among species whose roots are type A, and much less among those with roots of type B. The decline of B is caused by the slight coverage of grasses, while the increase of A is due to the dicotyledons. Type D also increases.

Cyperetosum

shape	Sum mean coverages	Number species
	(%)	(%)
R. generalized .	+ + (0.6)	5.4 + (5.4)
mushroom . . .	1.1 + (0.1)	16.4 + (8.2)
cylinder	0.2	2.7

cone	2.4	4.1
specialized. . .	0.3 + (+)	5.4 + (1.3)
hemispherical .	16.3 + (+)	1.3 + (2.7)
horsetail. . . .	+	1.3
umbrella . . .	66.8	2.7
disc.	9.4 + (1.8)	13.7 + (4.1)
shower	(+)	(1.3)
?	0.7	23.2

Curatelletosum

Shape	without *Curatella* Sum mean coverages (%)	Number species (%)	with *Curatella* Sum mean coverages (%)
R. generalized .	+ + (1)	4.0 + (5.4)	0.3 + (0.5)
mushroom . . .	2 + (1)	14.8 + (9.4)	30.1 + (0.5)
cylinder	4	2.7	3.1
cone	3	4.0	1.0
specialized . . .	0.8 + (+)	2.7 + (4.0)	0.5 + (0.1)
hemispherical .	+ + (+)	1.3 + (2.7)	0.3 + (+)
horsetail, . . .	—	—	—
umbrella . . .	57	2.7	40.3
disc.	16 + (+)	14.8 + (2.7)	11.4 + (0.3)
shower	+ + (6)	1.3 + (1.3)	+ + (4.4)
?	8	24.3	5.5

In general, the root systems exceed the projection of aerial portions. Shrubs and trees have horizontal roots of many meters. In both subassociations the specialized form of the primary root type is in the minority; the mushroom shape is the most common. The umbrella form prevails in the "fibrous" type, primarily by the dominance of *Trachypogon plumosus*. The hemispherical and disc shape follow next, horsetail and shower shape are both present with one species. Most species of the fibrous root type belong to the disc shape. In the *curatelletosum* we note a general increase in the primary root types in comparison with the cyperetosum. The hemispherical shape of the fibrous type decreases by the decline of the grasses. The disc shape increases, because some dicotyledons (Composites) also have this root form. The shower shape is due to *Heliconia psittacorum*. In the upper herb layer the umbrella shape has the highest coverage, in the medium herb layer the hemispherical shape and in the lowest herb layer the disc shape. There is no correlation between aerial portions and root types of the dicotyledons.

The root forms generalized, mushroom, cylinder, and umbrella reflect favourable conditions below the sod layer. They all have both superficial and deep roots. They also have rather extensive forms. This also is true for the disc shape. The superficial, horizontal expansion can also be correlated with the rapid penetration of rain water, and the favourable percolation rate through the soil. An extensive system is able to utilize more rain water than a system of slight horizontal dimension.

The rooting volume occupied by the plant may also be correlated with the mineral content of the soil. No further data are available on this point.

A discussion of the umbrella shape will be found under the treatment of the root system of *Trachypogon plumosus* (Ch. III.3.11.1).

The difference between both subassociations in the rooting method is correlated with the higher coverage of dicotyledons in the *curatelletosum*. The cause of this is not to be found in properties of the root system, nor in those of the soil.

Correlations

Rain water as a water source in soil with rapid penetration—spreading forms such as disc, specialized, and mushroom.

Moist layers below the sod layer during the growing season—many roots below the sod layer (type C).

Water supply of soil below the sod layer from percolating rain water—shapes spread also in depth such as umbrella, cylinder, and R. generalized.

Ground water deep but within reach—some roots down into the layers within reach of the ground water.

Desiccation to great depth during the dry season—only dicotyledons penetrate to the ground water.

Oxygen deficiency in layers within reach of the ground water—dicotyledon roots bent or branched strongly.

III. 3.5. **Mesoseto-Trachypogonetum** (Fig. 10)

There is no sharply defined, closed sod layer. The layer with dense root system reaches down to 10 or 15 cm. Roots are encountered frequently down to 40 cm, while *Trachypogon plumosus* extends to 80 cm and a few dicotyledons to the ground water level at 120 to 150 cm.

Distribution type	Sum mean coverages (%)	Number species (%)
A	22.3 + (10.9)	16.6 + (27.7)
B	3.5 + (0.8)	5.5 + (2.7)
C	61.9 + (+)	27.7 + (5.5)
?	1.3	13.8

The numbers in parentheses refer to species which were dug up in other units. On the basis of their behaviour in those units and the general root picture of the present association their behaviour was predicted. The largest share in the coverage is due to *Axonopus pulcher*, which was dug up in the two adjacent vegetation types.

There are many species of types A and C; type B is much less represented. Since the sod layer is not sharply delimited, the difference between types A and B is often arbitrary. Species with type C roots have the highest coverage. Type D is absent. Some dicotyledons, e.g. *Curatella americana*, *Cassia hispidula* and *Tetracera asperula*, reach the level of the ground water. Here they bend sideways or branch into a criss-crossing system of roots.

The upper herb layer is completely of type C, the low herb layer both A and C. The C in this layer is entirely due to *Mesosetum loliiforme* which reaches 40 cm. The medium herb layer has a varied root system.

It is known from soil data (Ch. II.3.), that water is rapidly absorbed after a shower and will sink through.

Since the vegetation mostly does not reach ground water, the source of water supply is rain.

The high coverage of root types A is in agreement with this situation. But rain water is also of importance below the sod layer. Since water sinks out of reach rapidly on the one hand, and evaporates on the other hand, there is an advantage in superficial root systems which catch as much of the precipitation as possible.

Root systems are shallow, although rain water percolates down to ground water and moistens the entire soil body. The question why more roots do not reach the ground water, may perhaps be answered by considering the long dry season. At that time the soil dries out completely down to the level of capillary water. Plants would have to be protected against drying out along the entire root system through these dry layers. For dicotyledons with protective cork layers this would be easier than for monocotyledons. The few roots which do reach the ground water are dicotyledonous.

Shape	Sum mean coverages (%)	Number species (%)
R. generalized .	(0.5)	(13.8)
mushroom . . .	10.5 + (+)	27.7 + (5.5)
cone	(0.9)	(2.7)
specialized . . .	0.7	5.5
hemispherical .	+ + (8.6)	2.7 + (2.7)
umbrella . . .	22.8	2.7
disc.	21.8	5.5 + (13.8)
shower	29.4	2.7
?	1.3	13.8

All species are rooted well beyond the projection of the aerial portions. Many species have very large root systems in proportion to the aerial dimensions.

In the low herb layer all species have a disc shaped system, except *Mesosetum loliiforme*, whose coverage is highest and whose root system is shower shaped. In the high herb layers there is one species with a disc shaped system.

Among the primary root type, the mushroom shape predominates in coverage and number of species; among the fibrous types a high coverage occurs in the umbrella, disc,and shower shapes. A better summary would be to say that small root systems are absent; even the shower form tends to fan out sideways.

This vegetation type is adapted to the interception of rapidly sinking rain water, by root systems with superficially extensive shapes such as disc and mushroom. In the mushroom shape there are many lateral roots and they grow very long. This will enable the vegetation to utilize rain showers even during the dry season.

Apart from the common disc shape, all other forms (mushroom, generalized, hemispherical, umbrella and shower) are able to utilize the percolating water in deeper layers. It should be remembered again, that the roots are not very dense and the sod layer is not closed.

Correlations

Rain water the principal water source, but rapidly percolating to great depth—very extensive horizontal systems (disc, specialized, and mushroom shape).

Rain water penetrates below the sod layer—deeply and widely spread systems (shower and umbrella shapes, type A, B and C).

Ground water within reach, but deep—some roots to depth within reach of the ground water.

Oxygen deficiency in the layers within reach of the ground water—the roots of dicotyledons bend sideways or branch strongly.

Desiccation to great depth during the dry season—only dicotyledonous roots down to ground water.

Pure white sandy soils—sod layer not closed and soil not occupied by dense root systems.

III. 3.6. **Vegetation types of pure white sands, wetter than Mesoseto-Trachypogonetum, particularly the Xyrido-Paspaletum** (Fig. 6)

In vegetation types on white sands of various degrees of moisture,

TABLE 1

Characteristics of root systems of species occurring

	Syngonantho-Lagenocarpetum				Xyrido-Paspaletum			
	typicum				typicum			
Ground water table								
rainy season								
own observation	surface				?			
Heyligers	surface				surface			
dry season								
own observation	110 cm				?			
Heyligers	60–100 cm				70–90 cm			
Hardpan								
own observation	130 cm				?			
Heyligers	–				–			
	depth (cm)	shape	distr. type	spreading (cm)	depth (cm)	shape	distr. type	spreading (cm)
Paspalum pulchellum	10	hemisph.	A	5	20	horse tail	B	5
Leptocoryphium lanatum . . .	5–25	shower	C	5		X		
Rhynchospora graminea					10	horse tail	B	5
Rhynchospora barbata var. glabra					5–15	hemisph.	A	5
Panicum micranthum					20–25	horse tail	C	5
Mesosetum loliiforme								
Bulbostylis circinata								
Trachypogon plumosus								
Date of field work	9–3–1959				2–4–1959			

root systems were excavated using the nail board. Drawings are represented of the nail boards from the *Syngonantho-Lagenocarpetum tremuli* typicum, the *Xyrido-Paspaletum* typicum, the *Bulbostylidetum circinatae* typicum and *bulbostylidetosum coniferae* (Fig. 6).

The habitats differ in the level reached by the water table during the long wet and the long dry season. Table 1 presents the highest and lowest levels together with the sizes, forms and distribution of the root systems of those species which occur in more than one of these types. For comparison the *Mesoseto-Trachypogonetum* is also included.

In these habitats there is an alternation of water surplus and deficiency, with transitional periods in between. The deeper soil is permanently saturated with water. Above it, there are saturated layers during parts of the year depending upon the schedule of ground water movements. If the ground water does not come up to the surface, the water supply of the upper layer is exclusively by precipitation. This means that there is a water deficit, except during or immediately following rain. Prolonged saturation and drought both influence the root systems. The vegetation units were arranged according to their water economy. At one extreme is the *Syngonantho-Lagenocarpetum* (1), with long lasting water surplus. The ground water rises above the surface during a part of the rainy

in different vegetation types on wet white sand

Bulbostylidetum circinatae								Mesoseto-Trachypogonetum			
typicum				bulbostylidetosum coniferae							
surface				?				± 100 cm			
20 cm – surface				40–20 cm				440 cm			
> 120 cm				?				200 cm			
80–120 cm				150–130 cm				540 cm			
120 cm				?				?			
–				–				–			
depth (cm)	shape	distr. type	spreading (cm)	depth (cm)	shape	distr. type	spreading (cm)	depth (cm)	shape	distr. type	spreading (cm)
25	shower	C	10								
20–40	shower	D	20–30	20–30	hemisph.	C	20				
30–50	horse tail	C	5	15–25	hemisph.	B	10–15				
10–20	hemisph.	A	5–10	5	disc	A	10	5	disc	A	10
30–35	horse tail	C	10–15	10–15	hemisph.	B	5–10				
30–35	horse tail	C	10	10	hemisph.	A	15	40–50	shower	C	20–25
15	hemisph.	A	15	5	disc	A	10–15				
				10	disc	A	25	80	umbr.	C	50
6 + 7–3–1959				3–4–1959							

season. There is nevertheless a dry superficial layer during the dry season. At the other extreme is the *Mesoseto-Trachypogonetum* (5), whose superficial layers never experience water surplus. The *Xyrido-Paspaletum* (2), *Bulbostylidetum circinatae* typicum (3) and *bulbostylidetosum coniferae* (4) constitute links between these two extremes. In the *B. circinatae b. coniferae* ground water just reaches the surface.

For species found in more than one vegetation type, we may note the following correlations between root systems and water economy.

Duration of water surplus increases: represented by the vegetation series 3-2-1: root systems become shallower. The following species conform to this pattern:

Paspalum pulchellum, studied in 3, 2, 1.
Leptocoryphium lanatum, studied in 3 and 1.
Rhynchospora graminea, studied in 3 and 2.
Rhynchospora barbata var. *glabra*, studied in 3 and 2.
Panicum micranthum, studied in 3 and 2.

The conclusion is justified, that root systems of these species tolerate water surplus for a certain length of time. With increasing saturation of the soil, and with progressively shallower soil layers whose saturation lasts for tolerably short periods, the root systems tend to grow shorter. If saturation lasts too long, the species will disappear.

The ground water forces the root system upward. This effect can be seen clearly in the nail board of types 3 and 2.

The same phenomena can be approached from the other direction, the *decreasing duration of water surplus*, exemplified by the series 1-2-3-4-5.

For the species already mentioned, root systems will of course increase in length. When vegetation types 4 and 5 are included, this increase in length appears to be limited.

Leptocoryphium lanatum: 1→3 root system deeper, 3→4 shallower.
Rhynchospora graminea: 2→3 deeper, 3→4 shallower.
Rhynchospora barbata var. *glabra:* 2→3 deeper, 3→4 shallower, 4→5 unchanged.
Panicum micranthum: 2→3 deeper, 3→4 shallower.
Mesosetum loliiforme: 3→5 deeper.
Bulbostylis circinata: 3→4 shallower.
Trachypogon plumosus: 4→5 deeper.

There is a break between types 3 and 4 in the behaviour of the root systems. This is also clearly expressed in the drawings of the nail boards.

The roots follow the ground water down to the zone where saturation does not last too long. When ground-water fluctuations occur at a deeper level, the duration of the dry period in the upper layers increases. The length of roots which traverse a dry layer for part of the year, increases accordingly. The species are not able to increase this length further and further. The critical length for these monocotyledons is obviously between vegetation types 3 and 4. Some dicotyledons, with corky bark, penetrate the dry soil down to ground water in type 4, and also in much drier vegetations (see Ch. III.3.5 and 3.8).

Increasing duration of the dry period, exemplified by the vegetation series 1-2-3-4-5.

Paspalum pulchellum: 1→2, root system equally extensive, 2→3 more extensive.

Leptocoryphium lanatum: 1→3 more extensive, 3→4 equally extensive.

Rhynchospora graminea: 2→3 equally extensive, 3→4 more extensive.

Rhynchospora barbata var. *glabra:* 2→3 equally extensive, 3→4 more extensive, 4→5 equally extensive.

Panicum micranthum: 2→3 more extensive, 3→4 less extensive.

Mesosetum loliiforme: 3→5 more extensive.

Bulbostylis circinata: 3→4 equally extensive.

Trachypogon plumosus: 4→5 more extensive.

In most cases the spread of the root system increases with increasing drought. With increasing drought the importance of precipitation as a water source enhanced. A more extensive root system intercepts more rain water.

In the drawings of the nail boards of vegetation types 2, 3, 4 and 5 this effect can be seen clearly.

Species which occur in both types 3 and 4 switch over from ground water to rain water in vegetation type 4.

Species from wet and dry habitats meet one another in the *Bulbostylidetum circinatae bulbostylidetosum coniferae.* The moisture-adapted species probably survive because of the ground water that reaches the surface, the drought-adapted ones in spite of this fact. For both categories the root system remains superficial. The wet category is forced to the surface by excessive drought, the dry category by water surplus during the period when ground water reaches the surface. *Mesosetum loliiforme* is the only species which belongs in both wet and dry habitats.

Vegetation types 1, 2 and 3 are therefore ground water vegetations, while 4 and 5 are dependent upon precipitation for their water supply. The shape of the root systems is correlated. In the habitat dependent on precipitation, the disc and umbrella shapes predominate; in the habitat dependent on ground water, the horsetail and shower shapes.

Since both environments offer the same nutrient content, we may conclude that lack of nutrients is not responsible for extensive root systems.

For the sake of completeness the following quantitative data concerning the roots of the *Xyrido-Paspaletum* are listed.

Distribution type	Sum mean coverages (%)	Number species (%)
A	13.9 + (25.4)	16.6 + (21.4)
B	9.7 + (6.7)	9.5 + (4.7)
C	29.3 + (0.6)	7.1 + (4.7)
D	(0.1)	(2.3)
?	13.7	33.3

Shape	Sum mean coverages (%)	Number species (%)
R. generalized .	(0.4)	(4.7)
cone	3.5	2.3
specialized. . .	3.4 + (0.3)	11.9 + (7.1)
hemispherical .	7.0 + (2.5)	7.1 + (11.9)
horsetail. . . .	39.1 + (5.0)	11.9 + (4.7)
?	38.1	38.0

The number of unknown species is especially high because therophytes were absent at the time of the field work. The dicotyledons, which were not mentioned in the previous discussion, are all rooted with specialized form in the sod layer. This is due to high water tables.

III. 3.7. **Clusia-Scleria scrub, Comolia-variant** (Fig. 12b and c)

The soil in the bush is covered by litter, varying in thickness. At the boundary of litter and sand a root mass may be found, formed especially by *Bactris campestris*. Even when this mass is absent, we can distinguish a sod layer. It reaches down to 10 or 15 cm. The deepest roots penetrate 60 cm (*Marlierea montana*).

Distribution type	Number species with high coverage	Number species (%)
A	4	54.5
B	2	9.0
C		(9.0)
D		4.5
E		4.5
?		18.1

The vegetation is almost exclusively dicotyledonous, rooted in the upper layer. One species, *Retiniphyllum schomburgkii*, is not rooted in the sand but is limited to the litter layer. The upper layer is the one with the shortest duration of water surplus, since ground water reaches the surface. This may be the cause of the superficial root system. But organic content is also the highest in the layer just below the litter layer.

The superficial rooting method means that there is water deficiency during the long dry season, even though ground water does not sink deeper than 70 cm.

Shape	Number species with high coverage	Number species (%)
specialized. . .	5	54.5
hemispherical .	1	9.0 + (9.0)
disc.		9.0
?		18.1

The specialized form predominates in coverage and number of species. This is correlated with the high ground water level, which causes oxygen deficiency. The roots of the dicotyledons prefer the most superficial layer, where aeration is best. The primary root dies off or runs horizontally in the sod layer. Many species have an extensive root system. The horizontal roots generally grow several meters long and reach well outside the projection of the aerial portion. The extensive root system enables the plants to benefit from rain water during the dry season, when ground water is out of reach.

Relation to litter area	Number species with high coverage	Number species (%)
within	2	40.9 + (4.5)
outside	(1)	(9.0)
within + outside	3	22.7 + (4.5)
?		18.1

See also map in Fig. 12c.

Many species are limited to the area of the litter (*Clusia fockeana, Conomorpha magnoliifolia, Bactris campestris, Ternstroemia punctata*). At the edge of the litter area the roots turn, so that they remain within the area covered by litter. Sometimes roots are found which have ventured outside the area. Their tips have died.

Underneath the litter layer, the content of organic material is higher. The litter layer also decreases evaporation from the underlying soil, so that the environment is more favourable for roots during the dry season, when the superficial layer would be bone dry. The roots which grow out of the litter area during the wet season, die off in the following long dry season.

There are species which are therefore limited to this environment with a litter layer. These are of course limited to the bushes. A few species which may also root outside the litter area (*Comolia vernicosa, Licania incana,* and *Tetracera asperula*) are also encountered as isolated shrubs in the *Xyrido-Paspaletum*, which occurs on the same pure white sandy soil with the same ground water regime. *Humiria balsamifera* and *Marlierea montana* will root outside the litter area, but do not occur as isolated individuals.

Correlations

High water table—very superficial root systems, specialized, A.

Drying of root layer in the dry season—extensive horizontal root systems, limited to litter area.

III. 3.8. **Ternstroemia-Matayba scrub, Humiria variant** (Figs. 13 and 14)

The objective for this vegetation was to gain an impression of the method of rooting. Not all species were excavated, only all dominants and a few companion species.

The sod layer in the bush is immediately below the litter layer and goes down to 10 or 15 cm. The sod layer has a dense root system, creating a real mat (see HEYLIGERS, 1963). Outside the bush the root layer is 15 to 25 cm below the surface. It is formed by the roots of plants within the bush, and is sparse.

Distribution type	Number species with high coverage	Number species (%)
A	2	9.6 + (12.9)
B	2	9.6
C	1	3.2 + (12.9)
D		—
E		3.2
F		6.4
?		41.9

The emphasis is on superficial root systems, A, B, E, and F. D is totally absent. Distribution type C is found only for *Clusia fockeana*. It may be expected for four other species, based on their rooting method in the *Mesoseto-Trachypogonetum*. The roots of *Clusia* penetrate to the hardpan at 2.50 m. Ground water is at least 2 m deep. Rain water is of great importance for this vegetation; for many species it is the only source of water. *Conomorpha magnoliifolia*, *Ormosia costulata*, and *Ternstroemia punctata* have a main root down to 2 m. The root is branched at this level.

The emphasis on superficial root systems is in accordance with the importance of rain water in the water supply. There are roots below the sod layer. They benefit from percolating rain water. As a result of the dense root mat the percolating rain water will be deficient in oxygen. This, and the greater organic content make the superficial soil layer more suitable for the roots.

It is remarkable that the root layer outside the bush is deeper than inside, and that no roots are found near the surface. One and the same root of *Clusia*, *Ternstroemia* or *Ormosia* occurs outside the bush at a deeper level than inside the bush.

Shape	Number species with high coverage	Number species (%)
generalized . .	1	3.2 + (12.9)
mushroom . . .	1	12.9
specialized . . .	2	9.6 + (6.4)
hemospherical .	1	6.4 + (9.6)
?		41.9

None of the forms of the primary root type appear to predominate. This is in accordance with the water economy. All forms have superficial roots which utilize rain water. The generalized and mushroom shapes utilize percolating rain water with their deeper roots, and ground water if they manage to penetrate deep enough. All horizontal roots become many meters long and reach well outside the projection of aerial portion. Most of them have few or no lateral roots. Only the ends are branched. Sometimes the end of the root bends down to a depth of 60 or 80 cm. Only along horizontal roots of *Humiria balsamifera* and *Marlierea montana* are there many small lateral rootlets.

Relation to litter area	Number species with high coverage	Number species (%)
inside	1	16.1 + (12.9)
outside		3.2
inside + outside	4	16.1 + (9.6)
?		41.9

The result of the litter layer is a higher content of organic material in the underlying soil layer, and probably higher moisture. Both results are favourable for root growth.

It is remarkable that the dominants are able to root outside the litter area, while the companion species are limited to it. The roots turn at the edge of the litter area (Fig. 14).

Only those species which are able to root outside the litter area, are found isolated outside the bushes.

Humiria balsamifera is a tall shrub inside the bush, a low shrub with procumbent branches at the edges. Only the rooting method of the latter form was determined. Very long horizontal roots run out beyond the litter area.

Correlations

Rain water the most important water source—very extensive root systems, mushroom and specialized, and superficial distribution, A, B, F and E.

Rapid water uptake—roots even below the sod layer, mushroom, generalized, B.

III. 3.9. Detailed discussion of certain species of the bushes on white sand

For a better understanding of the relationships between soil and scrub vegetation, it is necessary to compare the behaviour of root systems of those species which occur in both of the units discussed above. In addition, individuals of several species were excavated from sites with water economy intermediate between those of dry and wet bushes, corresponding with the water regime, of the *Bulbostylidetum circinatae bulbostylidetosum coniferae*.

We indicate these three vegetation types as wet (W), moist (M) and dry (D). See Table 2.

Conomorpha magnoliifolia (Figs. 12b, c, 13, 14) occurs in W. M and D, always rooted below the sod layer. Roots exceeding the litter area are dead.

Clusia fockeana (Fig. 15) occurs in W, M and D. In W we encounter very superficial horizontal roots only, below or at the boundary of the litter layer and sand, sometimes a little above the surface. They are limited to the litter area. The ends of roots which exceed the area were dead. In M there are horizontal roots both within and outside the litter area. Outside they run at a depth of about 20 cm. Vertical roots, attached to the horizontal ones, go down to 80 cm. In D the horizontal roots are both within and outside the litter area. Outside they are at a depth of 20 to 30 cm, inside just below or at

TABLE 2

Characteristics of root systems of shrubs in bushes on wet and dry white sand

spec. = specialized   mush. = mushroom
gen. = generalized   measures in cm

	vegetation-type	shape	distribution type	litter area	length	depth of horizontals	greatest depth
Conomorpha magnoliifolia	W	spec.	A	inside	50		20
	M	spec.	B	inside	300		30
	D	mush.	B	inside	400		180
Clusia fockeana	W	spec.	A	inside	350	0–10	10
	M	gen.	C	inside + outside	300	0–20	80
	D	gen.	C	inside + outside	1500	20–30	280
Humiria balsamifera	W	spec.	B	inside + outside	150	0–5 à 10	> 50
	M	spec.	B	inside + outside	400	0–10	60
	D	spec.	A	inside + outside	2000	20–30	30
Licania incana	W	spec.	A	inside + outside	200	0–10	20
	D	spec.	B	inside + outside	600	20	50
Retiniphyllum schomburgkii	W	spec.	E	inside	100		
	D	spec.	E	inside	300		
Ternstroemia punctata	W	spec.	A	inside	400	0–10	20
	D	mush.	C	inside + outside	1000	20	180
Marlierea montana	W	spec.	D	inside + outside	150	0–15	60
	M	spec.	D	inside + outside	400	20	60
	D	mush.	B	inside(+ outside)	800	0–10	80

the boundary of litter and sand. Vertical roots penetrate to the hardpan at 2.80 m.

The ground water level is clearly the determining factor for the depth of the horizontal roots and the length of the vertical ones.

Humiria balsamifera (Figs. 12b, c, 13, 14) occurs on white sand from very wet to very dry. The roots go preferably beyond the litter area. At the inner extreme of the underground trunk there is a root which runs underneath the litter layer. In W the roots are 10 cm below the surface. They are about 1.50 m long and remain thin. Only the tip of the underground trunk produces living roots, further back they are dead or have dead tips. The root at the inner end turned

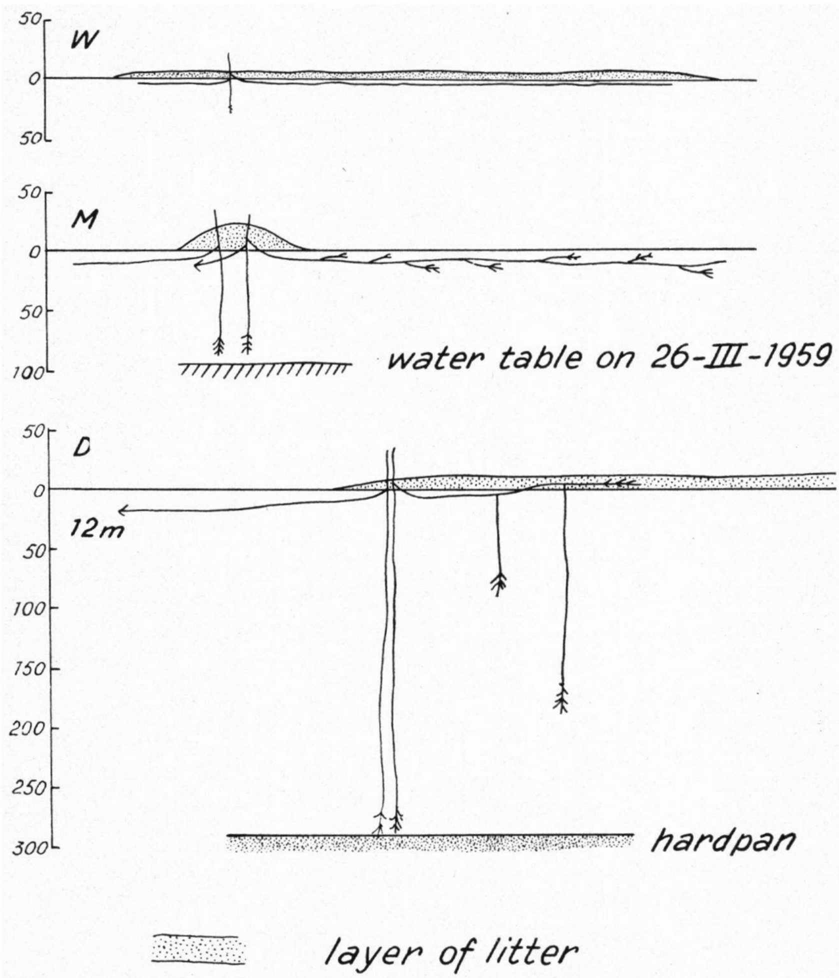

Fig. 15. Root system of *Clusia fockeana* in *Clusia-Scleria-Comolia* scrub (W). *Ternstroemia-Matayba-Humiria* scrub (D). Habitat with intermediary moisture conditions (M). 1/60 ×

vertically and reached down below 50 cm. In M the roots run 10 cm below the surface and remain thin. Some root tips bend down to a depth of 60 cm, and become 4 m long. In D the roots run to a depth of 25 to 30 cm, have a thick bark and lateral roots along their entire length. The length may be 20 m.

Licania incana (Figs. 12b, c, 13 and 14) occurs from dry to wet habitats. The roots in all habitats occur in sand both within and outside the litter area. There are only horizontal roots. In W the roots are 10 cm deep. The length was 2 m. In D the roots run underneath the litter at 25 cm depth, outside the litter area they are at a depth of between 10 and 30 cm. They grow 6 m long. One small root reached down to 60 cm. One treelike individual, which was excavated from a bush of the dry type, had many more roots than the small shrubs which occur isolated in dry sand.

Retiniphyllum schomburgkii (Figs. 12b, c, 13 and 14) occurs in bushes from wet to dry. The roots are always exclusively in the litter layer. The only difference is one of length: in W 1m, in D 3 m.

Ternstroemia punctata (Figs. 12b, c, 13 and 14) occurs both in wet and dry white sand. In W all roots are superficial above 10 or at most 20 cm. They are limited strictly to the area of litter. The length may be 4 m. In D the plants have a primary root in the sand which grows to a depth of 1.80 m. There are many horizontal roots, more than in W. These run both within and outside the litter area. They occur at a depth of 20 cm in the sand, while the tips may bend down to a depth of 60 cm. The length may reach 10 m.

Marlierea montana (Figs. 12b, c and 14) occurs in both wet and dry bushes. The roots grow through the sand both within and outside the litter area. In W there is only a horizontal primary root, at a depth of 15 cm. It may become 1.50 m long. The branching at the tip penetrated down to 60 cm. In M there are only horizontal roots at a depth of 20 cm in the sand. One root went down to 60 cm. The longest root which was excavated was 4 m. There are more roots than in W, which are moreover covered with many small lateral rootlets. In D there is a primary root down to 80 cm and many horizontal ones at 10 cm below the sand surface. They bear many lateral roots 10 cm long: their length may be 8 m.

Correlations with the environment

A *high water* table results in superficial root systems of *Conomorpha*, *Clusia*, *Licania* and *Ternstroemia*. In *Humiria*, *Clusia*, *Licania* and *Ternstroemia* the horizontal roots are much closer to the surface in wet environments than in dry ones.

A *dry environment* brings with it more extensive horizontal root systems in all of these species. As the ground water is deeper, the importance of rain water for the vegetation increases. An extensive root system is more suited to intercept rain water than a small root system. In dry soil a larger soil volume is needed per individual to collect enough water than in a moist soil.

Conclusions concerning species which root both within and outside the *litter area:*

1) The roots of *Clusia* and *Ternstroemia* are limited in the wet environment to the litter, while in the dry environment they are numerous outside of it. Apparently neither the nutrient content nor the water surplus limit the roots to the litter area, since similar water levels occur inside and outside the bushes.

2) In wet environments the high water table forces the roots outside of the litter area into the upper dm of the soil (*Humiria*, *Licania*, dead root tips of *Clusia*). In the dry habitat the roots are at a depth of 20 to 30 cm; no roots are found in the superficial layers (*Humiria*, *Clusia*, *Licania*, *Ternstroemia*).

3) In *Clusia*, *Ternstroemia* and *Ormosia costulata* in the dry habitat the same roots run at a deeper level outside the litter area than inside. At the edge they bend down to a deep layer.

As soon as the ground water permits, the roots select a deeper level outside the litter area. If this is impossible due to high water levels, then some species are limited to the litter area.

These facts suggest that conditions for root growth outside the litter area are more favourable at some depth than immediately below the surface. In the dry habitat the zone between 20 and 30 cm as well as the superficial layers, are entirely dependent on rain for water supply. Both layers are completely dry in the dry season. The superficial layer dries out completely in the wet habitat. Hence neither water supply nor drought are the cause of this behaviour. Although no measurements were done, it seems plausible that temperature is the primary determining factor. The superficial layer will be very hot, while 20 cm of sand offers some protection. In the wet environment the ground water prevents the roots from utilizing this layer which would be protected during the dry season. The litter layer does offer protection. The roots of *Clusia* and *Ternstroemia* are then limited to those soils which are covered with litter.

Humiria offers further proof. In wet habitats it forms thin roots outside of the litter area at a depth of 10 cm. These die off in the dry season, as shown by the dead tips on older stems. In dry habitats the horizontal roots outside the litter area are between 20 and 30 cm. They do not die during the dry season, but grow in thickness and form a protective cork layer.

The *companion species* remain mostly within the litter area (e.g. *Conomorpha* and *Retiniphyllum*). The cause is probably the better moisture condition, as well as a higher content of organic material.

For a discussion of the role of the litter layer and the rooting method in the origin and structure of the bushes, see Ch. VII.9.

III. 3.10. **Correlations for the white sand**

Water surplus

a) monocotyledons: short, superficial root systems, not extensive.

b) dicotyledons: superficial systems, extensive.

Ground water at some depth, but the major water source—monocotyledons: narrow deep root systems, such as horsetail and shower shape.

Ground water still deeper, rain water of importance—monocotyledons: greater spread, even in deeply rooted forms.

Ground water deep, rain water major water source—

a) monocotyledons: superficial systems, disc and hemispherical shapes.

b) dicotyledons: very extensive horizontal root systems (disc and specialized form), some deep roots down to ground water.

Deep layer permanently dry—

a) monocotyledons: roots do not penetrate.

b) dicotyledons: some roots penetrate.

High temperature—dicotyledons: roots die off, unless protected by layer of sand or litter.

Litter layer, greater organic content, better water economy—intensive root development immediately below the litter layer. Restriction to litter layer or litter area.

III. 3.11. **Detailed consideration of certain species**

III. 3.11.1. Species whose root system is known from several vegetation types

For species which occur on white sands only see Ch. III.3.6 and 3.9.

Vegetation units on heavy soils are the *Panicetum stenodoidis*, the *Schizachyrio-Rhynchosporetum mesosetosum* and *mitracarpetosum* and the *Polycarpaeo-Trachypogonetum.* The soils differ in texture, structure, ground water level and water economy. All these soil characteristics influence the root growth. A correlation of roots with one of the soil properties is not as clear as in species limited to white sand, especially since the soil properties are interdependent. In the discussion of the root picture of the vegetation types as a whole we considered the correlation with known or probable water economy. We encounter the same correlation and a corroboration of the supposed water economy by comparing the behaviour of root systems of those species which are found in more than one unit.

Monocotyledons (see Table 3)

For data concerning shape, distribution through the soil, and sizes of the root systems, see Ch. VIII.

Andropogon leucostachyus and *Mesosetum cayennense* are deeply rooted in the Panicetum, with little spreading. For their water supply they are adapted to ground water. In the *Schizachyrio-Rhynchosporetum mesosetosum* the roots remain superficial, they do not reach ground water. Their spread is greater than in the *Panicetum*, especially in *mesosetum.* Since they are not inhibited by high water levels, it is probable that their restriction to the superficial layer is caused by drought, although ground water reaches up to 30 or 50 cm below the surface.

TABLE 3

Characteristics of the root systems of species occurring in different vegetation types
X: occurring, shape unknown

	Panicetum stenodoidis				Schizachyrio-Rhynchosporetum							
					mesosetosum				mitracarpetosum			
	depth (cm)	shape	distr. type	spreading (cm)	depth (cm)	shape	distr. type	spreading (cm)	depth (cm)	shape	distr. type	spreading (cm)
Aristida tincta	40	hemisph.	C	15–20	25	hemisph.	B	15–20	20	hemisph.	B	20–25
Andropogon leucostachyus .	50	shower	C	15–20	20	hemisph.	B	15		X		
Axonopus pulcher	25	hemisph.	B	10	25	hemisph.	B	20	20	hemisph.	B	20
Mesosetum cayennense . .	50	horse tail	C	5–10	25 (1 × 40)	hemisph.	B	20–30				
Schizachyrium riedelii. . .		X			15–20 (1 × 50)	hemisph.	B	15		X		
Leptocoryphium lanatum .	90	horse tail	D	20	50	shower	D	35				
Rhynchospora barbata v.b.		X			20–25	hemisph.	B	15	15	hemisph.	A	5–10
Trachypogon plumosus . .	25 (1 × 40)	hemisph.	B	25	15 (1 × 40)	hemisph.	B	30	20	disc	B	25-30
	Polycarpaeo-Trachypogonetum				Mesoseto-Trachypogonetum							
Aristida tincta												
Andropogon leucostachyus .												
Axonopus pulcher	20	hemisph.	B	30		X						
Mesosetum cayennense . .												
Schizachyrium riedelii. . .	15–20 (1 × 50)	umbrella	B	40								
Leptocoryphium lanatum .												
Rhynchospora barbata v.b.												
Trachypogon plumosus . .	80	umbrella	C	60	80	umbrella	C	60				

Aristida tincta utilizes the ground water with a deep root system in the *Panicetum*. In the *Schizachyrio-Rhynchosporetum mesosetosum* rain water is the only source, because the root system does not reach ground-water level. This can only be explained by assuming a dry layer between the capillary ground water and the superficial water. In the *mitracarpetosum*, where capillary water does not come above 80—40 cm below the surface, the root system is limited to the upper 20 cm by drought of the underlying layer. The uptake of rain water in the *mitracarpetosum* is probably not better than in the *mesosetosum*. Yet we find a greater spread. Is this because of a minimal soil volume needed by the species? Greater depth in the *mesosetosum* would be replaced by greater spread in the *mitracarpetosum*.

Roots of *Axonopus purpusii* where excavated only in the *Schizachyrio-Rhynchosporetum*. In the *mesosetosum* there are many more roots below the sod layer (type C) than in the *mitracarpetosum*. In the *mitracarpetosum* spread is greater. In the *mesosetosum* there is probably more moisture in the layer below the sod. The greater extent may perhaps be explained on the basis of minimal soil volumes as in *Aristida tincta*. The prediction for the *Panicetum* is hemispherical shape and C, for the *Polycarpaeo-Trachypogonetum* hemispherical shape and D.

Rhynchospora barbata var. *barbata* is limited to the superficial layer in the *Schizachyrio-Rhynchosporetum*. The root system is both deeper and broader in the *mesosetosum* than in the *mitracarpetosum*. The expectation for the *Panicetum* is hemispherical and B.

Leptocoryphium lanatum is rooted almost entirely below the sod layer, type D, in the *Panicetum* and the *Schizachyrio-Rhynchosporetum mesosetosum*. The depths are 90 and 50 cm respectively. In the white sand the root distribution of the species is also type D. Here the depth is determined by the duration of high water tables. On the Coesewijne savanna, *Leptocoryphium* occurs on very heavy soil with very deep water tables. An explanation for the method of rooting in heavy soil is not easy on the basis of these data.

Axonopus pulcher has hemispherical root systems and type B in all units mentioned. The root system is always superficial and geared to rain water supply. In the *Panicetum*, the species utilizes the moist layer below the sod, where depth exceeds spread. Penetration of roots to greater depth will be prevented by long periods of water surplus. In the *Schizachyrio-Rhynchosporetum mesosetosum* and *mitracarpetosum* there is neither a moist soil below the sod layer, nor rapid wetting by the rain water. Roots are equally long in all directions. In the *Polycarpaeo-Trachypogonetum* rain water is absorbed rapidly and sinks down to deeper layers. *Axonopus pulcher* has an extensive root system which may intercept much rain water.

Schizachyrium riedelii is neither extensive nor deep in the *Schizachyrio-Rhynchosporetum mesosetosum;* a few roots penetrate to 50 cm. In the *Polycarpaeo-Trachypogonetum* the depth is the same, the extent is greater. The explanation is the same as for *Axonopus pulcher*. The expectation for *Panicetum* is hemispherical shape, type B, for *mitracarpetosum* hemispherical shape, type B.

Trachypogon plumosus. In a discussion of the species of white sands wetter than the *Mesoseto-Trachypogonetum* (Ch. III.3.6) it was shown that *Trachypogon* is limited to the superficial layer by water surplus. The same superficial root system is seen in the *Panicetum*. In the *Schizachyrio-Rhynchosporetum*, roots also are primarily in the sod layer. This must be explained however on the basis of the supposed dry layer, permanently or long persistent between superficial and ground water. In the *Polycarpaeo-Trachypogonetum* and the *Mesoseto-Trachypogonetum* the root system has its optimal development with roots in and below the sod layer, penetrating deeply and very extensive. In the *Polycarpaeo-Trachypogonetum* the root system is clearly umbrella shaped. Within the umbrella there are few deep roots. Some of the roots bend down at a distance of 30 to 40 cm. Rain water is the water source and the soil has a good percolation rate. Part of the precipitation will be intercepted by aerial portions. Some of this water will evaporate immediately, part of it will run down the leaves and culms, so that a large amount of water collects in the soil near the base of the plant which is widely spread out (Fig. 9). Near the base there are very many roots and rootlets, which utilize this water. That part of the soil which is shaded by Trachypogon, will receive less water; this water is intercepted and used by the horizontal roots in the superficial layer. The result is that little of the rain penetrates through the root layer, and that the soil underneath the root umbrella has little to offer. Only a few roots penetrate in this area. Outside the area shaded by the aerial portions, all rain water reaches the soil. At this distance from the base there are fewer roots, so that part of the water will sink to deep layers. The roots follow the water to these deeper layers. In this way we can explain the umbrella shape of the root system.

In the *Polycarpaeo-Trachypogonetum* the root systems of different individuals are contiguous. The question may be posed whether root competition might not force the roots to bend down at their meeting point. If we assume that the individuals are equivalent, the mechanism is difficult to imagine. One could visualize however, that roots of a young individual can not penetrate a soil which is already occupied by roots of a mature individual. These are already utilizing the available water. In this case, the shape of the mature individual is already fixed, independent of competition. Observation shows, that horizontal root systems of different individuals, even of different species are intermingled.

The closer to the base, the fewer extraneous roots we will find. This does seem to be a matter of competition for water. The many roots close to the base use up the available water, rendering the soil less attractive to the roots. In the *Mesoseto-Trachypogonetum*, the *Trachypogon* root systems are not contiguous. Their behaviour in this situation may yield further information concerning the question raised above. The weak tendency in specimens that were studied, to remain horizontal without bending downward is in agreement with the total root picture of this association, and is correlated with the rapid sinking down of rain water.

Correlations

High ground-water table—

a) part of the species exhibits a deep (type C) and narrow rooting method (horsetail shape)

b) a part of the species is limited to layers without long lasting ground water.

Rain water of importance—root systems are spreading.

Percolation of rain water—widely spread shapes.

Moist soil below the sod layer—roots occur below the sod layer.

The behaviour of root systems in the *Schizachyrio-Rhynchosporetum mesosetosum* and *mitracarpetosum* may be explained by assuming a permanent or long lasting dry layer between superficial and ground water. From a comparison of species occurring in both subassociations, we deduce that the former contains more moisture in the layer below the sod layer.

Whether this is derived from rain water or ground water we will not discuss.

Dicotyledons

Cassia hispidula occurs in the *Polycarpaeo-Trachypogonetum* and the *Mesoseto-Trachypogonetum.* In both we find long lateral roots in the sod layer, and a primary root down to capillary ground water. At this level the root bends sideways.

Eriosema crinitum occurs in both subassociations of the *Schizachyrio-Rhynchosporetum* and in both subassociations of the *Polycarpaeo-Trachypogonetum.* The species was excavated from a termite hill in the *Schizachyrio-Rhynchosporetum mesosetosum* and in the *Polycarpaeo-Trachypogonetum curatelletosum.* In both cases there was a tap root with some lateral rootlets at the tip down to 60 cm and some lateral roots in the sod layer to 40 or 50 cm long. By the excavation of the termite hill it was shown that *Eriosema* had stems starting at the original surface level. Hence the species was present before the hill was started. Perhaps the species maintains itself in this unit through better drainage caused by the burrowing of the termites.

Eupatorium amygdalinum occurs on termite hills in the *Schizachyrio-Rhynchosporetum mesosetosum,* in the *Schizachyrio-Rhynchosporetum mitracarpetosum* and in the *Polycarpaeo-Trachypogonetum.* The root system is always disc shaped in the sod layer.

These 3 species are rooted in a similar fashion in different vegetation units. In all cases the rooting method is in accordance with the water economy.

Eugenia punicifolia occurs in both subassociations of the *Schizachyrio-Rhynchosporetum* and of the *Polycarpaeo-Trachypogonetum,* and in the *Mesoseto-Trachypogonetum.* The root systems from the *Polycarpaeo-Trachypogonetum* and the *Mesoseto-Trachypogonetum* are known. In the former unit, the species roots entirely underneath the sod layer with a main root down to 2 m and many lateral roots along the main root, which become 1.50 m long (cylinder shape). In the *Mesoseto-Trachypogonetum* we also encounter a primary root, down to 80 cm.

At this level the roots which originate from the top of the primary root bend sideways. We may assume on the basis of measurements of ground water levels, that the capillary ground water penetrates to this depth. In both cases the depth of the primary root is probably correlated with the height reached by the capillary ground water. The distribution of the laterals along the main root may be correlated with the greater moisture below the sod layer in the *Polycarpaeo-Trachypogonetum*, and the rapid sinking of rain water in the *Mesoseto-Trachypogonetum* and the consequent necessity of catching as much rain water as possible.

The rooting method of *Hyptis atrorubens*, occurring in all units on soils heavier than white sand, is known only from the *Polycarpaeo-Trachypogonetum;* it is mushroom shaped, distributed according to B, greatest depth 50 cm and spread 50 cm. From this method the species may be modified in various ways. Probably the rooting method is always mushroom shape and B. In the *Panicetum* probably only A, owing to high ground water during the wet season.

The rooting method of *Sipanea pratensis* is as follows: in the *Polycarpaeo-Trachypogonetum*—mushroom shape and B, depth 25 cm and spread 30 cm; in the *Schizachyrio-Rhynchosporetum mitracarpetosum*—no primary root, many roots originate from a geopodium, the spread is 25 cm, an occasional root goes below the sod layer; in the *mesosetosum*—there is no primary root, spread is 40 cm, the deepest root down to 40 cm; in the *Panicetum*—specialized form, limited to the sod layer, spreading 30 cm. The species is geared to rain water. In the *Panicetum* the ground water forces the roots upward. The great spread even in soil where rain water is absorbed only slowly and where single showers cannot be utilized, is perhaps correlated with the necessary minimum soil volume.

Tibouchina aspera is found on white sand in *Mesoseto-Trachypogonetum*, and otherwise in all units on heavier soil. Drawings give a better picture of the root system in different habitats than a description (Fig. 16). In the *Panicetum* the roots are limited by high water levels to the superficial layer. In the *Schizachyrio-Rhynchosporetum mesosetosum* the specimen studied grew in a termite hill. It turned out that the plant was already present before the termite hill was formed. With the raising of the soil, the location of new shoots following the long dry period (fire) was moved up along the stem. The stem portion within the termite hill produces adventitious roots. The roots of the original geopodium go down to 40 cm, at which depth there are gley phenomena. Rain water will penetrate below the sod layer through the better drainage of the termite burrows. In the *mitracarpetosum* an individual 1.50 m tall was excavated, which had certainly withstood two long dry seasons without fire. The main root penetrates the dry layer below the sod down to moisture of the ground water table. Many long roots in the sod layer utilize rain water; they measured 70 cm, and bore many lateral rootlets. The tips reach below the sod layer (40 and 60 cm). It cannot be indicated to what extent the size of the root system was influenced by survival without fire. A burnt specimen would have to be excavated for comparison. In the *Polycarpaeo-Trachypogonetum* we find roots both in and below the sod layer, down to 40 cm. The distribution of roots through the soil is correlated with the good percolation rate of rain water and consequent moistening of the soil below the sod layer. In the *Mesoseto-Trachypogonetum* there is an extensive root network in the upper 15 cm of the soil, and only a short primary root. In this soil rain water sinks away rapidly without wetting the soil for any length of time. The plant benefits best by intercepting as much water as possible in the superficial layer, before it evaporates or sinks away. The excavated specimen had certainly survived two long dry seasons

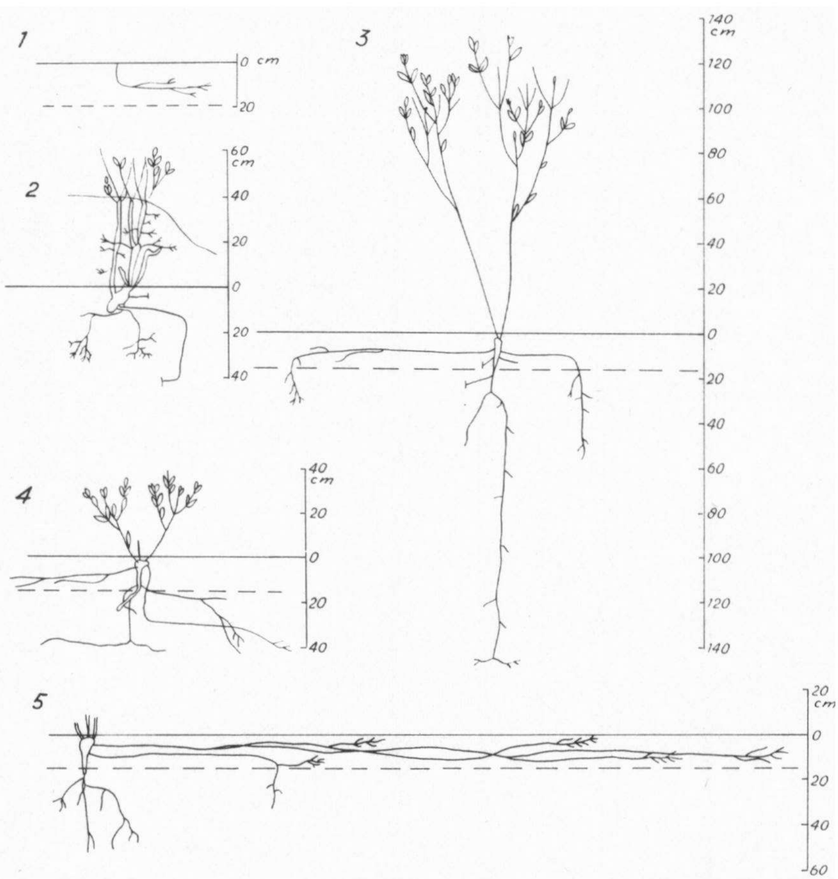

Fig. 16. *Tibouchina aspera.* ——— / - - - - } sod layer

1. *Panicetum stenodoidis.*
2. *Termitary* in *Schizachyrio-Rhynchosporetum mesosetosum.*
3. *Schizachyrio-Rhynchosporetum mitracarpetosum,* 2 years not burned.
4. *Polycarpaeo-Trachypogonetum.*
5. *Mesoseto-Trachypogonetum.*

without fire, like that of the *Schizachyrio-Rhynchosporetum mitracarpetosum.* The capillary ground water in both associations reaches 80 cm below the surface in the wet season. The difference in the behaviour cannot be explained on the basis of the available facts.

Curatella americana has roots only in the sod layer in the *Panicetum.* They are found at 10 to 25 cm below the surface and grow 6 m long. In the *Schizachyrio-Rhynchosporetum* there are also only horizontal roots. Their greatest depth is 50 cm in a tree-like individual. The roots run at 10 to 25 cm below the surface, the longest one that was studied being 13 m. In the *Polycarpaeo-Trachypogonetum* there was a primary root which bent horizontally at 1.20 m. The lateral roots were found to be 27 m long, usually at 20 to 25 cm depth, sometimes to 40 cm below the surface. In the *Mesoseto-Trachypogonetum* there is a main root down to 1.50 m, with copious branching at the end. The lateral roots are found at 20 to 25 cm below the surface, the longest being 18 m. The horizontal roots always have a diameter of about 2.5 cm. These different behaviour patterns are clearly correlated with ground water. A difference in length of horizontal roots is correlated with the height of the aerial parts. A causal relationship cannot be indicated.

Correlations

High water levels—roots exclusively superficial.

Ground water always at some depth—roots penetrate to the depth where water surplus is tolerable, here they bend or branch.

Rain water quickly sinking—root system superficial and very extensive.

Dry layer below the sod—barrier to most roots, except the main roots of some species which penetrate to ground water.

III. 3.11.2. Trees and shrubs

All trees and shrubs taller than 80 cm show great similarity in their root systems. 22 Species were excavated.

The root system is always limited to a few horizontal roots which reach many meters in length, well outside the projection of the crown, and which remain superficial. Two palms, Bactris campestris and Mauritia flexuosa, have very many roots of this type. When the water table is not too high, most species develop an insignificant vertical primary root. Its depth is similar in species of the same vegetation type, and correlated with the gley horizon. The vertical primary root is lacking in *Davilla aspera, Humiria balsamifera* and *Retiniphyllum schomburgkii.*

The roots have a corky bark, which flakes off like on the stems of many species.

In most cases there are few or no lateral roots along the long horizontal ones. Only the tip of the root is branched and sometimes penetrates somewhat deeper. This form of root system is completely in agreement with Kutschera (1960): "It is a sign of dry habitat, that the root systems of many species become limited to a few strong, often far reaching roots, which give rise to a large number of thin fibrous roots. These fibrous roots may die off during the dry period without great harm to the plants, so that a smaller root surface remains exposed to the increased suction force of the soil. At the beginning of the wet period they are rapidly regenerated and can then serve the water uptake function best with not or weakly developed cork layers."

The primary root often penetrates through a very dry layer into areas which are moistened by ground water. It is noteworthy that this is always done by the primary root. It may be supposed, that this root is supplied by water and assimilates from the higher portions of the plant. The primary root is always directly underneath the trunk, which conducts the rain water intercepted by the crown. At the base of the stem there will be a greater influx of water than elsewhere. The question arises whether perhaps a part of this water filters down along the vertical root or through the flaky bark, and thus creates a micro-habitat around the root tip which favors further growth in depth.

III. 4. Conclusions and correlations

III. 4.1. **Water economy**

It is shown conclusively that the water economy of the soil determines the method of rooting, both for individual species and vegetation types. Water surplus and drought are the main limiting factors in root distribution.

Water surplus is harmful through oxygen deficiency that comes with it. Apart from water and marsh plants which are adapted by special provisions to rooting underwater, all species are limited in their tolerance of the duration of excess and drought. These limits differ according to species. In the present study the dicotyledons generally show limited tolerance for water surplus, but resistance against drought, while the monocotyledons on the other hand will tolerate water excess of relatively long duration, and are more sensitive to drought. The exception is Trachypogon plumosus, which behaves like a dicotyledon in this respect. This behaviour of monocotyledons may be correlated with the larger intercellular spaces, which occur in the roots (Ch. III.1.4), and for dicotyledons with the corky bark which protects the root against drying.

There are two possible water sources for the vegetation: rain water and ground water. The rain moistens the soil from the top, so that the upper layer is the wettest. Water surplus is only indirect, but the disadvantage is that this supply fails during the dry season, apart from isolated showers. For root systems which are dependent upon rain water, the extensive form is characteristic.

Ground water moistens the soil from below. The advantage is that it is continuously available, the disadvantage is the concomitant oxygen deficiency. Deeply penetrating root systems are characteristic of species that utilize ground water as the main water source.

When ground water or capillary ground water is not permanently at the surface, rain water becomes important even for vegetation which uses ground water as the principal source. Rain water replenishes the ground water after the dry season. The shape of the root system depends upon the ratio between ground water and rain water.

The relationships are as follows:

Monocotyledons

Ground water at surface for long periods but not permanently—short root systems in the superficial layer, where the dry season becomes noticeable.

(However, in species which are characteristic of this habitat, deeper root systems are known).

Ground water deeper, but rapidly rising after the dry season due to rapid percolation or shrinkage crevices—narrow deep root systems; horsetail and shower shapes, type C.

Ground water still deeper, rain water most important in moistening the soil—root systems spreading both horizontally and in depth; primarily shower and hemispherical shapes, types C and B.

Ground water so deep, that the surface is reached only during the wettest season (possibly only by capillary water). There is a wide long lasting dry zone between superficial and the ground water. The rain water is most important in moistening the soil—spreading shapes in the superficial layers; hemispherical and disc shapes, types A and B.

Ground water never at the surface. The upper layers moistened only by rain water:

a) Soil with poor percolation, so that only a shallow layer is moistened and a dry layer remains underneath—roots superficial, moderately spread; hemispherical shape, types A and B.

b) Soil with good percolation, moisture even below the sod layer—greater spread and depth; hemispherical, disc, umbrella, and wide shower shapes, types A, B and C.

c) Soils with good percolation to great depth, so that rain water sinks rapidly through the root layers—as under B.

Dicotyledons

Ground water at the surface for some time—roots superficial only; specialized form and type A.

Ground water deeper—some roots penetrate to lower layers near ground water. Here the roots bend or branch without growing deeper. The most important part of the root system is in superficial layers. Distribution depends on percolation rate of the soil.

a) Soils with poor percolation, so that only a shallow layer is moistened, and a dry layer exists underneath—root systems superficial, more or less extensive; specialized and mushroom shapes, types A and B.

b) Soil with good percolation, moisture below the sod layer—deeper root systems; R. generalized, cylindrical, cone and mushroom shapes, types B, C, and sometimes D.

c) Soil with good percolation to great depth, so that rain water sinks rapidly—root systems are geared to the interception of the maximum amount of rain water, they are very extensive and superficial: specialized and mushroom shapes, types A and B.

III. 4.2. Texture and structure of the soil

Structure and texture of the soil influence the water economy. A correlation of properties of the root system with texture and structure directly is never clear. It is always connected with water economy.

III. 4.3. Nutrient content

Soil analyses have shown that sand underneath litter layers contains more organic material than outside. The content decreases with increasing depth.

The dense root network immediately below the litter layer can be correlated with this, but also with the water economy which is improved by the humus content and the overlying litter layer.

Nutrients are absorbed primarily in dissolved form. This means that it is often impossible to determine whether water or nutrient content determines the size of the root system.

The following facts may be correlated with nutrient content: *Aristida tincta* and *Axonopus purpusii* both occur in the *Schizachyrio-Rhynchosporetum mesosetosum* and *mitracarpetosum*. The soils of both units have poor percolation. The layer influenced by rain water in the *mitracarpetosum* is less deep than in the *mesosetosum*, judging from the roots of these units. Root systems of both species are deeper in the *mesosetosum* and are more widely spread in the *mitracarpetosum*. Spreading in these two soils cannot be correlated with interception of rain water. Hence it is possible to say that plants need a minimum soil volume for the supply of nutrients, which causes horizontal root growth since growth in depth is made impossible by drought. All trees and shrubs which occur in bushes on both wet and dry white sand have much larger roots in the dry white sand. Functionally this can be understood because the need for water in wet sand is satisfied in a smaller soil volume than in dry sand. From the smaller soil volume fewer nutrients are available, with the result that the plants remain smaller above ground in the wet than in the dry environment.

III. 4.4. Oxygen

The ground water limits growth of roots through oxygen deficiency (Ch. III.1.0).

A dense network of roots uses up the oxygen from rain water, so that only water poor in oxygen penetrates into the soil underneath the root layer. This could be the case underneath the dense root mat in the bushes on dry white sand. An explanation for the small amount of roots underneath the root mat must be sought in the deficiency of oxygen. The content of organic material and the water economy should also be considered.

III. 4.5. Temperature

In the discussion of the species in bushes on dry and wet white sand (Ch. III.1.11) the depth of the horizontal roots outside the litter layer in the dry environment and their limitation to the litter area in the wet habitat is for some species correlated with the possible adverse influence of high temperature during the dry season.

III. 4.6. Fire

In the discussion of the literature (Ch. III.1.14) it was shown that the removal of the majority of photosynthetic parts by mowing and grazing will limit the size of the root system. Although fires destroy the aerial parts, they only occur in the dry season, when vegetation above ground is largely dried out. So the fire would not be expected to influence the root system.

In species which are reduced in size by fires more than by drought, a smaller root system might possibly result. The only indication of this could be an excavated specimen of *Tibouchina aspera*, which had not been burned for at least two long dry seasons. This specimen had an unexpectedly large and deep root system (Ch. III. 3.11.1).

III. 4.7. Effects of animals

On the savannas two types of termite nests occur, the upright sugar-loaf, and a system of burrows in the soil with a hill constructed by the termites. The latter type is very common in the *Schizachyrio-Rhynchosporetum mesosetosum*, the former on white sandy soils.

In Chapter III. 3.2 we mentioned how a better and deeper moistening of the soil results in a deeper root system, through these termite burrows.

The most important plants on termite hills usually prove to have been present before the termites started their hills.

Where roots grow underneath a sugar-loaf nest, they are branched intensively (Photo 5).

III. 4.8. Competition

In the discussion of the rooting method of *Trachypogon plumosus* a possible competition for water is discussed (Ch. III.3.11.1).

A dense network of roots of a species will use up the available water, so that the environment is no longer attractive to other roots. Just below the tussocks, where the species itself has most of its roots, we rarely find roots of an neighbouring plant.

In the *Polycarpaeo-Trachypogonetum*, the distance between tussocks is determined by the competition between root systems.

In the *Panicetum stenodoides* the individuals stand close together with narrow deep root systems. The question is whether the plants stand close together and the roots are therefore forced down by competition, or whether the plants can stand close together because the narrow, deep root systems permit this? The explanation of the narrow deep root systems as a result of the water economy is satisfactory; in white sand under comparable conditions of water supply, we find the same kind of root systems, while the sod layer is not closed; species which are forced to root more widely, by water excess, are also found. These three arguments justify the position that the plants stand close together because the root systems permit them to do so.

In both subassociations of the *Schizachyrio-Rhynchosporetum*, the sod layer is closed, the vegetation above ground is not. Although this correlation exists, we may not conclude that root competition determines the distribution above ground. Factors such as ecesis and survival chances, and fires, may also play a role.

In the herbaceous vegetation on white sands, root competition is out of the question, because the sod layer is not closed.

III. 4.9. **Periodicity**

With respect to the periodicity in root growth we can only state that many monocotyledons were found with new roots and new root tips at the beginning of the wet season.

III. 4.10. **Mycorrhiza**

In *Retiniphyllum schomburgkii* and *Dimorphandra conjugata* coral-like branching was found in roots in the litter layer. This is indicative of mycorrhiza (Ch. III.1.3).

CHAPTER IV

STRUCTURE

IV. 1. Survey of the literature

IV. 1.1. **Structure of the vegetation**

The structure of the vegetation plays an important role in the general physiognomic classification of the vegetation. When authors recognize "Savanna" as a separate formation in the tropics, it is always primarily on the basis of structure, while xerophytic characteristics play a secondary part. The essential characteristic of savannas is that the herbaceous layer is the most important one, and consists of *Gramineae* and *Cyperaceae*. The occurrence of trees and shrubs is scattered and isolated.

Many have attempted to solve the problem of the origin of savannas, in other words the cause of such a vegetation structure. Usually the question is posed in the negative, i.e. why there is no vegetation consisting of more and especially higher, woody layers. BEARD (1953) and VAN DONSELAAR (1965) have reviewed this question.

There is general agreement that an alternation of wet and dry periods is required. As possible causes the following qualify:

1) The climate, in this case referred to as savanna climate. Annual precipitation and the number of dry months are of importance. The definition of a dry month differs from one author to another. For maximum precipitation MOHR and VAN BAREN (1954) indicate 60 mm, JAEGER (1952) gives 30–50 mm, while LAUER (1952) includes the temperature in the definition. Nowadays most authors deny the existence of a savanna climate.

2) Climate and soil together, in such a way that there is an alternation of dry and wet periods in the water supply of the vegetation. The climate brings with it an annually recurring dry period, the soil makes these felt by a) deep ground water tables, b) excessive drainage, c) poor water intake, d) impermeable layer at some depth.

Most authors stress the dry season which the species must be able to withstand. The length of the dry season determines what vegetation may occur. BEARD (1953) and FANSHAWE (1952) emphasize the importance of the alternation of shortage and surplus of water, which make both dry and wet season unfavourable.

Only few authors pose the question of causal relationship between vegetation structure and environmental factors. *Gramineae* and *Cyperaceae* go through a resting stage during the dry season and are not damaged by drought. The height of the grass layer is correlated with the water economy. SCHIMPER and VON FABER (1935) state that trees generally manage to survive a dry season by means of a deep root system, with which water reserves stored in deep soil layers may be utilized. "A soil which does not permit the deep penetration of moisture, is not suited for the growth of trees". On the other hand the following is stated: "For grasses moisture of the sub-soil is generally of little importance; on the other hand moisture of the top soil is essential." "Soils supporting grassy vegetation all have in common that they hold the moisture to some extent in the upper layer".

According to BEARD (1953), species of trees and shrubs may be adapted to either drought or excess of moisture, but not both.

According to GRAEBNER (1929) a dry period during the growing season inhibits the maximum productivity, which would result in a forest. It is therefore a matter of the build-up of materials, not of resistance to drought.

LANJOUW (1936) lists as an important factor of the origin of savannas the poverty of the soil as a result of leaching.

Most authors regard fires as an important secondary factor: Some authors ascribe the origin and maintenance of a majority of the savannas to fires. Fires occur during the dry season. Grasses and sedges, which are then in a resting stage, are hardly affected; but shrubs and trees are heavily damaged by fires.

IV. 1.2. Structure of the species

Apart from the vegetation as a whole, the species may also have a structure, typical of the environment or a single environmental factor.

Trees

The scattered trees are described by all authors of American savannas as gnarled, resembling fruit trees. WARMING (1893), BOUILLENNE (1930) and PHILLIPS (1936) give descriptions of the destruction by drought or fire of the terminal bud and sometimes also the youngest parts of branches which have not yet developed cork. The result is that dormant buds lower on the branches and protected by bark will develop. In this way a gnarled form develops resembling pruned fruit trees (TAMAYO, 1961). It is not explained why the new terminal bud does not keep the same direction of growth as the main branch. LEBRUN (1947) states that species which normally grow upright with straight branches will continue to do so after destruction of the terminal bud. The same is true for species with gnarled forms. Both drought and fire can destroy terminal buds. The resistance and protection against drought will differ according to species, so that some are only susceptible to fire.

Fires are especially damaging at a height of 3 to 4 m (WARMING, 1893; LEBRUN, 1947). Higher trees have already outgrown the dangerous fire zone.

The characteristic flat-top tree form described from Africa is lacking on the South American savannas.

Shrubs

Many species which reach the stature of trees elsewhere, are found as shrubs in the savanna. Aerial parts are damaged by drought and especially by fire in such a way, that rejuvenation buds develop close to or below the surface, resulting in a shrub with several stems (Warming, Lebrun). When this occurs repeatedly, the base of the plant becomes thick and woody and bears living branches and scars of dead ones, as on the burls of pruned willows. Lebrun describes this process. Many authors call these thickened organs characteristic of savanna plants. There is difference of opinion whether drought or fire is the cause, and also about the place of the burl in relation to the surface; positions above, at, and below the soil surface are known.

DU RIETZ (1931) calls an "orthogeocorm not or only slightly incrassate, a 'leptopodium'" and an "orthogeocorm more or less incrassate" and lignified, a "xylopodium."

Dwarf shrubs not higher than the herbaceous vegetation (about 80 cm) do not occur frequently. WARMING (1893) reports for a savanna near Lagoa Santa that the "heather form" is missing.

Half-shrubs

Drought and fire destroy the herbaceous portions; the plant develops from short, woody stem parts below, at, or immediately above the soil surface. Half-shrubs also possess thick, woody organs, resembling burls of the pruned willow. All authors who have dealt with life forms of savanna plants describe these. From the African savannas, very large underground organs have been described, which are said to have a water-storage function (DUVIGNEAUD, 1953; BEWS, 1929; LEBRUN, 1947). From American savannas underground organs are regularly described, but they are not extremely large and BOUILLENNE (1930) and BEARD (1953) state specifically, that they do not function as water-storage organs. Lebrun describes from savannas in the plains of Rwindi Rutshuru in the Congo that rejuvenation buds are above the surface, while most authors report for American savannas that the plants grow from below the soil surface.

A half-shrub generally sprouts from the woody portion of the stem above the ground. Lebrun reports for plants that were not burned, that the level of the rejuvenation buds becomes slightly higher each year.

Herbs

These underground organs are also described for herbs. BEARD (1953), BOUILLENNE (1930), LEBRUN (1947), PHILLIPS (1930), PILGER (1902) and WARMING (1893) report that herbs and half-shrubs commonly have several stems per individual. This is ascribed to drought and fire.

Many herbs have a woody base without being half-shrubs (GRISEBACH, 1884; LEBRUN, 1947; PILGER, 1902; FANSHAWE, 1952).

Therophytes are conspicuous by their scarcity (WARMING, 1893; BOUILLENNE, 1930; BEARD, 1953). It is assumed that seeds are destroyed by fire or that destruction occurs before the seeds are ripe. Lebrun says, however, that therophytes are especially fire resistant as seeds.

In grasses and sedges the tussock is the predominant structural form. Lebrun has measured the temperature in the center of the tussock while the front of the fire passed through. He found that the tussock offers good protection against rising temperature, so that little or no damage occurs at the level where the young shoots are found.

A tussock also reduces air-convection currents and thereby diminishes the evaporation. The tussock form is therefore a good adaptation to drought (MASSART, 1907, 1908, 1909; LEBRUN, 1947; PILGER, 1902; WARMING, 1893).

LUNDELL (1937) reports that tussocks may sprout with new shoots from below the surface.

All these conspicuous forms, gnarled trees, multiple stems and underground organs of shrubs, half-shrubs, and herbs, may be explained by the destruction of terminal buds and aerial parts by drought and fire. Thus Lebrun describes the plains of Rwindi Rutshuru as follows: "The pyrophytes of our regions are above all xerophytes, and the great effectiveness of their morphological arrangement which is protective in this respect, insures of course also a very real protection against damage caused by fires."

Underground woody organs are also described by BEADLE (1940) from the fire-adapted *Eucalyptus* trees in Australia. They are called lignotubers.

SPECHT and RAYSON (1957), working on Australian heaths which are burned regularly, report that all species with a fibrous root system have their overwintering buds at some depth below the soil, so that fires can be tolerated. Renewal buds are also underground in 68% of the species with a deep tap root and in 60% of the species with a shallow tap root.

Concerning the woodiness of the basal portion of the stem in herbs we may quote HAGERUP (1930), who reports that only woody stem portions can withstand a hot drought which occurs in the air layers directly above the soil in the steppe terrain in the dry season in Timbuctu. WARMING (1916) says: "The drier the habitat, the longer the main root will stay alive, and the more woody the basal shoot parts will be."

Another indication of the determining factors for savanna vegetation is the lack of forms commonly associated with certain conditions. Mosses and epiphytes generally correlated with high humidity are lacking (BEARD, 1953; WARMING, 1893). Algae and lichens also are absent, even from the tree trunks (WARMING, 1893).

But forms which would indicate extreme drought, such as succulents, bulbs and thorns, are also lacking. Rosette plants are also scarce or absent from savannas, as are true lianas. One does encounter shrubs with weak branches of species, which in woody vegetation occur as lianas. Creeping stems are rare. Species with rhizomes and stolons are also scarcely represented. (LEBRUN, 1947; WARMING, 1893). Warming relates this to the hardness of the soil.

IV. 2. METHODS

Little is known about the structural variety of vegetation and flora within the savanna formation. All of the characteristics mentioned before are described as pertaining to savannas in general. It is by detailed study of differences that we may establish correlations with environmental variations, and so perhaps reach a better understanding of the well known forms.

The several vegetation units will be compared with respect to the following:

a) The structure of the vegetation as a whole. The structure is described by means of vegetation coverage, the number of layers, height and coverage per layer and the number of species per layer. The coverage is always calculated by adding the mean coverages of the species (calculated according to TÜXEN & ELLENBERG, 1937). Usually this sum is expressed as a percentage of the sum of all species of the vegetation unit. The results are recorded in a structure diagram. These mean coverages are also utilized in the diagrams.

b) The structure of the species. The main forms are trees, shrubs, half-shrubs, herbs, and tussock plants (following DU RIETZ, 1931). Herbaceous plants were divided into non-tussock forming herbs and tussock plants. Non-tussock forming plants are simply designated as "herbs". A schematic drawing of the habit of each species was drawn, partly in the field, partly from herbarium material.

The following characteristics of all species are noted in Ch. VIII: Number of stems; categories: stemless, single stem, several stems, tussock forming, individuals loosely connected e.g. by a rhizome. Branching; categories: stem unbranched, branches near the base, and branches only in the upper portion of the stem.
Woodiness; categories: completely woody, base woody, entirely herbaceous.
Position of the stem; categories: erect, oblique, prostrate, creeping, climbing or winding.

Vegetation units were compared with respect to these characteristics whenever feasible.

IV. 3. Results

IV. 3. **Structure of the plant cover and component species according to vegetation unit**

IV. 3.1.1. *Panicetum stenodoidis* (Fig. 5, Tables 4 and 5)

Coverage of vegetation is almost always 100%. The sum of the mean coverages of the species (*T* & *E*) is 138.54. The number of species is 26.

Three layers may be distinguished:

	Height in vegetative state	Sum mean coverages	Number species
emergent layer . . .	1 m	0.1 = + %	1 = 3.8 %
high herb layer . . .	50–60 cm	49.68 = 36 %	11 = 42.3 %
low herb layer . . .	20 cm	88.85 = 64 %	14 = 53.8 %

Curatella americana is the only species in the emergent layer. In the herbaceous layer, plants stand close together leaving no open space.

	Sum mean coverages (%)	Number species
trees	—	—
shrubs	+	1 = 3.8 %
half-shrubs	2	4 = 15.3 %
herbs	0.2	8 = 30.7 %
tussocks	97.8	13 = 50.0 %

As was seen in the chapter on root systems, high water tables result in superficial root systems among the dicotyledons. This severely limits the rooting space for the dicotyledons; no trees or tall shrubs develop. *Curatella* is the only taller shrub that occurs.

The grasses and sedges experience less hindrance from high water tables. Compared to other units they have more soil volume at their disposal: the highest herb layer has a high coverage compared with other units, and the total coverage is great.

The alternation between high water tables near soil surface and total desiccation of the upper soil layers make this an environment of extremes; the number of forms is small, tussock forms predominate in coverage and numbers. Other forms do not play an important role in the vegetation.

The individuals stand close together. This is made possible by small root systems and roots which generally do not exceed the aerial portions in extent.

IV. 3.1.2. *Schizachyrio-Rhynchosporetum mesosetosum* (Fig. 7, Tables 4 and 5)

Coverage of vegetation averages 80%. The sum of the mean coverages of the species (*T* & *E*) amounts to 101.45. The number of species is 31.

Four layers may be distinguished:

	Height in vegetative condition	Mean coverages	Number species
layer of scattered trees	10 m	0.16 = 0.1 %	5 = 16.1 %
high herb layer . . .	50 cm	15.15 = 14.8 %	3 = 9.6 %
medium herb layer .	20–30 cm	84.4 = 83.1 %	12 = 38.7 %
low herb layer . . .	10 cm	0.85 = 0.8 %	4 = 12.9 %

Small hills occur in this vegetation type, measuring between 60 and 80 cm in height and from 1 to 2 m² in area. They are made by termites. The vegetation on the hummocks is distinct especially structurally. Dicotyledons are more numerous and taller than elsewhere in the subassociation. There are 7 species (=22.5%), which are mainly or exclusively restricted to the hummocks, with an average coverage of 0.89=0.8%.

	Sum mean coverages (%)	Number species
trees	0.1	5 = 16.1 %
shrubs	0.8	3 = 9.6 %
half-shrubs	1.5	4 = 12.9 %
herbs	0.5	8 = 25.8 %
tussocks	96.8	11 = 35.4 %

The shrubs occur preferentially on the termite hills. The half-shrubs occur in the medium herb layer and on the hummocks.

The vegetation is found on soils with less high water tables than the *Panicetum*. The rooting space for the dicotyledons is thus larger: trees are present.

The *Gramineae* and *Cyperaceae* are dependent on the upper soil layer which receives its moisture from rain water. This is only a shallow layer. Compared with the *Panicetum* a smaller volume of soil is available to these plants: the medium herb layer has the largest coverage, approximately equalling that of the *Panicetum;* the high herb layer has much less coverage than in the *Panicetum*. The vegetation is not as tall.

On the termite hills, drainage is better and the available soil volume larger: the vegetation is taller and the structure more differentiated.

Since water excess does not extend to soil level, the environment is less extreme than that of the *Panicetum:* there is a greater diversity of forms.

Roots more widely spread than in the *Panicetum:* the plants are less densely arranged, the coverage is less than 100%.

IV. 3.1.3. *Schizachyrio-Rhynchosporetum mitracarpetosum* (Fig. 8, Tables 4 and 5)

The vegetation coverage averages 75%. The sum of the mean coverages (*T* & *E*) of the species is 113.04. The number of species is 45.

Five layers may be distinguished.

	Height in vegetative condition	Sum mean coverages	Number species
layer of scattered trees	10 m	0.84 = 0.7 %	9 = 20 %
emergent layer . . .	2 m	6.43 = 5.6 %	4 = 8.8 %
high herb layer . . .	60–70 cm	38.83 = 34.2 %	9 = 20 %
medium herb layer –	30 cm	47.23 = 41.8 %	17 = 37.7 %
low herb layer . . .	15 cm	19.71 = 17.4 %	6 = 13.3 %

The emergent layer consists of a few shrubs and a high herb.

	Sum mean coverages (%)	Number species
trees	0.7	9 = 20 %
shrubs	11.4	5 = 11.1 %
half-shrubs	3.3	8 = 17.7 %
herbs	2.0	11 = 24.4 %
tussocks	82.6	12 = 26.6 %

The gley horizon occurs at a depth of 40–80 cm. There is no excess water in the upper layers. The Dicotyledons enjoy a larger soil volume for root systems than in *mesosetosum* and *Panicetum:* the non-tussock formers have a larger share in the vegetation and flora.

During much or all of the year there is a dry layer separating the ground water from the rain water in the upper layers; only roots of trees and shrubs penetrate to the level of the ground water table: especially the shrubs increase in coverage (primarily due to *Tibouchina aspera*).

The roots extend beyond the area covered by the aerial parts in general: the vegetation cover is not closed.

Rain water is absorbed into the soil only slowly, so that the soil volume available to roots of monocotyledons is small: the vegetation is mostly low; the high and medium herb layers have almost the same coverage.

IV. 3.1.4. *Polycarpaeo-Trachypogonetum cyperetosum* (Fig. 9, Tables 4 and 5)

The vegetation covers 85% on the average. The sum of the mean coverages (*T* & *E*) of the species is 108.82. There are 73 species.

Five layers may be distinguished.

	Height in vegetative condition	Sum mean coverages	Number species
layer of scattered trees	10 m	0.10 = 0.1 %	9 = 12.3 %
emergent layer . . .	80–100 cm	0.37 = 0.3 %	5 = 6.8 %
high herb layer . . .	60– 80 cm	77.15 = 70.8 %	27 = 36.9 %
medium herb layer .	30– 40 cm	18.76 = 17.2 %	20 = 27.4 %
low herb layer . . .	10– 20 cm	12.44 = 11.4 %	12 = 16.4 %

The emergent layer consists of tall herbs, half-shrubs and shrubs. The herb layers consist mainly of grasses: some forbs and half-shrubs grow interspersed.

	Sum mean coverages (%)	Number species
trees	+	9 = 12.3 %
shrubs	0.5	5 = 6.8 %
half-shrubs	1.2	19 = 26.0 %
herbs	5.7	28 = 38.3 %
tussocks	92.3	12 = 16.4 %

The gley horizon is deep, there is no water excess; the soil absorbs all rain water, so that moisture penetrates even below the sod layer. Thus there is a large soil volume with a better water economy: the high herb layer has the highest coverage, and productivity is higher.

Herbs and half-shrubs are much more abundant than in the vegetation types already mentioned. This may also be correlated with the larger soil volume and water economy. Another possible factor is the greater protection against insolation offered by the grasses with their high coverage in the highest herb layer. The micro-climate may be somewhat more favourable, improving the chance of survival for herbs and half-shrubs (see also Ch. IV.3.2).

The lesser coverage of grasses in the low herb layer may also be the result of the higher coverage of the upper layers. The amount of light that penetrates to the lower layers is less. It is known that grasses are heliophiles.

The roots spread and form a closed layer: the basal area of the vegetation is not closed. The tussocks (especially of *Trachypogon plumosus*) maintain a certain distance and so are able to fan out from the base. The interval between the tussocks is determined by the root systems.

IV. 3.1.5. *Polycarpaeo-Trachypogonetum curatelletosum* (Fig. 11, Tables 4 and 5)

The average coverage of vegetation is 95%. The sum of mean coverages (*T* & *E*) of the species is 143.43. There are 74 species. We may distinguish 5 layers.

	Height in vegetative condition	Sum mean coverages	Number species
tree layer	8–10 m	41.09 = 28.6 %	8 = 10.8 %
emergent layer . . .	1.5– 2.5 m	0.22 = 0.1 %	6 = 8.1 %
high herb layer . . .	60–80 cm	86.67 = 60.4 %	30 = 40.5 %
medium herb layer .	40 cm	6.53 = 4.5 %	20 = 27.0 %
low herb layer . . .	15 cm	8.92 = 6.2 %	10 = 13.5 %

The tree layer covering 40% on the average, is almost exclusively made up of *Curatella americana.* In the high herb layer, *Trachypogon plumosus* has the highest coverage (55.7%). The remainder of the coverage is due to herbs and half-shrubs. The medium herb layer consists of a few grasses and for the rest of herbs and half-shrubs. The low herb layer consists of *Cyperaceae* and annual herbs.

	Sum mean coverages (%) total	herb layer	Number species
trees	28.6	+	8 = 10.8 %
shrubs.	3.1	4	6 = 8.1 %
half-shrubs.	2.6	3	17 = 22.9 %
herbs	17.8	25	32 = 43.2 %
tussocks	47.6	68	11 = 14.8 %

The most important tree, *Curatella americana,* is of the well known gnarled fruit tree form (see Ch. IV.3.2).

The species composition is very similar to that of the *cyperetosum.* The differences between the two subassociations are primarily quantitative. The soils of both are entirely parallel.

This soil is apparently able to support a tree layer. This must be regarded as related to the greater depth of root systems along with a better water economy as compared with the *Schizachyrio-Rhynchosporetum* and the *Panicetum.*

A comparison of coverages of the herbaceous layers of the *cyperetosum* and *curatelletosum* shows differences which are due to the presence of the tree layer. The tree layer tends to lower the insolation and thereby the temperature and evaporation. The result will be that the water economy becomes more favourable for plants. Light intensity under the canopy will also be lower, although the crown of *Curatella* has sparse foliage.

The non-tussock-forming herbs have increased in coverage compared with the *Cyperetosum.* The herbs are the most drought sensitive during the growing season. Their increase must therefore be correlated with the more favourable water economy underneath the trees (see also Ch. IV.3.2).

The share of the tussock forming grasses is diminished under the tree layer. The sum of their mean coverages is reduced from 100.51 to 68.39. The cause of this must be the lower light intensity.

IV. 3.1.6. *Mesoseto-Trachypogonetum* (Fig. 10, Tables 4 and 5)

The vegetation has mean coverage of 52%. The sum of the mean coverages (T & E) of the species amounts to 80.20. The number of species is 36.

Four layers may be distinguished.

	Height in vegetative condition	Sum mean coverages	Number species
emergent layer . . .	ca. 1 m	8.11 = 10.1 %	4 = 11.1 %
high herb layer . . .	60 cm	18.90 = 23.5 %	3 = 8.3 %
medium herb layer .	40 cm	9.07 = 11.3 %	17 = 47.2 %
low herb layer . . .	15 cm	44.12 = 55 %	12 = 33.3 %

In the emergent layer an occasional *Curatella* reaches 3 m in height. In the low herb layer only herbs and tussocks occur; in the high and medium layers also shrubs and half shrubs.

	Sum mean coverages (%)	Number species
trees	+	1 = 2.7 %
shrubs	10.8	6 = 16.6 %
half-shrubs	1.6	6 = 16.6 %
herbs	2.9	13 = 36.1 %
tussocks	84.5	10 = 27.7 %

Trees and tall shrubs are very scarce.

The ground water is very deep, there is a large soil volume: dicotyledonous species are numerous.

The water economy is unfavourable, because all rain water sinks out of reach immediately. Moreover, the soil is very poor in nutrients: the vegetation is low. The low herb layer is the most important. There is little productivity. This is also evident from the fact that the species have very extensive root systems, but nevertheless remain small.

The shrubs have a relatively large part in the coverage. The vegetation is thin. Although the root systems are horizontally very extensive, the sod layer is not closed. Roots are not the determining factor in the density of vegetation. Germination and ecesis of the young plant probably determine vegetation density.

IV. 3.1.7. *Xyrido-Paspaletum* (Fig. 12a, Tables 4 and 5)

The vegetation has a mean coverage of 25% according to HEYLIGERS (1963). The maximum coverage is 40%. For the present study a stand of *Xyrido-Paspaletum* was investigated which had a coverage of 60%. The sum of mean coverages (T & E) of the species is 36.77, calculated from the table of Heyligers. The number of species is 42.

We can distinguish two layers.

	Height in vegetative condition	Sum mean coverages	Number species
high layer	50 cm	0.49 = 1.3 %	10 = 23.8 %
low layer	10–20 cm	36.28 = 98.6 %	32 = 76.1 %

The high layer consists of three grasses and sedges and for the rest of small shrubs, which occur occasionally and singly. Most species of the low layer do not exceed 10 cm. Many species have a rosette flat on the ground.

	Sum mean coverages	Number species
trees	—	—
shrubs	1.53 = 4.1 %	10 = 23.8 %
half-shrubs	1.30 = 3.5 %	1 = 2.3 %
herbs	7.48 = 20.3 %	12 = 28.5 %
tussocks	26.41 = 71.9 %	18 = 42.8 %
?	0.05 = + %	1 = 2.3 %

It is difficult to distinguish tussocks from non-tussock formers. There are several species with small rosettes of flattened leaves, forming aggregations of individuals which originated vegetatively from one parent plant. They are counted as tussocks, e.g. *Abolboda americana* and *Xyris* species.

The ground water reaches the surface for a part of the year. There is only little rooting space for dicotyledons: trees are lacking, shrubs are sporadic and remain small. There are many herbs of which 8 are therophytes, which are present only in the wet season.

The environment is extreme in its alternation of water surplus and desiccation: the most common herbs are adapted to only one situation as therophytes.

As a result of prolonged periods with high water tables, the root volume for monocotyledons is also limited. Moreover, the soil is poor: the vegetation remains extremely low.

The vegetation is thin, although the roots do not spread and the sod layer is not closed. The reason must be sought in germination and survival chances in this extreme environment.

IV. 3.1.8. *Clusia-Scleria* scrub, *Comolia* variant (Fig. 12b, Tables 4 and 5)

Structurally, this scrub does not belong to the savannas. *Gramineae* and *Cyperaceae* do not play a part in the vegetation which is primarily made up of woody species. This scrub always occupies a small area of a few m². It is scattered through vegetation types which do have a savanna structure. Soils and ground-water changes are identical with those of surrounding savannas.

Coverage according to Heyligers amounts to 15–40%. The present investigation was carried out in scrub with higher coverage, from 60 to 100%. The herb layer was accordingly less important than indicated by Heyligers. The total number of species is 22. In addition there were 2 mosses.

Three layers may be distinguished.

	Height	Number species with high coverage	Number species
high shrub layer . .	1.5 m	3	8 = 36.3 %
medium layer . . .	60–100 cm	2	12 = 54.5 %
herb layer	15– 20 cm		2 = 9.0 %

Some shrubs emerge from the upper layer up to 3 m. The herbaceous layer consists of two species, which grow especially at edges of the scrub.

	Number species with high coverage	Number species
trees		1 = 4.5 %
shrubs	5	13 = 59.0 %
half-shrubs		—
herbs		5 = 22.7 %; 1 = 4.5 %
tussocks		2 = 9.0 %

The essential environmental difference between this shrubby vegetation and the *Xyrido-Paspaletum* is the litter layer, which covers the ground. The litter increases the organic content, improves water economy and lowers the maximum temperature of the underlying sandy soil. Once the bush is established, the micro-climate inside is probably less extreme.

The increase in organic material is possibly the most important factor for the occurrence of scrub. But it is also possible that the mineral soil could produce shrubby vegetation, but that the extreme alternation of water surplus and drought with high temperatures are limiting factors. The litter layer takes the edge off the harshness of the environment, improving survival chances for woody plants.

Rooting space is limited: the scrub remains low.

The reduction of light intensity inside the bush will prevent the occurrence of *Gramineae* and *Cyperaceae*.

IV. 3.1.9. *Ternstroemia-Matayba* scrub, *Humiria* variant (Fig. 13, Tables 4 and 5)

As was the case with the *Clusia-Scleria* scrub, these groups of shrubs are structurally not savannas; nor can this be said of the very thin vegetation between the bushes. The species composition of both shrubby vegetation types shows great similarity. A comparison of the structure of both is very interesting, since the only environmental difference is the level of the water table.

According to Heyligers, coverage of the canopy layer amounts to 75%. The coverage of the undergrowth varies considerably: from a few percent to 75%. The number of species given by Heyligers is 31.

These bushes are always rounded and dome shaped. The closed canopy reaches the ground around the periphery, because of the low creeping branches of *Humiria balsamifera* around the outside. The small patches of scrub frequently consist of one large specimen of *Ternstroemia punctata* or *Clusia fockeana*, with a few shrubs underneath.

We may distinguish four layers.

	Height	Number species with large coverage	Number species
layer of emergent trees	5 m		6 = 19.3 %
closed canopy . . .	2.5– 5 m	4	11 = 35.5 %
undergrowth	to 2 m		6 = 19.3 %
herb layer	to 50 cm		8 = 25.8 %

The emergents are sometimes complete trees, sometimes single branches. A few species which appear to prefer the edge of the scrub have been counted in the herb layer.

	Number species of high coverage	Number species
trees } shrubs }	4	23 = 74.1 %
half-shrubs		1 = 3.2 %
herbs		4 = 12.9 %
tussocks		3 = 9.6 %

It is difficult to distinguish trees from shrubs. Many species have sometimes one trunk, sometimes several. Tree and shrub forms are combined. Tussocks occur only at the edges of the bush.

The same reasoning applied to the litter layer of the scrub on wet white sand, is also valid in the present case.

The structural difference between shrub communities is one of dimension, both in height and in area. The difference in environment is a matter of water-table levels, which are deeper in the *Ternstroemia-Matayba scrub*. This causes more severe drought, but on the other hand the omission of a period of water excess. Both conditions are responsible for a greater soil volume for root systems, in view of the necessity of reaching out to water, and the better aeration. A higher productivity can be noticed: plants are larger, even in species which occur in both types of scrub.

The dome shape of the bushes can be correlated with 1) drought damage to those terminal buds which emerge from the canopy, 2) the rooting volume, which is more limited for species at the edge of the litter area, than for those which grow in the center of the bushes; roots appear to limit themselves to areas covered by litter.

Humiria balsamifera, which fills the lowest zone, roots outside the litter. It seems plausible, that light intensity is the factor which causes *Humiria* to emerge from underneath the canopy.

IV. 3.2. **Detailed consideration of some forms**

Trees

The gnarled fruit-tree type is the dominant tree form in savannas, as is confirmed by literature reports. Only a few species adopt this form. In the Lobin savanna it is only *Curatella americana*. In other savannas of North Suriname these forms are assumed by *Byrsonima* *crassifolia* and *B. coccolobaefolia* and by *Anacardium occidentale*, which is planted around Indian settlements. All other tree species have a normal form with well developed trunk and a crown at some height above the ground. Although the terminal buds of every species succumb to fire, the resulting tree form still depends upon the species, as was also observed by LEBRUN (1947). It is not clear why the gnarled form is dominant and apparently better adapted to the situation.

Both fires and drought may destroy the terminal bud. In cases of serious fire damage to the aerial portions, the species sprout from below the surface, often with several stems. This causes a shrubby habit.

When the trees have reached a height of several meters, the crown will not be damaged seriously by grass fires, as is also known in the literature.

Curatella americana is the most generally distributed species in the associations discussed above. It shows the fruit-tree form very clearly. The terminal bud, which is enveloped by the most recently formed young leaf, dries out even in the short dry season. The direction in which the new terminal bud develops, is at a wide angle with the main branch. Often the old branch dies back above the new bud and falls off. This gives rise to branches of irregular form. The wood of *Curatella* is soft and juicy. Thick branches may be cut of with one (practiced) blow of the machete. *Curatella* may be a tree or shrub. The shrubs always turn out to have a xylopodium below soil level, on which fire scars are frequently visible. Obviously the shrub form is the result of destruction of the aerial parts. In the *Panicetum* and the *Schizachyrio-Rhynchosporetum*, *Curatella* is scarce and mostly shrubby. The tree form is very rare, since annual fires prevent its development. Where fires occasionally skip a year the species may outgrow the influence of the fire.

In the *Polycarpaeo-Trachypogonetum*, *Curatella* is usually a tree, although this vegetation type burns annually. This may be explained by supposing that the environment with its larger soil volume and relatively favourable water economy makes rapid growth possible, so that plants may outgrow the fire zone with one or two branches in the interval between two fires, i.e. one years time.

Shrubs

A total of 31 species are found in the associations mentioned above, including the scrub on white sand. Only five of these have a single stem. All others have several stems per individual, arising from the xylopodium below the surface. The xylopodium is an outgrowth of the base of the stem, which arose by the destruction of aerial parts and the sprouting of buds into new, full-fledged trunks, as was also described by LEBRUN (1947). He made the correct comparison with the burl of a pruned willow. On the xylopodium we may find scars of old stems, sometimes also burnt remains.

Although the ability to sprout from the base of the stem below the surface would be a good adaptation to drought, the great frequency of xylopodia and multiple stems appears to be primarily due to fire. Fire damage is often so heavy that only underground buds remain intact. The damage to the aerial portions and the possibility of sprouting above the ground depend upon the intensity of the fire and the resistance of the species. Thus, shrubs were observed to sprout along the entire length of the stem following the rapid passing of the front of the fire; and species of a *Ternstroemia-Matayba* bush sprouted from far below the surface following days of smoldering in the thick litter layer.

Eight species fall in the category of dwarf shrubs. They remain within the herb layer in most cases.

Half-shrubs

Twenty-three half-shrubs were found in the vegetation units studied. All but three have multiple stems. All but four have an underground xylopodium.

It was assumed that occasional individuals which were not burned had produced new stems form the woody stem base above the surface, following the dry season. The great frequency of xylopodia must be ascribed to fire damage. There are no instances of extremely large underground organs, which might function in water storage.

Generally, the occurrence of half-shrubs indicates drought. In this vegetation with annually recurring fires, which could be regarded as intensified drought, half-shrubs have a better chance of survival than herbs and dwarf shrubs.

Non-tussock forming herbs

In the units discussed above, 47 herbs occur altogether. Of these, 24 are limited to or prefer the *Polycarpaeo-Trachypogonetum*, with higher coverage in the sub association *curatelletosum;* 8 are limited to the *Xyrido-Paspaletum*, 1 to *Clusia-Scleria* vegetation, 2 to the undergrowth of the *Ternstroemia-Matayba* vegetation. No special preference can be reported for the remaining 12 species. The herbs apparently favour habitats with either long periods of high water table or a more favourable micro-climate as a result of tree cover.

Of the 47 herbs, 11 have multiple stems, 10 of them perennial; 36 have single stems, 10 of them perennial and 26 therophytic. Apparently the therophytic habit is correlated with single stems.

Survival of the dry season

For therophytes the dry season poses no problem. They disappear. 14 of the 20 perennial species survive underground, 5 remain above ground; the behavior of one species is unknown. The 14 species whose aerial parts dry out in the dry season, are not affected by fires. Some are able to continue a marginal existence if the dry period is not too severe. A leptopodium occurs in 11 species, one forms a bulb, one a corm, and one a rhizome. Herbs that retire underground, are missing in the *Xyrido-Paspaletum*, probably owing to high ground water levels. Of the 5 species that do not dry up in the dry season, none has any special morphological peculiarities for this purpose.

Two of them occur in the *Xyrido-Paspaletum*, one in the *Clusia-Scleria* vegetation, one in the *Polycarpaeo-Trachypogonetum curatelletosum*, and one species occurs in several units.

Adaptations to drought during the growing season (see Ch. VI.2)

Dense aggregations of stems or densely branched stems will reduce air-convection currents and thereby diminish transpiration. Individuals with multiple stems are always perennials sprouting from underground parts. Of the 36 single-stemmed species, 29 remain unbranched or ramify at some height. We may conclude, therefore, that this "adaptation" to drought does not play a role.

A woody stem base will increase resistance against desiccation due to high temperatures near the soil (HAGERUP, 1930; WARMING, 1893). A woody stem base occurs in 16 herbs. None of the herbs of the *Xyrido-Paspaletum* has this property.

Herbs occur primarily in the *Xyrido-Paspaletum* and the *Polycarpaeo-Trachypogonetum*. They attain the greatest coverage in the subassociation *curatelletosum* of the latter association.

The prevalence of herbs, and the lack of woody stem bases in the *Xyrido-Paspaletum* may be correlated with the high water tables, which form an effective protection against drought during the growing season. At the same time the high water table must also be the cause of the lack of species which retire underground during the dry season. Of the 8 herbs, 6 are therophytes.

In the *Polycarpaeo-Trachypogonetum*, water supply during the growing season is relatively good at some depth, while the closed tall grass layer may offer some protection against high temperatures and consequent desiccation. The increased coverage in the subassociation *curatelletosum* may be correlated with a similar protective action of the canopy of *Curatella*. Of the 24 species, 13 have a woody base. This may be correlated with the incidence of drought during the growing season. Besides 16 therophytes, there are 8 perennial species. Of these, 7 retire underground during the dry season, without obstruction by high water tables. The increase in coverage of herbaceous species in the *curatelletosum* as compared with the *cyperetosum*, is due to completely herbaceous species more than to those with woody stem bases.

Non-tussock forming *Gramineae* and *Cyperaceae*

Only eight species belong in this group. Their distribution over the associations is as follows: 2 in the *Polycarpaeo-Trachypogonetum curatelletosum;* 1 also in the *cyperetosum;* 3 in units with high water tables during the growing season, i.e. 1 in *Xyrido-Paspaletum*, 1 in *Clusia-Scleria-Comolia* vegetation, 1 in *Panicetum* and *Xyrido-Paspaletum;* 1 in *Schizachyrio-Rhynchosporetum mesosetosum;* 1 in several units. This distribution fits in well with that of the herbs discussed before.

Tussocks

The tussock is the favourite growth form in all units except the scrub. It offers protection against fires and desiccation (MASSART, 1907, 1908, 1909; LEBRUN, 1947; PILGER, 1902; WARMING, 1893).

Following fires, all tussock species produce new sprouts around the old ones.

The young shoots arise several cm below the surface in almost all species (see Ch. V.2.2).

Further remarks

Climbing stems occur in 11 species. They may be herbaceous, woody, or woody only at the base. No special correlation with the several units can be noted.

Decumbent stems are seen in 4 species; 1 shrub, 2 half-shrubs, 1 herb.

As is also reported in the literature, certain forms are scarce or absent in these vegetation types: mosses, epiphytes, succulents, bulbs, thorns, rhizomes, and stolons. Rosettes of prostrate leaves are found apart from the *Xyrido-Paspaletum*, in only two species of *Polycarpaeo-Trachypogonetum*.

IV. 3.3. **Discussion of some species**

Byrsonima crassifolia occurs in the Lobin savanna as a tall tree (about 7 m) in units on soils heavier than white sand. On dry white sand, it is a low shrub. In the Gross savanna, the species assumes the fruit tree form (VAN DONSELAAR, 1965).

Licania incana occurs as isolated low shrubs on white sand. Inside bushes it becomes a small tree. One specimen of each form was dug up. The tree had many more roots than the little shrub. The environment inside a bush is less extreme than outside. Higher content of organic material, soil moisture, and atmospheric moisture within the bush, may account for the development of the tree form. In open sand the low nutrient content limits the dimensions of the individual, and the extreme drought stimulates the development of buds at the base of the stem, since higher buds dry out. Possibly, the number of roots is also limited outside bushes (and consequently the dimensions above ground), because roots perish during the dry season.

Many species have larger dimensions in dry white sand than in wet white sand where roots occupy a smaller soil volume. Examples: *Clusia fockeana*, *Conomorpha magnoliifolia*, *Ternstroemia punctata*, *Humiria balsamifera*, *Tetracera asperula* and *Cassia ramosa* var. *ramosa*.

IV. 4. CORRELATIONS AND CONCLUSIONS

IV. 4.1. **Correlations of characteristic forms of savanna plants with environment**

The fruit-tree form is the most conspicuous tree type. Not all tree species have this stunted form. The cause of the prevalence of this type is not known.

Many species which are elsewhere tree-like occur on the savanna as shrubs with several stems, which sprout from a xylopodium. Fire is a primary cause of multiple stems.

Trees and shrubs occur in all habitats mentioned, except wet white sand, where trees and tall shrubs are absent.

Half-shrubs, whose woody stem bases remain above ground during the dry season, are forced underground by fires. On white sand they are less numerous than on heavier soil types.

Some of the herbs have woody stem bases, as adaptations to incidental drought during the growing season. Few species remain above ground during the long dry season. Most perennial species retire underground, so that fire has little effect on them. Species with simple as well as multiple stems exist.

Almost all therophytes have single stems. Most species have no branches or branch at some height above the ground. Woody stem bases occur regularly.

Perennial and annual herbs prefer environments with the least chance of drought during the growing season, viz. the *Xyrido-Paspaletum*, and the *Polycarpaeo-Trachypogonetum*, especially the *curatelletosum*. Why they are not more abundant in the *Panicetum stenodoidis* is not clear. Species perennating underground, are lacking in the *Xyrido-Paspaletum*, as are species with woody stem bases. This is correlated with excessive water and with permanent water supply during the growing season, respectively.

Grasses and *Cyperaceae* which are not tussock forming are scarce. Their occurrence corresponds with that of perennial herbs.

The tussock is the dominant structural form in all herbaceous vegetations. Their absence from bushes on white sand can be correlated with the diminished light intensity.

Thick woody organs are always underground. They are in most cases caused by repeated fires. They are never extremely large as is described in the literature for some species. There are no indications that their primary function is water storage.

IV. 4.2. Correlations between vegetation structure and environment

The effect of the climatically controlled long dry period is noticeable in all vegetations investigated. The adaptations, which result from the long dry period, are treated in Chapter V.

The structural differences of vegetation in optimal condition are primarily caused by differences in the environment during the growing season.

The water economy of the soil appears to be the most important factor. It determines the rooting volume. The relationship between root volume and water economy is treated in Chapter III.3.3.

Greater rooting volume is always accompanied by a greater number of forms, greater differentiation of layers, and increase in coverage of the higher layers. It is, in other words, accompanied by a greater productivity. The growth rate per growing season must be determined by the available rooting volume, but also by the nutrient content. Where the roots of the dicotyledons are limited to the upper part

TABLE 4

Data on the structure of the vegetation types

	total coverage		low herb layer		medium herb layer		high herb layer		emergent layer		tree or shrub layer	
	mean	sum mean cov. T & E	height in cm	sum mean cov. T & E	height in cm	sum mean cov. T & E	height in cm	sum mean cov. T & E	height in cm	sum mean cov. T & E	height in cm	sum mean cov. T & E
Panicetum stenodoidis	100	138,54			20	*88,85*	60	*49,68*	100	0,1		
Schizachyrio-Rhynchosporetum mesosetosum	80	101,54	10	0,85	30	*83,1*	50	15,15	70	0,89	1000	0,16
Schizachyrio-Rhynchosporetum mitracarpetosum	75	113,04	15	19,71	30	*47,23*	60	*38,83*	200	6,43	1000	0,84
Polycarpaeo-Trachypogonetum cyperetosum	85	108,82	15	12,44	40	18,76	70	*77,15*	100	0,37	1000	0,10
Polycarpaeo-Trachypogonetum curatelletosum	95	143,43	15	8,92	40	6,53	70	*86,67*	200	0,22	1000	*41,9*
Mesoseto-Trachypogonetum	52	80,02	15	*44,12*	40	9,07	60	*18,90*	200	8,11		
Xyrido-Paspaletum	25	36,77	10	*36,28*			50	0,49				
Clusia-Scleria-Comolia scrub	15–40		15	± 10 %			80	10 %			300	± *20* %
Ternstroemia-Matayba-Humiria scrub	75				50	little	200	little-75 %	500	little	< 500	*70* %

of the soil by an alternation of excessive water and desiccation, trees and tall shrubs do not occur.

TABLE 5

Distribution of the types of structure of the species according to vegetation units

A Sum mean coverages (T & E) of the species in % of the total sum
B Number of species in %

	tree	shrub	half-shrub	herb	tussock
A					
Panicetum stenodoidis	—	+	2	0.2	97.8
Schizachyrio-Rhynchosporetum mesosetosum	0.1	0.8	1.5	0.5	96.8
Schizachyrio-Rhynchosporetum mitracarpetosum	0.7	11.4	3.3	2.0	82,6
Polycarpaeo-Trachypogonetum cyperetosum	+	0.5	1.2	5.7	92.3
Polycarpaeo-Trachypogonetum curatelletosum	28.6	3.1	2.6	17.8	47.6
Mesoseto-Trachypogonetum	+	10.8	1.6	2.9	84.5
Xyrido-Paspaletum	—	4.1	3.5	20.3	71.9
B					
Panicetum stenodoidis	—	3.8	15.3	30.7	50.0
Schizachyrio-Rhynchosporetum mesosetosum	16.1	9.6	12.9	25.8	35.4
Schizachyrio-Rhynchosporetum mitracarpetosum	20.0	11.1	17.7	24.4	26.6
Polycarpaeo-Trachypogonetum cyperetosum	12.3	6.8	26.0	38.3	16.4
Polycarpaeo-Trachypogonetum curatelletosum	10.8	8.1	22.9	43.2	14.8
Mesoseto-Trachypogonetum	2.7	16.6	16.6	36.1	27.7
Xyrido-Paspaletum	—	23.8	2.3	28.5	42.8
Clusia-Scleria-Comolia scrub	4.5	59.0	—	27.2	9.0
Ternstroemia-Matayba-Humiria scrub	74.1		3.2	12.9	9.6

All *soil types* which were discussed prove to be capable of supporting trees and tall shrubs, even the pure white sandy soil. In this soil many shrubs require a litter layer, which is supplied by the local vegetation.

The vegetation is much lower on wet white sand than on wet heavy soils (*Xyrido-Paspaletum* and *Panicetum stenodoidis* respectively). On white sand a large root system is accompanied by relatively small proportions of the aerial parts.

Fire does heavy damage to aerial portions. Above a height of 3 to 4 m, fire damage is never so heavy as to be irreparable. The assumption is justified, that a vegetation with high woody layers is made possible by rapid growth through high productivity, or by decreased frequency of fires. The coverage of this higher tree and shrub layer will also depend upon other factors, such as germination and survival chances of the seedlings.

The extent of root systems depends upon the water supply by ground and rain water, and the rate of penetration into the soil of rain. The extent of root systems is correlated with the distance between individuals above ground. However, this is not true for vegetation on white sand. Factual evidence is too limited to conclude, that the distance between individuals is determined by root competition in every case.

On both wet and dry white sand, the herbaceous vegetation is sparse, and the root layer is not closed. Here the distance between individuals is certainly not determined by root competition. Such factors as germination and survival of the first drought must play an important role. During the dry season the white sand is probably a less favourable environment than heavier soil, owing to the greater aeration, and higher temperature, resulting from insolation. A litter layer will improve conditions during the dry season, so that more plants germinate and survive the dry season, resulting in denser vegetation.

A tall layer with considerable coverage will influence the micro-environment. It seems probable that in this case the low incidence of tussocks in the low layer is due to diminished light intensity. Increase in number and coverage of herbs, the most drought-sensitive growth form, may have to do with diminished transpiration under the tall layer due to diminished insolation, and hence less extreme heat.

CHAPTER V

PERIODICITY OF THE VEGETATIVE STRUCTURES

V. 1. Introduction

In a tropical climate with alternating dry and wet seasons, conditions for plant growth are not equally favourable throughout the year, unless edaphic factors nullify this alternation.

In contrast to the temperate regions, where low temperatures retard the physiological processes even when the building materials are present, these physiological processes are always possible in the tropics, but the raw materials are the limiting factor (Beard, 1942). During drought, water is limiting, during excessively wet periods, the oxygen is the limiting factor.

During the unfavourable season the activity of the vegetation slows down. There is a periodicity correlated with the seasons: "seasonal rhythm."

In different species and environments, the ways in which plants spend the unfavourable season, in other words, the extent to which activity is reduced, depends upon the severity of the unfavourable season, and the sensitivity of the species. The aspect of the plants and the vegetation changes with the season: "seasonal aspect".

By following these seasonal rhythms we find the answer to the question, which seasons are the least favourable for plants (vegetation).

By noting the seasonal aspects, one gains information about the imprint left by the unfavourable season upon the plant and the vegetation.

If drought is the unfavourable factor, the reduction in activity is not only a direct consequence, it is also functional. The effect of drought is reduced, by a reduction of water usage.

MASSART (1907, 1908, 1909) classified in a more or less similar manner the plants of the Belgian dunes. He created groups using combinations of characteristics which are here indicated as rhythm and aspect.

Since the climate of all vegetation types of this study is the same, it is perhaps possible to find a correlation with environmental factors other than the macroclimate, by following the changes in aspect of species and vegetation types through the seasons, and by comparing these data for different vegetation types.

V. 1.1. Seasonal rhythm

The climatic cycle includes a long wet season, a long dry period, a short wet season and a short dry period. In the following account these seasons are indicated with W, D, w and d, respectively. The seasons in which each species has vegetative organs, in good condition, was noted. By this method we discover the following possibilities in the vegetation types of this study.

WDwd: Activity similar in all seasons.
W*D*wd: Diminished activity during the dry season, but functional.
Wwd : No activity apparent during the long dry season; the plant has a resting stage.
W-wd : Normally belonging to Wwd, but sometimes leading a marginal existence during the dry season owing to favourable habitat or rainfall. Even following renewed rainfall the species does not resume normal activity.
W : Active only during long wet season.
W/w/d: Period of activity whenever conditions are favourable.
Wd : Active following short wet season, during short dry season and subsequent wet season.
wd : Active during the short wet and short dry seasons.

V. 1.2. Seasonal aspects

The most spectacular seasonal change is leaf fall. Leaf fall is frequently the only information available concerning periodicity of a vegetation type. In those types where trees and shrubs determine the aspect and form ecologically dominant layers, leaf fall data are frequently adequate for the classification into larger units. When trees and shrubs are absent or not dominant, as in savanna vegetation, a classification of seasonal aspects of non-woody species is necessary.

With respect to leaf fall, the common distinction is between evergreen and deciduous plants. This dichotomy proved inadequate for tropical vegetation; there are species intermediate between the two groups. DANSEREAU (1951) designates as semi-deciduous those "plants that lose some of their leaves during the dry or cold period but never all of their leaves at any one time". As an example he names tropical savanna trees. RICHARDS (1952) says concerning leaf fall: "... but some species of large trees have a short leafless period lasting from a few days to a few weeks and may be described as semi-deciduous." BEARD (1942) says: "Three other species may be described as semi-deciduous species, affecting a short leafless or almost leafless period coinciding with flowering, but cannot be said to be related with it." He furthermore distinguishes "incompletely deciduous": "This class of trees would now be better described as incompletely deciduous since they show a period varying in length according to the intensity of the drought when they may lose a large proportion or even all of their leaves." The definitions of semi-deciduous by Beard and Richards agree, while Dansereau's definition of semi-deciduous agrees with Beard's definition of incompletely deciduous.

In the present study it proved necessary to recognize an incompletely deciduous category sensu Beard in addition to the deciduous and evergreen groups.

For the non-woody species, in which the same categories occur, there proved to be a difference in the degree in which aerial portions disappear during the resting stage, i.e. the extent to which plants are exposed to desiccation. Besides desiccation the temperature also plays an important part, because it may rise considerably owing to insolation (Phillips, 1930; Beadle, 1940).

The following possibilities may be distinguished:

Eg : Plant evergreen.
Id : Incompletely deciduous, the plant loses part of its foliage so that activity is reduced but not halted.
D : Deciduous, the plant loses all its foliage, halting assimilation and transpiration.
Sh : Stem shortened, the plant loses the aerial portions, except the short woody stem base.
Vs : Aerial portions of the plant disappear, down to soil level.
Vb: Aerial portions of the plant disappear including several cm below soil level.
S : Only seeds remain, the vegetative plant disappears.

It is clear that the rejuvenation buds enjoy better protection in groups Vs and Vb.

V. 2. Results

V. 2.1. Seasonal rhythm

The distribution of all species found in the vegetation units studied, is as follows:

WDwd	48 species, of which 20 in bushes on white sand only.
W*D*wd	17 species.
Wwd	67 species, of which 5 exclusively in bushes on white sand.
W-wd	16 species.
W	8 species.
W/w/d	3 species.
Wd	1 species.
wd	2 species.
w	1 species.

Unknown 11 species, 2 exclusively in bushes on white sand.

This distribution shows, that the long dry season is the least favourable for plant growth. The long wet season does not inhibit activities. This is not in agreement with Beard (1953), who says about most woody plants: "If the soil becomes water logged later in the rains, they die down into a dormant state."

WDwd: The trees and shrubs all belong to this group, with the exception of 6. 5 of the exceptions belong to the W*D*wd group, and 1, *Galactia jussieuana* is Wwd. In addition to woody species, 6 herbaceous species belong to the WDwd group. 5 of these are limited to wet white sand, where water is always or usually available, owing to the high water table. One species (*Heliconia psittacorum*) occurs in the *Polycarpaeo-Trachypogonetum curatelletosum*. This is correlated with the supposed better micro-climate under the tree canopy.

The seasonal rhythm could not be determined for all trees and shrubs in the field. For some, herbarium material and information from the flora of Surinam had to be used. Possibly, a few species will turn out to belong in the W*D*wd group.

The occurrence of trees and shrubs in the various vegetation units was discussed in Chapter IV under structure. A correlation with root volume was established. No reason can be given why all woody species belong in the WDwd group and the W*D*wd group. The following possibilities exist: a) the root systems reach the ground water, so that water is always available. On dry white sand this is not the case for most species. In heavier soils many species have roots which reach down to ground water level. But usually this is an insignificant part of the entire root system. Even species with superficial roots belong in this group. b) The environment well above soil level may be better than closer to the ground, since the temperature of the upper air strata is not influenced by the emission of heat from the soil. However, no temperature measurements were done. Even dwarf shrubs belong to the WDwd or W*D*wd group. c) Woody and corky portions are a good protection against evaporation, so that only the leaves are transpiring. The leaves are generally scleromorphic and shiny on the upper surface. Perhaps the vessels of the wood serve as water storage. In *Curatella americana*, the wood certainly is juicy and brittle.

W*D*wd: This group includes 5 woody species, i.e. 2 trees and 3 dwarf shrubs: *Curatella americana*, *Licania incana*, and *Cassia ramosa*, *Tibouchina aspera* and *Comolia lythrarioides*. When we consider that there are 8 dwarf shrubs, then the percentage of W*D*wd dwarf shrubs is high. Possibly this is also related to the supposedly poor micro-environment closer to the soil.

The remaining W*D*wd species are herbaceous, or woody at the base. The distribution of the 13 species over the units of vegetation is as follows:

3 species in units on heavier soils and not on white sand: *Hyptis atrorubens*, *Sipanea pratensis*, *Scleria bracteata*.

2 species only on wet white sand.

5 species limited to the *Polycarpaeo-Trachypogonetum*, 4 with highest coverage in the *curatelletosum*, 1 exclusively in the *cyperetosum*.

3 species exclusively or preferentially in the *Mesoseto-Trachypogonetum*.

Most of the W*D*wd species, apart from the woody ones, occur on soils with rapid water uptake. This means that rain showers in the dry season come within reach of the root systems. Only those species which have retained some foliage would be able to profit from these rain showers.

Which is the cause and which the effect in this case, remains a question.

Wwd: This group is the largest in terms of numbers of species. It also has the highest coverage in all savanna vegetation, not counting bushes on white sand. All tussocks belong here, except 3 therophytic tussock species with short periods of activity. 9 half-shrubs, most therophytes, and perennial herbs, and 1 shrub belong to the Wwd group.

There are 27 non-tussock species. They occur in all units. Of these, 15 are restricted to the *Polycarpaeo-Trachypogonetum*, which is generally distinguished from other units by the large number of non-tussock species.

It is noteworthy that only 1 species of this group occurs in the *Xyrido-Paspaletum*, with its high water table.

W-wd: Besides the species of the Wwd group, there are 16 other non-tussock forming species, which under favourable circumstances manage to extend through the dry season. 13 of these occur in units with permeable soils, so that they can utilize occasional showers.

1 species is exclusive for the *Xyrido-Paspaletum*.

1 species occurs in *Panicetum* and *Xyrido-Paspaletum*, both units in an environment with high water table.

1 species occurs on all soils heavier than white sand (*Cassia cultrifolia*).

There is a clear preference for habitats with occasional water supply in the dry season.

There are several grasses, *Trachypogon plumosus*, *Schizachyrium riedelii*, and *Axonopus pulcher*, of which occasional specimens were observed with green leaves on the tips of old culms. The vitality was clearly reduced. No note was made of the vegetation units where these specimens were found.

W and W/w/d: 11 species belong to these groups, all therophytes. They occur in all units. The largest coverage is found in the *Xyrido-Paspaletum*, where water shortage is never acute, due to high water levels.

wd and w: *Oxypetalum capitatum* and *Myrosma cannifolia* belong in the wd group and *Scleria hirtella* is the one species which is in evidence during the short wet season only.

Possibly there is a correlation with fire. But causal relationships are not known. *Zornia diphylla* (Wwd) has its optimum in the short wet and dry periods.

dW: *Riencourtia glomerata* is the only species in this group.

V. 2.2. Seasonal aspects

The distribution of all species over the categories, is as follows:
Evergreen: 48 species, of which 20 exclusively in the bushes on white sand.
Incompletely deciduous: 17 species.
Deciduous: 3 species.
Shortened: 12 species.
Disappearing to soil level: 5 species.
Disappearing to below soil level: 46 species.
Seed: 30 species.
Unknown: 13 species.

Evergreen (Eg): All WDwd species belong of course in this group. What was said about them before could be repeated here.

Incompletely deciduous (Id): By definition all W*D*wd species belong here. They are 8 half-shrubs, 5 woody species and 4 herbs. Following the dry season, 8 half-shrubs sprout with new shoots from the woody stem base, and 2 herbs from below soil level. The other 2 herbs may also sprout from below the surface, but it was not determined whether this is the rule.

Deciduous (D): Only 3 species are counted as deciduous: the shrub *Galactia jussieuana* and the half-shrubs *Cassia hispidula* and *C. faginoides*. The latter 2 sprout both from the winding stems and the woody bases following the dry season.

Shortened aerial parts (Sh): Only half-shrubs belong in this category. But not all half-shrubs are Sh. There are 12 species, of which 9 occur only on permeable soils, in the *Polycarpaeo-Trachypogonetum* and *Mesoseto-Trachypogonetum*. 1 species is found in bushes on dry white sand, one in the *Xyrido-Paspaletum*, and 1 in the units of heavier, less permeable soils.

Disappearing to soil level (Vs): 5 tussock forming species belong here. 4 of them are on white sand, with 2 exclusively on wet sand. 1 species occurs in the *Panicetum stenodoidis*.

Disappearing to below soil level (Vb): All tussocks belong in this group, except the 5 Vs species and 3 S species. In addition, 15 herbs and 2 half-shrubs are Vb.

8 of these species are limited to the *Polycarpaeo-Trachypogonetum*, with highest coverage in the *curatelletosum*. Two *Schizaeaceae* occur in the bushes on white sand. The remaining 7 species are distributed irregularly over several different units.

The largest number of perennial non-tussock forming herbs are present in the *Polycarpaeo-Trachypogonetum*. It is noteworthy that the only Vb species in the *Xyrido-Paspaletum* is a sedge. Dicotyledons which retire into the soil are lacking in this habitat with long periods of high water table.

Seed (S): 28 dicotyledons and 3 tussocks remain through the dry season as seeds. There are 3 species which occur in almost every unit (*Polygala adenophora*, *P. longicaulis*, and *Cassia cultrifolia*).

7 species limit themselves to the *Xyrido-Paspaletum*.

18 species are restricted to the *Polycarpaeo-Trachypogonetum*, with highest coverage in the *curatelletosum.*

2 species occur in the *Schizachyrio-Rhynchosporetum*, in addition to the *Polycarpaeo-Trachypogonetum.*

1 species occurs in the *Panicetum stenodoidis.*

It may be concluded from this distribution, that the presence of these plants is determined by conditions during the growing season, not those of the dry season, because there is less chance of water shortage during the growing season in the *Polycarpaeo-Trachypogonetum* and the *Xyrido-Paspaletum* than in other types of vegetation.

From the distribution of the non-woody species over the classes of seasonal aspects we may conclude that conditions in the vicinity of the surface are unfavourable (few species retire to the surface; species which remain above the surface have woody stem bases; most species retire several cm into the soil). This may be related to the intensive insolation during the dry season, and the resulting high temperature.

V. 2.3. **Discussion of the periodicity of the vegetation units**

Since all woody species are WDwd, Eg, a comparison of the distribution of this group is not interesting. Their distribution has already been discussed in Chapter IV. A correlation was shown with the root volume and with fire. The W*D*wd woody species *Curatella americana* and *Tibouchina* occur in all units, except those on wet white sand. The remaining 3 woody W*D*wd species are limited to sand.

The WDwd and W*D*wd species which are woody, will be left out of the discussion of vegetation units.

All tussocks are Wwd and Vb, except 5 species which are Vs, and 3 therophytes. 4 of the 5 Vs species occur on white sand, 1 in the *Panicetum stenodoidis*. The therophytic tussocks are counted with the other therophytic herbs. There is little reason to include the tussock forming plants in the discussion of periodicity of the vegetation units.

For comparisons, the only useful plant forms are the half-shrubs, the perennial non-tussock formers and the therophytes. Even among these, there are several species which occur in almost every vegetation type, except on white sand: the half-shrubs *Hyptis atrorubens* and *Sipanea pratensis*, both W*D*wd and Id; *Scleria bracteata* W*D*wd and Id; *Cassia cultrifolia* W-wd and S; *Polygala adenophora* and *P. longicaulis*, both W/w/d and S.

Table 6 shows the sum of the mean coverages of these species, calculated according to Tüxen & Ellenberg, and expressed as percent of the sum of all species of the unit, as well as the number of species in percent per unit.

Panicetum stenodoidis: There are no W*D*wd, Id species, apart from *Hyptis atrorubens*, *Sipanea pratensis*, and *Scleria bracteata*, which occur in all units other than those of white sand. Neither do we find WDwd, Eg species. Thus, all species have a resting stage in the dry period.

TABLE 6

Distribution of the periodicity classes of the non-tussock forming herbs and half-shrubs according to vegetation units

		I						II						III						IV					
		Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S
WDwd	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1,3	.	.	.	.	.
W*D*wd	A	.	*1,3*	.	.	.	.	.	*1,5*	.	.	.	.	.	*4,1*	.	.	.	.	.	0,8	.	.	.	.
	B	.	*11,5*	.	.	.	.	.	*9,6*	.	.	.	.	.	*8,8*	.	.	.	.	.	8,2	.	.	.	.
Wwd	A	.	.	.	.	+	.	.	.	.	+	0,1	.	.	.	+	0,1	+	+	.	.	.	0,1	0,2	0,2
	B	.	.	.	.	7,7	.	.	.	.	3,2	6,4	.	.	.	2,2	2,2	8,8	2,2	.	.	.	6,8	9,5	12,3
W–wd	A	.	.	.	.	0,1	±	.	.	.	+	.	*0,1*	.	.	.	+	.	*0,3*	.	.	0,1	0,1	.	2,4
	B	.	.	.	.	3,8	*3,8*	.	.	.	3,2	.	*3,2*	.	.	.	4,4	.	*2,2*	.	.	2,7	8,2	.	8,2
wd	A	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	0,3	.
	B	.	.	.	.	3,8	.	.	.	.	.	6,4	.	.	.	.	.	2,2	.	.	.	.	.	2,7	.
W + W/w/d	A	.	.	.	.	.	0,9	.	.	.	.	.	0,6	.	.	.	.	.	0,9	.	.	.	.	.	2,5
	B	.	.	.	.	.	11,5	.	.	.	.	.	12,9	.	.	.	.	.	13,3	.	.	.	.	.	6,8

		V						VI						VII						VIII					
		Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S	Eg	Id	D	Sh	Vb	S
WDwd	A	6	.	.	.	.	.	.	.	.	.	.	.	10,5	.	.	.	.	.	.	.	.	.	.	.
	B	1,3	.	.	.	.	.	.	.	.	.	.	.	7,1	.	.	.	.	.	9,0	.	.	.	.	.
W*D*wd	A	.	4,0	.	.	.	.	.	0,5	.	.	.	.	.	7,0	.	.	.	.	.	.	.	.	.	.
	B	.	9,4	.	.	.	.	.	11,1	.	.	.	.	.	4,7	.	.	.	.	.	.	.	.	.	.
Wwd	A	.	.	.	0,8	4,0	2,5	.	.	.	+	0,9	+	.	.	.	.	+	0,1	.	.	.	.	.	.
	B	.	.	.	6,7	10,8	10,8	.	.	.	5,5	13,8	5,5	.	.	.	.	2,3	4,7	.	.	.	.	9,0	.
W–wd	A	.	.	0,4	0,9	.	3,0	.	.	1,0	.	.	.	.	.	.	.	.	0,1	.	.	.	.	.	.
	B	.	.	2,7	8,1	.	9,4	.	.	2,7	.	.	.	.	.	.	.	.	2,3	.	.	.	.	4,5	.
wd	A	.	.	.	.	6,0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	B	.	.	.	.	4,0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
W + W/w/d	A	.	.	.	.	.	0,8	.	.	.	.	.	0,8	.	.	.	.	.	17,8	.	.	.	.	.	.
	B	.	.	.	.	.	5,4	.	.	.	.	.	11,1	.	.	.	.	.	14,2	.	.	.	.	.	.
unknown	A													+	.	.	.	.	.	24,9	.	.	.	.	.
	B													2,7	.	.	.	.	.	14,2	.	.	.	.	.

I = Panicetum stenodoidis
II = Schizachyrio-Rhynchosporetum mesosetosum
III = Schizachyrio-Rhynchosporetum mitracarpetosum
IV = Polycarpaeo-Trachypogonetum cyperetosum
V = Polycarpaeo-Trachypogonetum curatelletosum
VI = Mesoseto-Trachypogonetum
VII = Xyrido-Paspaletum
VIII = Clusia-Scleria-Comolia scrub

A = Sum mean coverages (T & E) in % B = number of species in % Italics = only species occurring in all units of heavier soil

During this time they are Vb or S. This behaviour can be correlated with drought that is extremely effective, owing to the very superficial root systems of the dicotyledons caused by the high water table.

Schizachyrio-Rhynchosporetum mesosetosum: W*D*wd, Id species do not occur, apart from the species *Hyptis atrorubens*, *Sipanea pratensis*, and *Scleria bracteata*. Nor do we encounter WDwd, Eg species. All species are inactive in the dry season. The aspect types Sh, Vb, and S were noted, most species being S, W/w/d; coverage for Vb and Sh species is small, with a larger number of species in the former group.

The species on the termite hills do not show a different behaviour during the dry season from those in the remainder of the vegetation. Apparently the dry season is so unfavourable, that almost the entire vegetation goes through an inactive stage.

Schizachyrio-Rhynchosporetum mitracarpetosum: Hyptis atrorubens, *Sipanea pratensis* and *Scleria bracteata*, occurring in all units except on white sand reach their highest coverage in this subassociation. In addition there is 1 W*D*wd species. Otherwise the distribution is practically the same as in the other subassociation.

Polycarpaeo-Trachypogonetum cyperetosum: One species with low coverage is WDwd, Eg. *Hyptis atrorubens* and *Sipanea pratensis* are no longer the main component of the W*D*wd, Id species, neither in coverage nor in numbers. The percentage of W-wd species is higher than in the units mentioned above, indicating better conditions during the dry season. We may connect this with the more rapid water uptake of the soil. Occasional showers which fall during the dry season will also benefit the vegetation.

The larger number of Wwd, S and W-wd species indicate better conditions during the growing season. As was mentioned in Chapter IV under structure, we may correlate this with the deeper root systems and improved micro-environment, made possible by the high herb layer.

Polycarpaeo-Trachypogonetum curatelletosum: The distribution of species over the categories is practically the same as in the *cyperetosum*. The coverage increases in all groups. The W/w/d, S group is an exception: it decreases. The increase of all other groups may be correlated with the improved micro-climate under the tree canopy.

Mesoseto-Trachypogonetum: The W*D*wd group has a relatively high percentage of species. This may be correlated with the fact that rain water is the only water source, which disappears rapidly into the well drained soil. It is of great importance for the plants that every rain shower be utilized, even in the dry season. This is only possible when photosynthetic organs are present. The relatively high coverage of shrubs of the WDwd or W*D*wd type may be correlated also.

Xyrido-Paspaletum: There are relatively many WDwd, Eg species with a large share in the coverage of the vegetation. The W*D*wd group also has a major share in the coverage. Contrariwise, there are few Wwd species and there are no dicotyledonous Vb. Many S species are present with a short life span. All of these facts may be related to the high water table of this environment. This insures water supply during the growing season (S, W/w/d species) and is responsible for the short duration or absence of an effective dry season, since roots reach down to the ground water (WDwd and W*D*wd species). Finally, it prevents the retirement of dicotyledons into the soil (Vb species).

Clusia-Scleria-Comolia scrub.: The WDwd, Eg species may be related to the high ground water level and the protection of the crowns of the shrubs The Wwd, Vb species are always along the periphery of the bush

Ternstroemia-Matayba-Humiria scrub.: In this unit 3 non-tussock formers are present, 2 ferns which are Wwd, Vb, and 1 half-shrub which is Wwd, Sh. The periodicity of 2 herbs which are found in the bush is not known.

V. 2.4. **Fire**

Almost every type of vegetation is burned once a year, usually in the long dry season. In vegetation on wet white sand fires are less regular The vegetation is too sparse and low to sustain the fire. The desiccated tall, dense vegetation of the other units is very inflammable. The fire cleans out the dry vegetation. Of course, this affects the aspect of the plants and the vegetation, and the point from which the plants will sprout following the dry season.

The changes are as follows:

Evergreen species: In trees and shrubs above 3 to 4 m, fire generally results in a change from Eg to D.

For 11 of these species it was established with certainty that they form new sprouts from below soil level, following destruction of the aerial portions by fire, giving rise to a xylopodium. Eg becomes Vb.

In 7 lower shrubs, which remain in the heavy fire damage zone, it was noted that they also regenerate from below the soil, causing a xylopodium: Eg becomes Vb.

Two evergreen herbs sprout from a rhizome following fires. The behaviour of 3 herbaceous species of the *Xyrido-Paspaletum* is unknown. One of them was destroyed completely by fire, so that reestablishment is only possible by seed.

Occasionally bushes of dry white sand, belonging to the *Ternstroemia-Matayba-Humiria* scrub, are burned down. The litter layer may smolder for days, so that the aerial parts if not completely burnt, are certainly killed. Yet certain species were observed to sprout from below the surface, sometimes several dm below the original litter surface.

It has been established that through fire 6 Eg species become D; 18 have recourse to the possibility of Vb, and 1 species becomes S.

Incompletely deciduous: *Curatella americana* as a tree, loses all its leaves (D) in a fire. As shrub, it becomes Vb. *Licania* can sprout just above and below the surface after fires (Vb or Sh).

The other Id species, both the one shrub and the half-shrubs and herbs, become Vb. Only 2 half-shrubs on dry white sand become Sh.

Deciduous: (3 species). *Cassia hispidula* and *Galactia jussieuana* become Vb, *Cassia faginoides* becomes Sh.

Shortened aerial portions: 10 of the 11 Sh species become Vb with xylopodium. The remaining species does not survive fires and has to be reestablished from seed.

Disappearing below the surface: Most Vb species are not affected by fires in the dry season. However, 2 species die and must come up from seeds.

Remaining as seeds: There are no indications that seeds are destroyed by fire, as WARMING (1893) supposes.

All perennial grasses and Cyperaceae form new leaves inside the old sheaths, immediately following the fire and regardless of rainfall. Many species flower as a reaction to fire.

Thus, fire has the effect of a very severe drought. Most species do not die, but behave as if they were adapted to a more severe dry period.

Since fires occur annually in the *Panicetum stenodoidis*, the *Schizachyrio-Rhynchosporetum*, the *Polycarpaeo-Trachypogonetum*, and the *Mesoseto-Trachypogonetum*, fire-related seasonal aspects are the rule. This means that after a fire almost the entire vegetation normally disappears from view, and has the aspect Vb or S. Only tall trees and shrubs remain, without leaves. Only in accidentally unburned places do we find the species in their normally drought-adapted form. The question to what extent the vegetation would change if fires did not occur, is beyond the scope of this study.

V. 3. Conclusions and correlations

The long dry period is the unfavourable season. This is apparent from the fact, that the periodicity groups Wwd, including Sh, Vb, and S, have the greatest numbers of species, as well as coverage. Almost all tussocks belong to the Wwd and Vb category. Conditions at soil level are unfavourable; there are only 5 Vs species.

Some facts and possible explanations of less strict adaptations to the long dry season are:

1) All trees and shrubs are WDwd, Eg or W*D*wd, Id. This cannot be accounted for.

In the following data, tussocks and woody species are not included.

2) In the *Xyrido-Paspaletum* many herbaceous WDwd species are found, and the WDwd and W*D*wd species have a relatively large share in the coverage. This may be correlated with the long period of high water table, causing at most a very short interruption of the water supply.

3) In the *Polycarpaeo-Trachypogonetum* we find a herbaceous WDwd, Eg species, and more species of the W*D*wd and W-wd groups. The coverage of these species increases considerably in the *curatelletosum* This may be correlated with improved micro-climate under the tree canopy and among the high herb layer with high coverage; and with the possible utilization of rain showers in the long dry period owing to rapid uptake by the soil.

4) In the *Mesoseto-Trachypogonetum* we find relatively many W*D*wd species. This is also correlated with the rapid intake of rain water, even in the dry season.

Facts indicating better conditions during the growing season, and possible correlations:
1) Increase of therophytes (Wwd) in the *Polycarpaeo-Trachypogonetum*, and with respect to coverage especially in the *curatelletosum*. This may be correlated with the more favourable water economy during the growing season, owing to more rapid wetting to greater depth of the soil on the one hand, a more favourable micro-environment due to the high coverage of the tall herb layer and especially in the *curatelletosum* of the tree layer on the other hand.
2) Increase in therophytes of type W in the *Xyrido-Paspaletum*. Undoubtedly this is correlated with high water tables during the growing season, permitting continuous water supply.

Remarks about the occurrence of groups Sh-Vs-Vb-S.
1) Sh: Almost exclusively on permeable soils. Why?
2) Vs: 4 species on white sand and 1 species in the *Panicetum stenodoidis*. We can only state the fact.
3) Vb: Vb dicotyledons are lacking in the *Xyrido-Paspaletum*. Excessive water in this environment must be the cause.
4) Fire affects the vegetation as if a severe drought had occurred.

CHAPTER VI

OTHER CHARACTERISTICS

VI. 1. Leaf size

VI. 1.1. **Review of the literature**

"That the environment affects leaf size is often immediately obvious" (Raunkiaer 1934). In order to make comparisons possible, Raunkiaer classified leaves according to size in the following classes:

leptophyll	< 25 mm²	mesophyll	2025–18225 mm²
nanophyll	25–225 mm²	macrophyll	18225–164025 mm²
microphyll	225–2025 mm²	megaphyll	> 164025 mm²

The leaflets of a compound leaf are considered separately in size determinations. The size limits set by Raunkiaer have proved satisfactory in practice, when applied by various authors. In comparing vegetation types Raunkiaer determines leaf size for each life-form category.

In this way he compared four evergreen shrub formations in Europe, differing primarily in different moisture regimes. He shows that leaf size of the shrubs decreases with decreased stature of the vegetation. Both phenomena are linked with decreasing moisture in the enviroment. The generally accepted correlation of decreasing moisture with decreasing leaf size, and the conclusion that smaller leaves are apparently more drought resistant than large leaves, was taken as a point of departure in the present study to explain the observed facts.

VI. 1.2. **Results**

The species occurring in the communities studied, have been classified as to leaf size according to Raunkiaer. Where leaf size fell approximately between two classes, the class in which most of the studied specimens belonged, was chosen.

Tussocks: The tussocks, which have the largest share in the coverage, consist of erect, basal leaves. The length, and hence the size, of the leaf increases with the height of the tussock. The height of the tussock determines the height of the herb layers. Thus, the leaf size is directly related to the height of the herb layers.

Vegetation types differ in the height and coverage of the component layers. From the above, it follows that they are therefore different in leaf size. Table 7 shows the share of the different leaf size classes

TABLE 7

Distribution of the species over the leaf-size classes according to vegetation types

A sum of the mean coverages (T & E) of the species as a percentage of the total sum of the vegetation unit.

B number of species as a percentage of all species of the vegetation unit.

		lepto	nano	micro	meso	macro	?
Panicetum stenodoidis	A	+	16.6	83.0	0.3	–	–
	B	7.7	19.2	61.5	7.7	–	–
Schizachyrio-Rhynchosporetum mesosetosum	A	0.8	5.2	93.5	0.1	+	–
	B	9.6	22.5	38.7	25.8	3.2	–
Schizachyrio-Rhynchosporetum mitracarpetosum	A	7.7	1.6	67.7	22.9	+	–
	B	13.3	15.5	46.6	22.2	2.2	–
Polycarpaeo-Trachypogonetum cyperetosum	A	11.5	0.4	27.4	60.5	+	–
	B	19.1	21.9	41.0	16.4	1.3	–
Polycarpaeo-Trachypogonetum curatelletosum	A	6.8	2.9	14.8	75.4	+	–
	B	16.2	18.9	43.2	20.3	1.3	–
Mesoseto-Trachypogonetum	A	33.0	31.0	10.9	23.6	–	–
	B	38.8	25.0	16.6	16.6	–	–
Xyrido-Paspaletum	A	23.4	69.3	6.5	0.2	–	0.2
	B	19.0	42.8	26.1	2.3	–	7.1
Clusia-Scleria-Comolia scrub	B	–	4.5	77.2	9.0	4.5	–
Ternstroemia-Matayba-Humiria scrub	B	–	6.9	45.1	41.9	–	–

in the coverage of different vegetation types. It appears that leaf size generally parallels the height of the vegetation.

The distribution of the tussock forming species, except for 3 therophytes, is as follows: leptophyll 7, nanophyll 14, microphyll 15, mesophyll 5.

Non-tussock forming species of the herb layers: The distribution of the leaf size is as follows: leptophyll 18, nanophyll 25, microphyll 36, mesophyll 5.

Leaf size changes with the height of the layer, even for non-tussock forming species of herbs. Table 8 shows, that the distribution of species over the size classes is clearly related to the height of the layer; small-leaved species occur in the low herb layer with larger numbers and coverage and the large leaved species occur, if not

TABLE 8

Leaf-size classes of the non-tussock forming herbs in different herb layers according to different vegetation units

A sum mean coverages (T & E) B number of species () number of therophytes included

Panicetum stenodoidis

		lepto	nano	micro	meso
low herb layer	A	0.07	0.05	2.81	–
	B	1(1)	2(2)	3	–
high herb layer	A	–	–	0.28	–
	B	–	–	5(1)	–

Schizachyrio-Rhynchosporetum mesosetosum

		lepto	nano	micro	meso
medium herb layer	A	0.34	0.21	1.55	–
	B	2(2)	3(1)	2	–
termite hills	A	–	–	0.08	–
	B	–	–	6	–

Schizachyrio-Rhynchosporetum mitracarpetosum

		lepto	nano	micro	meso
low herb layer	A	–	0.40	–	–
	B	–	1(1)	–	–
medium herb layer	A	0.31	0.42	3.60	–
	B	3(2)	3(2)	8(1)	–
high herb layer	A	–	–	7.72	–
	B	–	–	5	–

Polycarpaeo-Trachypogonetum cyperetosum

		lepto	nano	micro	meso
low herb layer	A	2.71	–	–	–
	B	5(4)	–	–	–
medium herb layer	A	0.07	0.31	0.57	–
	B	2	9(5)	7	–
high herb layer	A	0.03	0.13	1.06	0.29
	B	2(1)	4(3)	16(3)	1

Polycarpaeo-Trachypogonetum curatelletosum

		lepto	nano	micro	meso
low herb layer	A	0.87	–	–	–
	B	4(4)	–	–	–
medium herb layer	A	0.75	1.41	3.56	0.36
	B	2	7(4)	7	1
high herb layer	A	0.46	2.36	15.01	6.44
	B	2(1)	5(4)	17(4)	2

Mesoseto-Trachypogonetum

		lepto	nano	micro	meso
low herb layer	A	1.56	–	–	–
	B	5(4)	–	–	–
medium herb layer	A	0.45	0.72	0.93	–
	B	4	6(2)	3	–
high herb layer	A	–	–	–	0.60
	B	–	–	–	2

Xyrido-Paspaletum

		lepto	nano	micro	meso
low herb layer	A	7.26	2.62	–	–
	B	6(5)	6(1)	–	–
high herb layer	A	–	0.02	0.04	–
	B	–	1	2	–

exclusively, certainly in larger numbers and with higher coverage in the upper herb layers.

The therophytes appear to have small leaves: leptophyll 12, nanophyll 13, microphyll 5, mesophyll 0. This includes the 3 tussock forming therophytes. The therophyte species appeared to be adapted to drought even in leaf size, while in previous Chapters it has been shown that they occur in environments where there is less chance of interruption of water supply during the growing season (*Xyrido-Paspaletum*), or where a tree layer has a favourable influence on water economy (*Polycarpaeo-Trachypogonetum curatelletosum*). This reduction in leaf size will contribute to survival of occasional drought during the growing season.

Microphylls predominate among the perennial non-tussock formers in the herb layers: leptophyll 6, nanophyll 12, microphyll 31, mesophyll 5.

There appears to be no correlation between leaf size and seasonal rhythm of the species.

TABLE 9

Distribution of the non-tussock forming species in the herb layers over the leaf-size classes according to vegetation units

A sum of the mean coverages (T & E) of the species as a percentage of the total sum of the vegetation unit.

B number of species as a percentage of all species of the vegetation unit.

		lepto	nano	micro	meso
Panicetum stenodoidis	A	+	+	2.2	–
	B	3.8	7.7	30.7	–
Schyzachyrio-Rhynchosporetum mesosetosum	A	0.3	0.2	2.3	–
	B	6.4	9.6	25.8	–
Schyzachyrio-Rhynchosporetum mitracarpetosum	A	0.2	0.7	10.0	–
	B	6.6	8.8	28.8	–
Polycarpaeo-Trachypogonetum cyperetosum	A	2.5	0.4	1.5	0.2
	B	12.3	17.8	3.5	1.3
Polycarpaeo-Trachypogonetum curatelletosum	A	2.0	4.4	18.0	7.0
	B	10.8	16.2	32.4	4.0
Mesoseto-Trachypogonetum	A	2.5	0.9	1.1	0.7
	B	25.0	16.6	8.3	5.5
Xyrido-Paspaletum	A	19.7	7.1	0.1	–
	B	14.2	16.6	4.7	–

In Table 9, the coverages and the numbers of species, in percentages of the total for the vegetation type, are given for each leaf-size category, in order to express the share of non-tussock forming species in the herbaceous layers of the vegetation.

In comparing vegetation types, it is noted that microphyll and mesophyll increase in coverage in the *Polycarpaeo-Trachypogonetum curatelletosum*, as compared with the *cyperetosum*. This may indicate an improvement of the micro-climate, caused by the tree layer.

In the *Mesoseto-Trachypogonetum*, the small leaved species increase, especially as to the number of species. The same is seen in the *Xyrido-Paspaletum*. In the latter unit, this increase is caused by the abundance of therophytes. In the *Mesoseto-Trachypogonetum*, small leaf size may be explained by the fact that rain water, the principal water source of the vegetation, sinks out of reach very rapidly. Thus, the species must be able to tolerate dry periods even in the growing season.

Trees and tall shrubs: Among the trees and shrubs more species with small leaves occur on white sand than on other soil types (see Table 10).

TABLE 10

Number of trees and tall shrubs in leaf-size classes on white sand as compared with other soil types combined

	Nano	Micro	Meso	Macro
white sand . .	1	11	11	1
other soils . . .	–	4	11	1
total	1	15	22	2

These data are not entirely comparable, since many species of white sand are found in bushes, while the species of other soil types occur singly. However, it is to be expected that leaf size would increase, owing to the greater protection derived from adjacent crowns or a higher canopy. It is all the more conspicuous that the species of white sand have small leaves. This may be related to excessive drainage, as was supposed for previously mentioned groups of species.

In general trees and shrubs have larger leaves than the lower species. Hence the correlation of leaf size with height of the species extends to the tree layer.

VI. 1.3. **Conclusions and correlations**

Therophytes have smaller leaves than comparable perennial species. This may be related to the fact that therophytes are more drought sensitive than other species (deduced from the fact that they are annuals, and from their distribution in the vegetation units).

Leaf size differs from layer to layer in the vegetation. Species of the higher layers generally have larger leaves than those of lower layers. Most trees and shrubs have larger leaves than the herbs of the upper herb layer, etc. The occurrence of small leaves in the lowest herb layer may be correlated with the fact that species of this layer almost always have superficial root systems. This means that drought during the growing season is more quickly felt than in the more deeply rooted species. No other correlation with the environment was found, and no acceptable explanation.

The increase in coverage of the microphyll, non-tussock forming species in the herb layer of the *Polycarpaeo-Trachypogonetum curatelletosum* is correlated with an improvement of the micro-climate resulting from the tree layer.

On dry white sand more species with small leaves are found than on non-white sand. This may be related to the excessive drainage and consequent drought during the growing season.

In the *Xyrido-Paspaletum* small-leaved species predominate. This is due to the many therophytes with small leaves.

VI. 2. Scleromorphy of the leaf

VI. 2.1. **Introduction**

In physiognomic descriptions of vegetation the stiffness of the leaves is frequently mentioned. It is generally known that leaves tend to be thin and tender in environments with high humidity of the air, while in environments with dry periods the leaves are stiff and leathery.

Dansereau (1951) includes the following leaf-texture possibilities in his system of notation for the description of vegetation: filmy, membranous, sclerophyll, and succulent.

Iversen (1936) describes a method to determine the scleromorphy of the leaf or the entire plant. The reasoning is as follows: turgor plays an important part in the stiffness of leaves and shoots. When a loss of turgor occurs due to an excess of evaporation over water supply, the leaf will wilt, unless special provisions are made. Wilted leaves are easily damaged mechanically, e.g. by a sudden breeze. Leaves then develop "kinks" and "water lines" are interrupted. The transpiration flow is broken at the kink, so that the portion distal to it die off. Plants with leaves that remain stiff in spite of loss of turgor, are better able to survive a dry period and water loss than species whose leaves will wilt. In addition, a wilted leaf which is moved by the wind acts as a fan, increasing the transpiration.

Stiffness of the leaf is caused mainly by the amount of mechanical supporting tissue, but also by leaf size, thickness of the cuticle, and the rolled-up margin or entire leaf, as in a graminoid leaf.

Iversen eliminated turgor pressure by killing the leaves (plants) in steam. He recognizes three possibilities for the behaviour of the leaf (plant) without turgor pressure:

scleromorphic: no physical changes

hygromorphic: total wilting occurs

mesomorphic: an intermediate condition; the leaf (plant) is neither completely stiff, nor completely wilted.

One reservation is, that leaves must be mature. Young leaves always wilt. Even from herbarium specimens, scleromorphy may be determined by soaking and boiling the leaves.

Thus, scleromorphy is primarily a protection against mechanical damage. Zonneveld (1960) shows, that scleromorphy (determined by Iversen's method) is related to movement of water in habitats where strong currents prevail. Massart (1907, 1908, 1909) calls the "rigidity of aerial organs" an adaptation to damage by wind in plants of the sea coast.

The method of Iversen is simple and yields objective data for comparison. It is preferable to the designations by Dansereau, which are based on subjective judgments.

The scleromorphy of leaves was determined by Iversen's method for all species.

VI. 2.2. **Results and correlations**

The great majority of species has scleromorphic leaves. These species also have the largest share in the coverage of the vegetation units. All tussocks have scleromorphic leaves, and all trees and shrubs except 4.

There are 16 species with mesomorphic leaves, and 10 with hygromorphic leaves. The distribution over the vegetation units is as follows:
Species with mesomorphic leaves:
5 species in the *Polycarpaeo-Trachypogonetum*, 2 of them limited to the *curatelletosum*, the others with the highest coverage in same; 4 species are therophytes
3 species in *Xyrido-Paspaletum;* 2 are therophytes.
1 species in *Clusia-Scleria-Comolia* scrub.
1 species in *Ternstroemia-Matayba-Humiria* scrub, in the undergrowth.
1 species in the *Panicetum stenodoidis* and the *Polycarpaeo-Trachypogonetum.*
4 species in various units not on white sand soils; 1 species is a therophyte.
1 species is epiphytic.
Species with hygromorphic leaves:
6 species in the *Polycarpaeo-Trachypogonetum*, of which one is limited to the *curatelletosum*, the others with highest coverage in this subassociation; 3 are therophytes
1 species in the *Polycarpaeo-Trachypogonetum* and the *Mesoseto-Trachypogonetum;* therophytic.
1 species in the *Panicetum-stenodoidis* and the *Schizachyrio-Rhynchosporetum mitracarpetosum;* therophyte.
1 species in the *Schizachyrio-Rhynchosporetum mitracarpetosum.*
1 species in several units.

These species with non-scleromorphic leaves are found in those habitats, where the growing season has a more favourable water economy, either by high water tables or by the effect of a tree canopy or closed high herb layer. This is completely in agreement with the fact that species with mesomorphic and hygromorphic leaves are less drought adapted.

It is entirely possible, that these species compensate for the lack of scleromorphy of the leaves, by other adaptations, such as:

1) Limitation of the growing period to the favourable season; 2) Extensive root system; 3) Small leaves.

In relation to item 1: the distribution of species with mesomorphic and hygromorphic leaves among the categories of seasonal rhythm is as follows:

WDwd:	0	wd:	1
W*D*wd:	1	W/w/d + W:	4
W-wd :	2	unknown :	4
Wwd :	14		

A relatively large number of species appear to have a growing period shorter than Wwd. Only one species has a longer growing period. The seasonal rhythm of almost all species with mesomorphic and hygromorphic leaves makes an adjustment to the long dry season.

In connection with item 2: A very extensive, superficial root system is found in one species: *Oxypetalum capitatum.*

In connection with item 3: Among the perennial species with hydro- and mesomorphic leaves, two are nanophyll, the others are micro- or mesophyll. The two nanophyll species are exactly those, which are not restricted in their occurrence to the more favourable habitats (*Mitracarpus discolor* and *Phaseolus longepedunculatus*). The hygro- or mesomorphic therophytes are mostly lepto- and nanophyll; 3 are microphyll.

A number of the species with hygro- or mesomorphic leaves do indeed compensate, either by means of leaf size, or by seasonal rhythm. Moreover, they have a clear preference for habitats with favourable water economy during the growing season.

Two species should be mentioned which have mesomorphic leaves, in spite of the fact that they occur in many units, without notable adaptation to drought: *Zornia diphylla*, Wwd, Vb, microphyll, and without extensive root system; *Sipanea pratensis*, W*D*wd, Id, microphyll, and without a large root system.

For the sake of completeness, Table 11 will show the number of species and the coverage in different vegetation units of plants with hygro-mesomorphic leaves.

TABLE 11

Number of species with hygro- and mesomorphic leaves, and coverage in the vegetation units

	Sum mean coverages (T & E) of species (as % of total sum)		Number species	
	meso-morphic	hygro-morphic	meso-morphic	hygro-morphic
Panicetum stenodoidis	1.4	+	3 = 11.5 %	1 = 3.8 %
Schizachyrio-Rhynchosporetum mesosetosum	1.7	+	2 = 6.4 %	1 = 3.2 %
Schizachyrio-Rhynchosporetum mitracarpetosum	2.8	+	4 = 8.8 %	3 = 6.6 %
Polycarpaeo-Trachypogonetum cyperetosum	0.2	0.1	7 = 9.5 %	7 = 9.5 %
Polycarpaeo-Trachypogonetum curatelletosum	2.2	2.2	9 = 12.1 %	8 = 10.8 %
Mesoseto-Trachypogonetum	0.1	0.8	2 = 5.5 %	3 = 8.3 %
Xyrido-Paspaletum	6.5	—	4 = 9.5 %	—
Clusia-Scleria-Comolia scrub	—	—	1 = 4.5 %	—
Ternstroemia-Matayba-Humiria scrub	—	—	1 = 3.2 %	—

VI. 3. Consideration of the findings of leaf size and scleromorphy

It was shown that of the 30 therophyte species, 12 are leptophyll, and 13 nanophyll, while only 5 were microphyll. The small leaf type is in the great majority.

Of these 30 therophytes, 8 species are mesomorphic, 5 hygromorphic, while 17 have scleromorphic leaves; there are relatively many species with non-scleromorphic leaves.

If we suppose, that it is more economical for therophyte species to make little mechanical tissue during their short existence, then the large number of species with small leaves can be understood. Small leaves need less supporting tissue to remain stiff. It is also understandable, that only two of the microphyllous therophytes have scleromorphic leaves.

These properties go together with the preference for habitats with relatively better water supply during the growing season.

It is tempting to extend this reasoning to perennial, non-tussock forming herbs, half-shrubs and evergreen woody species. It would be advantageous to the woody species to make relatively large leaves with the necessary supporting tissue, since these leaves have a long life span (see also Ch. V.2.1 under WDwd).

Perennial herbs and half-shrubs are intermediate between therophytes and woody species, both in leaf size and scleromorphy. Seasonal rhythm and aspect of this group as a whole is also intermediate.

VI. 4. Hydrotypes

VI. 4.1. **Introduction**

There are many adaptations to the moisture condition of the environment. Iversen (1936) devised a system, in which he arranged the plants according to the adaptation to the water factor of the environment, taking many possible adaptations into account. The principal categories are: I Terriphytes, II Telmatophytes, III Amphiphytes, and IV Limnophytes.

In the present study we are dealing with Terriphytes only. The classification of this group is as follows:

a) Seasonal xerophytes: Roots superficial. The plants are able to tolerate a complete interruption of water uptake for several weeks.

b) Euxerophytes: The root system is exceptionally strongly developed in proportion to the mass of transpiring parts. When water uptake is interrupted, the shoots die off quickly. Subdivisions: succulent, scleromorphic, white-felty, and mesomorphic euxerophytes.

c) Root systems moderately developed: Shoots die quickly when the water uptake is interrupted.

c1 hemixerophytes: sprouts clearly xeromorphic. Subdivisions: succulent, scleromorphic, and white-felty hemixerophytes.

c2 mesophytes: the shoots are mesomorphic. They wilt partially when losing turgor.

c3 hygrophytes: the shoots, or at any rate the leaves, wilt completely with loss of turgor.

Iversen was able to characterize vegetation units using the hydrotype spectra. A clear correlation was shown to exist with differences in the water economy of environments.

However, one adaptation which was not included in the hydrotypes, is the disappearance of photosynthetic organs during periods of water shortage. Iversen determined separate spectra for the various seasons.

In the present study, hydrotypes was determined according to seasonal rhythm, not during each season.

VI. 4.2. **Results**

In the vegetation units of this study, only Terriphytes occur. Seasonal xerophytes were not observed. Perhaps *Paepalanthus polytrichoides* may be counted as one; not enough data are available for a well founded opinion.

Euxerophytes are distinguished on the basis of the extent of root systems in relation to the size of aerial parts. This judgment is subjective. It was shown in the discussion of root systems in Chapter III, that extensive root systems, especially horizontal ones, occur primarily in soils which absorb rain water rapidly. The occurrence of Euxerophytes is therefore also related to this factor. The distribution of Euxerophytes is as follows:

3 species in soils heavier than white sand, but preferably on soils with good percolation (*Polycarpaeo-Trachypogonetum*)

3 species in vegetation types on wet white sand

6 species in vegetation types on dry white sand.

Added to this are 7 species which are euxerophytic depending on the environment. They are all euxerophytic on dry white sand. 6 are hemixerophytic in wet white sand and 1 on heavier soil.

For the 6 species of wet and dry white sand, there is a clear connection between euxerophytic condition (possession of an extensive root system) and drought. Among the other species it is not clear which factor plays the most important part: drought, rate of water uptake by the soil or low nutrient content.

The seasonal rhythm of all scleromorphic euxerophytes is WDwd of W*D*wd. The euxerophytic habit is apparently an adaptation to the dry season. However, not all WDwd and W*D*wd species are euxerophytic. Members of this rhythm category are able to withstand the long dry season even without an extremely large root system.

One of the euxerophytes has mesomorphic leaves: *Oxypetalum capitatum*, found in the *Polycarpaeo-Trachypogonetum curatelletosum*. The rhythm of this species is wd.

The other terriphytes are subdivided on the basis of the scleromorphy of their shoots. In most cases this is a matter of leaf scleromorphy; for this investigation the leaf was used as the criterion.

The scleromorphic hemixerophytes constitute the majority of the flora and the vegetation, in all classes of seasonal rhythm.

Apart from a single mesomorphic euxerophyte, the species belonging to the mesophytic and hygrophytic categories correspond completely with the groups established on the basis of mesomorphic and hygromorphic leaves. For environmental correlations we may refer to Chapter VI. 2.2.

VI. 4.3. **Conclusions**

All euxerophytes, except one, retain their photosynthetic parts during the long dry season. Hence, this form of xerophytism represents an adaptation to the long dry season. The ratio of root system to aerial organs is also determined by the nutrient content of the soil, while the size of the root system also proves to be related to the permeability of the soil to rain water. The euxerophytes are found almost exclusively on permeable soils.

All mesophytes and hygrophytes except 3 lose their photosynthetic portions during the long dry season. Their presence is indicative of better hydrologic conditions during the growing season. They are found primarily in the *Polycarpaeo-Trachypogonetum*, preferentially in the *curatelletosum* and in the vegetation types on wet white sand.

In the vegetation types of this study, Iversen's hydrotypes hardly yield any more information than the separate aspects of root systems and leaf scleromorphy.

VI. 5. Life forms according to Raunkiaer

Raunkiaer (1904) wrote: "Those structural characters which enable plants to harmonize the demands of their vegetative organs with their environment are on the whole the characters which make the most obvious impression on vegetation. From the nature of the case, however, the difference between the favourable season of two regions must be far less than the difference between their unfavourable season. This makes it exceedingly probable that those structural differences which enable plants to survive unfavourable seasons are greater than those which harmonize the same plants with the favourable seasons."

Starting from these considerations, Raunkiaer distinguished his generally accepted life forms based on the protection of the rejuvenation buds.

Since 1904 many authors have constructed life-form spectra according to Raunkiaer for floras. Generally, there is a climatic correlation, as Raunkiaer supposed. This supports the view that in most cases the climate is really the determining factor for the location of the rejuvenation buds. Where we find deviations from the ratio expected on the basis of climate, we may find the explanation in historical factors (such as glaciation), which have eliminated certain elements from the flora and given others a chance, or in factors other than climate (such as light intensity under a closed tree canopy), which influences the location of rejuvenation buds directly or indirectly.

Life-form spectra have also been constructed for vegetation units (LEBRUN, 1947; LINDEMAN, 1953). These are thought to be correlated with limiting factors in the unfavourable season in general, not necessarily the climate alone. Edaphic factors are, of course, of great importance. In many cases the spectrum is merely noted, without an attempt at environmental correlation.

The relationship of the rejuvenation buds to ground level is related to the structural form of the plant. The relationship of structure to environment is treated in Chapter IV. It was shown that the occurrence of trees and shrubs and the height which they attain is correlated with root volume, fire, and annual growth rates. The root volume (see Ch. III) and annual growth rate are determined especially by conditions during the favourable season. The structure and height of the plants and so the location of rejuvenation buds, are therefore also determined by conditions during the favourable season. The occurrence of phanerophytes and some of the chamaephytes is therefore not correlated with adaptation to conditions during the unfavourable season.

In an environment where drought is the unfavourable factor, with temperatures that would permit physiological processes to occur normally, adaptations other than the location of the rejuvenation buds are of great importance for flora and vegetation, for example the presence or absence of leaves during the dry period. This is why the chamaephytes are an unsatisfactory group. There are species with diversity of adaptations to drought. Such distinct forms as low evergreen herbs, half-shrubs, and dwarf shrubs which may or may not be evergreen, all must be included.

The hemicryptophytes also include species whose functional parts disappear from above ground, and species whose rosette is functional throughout the unfavourable season.

The geophytes and therophytes on the other hand, are entirely satisfactory. The seasonal-aspect categories Vb and S are identical with geophytes and therophytes, respectively. For a discussion of the relationship between these groups and the environment we may refer to Chapter V.2.2 and 2.3.

On the basis of this information, it is clearly pointless to construct life-form spectra accordingly to Raunkiaer for the various vegetation types. It does not add materially to the information already obtained. At most it obscures our insight by bringing together into one group species with very different characteristics, essential to their survival. In other words: in the vegetation units of this study the location of rejuvenation buds is not a proper criterion for the description of the effects of the unfavourable season in the vegetation.

A life-form spectrum of the flora of the savannas of Northern Surinam, or a part thereof does not mean much, neither for purposes of comparison, nor for climatic correlation, since savannas always occur as a mosaic with forest under similar climatic conditions.

For the sake of completeness, the species list has been annotated with the life forms. In determining the life form, Raunkiaer's premise was used as a guide line: "The kind of protection which enables the growing points to survive the unfavourable season." This led to the distinction of several new subdivisions:

1) Almost all cespitose *Gramineae* and *Cyperaceae* produce rejuvenation buds several cm below the surface. For this reason they are counted as geophytes: geophyta caespitosa.

2) A small, evergreen, upright perennial herb (*Paepalanthus polytrichoides*) must be classified as a chamaephyte, but does not fit in any of the existing subdivisions. It appears justified to distinguish chamaephyta herbacea.

3) A few half-shrubs and perennial herbs spend the long dry season underground. The rejuvenation buds are found on a leptopodium or xylopodium several cm below the surface: geophyta geopodiosa. Most shrubs, half-shrubs and perennial herbs also sprout from underground xylopodium after fires. If fire is an annual phenomenon then species must be counted as geophyta geopodiosa.

The maximum height above ground of the buds of chamaephytes is also a point of discussion. In the determination of the life form of a species with rejuvenation buds between 30 and 50 cm above the ground, the height of the surrounding vegetation was taken into consideration. Where this vegetation offered some protection, the species was counted as a chamaephyte. Species which surpassed the surrounding vegetation were counted as nanophanerophytes.

Annual fires change the life forms of all non-tussock forming species profoundly. The evergreen phanerophytes lose their leaves or become geophyta geopodiosa. Half-shrubs and perennial herbs become geophyta geopodiosa and therophytes.

In the species list, the life form is given for both dry seasons without fire and dry seasons with fire (Ch. VIII).

VI. 6. Protection of the buds

"The young embryonic tissue of the growing points is the most sensitive of all, and since it is this very tissue on which the plant's continued growth depends, it is of the greatest possible importance that it should survive the unfavourable season unscathed" so writes Raunkiaer (1904). This author, Lebrun (1947), and Richards (1952) enumerate the possibilities for protection of the primordia.

Primordia occur in two conditions: those which are active at the tips of the branches and those which are dormant lower on the branches. Dormant buds are generally equipped to survive unfavourable season, so that they may develop subsequently. The active primordia are present only during the favourable season, the growing season. The active primordia in an environment such as the savanna, are forced to endure dry spells during the growing season.

On the dormant buds of species in the vegetation types of this study, the following protective characteristics were noted: bud scales; distended petiole of the subtending leaf; stipules of the subtending leaf; bark. Unprotected buds were also noted.

For the growing primordia of species in the vegetation types of this study, the following protective characteristics were noted:

bud scales, e.g. *Ilex jenmani;*

primordium surrounded by involute or folded young leaves, e.g. *Curatella americana, Ternstroemia punctata;*

primordium imbedded between adjacent members of a pair of incompletely expanded leaves, e.g. *Retiniphyllum schomburgkii*;

primordium protected by petioles of subtending leaves: a) base of the petiole, e.g. *Clusia fockeana*; b) winged petiole, e.g. *Byrsonima coccolobifolia*;

primordium inside the sheath of the last leaf;

primordium protected by stipules of the preceding leaf: a) fused, e.g. *Rubiaceae*; b) separate, e.g. many *Papilionaceae*;

dense pubescence, mostly reddish brown in color. The hairs may or may not be combined with one of the other possibilities;

a resin layer, long persistent on the leaves and branches, finally flaking off;

primordium located between many crowded young leaves.

Young leaves may be protected in the same way as the growing primordia and may be folded or rolled up themselves.

Unfortunately, data for savanna plants are too fragmentary to permit further elaboration.

VI. 7. Indument of the leaf

Dense pubescence diminishes insolation and air movements around the stomata, resulting in decreased transpiration.

In the vegetation types of this study, approximately half of the species of the herbaceous layers have leaves with some form of pubescence, the remainder being glabrous.

Trees and tall shrubs have glabrous leaves, with a few exceptions. The leaves of most species have a glossy upper surface. Some species do have immature leaves with rusty brown pubescence.

Species with felty, tomentose leaves are practically absent. A dense pubescence is found in some species, e.g. *Pavonia speciosa.* In most species the pubescence is more sparse. To what extent the transpiration is influenced by such pubescence, cannot be indicated.

The portions of plants with glabrous and with pubescent leaves in the coverage of the different vegetation types show a correlation with water supply during the growing season (Table 12).

Pubescent leaves have the largest share in the coverage of all open savanna vegetation, but not in the bushes.

In environments where the ground water insures water supply during the growing season (*Xyrido-Paspaletum* and *Panicetum stenodoidis*) the coverage of species with glabrous leaves is clearly higher than in environments where the vegetation is dependent upon rain water, which is more irregular.

In the *Polycarpaeo-Trachypogonetum curatelletosum* the share of species with glabrous leaves is also greater, owing to the tree layer.

In the bushes, species with glabrous leaves and glossy upper surfaces predominate.

TABLE 12

Distribution of species with glabrous and pubescent leaves in the vegetation types

A sum mean coverages (T & E) of species (in % of the total sum).
B number species (in %).
x remainder unknown.

		glabrous		pubescent	
Panicetum stenodoidis	A	33.8		66.1	
	B		50.0		50.0
Schizachyrio-Rhynchosporetum mesosetosum	A	11.4		88.5	
	B		48.3		51.6
Schizachyrio-Rhynchosporetum mitra-carpetosum	A	18.9		81.0	
	B		62.2		37.1
Polycarpaeo-Trachypogonetum cyperetosum	A	17.4		82.4	
	B		47.8		52.0
Polycarpaeo-Trachypogonetum curatelletosum	A	39.3		55.6	
	B		45.9		52.6
Mesoseto-Trachypogonetum	A	27.2		72.5	
	B		61.1		36.0
Xyrido-Paspaletum	A	49.5		49.9	
	B		59.5		30.8 x
Clusia-Scleria-Comolia scrub	B		86.3		9.0 x
Ternstroemia-Matayba-Humiria scrub	B		83.8		6.4 x

VI. 8. LEAF MOVEMENTS

Folding and rolling-up of the leaf decreases the exposure to air currents and light. The result is a reduction of transpiration (MASSART, 1907, 1908, 1909).

Almost all species with graminoid leaves curl or fold along the midrib. Most species with compound leaves have joints which enable the leaflets and sometimes the whole leaf to move. The bending together of a pair of leaflets, as in certain Papilionaceae, has the same effect as folding of the leaf along the midrib.

Another effect of leaf movements is that the orientation of the leaf in relation to the sun may be changed. Insolation can be regulated to some extent.

13 of the 39 trees and shrubs have compound leaves. 21 of the 78 dwarf shrubs, half-shrubs and non-tussock forming herbs have compound leaves.

CHAPTER VII

DESCRIPTION OF THE VEGETATION TYPES AND HABITAT CORRELATIONS

VII. 1. Panicetum stenodoidis (Fig. 5)

The environment of the association *Panicetum stenodoidis* is extreme. The soil consists of silty clay loam. There is an alternation of water surplus and drought. During the long wet season, the soil becomes moist rapidly to relatively great depth, owing to the collection of runoff water in the crevices resulting from drying and shrinkage and to rising ground water. The vegetation is composed almost entirely of tussock forming grasses and *Cyperaceae*. There are more species of these families than in other units. The grasses and Cyperaceae have a relatively large rooting volume available to them, so that the vegetation becomes rather tall compared with other units, and coverage is high. Root systems are generally deep and narrow. The tussocks stand close together and upright.

Excessive water makes the habitat unfavourable for dicotyledons. Root systems remain superficial, and as a result of this are subject to drought. There are few dicotyledonous species, and their coverage is slight. None of the species is characteristic for this vegetation unit: the species also occur in many other vegetation units. They are *Curatella americana*, *Tibouchina aspera*, *Hyptis atrorubens* and *Sipanea pratensis*. In addition there are several therophytes of wide distribution.

All grasses and Cyperaceae dry out during the dry season (Vb). They are an easy prey to fires. Every year the vegetation burns at least once. This also forces dicotyledons under ground (Vb). Not a single unburned spot could be found in this vegetation, so that the behaviour of the dicotyledons without fire could not be established. Five species are potentially W*D*wd, Id. These are widespread species in the associations under discussion. The other species of dicotyledons, when growing in places where no fire occurs, are S or Vb, just like the tussocks.

Tall trees and shrubs do not occur. The environment is extreme, there is little rooting space, and the annually recurring fire destroys any specimens that might germinate. Only one *Curatella americana* of treelike habit was encountered. This shows nevertheless that the production of a tree is possible. The reason that not more specimens are found, appears to be that annual growth is not sufficient to raise the plant above the zone of fire influence. Only areas bypassed by the fire may support a tree. Another possible explanation is that the trees drown during extremely wet years.

The species are primarily microphyllous, even in the low herb layer. All perennial dicotyledons are also microphyllous offering a relatively large leaf surface. This may be correlated with the fact that during the wet season no water shortage occurs, due to the high ground water table.

All leaves are scleromorphic, except the leaf of *Sipanea pratensis* and *Polygala adenophora.*

VII. 2. SCHIZACHYRIO-RHYNCHOSPORETUM, SUBASSOCIATION MESOSETOSUM (Fig. 7)

The root layer is practically restricted to the upper 20 cm, although ground water is already noticeable at about 40 cm below the surface, as evidenced by the gley horizon. Some roots reach down to 30 cm, and some very exceptional ones to 50 cm. The soil consists of coarse-sandy clay loam.

From features of the root systems and properties of the soil, such as relatively low percolation rates, considerable runoff, and the lack of shrinkage crevices, it may be concluded that the vegetation is dependent upon rain water, and that the rain water penetrates only into the superficial soil layer, to about 20 cm. Probably there is a permanent or long persistent dry layer separating the surface moisture from the capillary ground-water area, which blocks the downward growth of roots.

The uptake of rain water is slow; much is lost in runoff, and the root systems do not have large horizontal dimensions. They do reach outside the area covered by the aerial portions in many species.

The plants therefore have a small rooting volume with the result that the vegetation remains low and is not closed. The root layer is closed. It is possible that root competition determines the coverage above ground, but not certain.

There is no excess water in the upper decimeters, so that the dicotyledons have a larger soil volume available to them than in the *Panicetum*, but less than in the subassociation *mitracarpetosum.* The variety of forms is greater than in the *Panicetum*, less than in the other subassociation.

There are termite hills. Their soil contains slightly more organic material. The values for percolation rates are less than in the rest of the vegetation. The vegetation on these termite hills is taller, there are more dicotyledons, and roots penetrate more deeply.

We may explain the change in the vegetation by assuming that drainage in and under the termite hills is better through the termite tunnels, which make for better moisture distribution through the soil.

There is evidence that most dicotyledons were already present before the termite hill was formed. They kept pace with the growth of the hill. These species occur more frequently on the hills than in the rest of the vegetation. It may be assumed that they can maintain themselves more easily than elsewhere in the habitat, due to the better drainage. The termite hills improve survival chances.

The vegetation burns annually, so that all species spend the rest of the dry season underground (Vb) or as seeds (S). In spots that were missed by the fire, which are found occasionally, it turns out that one dicotyledon is WDwd, Eg, and four others W*D*wd, Id, viz. *Sipanea pratensis*, *Hyptis atrorubens*, *Curatella americana* and *Tibouchina* *aspera. Scleria bracteata* is also W*D*wd, Id. They are all species which are widely distributed through the vegetation units of this study. They are most common on termite hills.

Fires do not find as much fuel in this open, low vegetation, as in the *Panicetum* and *Polycarpaeo-Trachypogonetum*. This is perhaps why unburned spots are more common, or the influence of fire is less disastrous. It explains, that trees will develop here and there, having outgrow the zone ravaged by fire. Six species of trees were observed. Their occurrence shows, that the environment can support trees. The trees are WDwd, Eg, they have leaves with glossy upper surfaces. The only evergreen shrub in the herb layer also has leaves with glossy upper surface.

All species have scleromorphic leaves, except *Sipanea pratensis*, *Polygala adenophora* and *Mitracarpus discolor*, all 3 with a wide distribution.

Most species have microphyllous leaves, the trees are meso- and macrophyllous.

VII. 3. Schizachyrio-Rhynchosporetum mitracarpetosum (Fig. 8)

The soil down to 40 cm consists of sandy loam, below that of coarse-sandy clay loam.

As in the subassociation with *Mesosetum cayennense*, the soil is slow to take up rain water. There is much runoff. The influence of the ground water extends up to 80 to 40 cm below the soil, as shown by the gley horizon, hence is deeper than in the other subassociation. On the basis of these data and the root systems, which are mostly shallower than 20 cm, we must conclude that rain water does not penetrate deeper than about 20 cm. Probably there is a permanently dry layer between the surface moisture and the capillary ground water.

The great majority of the vegetation, both in coverage and number of species, depends for its water supply on rain water, of which much is lost by runoff. The root volume is small, the vegetation remains low.

The roots extend beyond the area of the aerial portions, so that the root layer is continuous while the vegetation above ground is not closed.

There is no excess water, and the variety of forms and differentiation into layers is more pronounced than in the other subassociation.

Part of the trees and shrubs penetrate with the primary root down to the depth of the ground water. There they ramify strongly or bend sideways due to oxygen shortage. The water supply of these species should be better than for the rest of the vegetation, especially outside the long wet season. This may also explain the greater stature of these species.

In spite of annual fires, trees of various species are found. We also encounter bushes in this vegetation unit, forming little islands among the grassy vegetation. They are not discussed here. The fact that a large part of the vegetation is Wwd, shows the profound influence of the long dry season. Most of the plants disappear underground (Vb).

Three species are Sh, and 8 species remain as seeds. Apart from trees and shrubs, which are WDwd, Eg or W*D*wd, Id, and the W*D*wd species with wide distribution, there is only one W*D*wd species present.

Of the wide spread species, *Hyptis atrorubens*, *Sipanea pratensis*, and *Tibouchina aspera* reach their greatest coverage in this vegetation unit. *Tibouchina* is rooted within the zone of ground water, at least the taller specimens.

The larger portion of the vegetation is microphyllous. The mesophyll species attain a considerable coverage, especially due to *Trachypogon plumosus*. The leaf of *Trachypogon* is here small mesophyll, while in the other association it must be counted as a large microphyll. Tussocks in the *Schizachyrio-Rhynchosporetum mitracarpetosum* are also more sturdy than in the *mesosetosum*.

In addition to *Sipanea pratensis*, 1 tree, 2 therophytes, and 3 perennial herbs have meso- or hygromorphic leaves.

Comparison of the two subassociations of the *Schizachyrio-Rhynchosporetum*

Both subassociations have in common: a small rooting volume, due to the superficial wetting by rain water and a dry layer separating rain water from the capillary ground water; the resulting structure above ground, namely a low open vegetation, with an occasional higher tussock and sparse occurrence of dicotyledons.

While the ground water never reaches the root system of the *mitracarpetosum*, it may occasionally do so for short periods in the *mesosetosum*. This is perhaps responsible for the differences between the subassociations, such as more dicotyledons, greater coverage of *Trachypogon plumosus*, more tree species, et. in the *Schizachyrio-Rhynchosporetum mitracarpetosum*.

VII. 4. Polycarpaeo-Trachypogonetum cyperetosum (Fig. 9)

The soil consists of loamy sand; the gley horizon occurs at a depth of 60 to 120 cm below the surface, depending upon the elevation of the savanna. The soil absorbs all rain water so that there is no runoff. At a depth of approximately 80 cm the percolation rate decreases, so that rain water does not immediately sink out of reach. The soil has a favourable water economy during the long wet season.

Accordingly, the species are able to develop extensive superficial root systems which capture the percolating rain water, as well as deeper roots below the sod layer. The sod layer extends down to 15 or 20 cm, but roots penetrate to 40 or 50 cm, and occasional dicotyledonous roots reach depths near the ground water level.

Compared with other associations, there is a considerable rooting space for the plants, and no surplus of water. The vegetation is higher; the high herb layer is a closed one, and there is greater differentiation of forms. Although non-tussock forming species have a low coverage, their number is relatively large. The sod layer is closed and the roots generally extend beyond the projection of the aerial parts. Near the surface the vegetation is not closed. The tussocks, chiefly *Trachypogon plumosus* are widely spaced, so that they fan out. The result is that the vegetation as a whole appears closed.

The closed high herb layer causes a decrease in the light intensity for the lower layers. This is probably the reason why fewer grasses occur in these layers.

During the growing season the micro-environment is more favourable for forbs and half-shrubs, due to the decrease in insolation underneath the high herb layer. The occurrence of 7 species with mesomorphic leaves and 7 with hygromorphic leaves may also indicate a more favourable micro-environment during the growing season.

In this well percolated and aerated soil the dry season is clearly noticeable. Practically the entire vegetation has a seasonal rhythm of Wwd. Apart from trees and shrubs there is one species of very low coverage with a periodicity WDwd, Eg. In addition to the wide spread species there are others, important in number and coverage which belong to the WDwd, Id group. There are many more species of the type W-wd than in the units previously discussed. They may be Sh, Vb or S. Their occurrence is correlated with rapid water intake of the soil, so that a rain shower during the long dry season may be utilized. Growth can be sustained from one rain shower to the next.

The major part of the vegetation is microphyllous, mainly due to *Trachypogon plumosus*. The majority non-tussock forming species in the herb layers have relatively large leaves, belonging to the category of the microphylls.

Fires are fierce in this vegetation of high, dried tussocks. Practically the entire vegetation survives fires only below the surface. Part of the flora survives only as seed.

There are fewer tree species than in the *Schizachyrio-Rhynchosporetum mitracarpetosum*, perhaps correlated with the intensity of fires.

Individuals of *Curatella americana* are able to outgrow the critical fire zone. This occurs so often that a tree layer is created: sub-association of *Curatella americana*. Isolated shrubby specimens with a xylopodium below the surface show, that not every specimen manages to outgrow the destructive influence.

VII. 5. Polycarpaeo-Trachypogonetum curatelletosum (Fig. 11)

It must be assumed that the growth of *Curatella americana* is sufficiently rapid to permit some branches to grow above the fire zone between the fires of two successive long dry seasons: probably this is correlated with the possibility of deep root systems in this soil where no rain water is lost by runoff or excessive drainage. In several vegetation units we encounter low specimens of *Curatella*, whose shrubby habit is obviously caused by fire. Since fire is very intensive in the *Polycarpaeo-Trachypogonetum*, due to the large dry tussocks, all buds on branches which are within the fire zone will be destroyed. Only those specimens whose branches are tall enough will be able to sprout after the fire high above ground.

The tree layer is responsible for an improvement of the micro-environment. Since *Curatella* is incompletely deciduous, this improvement will be noticeable to a greater or lesser extent throughout the year. There is one WDwd herb with high coverage. The number and coverage of non-woody species of the category W*D*wd, Id is larger than in other units. Compared with the *cyperetosum*, where most of these same species occur, the coverage is considerably higher.

Both subassociations occur on similar soil. The floristic composition is also very similar. There are only a few species which are limited to one or the other subassociation. In the discussion of the *cyperetosum* it was shown that the occurrence of many non-tussock forming species may be correlated with a better water economy of the soil and probably with a better micro-environment under the dense high herb layer. The higher coverage of these species in the *curatelletosum* is correlated with the improved micro-environment, especially during the growing season, in the layers below the tree layer.

Therophytes, perennial herbs and half-shrubs increase. Apart from the WDwd and W*D*wd species, all others are Wwd of W-wd. So the long dry season is very severe under the *Curatella* canopy. Species which survive as W-wd by utilizing every rain shower of the long dry season, do not reach much higher coverage in the *curatelletosum* than they did in *cyperetosum*.

Other characteristics correlated with a better water economy are also encountered in the *Polycarpaeo-Trachypogonetum curatelletosum*. The coverage of non-tussock forming micro- and mesophyllous species is relatively high. Likewise there is a considerable increase in coverage of species with hygro- and mesomorphic leaves.

The importance of grasses decreases, relatively, by the increase of other herbs, but also in absolute terms, probably as a result of diminished light intensity.

The aspect of the *Polycarpaeo-Trachypogonetum curatelletosum* is more luxuriant than any other type of vegetation studied, due to the many dicotyledons and non-tussock forming monocotyledons.

VII. 6. Mesoseto-Trachypogonetum (Fig. 10)

The soil consists of pure white sand down to a considerable depth. Ground water in the vegetation studied reaches up to 1.20 to 1.50 m below the surface. All rain water, the water source for the major part of the vegetation, is quickly absorbed and sinks down to great depth. To utilize rain water, it has to be intercepted before it can sink down.

Many species have very extensive superficial roots. Grasses also have an extensive root system in deeper layers. The form of the root system is always spreading.

Although percolating rain water will soak through the entire soil down to ground water, we only find a few dicotyledonous roots within the reach of the ground water. The aeration, inherent in white sandy soils, causes a rapid drying of the soil after the rainy season. The roots which reach down to ground water are exposed for their entire length to desiccation. Dicotyledons can tolerate this, monocotyledons cannot.

The percentage of species with periodicity WDwd and W*D*wd is relatively high, correlated with the utilization of rain showers during the long dry season. The WDwd species are dwarf shrubs, W*D*wd species are half-shrubs and dwarf shrubs.

The woodiness of these groups is correlated with the survival through drought and high temperatures.

The predominance of lepto- and nanophyllous species, not counting the tussocks, may also be related to the survival of dry periods.

Concerning the other categories of seasonal rhythm and aspects: the majority of the vegetation and the species are Wwd, because desiccation is severe in spite of occasional rain showers. It is remarkable that only two species are Sh, while *Mesosetum loliiforme*, a grass, is not Vb but Vs.

In spite of the extensive root systems of the species, the vegetation remains low. This must be attributed to the low nutrient content of the sand and to the unfavourable water supply.

The vegetation is sparse, but even the root layer is not closed although the roots are always widely spread. Both under and above ground there is room for more plants. It is probable that the dry seasons, with their high temperature, reduce the survival chances of seedlings so much, that no closed vegetation develops.

The annual occurrence of fires forces thc whole vegetation underground. One does encounter occasional unburned patches, owing to the low stature and coverage of the vegetation. That there are nevertheless no trees, must be ascribed to the combination of drought, high temperatures and low nutrient content, reducing survival chances and annual growth.

VII. 7. Xyrido-Paspaletum (Fig. 12a)

Ground water is at a high level in the white sandy soil. During the long rainy season it stands at or above soil level and in the long dry season 90 to 70 cm below the surface, while capillary water reaches up to 60 to 40 cm. The upper 40 cm are therefore bone dry during the long dry season.

The roots of most dicotyledonous species are forced to stay in the upper layer by the high ground water level. This limits the rooting space and promotes drying out. The plants remain small above ground.

The monocotyledons are rooted more deeply, but their occurrence is also limited by long-term water surplus. In this environment with high water tables during most of the year, rooting space is small even for most monocotyledons. This, and the low nutrient content, explains the small dimensions of plants above ground.

The root systems of the monocotyledons do not spread, but are narrow and deep, due to the fact that the ground water is the principal source of water.

The vegetation is thin and the root layer is not closed. As is the case in the *Mesoseto-Trachypogonetum*, the extreme drought, together with high temperature, probably decreases the survival chances of seedlings in such a way that no closed vegetation develops.

During the long rainy season the water supply is uninterrupted. There are relatively many therophytes, which are herbaceous. They do not need to survive the dry season.

The situation is different for the perennial dicotyledons. High water tables prevent their withdrawal into the soil. Although the rain which falls during the long dry season penetrates into the soil, drought is extreme. Moreover, temperatures will be very high due to the insolation. The perennial species are mainly dwarf shrubs with small leaves (lepto- and nanophyll). Both woodiness and small leaves may be regarded as adaptations to drought. Half-shrubs and perennial herbs are practically absent.

The small shrubs are WDwd, Eg and W*D*wd, Id, so that they can profit from the occasional rain showers in the long dry period.

Most tussock forming species are rooted so shallowly, that the long dry season is highly effective. Almost all of them are Wwd. Most species disappear into the soil. Four species however, are Vs. *Xyris surinamensis* and *Abolboda americana*, both characteristic for this environment, are W*D*wd and WDwd, respectively. They are rooted to 30 cm depth, which is deeper than most other tussock formers

There are four species with mesomorphic leaves. Three of these are therophytes.

The root system and periodicity of a large number of species could not be ascertained. Some of these are therophytes, which were absent during the field work in the short dry season.

The vegetation burns once in a while, not every year. The low isolated tussocks do not give the fires much chance. Fire is not very intensive.

VII. 8. Clusia-Scleria scrub, Comolia variant (Fig. 12b and c)

On dry white sands bushes of *Clusia-Scleria* scrub occur as islands in a vegetation such as the *Xyrido-Paspaletum.*

The soil and ground water regime are the same as in the *Xyrido-Paspaletum.* The major difference is the litter layer, which covers the ground in these bushes. This reduces evaporation and insolation, thereby reducing water loss and temperature of the soil during the long dry season. Organic material is also increased in the upper layers of sand. The environment is improved by the litter layer.

The shrubs, which are practically the sole components of the vegetation, are rooted superficially as a result of water excess. Except for five species, all roots are limited to the litter area. It is very probable that the root systems of some species are limited to this area by the high temperature during the dry season outside of the area covered by litter. Others may respond to the increase of moisture and organic matter in the litter area. Only one species is rooted in the litter itself. The roots of other species are found primarily at the interface of sand and litter, or in the sand.

All species are rooted well beyond the projection of their aerial parts. Nevertheless, the space occupied by roots is small in comparison with the *Ternstroemia-Matayba* scrub. The shrubs remain low.

The vegetation is composed almost exclusively of shrubs. Only along the edges of the bush there are a few tussocks. These are Wwd, Vb. The reduction of light inside the bushes will limit the grasses and the *Cyperaceae*.

There is only one herb, perennial and evergreen. Half-shrubs are lacking entirely. This may be due to the same environmental conditions as in the *Xyrido-Paspaletum*.

The shrubs are always leafy. Most of them are WDwd. This may be correlated with the fact that the precipitation which falls during the long dry season reaches the root layer.

The species are mostly microphyll, the leaves are scleromorphic and mostly glabrous with a glossy upper leaf surface. Only one mesomorphic species is noted. These properties are correlated with the occurrence of periods in which the root layer is bone dry.

Fires may occur, but certainly not annually. Many of the species have a xylopodium and sprout from below the surface after the fire.

Some species die as a result of extremely dry times, which occur now and then (e.g. *Bactris campestris*). The dead individuals persist for years as bald, bleached snags. In view of the behaviour of the roots, and the low tolerance for water surplus, extremely long periods of high water tables will also cause the death of shrubs.

The bushes are never larger than a few dozen square meters. The destructive action of a dry spell or an extremely long wet season must be the cause of this.

Finally it should be mentioned that most species only bear leaves at the tips of the branches. This means that no buds will develop along the branch as long as the terminal bud is alive, even if the older leaves fall off.

VII. 9. Ternstroemia-Matayba scrub, Humiria variant (Figs. 13 and 14)

On dry white sand the bushes belong to the *Ternstroemia-Matayba* scrub. Between the bushes there is practically no plant growth. The white sand is the same as in the *Clusia-Scleria* scrub. Differences are due to the ground water, which is very deep.

A hardpan may occur at a depth of several meters, but according to Heyligers it is not essential. It was encountered once in the present study at a depth of 2.50 m.

The litter layer on the soil appears to be essential. The improvement of the environment is the same as that mentioned for the *Clusia-Scleria* scrub.

It can be shown that some of the species are rooted both underneath and outside the litter layer (*Clusia fockeana, Ternstroemia punctata, Humiria balsamifera, Licania incana*). However, most species are limited to the sand underneath the litter layer, while an occasional species is rooted in the litter itself.

Most roots occur in the upper 15 cm of the sand below the litter layer, but deeper roots are also found. Water surplus, which would inhibit root growth, does not occur. The high concentration of roots in the upper layer can be correlated with the increase in organic material, rain water which is the sole water source, and oxygen supply.

A few species have a primary root down to 2 m. At the tip it is branched profusely. This makes the impression of water surplus. This is plausible in view of the hardpan at 2.50 m.

Most species are rooted with many horizontal roots of several meters, an adaptation to an environment in which rain water is the main supply, and the soil is well drained.

The root systems become much larger than in the *Clusia-Scleria* scrub, even for species which are common to both units. This again is correlated with water supply, which is assured in the wet sand. The dimensions above ground correspond with those of the root systems.

The behaviour of the roots means, that a hardpan at several meters depth has little or no influence on the vegetation.

The horizontal roots which exceed the litter area are found at a depth of 20 to 30 cm, which is deeper than within the litter area. Probably the high temperature during the dry season forces the roots down to this level.

The bushes are composed entirely of shrubs. In the undergrowth two orchids are found, which were not investigated further. At the edges, one encounters some tussocks and two *Schizaeaceae*, which dry out in the dry season.

The shrubs are evergreen. This may be related to the fact that some rain falls during the dry season, which may be utilized by plants.

50% of the species are microphyll. There are several borderline cases.

The leaves are scleromorphic (except one shrub), generally glabrous and with glossy upper surface. The leaf characteristics indicate survival through a dry period.

As in the *Clusia-Scleria* scrub, many species have leaves only at the tips of branches.

The dome-shape of the bush is perhaps due to the drying out of terminal buds, which project beyond the protection of the crown layer, and to the reduction in rooting space for those species which grow at the edge of the litter area. *Humiria balsamifera*, which always occupies the lowest zone, decreases in vitality as soon as it is shaded. One might say that it crawls out from under the crown layer.

The bushes vary in size from one high shrub with some undergrowth to an area of several 100 square meters.

One may imagine the origin of a bush along the following lines:

in dry white sand with high temperatures during the long dry season, the survival of seedling plants is slight. Only a small number of species can take root in the white sand without the protection of a litter layer. Individuals of these species will become established at scattered points. By forming a small cluster of leaf litter they serve as a point of origin for a bush (Figs. 13 and 14). In this litter layer species germinate whose demands are higher. The litter layer increases in thickness, shading increases also. Through the growth of individuals and the germination of new species and individuals the litter layer will be extended and the bush will grow in area. Especially due to the crawling outward of *Humiria balsamifera*, the area of litter is continually extended.

Several bushes were observed which had left only a narrow strip of bare sand between the *Humiria* borders and litter layers. One bush was investigated which clearly consisted of two smaller bushes which had been merged. The circumference showed a notch at the meeting place and a map of the location of all shrubs growing in the bush showed that no shrubs occurred at the border between the two original bushes, although there was a litter layer and a closed canopy. The origin of shrub savannas may be thought of as a growing together of isolated bushes.

In such larger bushes the microclimate will be changed, resulting in different floristic compositions.

The occasional fires destroy the slowly growing vegetation above the ground. The dry litter layer may smolder for days, so that all aerial parts are thoroughly killed. Nevertheless, many species will sprout several decimeters below the original litter surface, sometimes months after such a fire. For years to come, the partly burned, blackened trunks will bear witness to the fire.

The fire does not always recreate a pristine sandy soil by any means. On the other hand it is probable, that an extremely long dry season in this already extreme environment may result in the death of the entire vegetation, resulting in a bare soil.

CHAPTER VIII

LIST OF SPECIES AND THEIR CHARACTERISTICS

(pages 133–149)

VIII. 1. Legend

× : in Chapter VIII.2 some characters are discussed in detail
— : not known
() : probably

Vegetation units

Following each species, the mean coverage in the vegetation units has been noted, calculated according to T & E (Ch. I.3).

Species whose root systems was dug out in the unit under consideration, are indicated by underscoring.

Pan sten	= Panicetum stenodoidis
Sch-Rhyn mes cay	= Schizachyrio-Rhynchosporetum mesosetosum
Sch-Rhyn mitr	= „ „ mitracarpetosum
Pol-Trach cyper	= Polycarpaeo-Trachypogonetum cyperetosum
Pol-Trach curat	= „ „ curatelletosum
mes-Trach	= Mesoseto-Trachypogonetum
Xyr-Pasp	= Xyrido-Paspaletum
Clus-Scl Com var	= Clusia-Scleria scrub, Comolia variant
Tern-Mat Hum var	= Ternstroemia-Matayba scrub, Humiria variant

Structure (Ch. IV.2)

height: in cm

sm = several meters
– = to

habit

tr = tree
sh = shrub
sf = half-shrub
h = a herb
t = tussock
c = climbing or winding
e = epiphytic

shoots

0 = stemless
1 = 1 stem
sv = several stems
t = tussock forming
l = individuals loosely connected

branching

no = no branches
up = branching at some height
bas = branching from base

posture

er = erect
pt = oblique, ascending
pr = prostrate
cr = creeping
cl = climbing

foliage

scat = leaves scattered along the branches
term = leaves on terminal portion of the branches
ros = leaves in rosette
bas = leaves only on the base of the stem
none = leaves absent

woodiness

lign = completely woody
herb = completely herbaceous
bas = with woody base

Life forms according to Raunkiaer (Ch. VI.5)

Under the heading "normal" the life form is indicated for the species when not subject to fire; under "fire" the life form resulting from fire.

Ph = phanerophyta
mm = meso-
m = micro-
n = nano-
h = herbaceous
HC = hemicryptophyta
sc = scaposa
b = bulbosa
r = rosulata
c = caespitosa
Ch = chamaephyta
s = suffruticosa
r = reptantia
gr = graminoidea
fr = frutescentia
h = herbacea
G = geophyta
rh = rhizomatosa
b = bulbosa
gp = geopodiosa
c = caespitosa
Th = therophyta

Periodicity

seasonal aspects (Ch. V.1.2)

Under the heading "normal" the aspect of the species is given when not subject to fire; under "fire" the aspect following a fire.

- Eg = evergreen
- Id = incompletely deciduous
- D = deciduous
- Sh = plants become shortened
- Vs = plants dying back to the surface
- Vb = Plants dying back to several cm below the surface
- S = remaining as seed only

seasonal rhythm (Ch. V.1.1)

WDwd	W
W*D*wd	W/w/d
W wd	W d
W - wd	w

Hydrotypes of Iversen (Ch. VI.4)

- Eux = euxerophytes
- Hx = hemixerophytes
- Mes = mesophytes
- Hyg = hygrophytes

Leaf

scleromorphy (Ch. VI.2)

- skl = scleromorphic
- mes = mesomorphic
- hyg = hygromorphic

size

- lepto = leptophyll
- nano = nanophyll
- micro = microphyll
- meso = mesophyll
- mega = megaphyll

shining

+ indicates species with glossy upper surface

shape

- sp = simple
- gr = graminoid
- cp = compound

hairiness

- gl = glabrous
- v = lower surface hairy
- d = upper surface hairy
- d + v = both sides hairy
- cil = ciliate

Root system (Ch. III 2.2)

shape

- gen = generalized form
- mush = mushroom shape
- cyl = cylinder shape
- con = cone shape
- brush = brush shape
- R. gen = rest generalized
- spec = specialized form
- disc = disc shape
- h. glob = hemispherical shape
- umbr = umbrella shape
- show = shower shape
- h. tail = horsetail shape

distribution

A
B
C
D
E
F

litter area

- under = roots limited to litter area
- not = roots only outside litter area
- both = roots both within and outside

VIII. 2. List of species

		Community									height in cm
		Pan sten	Sch-Rhyn mes cay	Sch-Rhyn mitr	Pol-Trach cyper	Pol-Trach curat	Mes-Trach	Xyr-Pasp	Clus Scl Com var.	Tern-Mat Hum var.	
Abolboda americana (Aubl.) Lanj.		.	.	.	.	.	.	1.30	.	.	2
Actinostachys pennula (Sw.) Presl.		.	.	.	.	.	.	.	+	+	20
Aeschynomene brasiliana (Poir.) DC.		.	.	0.01	0.05	0.74	.	.	.	.	40
Aeschynomene hystrix Poir.		.	.	.	0.02	0.01	0.07	.	.	.	40
Aeschynomene paniculata Willd. ex Vog.		.	.	0.01	0.05	0.10	.	.	.	.	150
Amazonia campestris (Aubl.) Moldenke		.	.	.	0.01	0.37	.	.	.	.	80
Andropogon leucostachyus H. B. K.	X	1.9	.	0.2	.	0.01	.	.	.	.	30
Anthurium gracile (Rudge) Lindl.		.	.	.	.	+	.	.	.	.	30
Araliacea spec.		.	.	0.05	.	.	.	.	.	.	sm
Aristida tincta Trin. et Rupr.	X	1.5	4.8	0.6	.	.	.	.	.	.	30
Aristida capillacea Lam.		.	0.30	0.20	.	.	.	.	.	.	10
Astrocaryum segregatum Brude		.	0.01	0.05	0.01	0.01	.	.	.	.	1000
Axonopus attenuatus (Presl.) Hitchc.		.	.	.	.	.	.	.	.	±	50
Axonopus pulcher (Nees) Kuhlm.	X	4.0	8.5	38.2	17.8	0.43	6.90	.	.	.	30
Axonopus purpusii (Mez) Chase	X	0.01	2.0	4.1	0.01	0.01	.	.	.	.	20
Axonopus purpusii narrow leaves		4.4	.	.	.	.	.	.	.	.	30
Ayenia tomentosa L.		.	.	.	.	0.37	.	.	.	.	60
Bactis campestris Poepp.		.	.	.	.	.	.	.	±	.	400
Bombax flaviflorum Pulle		.	.	.	.	.	.	.	.	+	500
Borreria latifolia (Aubl.) K. Sch.		.	.	.	0.01	0.03	.	.	.	.	60
Borreria suaveolens G. F. W. Meyer		.	.	.	.	.	.	.	.	+	30
Bredemeyera densiflora fo. glabra Benn.		.	.	.	.	.	.	.	.	+	150
Buchnera palustris (Aubl.) Spreng.		0.04	0.10	0.01	.	.	0.04	.	.	.	40
Bulbostylis capillaris (L.) Kunth		.	.	0.01	7.05	7.18	0.28	.	.	.	15
Bulbostylis circinata (Nees) Kunth		.	.	.	.	.	.	.	.	.	10
Bulbostylis conifera Kunth		.	.	.	.	.	16.1	.	.	.	5
Bulbostylis fasciculata Uitt.		.	.	.	0.27	0.37	0.58	.	.	.	10
Bulbostylis junciformis (H. B. K.) Kunth		0.01	0.50	8.4	2.3	0.04	1.43	.	.	.	10
Burmannia bicolor Mart.		.	.	.	.	.	.	0.03	.	.	25
Byrsonima coccolobifolia Kunth		.	.	.	.	.	.	.	.	.	400
		.	.	.	.	.	.	.	.	.	40
Byrsonima crassifolia (L.) Rich.		.	0.1	0.5	0.03	0.03	.	.	.	.	1000
		.	.	.	.	.	0.59	.	.	.	50
Byrsonima verbascifolia (L.) L. C. Rich.		.	.	.	.	.	.	.	.	.	30
Calycolpus revolutus (Schauer) Berg		.	.	.	.	.	.	.	.	+	300
cf Casearia		.	.	0.01	.	.	.	.	.	.	sm
Cassia cultrifolia H. B. K.		0.01	0.10	0.40	0.09	0.07	.	.	.	.	50
Cassia faginoides Vog.		.	.	.	0.01	.	.	.	.	.	40
Cassia flexuosa L.		.	.	.	0.01	0.03	0.02	.	.	.	60
Cassia hispidula Vahl		.	.	0.01	0.09	0.44	0.88	.	.	.	100
Cassia patellaria DC.		.	.	.	0.02	0.43	.	.	.	.	60
Cassia ramosa fo. ramosa Vog.		.	.	.	.	.	6.13	.	.	.	-150
Cassytha filiformis L.		.	.	.	.	.	0.02	0.06	+	.	±100
Centrosema brasilianum (L.) Benth.		.	.	.	0.01	0.03	.	.	.	.	±100
Clusia fockeana Miq.	X	.	.	.	.	.	.	0.10	±	±	-400
Clusia nemorosa G. F. W. Meyer		.	.	.	.	.	.	.	.	+	-400
Commelina erecta L.		.	.	.	.	0.05	.	.	.	.	20
Comolia lythrarioides Naud.	X	.	.	.	.	.	0.02	0.10	.	.	30
Comolia vernicosa (Benth.) Triana		.	.	.	.	.	.	0.02	±	.	100
Comolia veronicaefolia Benth.		.	.	.	.	.	.	0.02	.	.	(30)
Conomorpha magnoliifoila Mez	X	.	.	.	.	.	.	.	±	±	-300
Conyza chilensis Spreng.		.	.	.	0.02	2.20	.	.	.	.	5/50
Coutoubea spicata Aubl.		0.02	.	0.01	.	.	.	.	.	.	40
Crotalaria stipularis Desv.		.	.	.	0.04	0.07	.	.	.	.	60
Croton hirtus L'Hérit		.	.	.	0.01	0.06	.	.	.	.	60
Croton hostmanni Miq.		.	.	.	.	.	.	.	+	.	100
Curatella americana L.	X	.	.	+	.	41.0	0.02	.	.	.	800
		0.01	0.01	.	0.29	.	.	.	.	.	150
Cyperus amabilis Vahl		.	.	.	0.06	.	.	.	.	.	5
Cyperus flavus (Vahl) Nees		.	.	.	0.28	0.04	0.01	.	.	.	40
Davilla aspera (Aubl.) R. Ben.		.	.	0.01	.	0.01	.	.	.	.	±300
Desmodium asperum (Poir.) Desv.		.	.	.	0.01	0.05	.	.	.	.	50
Desmodium barbatum (L.) Benth.		.	.	.	0.08	0.43	0.02	.	.	.	40

Structure						Raunkiaer		Seasonal				Leaf					Rootsystem		
								asp		rhyt									
habit	shoots	branching	posture	foliage	woodiness	normal	fire	normal	fire		hydrotype	sklero morphy	size	shape	hairiness	shining	shape	distribution	litter area
t	t	no	er	ros	herb	HCr	?	?	?	WDwd	Eux	skl	lepto	gr	gl	+	h.tail	C	
h	1	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	Hx	skl	micr	gr	gl		(h.glob	A)	both
sf	sv	bas	pt	scat	bas	Chs	(Ggp)	Sh	Vb	W -wd	Hx	skl	lepto	cp	gl		(mush	B)	
sf	sv	bas	pt	scat	bas	Chs	Ggp	Sh	Vb	W -wd	Hx	skl	lepto	cp	gl		mush	B	
h	1	up	er	scat	bas	(Th)	Th	S	S	W wd	Hx	skl	lepto	cp	gl		(spec	A)	
sf	1	no	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	Hyg	hyg	micr	sp	d		spec	C	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micr	gr	gl		X	X	
e.h	1	no	er	bas	herb	Phh	-	Eg	-	WDwd	(Mes)	mes	meso	sp	gl		between		bark
t	1	up	er	scat	lign	(Phm)	-	Eg	-	WDwd	-	hyg	meso	cp	d		-	-	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	gl		X	X	
t	t	no	er	bas	herb	Th	Th	S	S	W	Hx	skl	nano	gr	gl		-	-	
t	1	no	er	ros	lign	Phmm	Phmm	Eg	Eg	WDwd	-	(skl)	macro	cp	gl	+	-	-	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	gl		h. glob	A	both
t	t	no	er	scat	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	d+v		h.globX	B	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	cil		X	X	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	d+v		h.tail	C	
h	1	no	er	scat	bas	Th	Th	S	S	W -wd	Mes	mes	micro	sp	d+v		-	-	
t	sv	no	er	ros	lign	Phm	Ggp	Eg	Vb	WDwd	Eux	skl	macro	cp	gl	+	disc	A	under
(t)	1	up	er	term	lign	Phm	-	Eg	-	WDwd	-	skl	meso	cp	-	+	-	-	
h	1	bas	er	scat	herb	Th	Th	S	S	W -wd	Hx	skl	micro	sp	d+v		-	-	
sf	sv	bas	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	Hx	skl	nano	sp	gl		(gen	C)	
c.sh	-	-	cl	scat	lign	Phm	-	Eg.	-	WDwd	-	skl	micro	sp	gl	+	-	-	
h	sv	up	er	scat	herb	ThGg	ThGg	Vb	Vb	W wd	Hx	skl	nano	sp	gl		-	(A)	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	lepto	gr	gl		disc	A	
t	t	no	pt	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx'	skl	lepto	gr	d+v		h.glob	A	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	lepto	gr	gl		disc	A	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	lepto	gr	gl		(disc	A)	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	lepto	gr	gl		disc	A	
h	1	no	er	scat	herb	Th	Th	S	S	W	Mes	mes	nano	gr	gl		-	(A)	
t	1	up	er	term	lign	Phm	-	-	-	-	Hx	skl	meso	sp	gl	+	spec	(D)	
sh	sv	-	er	-	lign	Chfr	Ggp	-	-	-	(Hx)	skl	meso	sp	gl	+	-	-	
t	1	up	er	scat	lign	Phmm	Phmm	Eg	D	WDwd	Hx	skl	meso	sp	gl	+	r.gen	D	
sh	sv	up	pt	scat	lign	Chfr	Ggp	Eg	Vb	WDwd	Hx	skl	meso	sp	gl	+	spec	C	
sh	sv	bas	pr	bas	lign	Chfr	Chfr	(Eg	Sh)	-	Hx	skl	meso	sp	d+v		mush	(D)	
sh	sv	up	er	scat	lign	Phn	-	Eg	-	WDwd	-	skl	micro	sp	gl	+	-	-	
t	1	up	er	scat	lign	Phm	Phm	(Eg)	-	-	-	skl	micro	sp	gl		-	-	
h	1	no	er	scat	bas	Th	Th	S	S	W -wd	Hx	skl	nano	cp	gl		(gen	A)	
c.sf	sv	bas	cl	scat	bas	Chs	Chs	D	Sh	W -wd	(Hx)	skl	nano	cp	-		-	-	
sf	sv	no	er	scat	bas	Chs	Ggp	Sh	Vb	W -wd	Hx	skl	lepto	cp	gl		mush	A	
c.sf	sv	bas	cl	scat	bas	Chs	Ggp	D	Vb	W -wd	Hx	skl	micro	cp	gl		mush	C	
h	1	no	er	scat	bas	Th	Th	S	S	W -wd	Hx	skl	lepto	cp	d+v		gen	(A)	
sh	sv	bas	er	scat	lign	Phn	Ggp	Id	Vb	WDwd	Eux	skl	lepto	cp	d+v		mush	C	
c.h	sv	up	cl	none	herb	-	-	-	-	-	-	-	-	-	-		-	-	
c.sf	sv	bas	cl	scat	bas	Ggp	Ggp	Vb	Vb	W wd	(Hx)	skl	micro	cp	d		-	-	
sh	sv	bas	er	term	lign	Phm	Ggp	Eg	Vb	WDwd	Eux	skl	meso	sp	gl	+	X	X	X
sh	sv	bas	er	term	lign	Phm	Ggp	Eg	Vb	Wdwd	(Eux)	skl	meso	sp	gl	+	-	-	-
h	sv	up	pr	scat	herb	Grh	Grh	Vb	Vb	W wd	Hyg	hyg	micro	sp	d+v		disc	A	
sh	sv	bas	er	scat	lign	Chfr	Ggp	Id	Vb	WDwd	Hx	skl	nano	sp	gl	+	mushX	C	
sh	sv	bas	er	term	lign	Phn	Ggp	Eg	Vb	Wdwd	Hx	skl	nano	sp	gl	+	spec	B	both
sh	sv	bas	er	scat	lign	Chfr	-	-	-	-	-	mes	nano	sp	d+v		-	-	-
sh	sv	up	er	term	lign	Phm	Ggp	Eg	Vb	WDwd	Hx	skl	meso	sp	gl	+	X	X	under
h	1	no	er	ros	herb	Ggp	Ggp	Vb	Vb	W wd	Hyg	hyg	micro	sp	d+v		disc	A	
h	1	up	er	scat	herb	Th	Th	S	S	W	Hyg	hyg	micro	sp	gl		-	-	
h	1	up	er	scat	bas	Th	Th	S	S	W wd	(Mes)	mes	micro	sp	d+v		-	-	
h	1	up	er	scat	herb	Th	Th	S	S	W wd	Hyg	hyg	nano	sp	d+v		-	-	
sh	(sv	bas)	er	-	lign	Phn	-	-	-	-	-	mes	micro	sp	gl		-	-	
t	1	up	er	scat	lign	Phm	Phm	Id	D	WDwd	X	skl	meso	sp	gl		mush	C	
sh	sv	up	er	scat	lign	Phn	Ggp	Id	Vb	WDwd	Hx	skl	meso	sp	gl		spec	A	
t	t	no	er	bas	herb	Th	Th	S	S	W	Hx	skl	lepto	gr	gl		(disc	A)	
t	1	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	Hx	skl	meso	gr	gl		disc	A	
c.sh	1	bas	cl	scat	lign	Phm	Phm	Eg	D	WDwd	Hx	skl	meso	sp	gl	+	spec	A	
sf	sv	up	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	Hx	skl	meso	cp	d+v		r.gen	C	
sf	sv	bas	er	scat	bas	Chs	Ggp	Id	Vb	WDwd	Hx	skl	nano	cp	v		spec	A	

List of species (*continued*)

		Community									
		Pan sten	Sch-Rhyn mes cay	Sch-Rhyn mitr	Pol-Trach cyper	Pol-Trach curat	Mes-Trach	Xyr-Pasp	Clus-Scl Com var.	Tern-Mat Hum var.	height in cm
Dichronema ciliata Vahl		.	.	.	0.02	0.40	.	.	.	.	20
Dimorphandra conjugata (Splitgerber) Sandwith	X	.	.	.	.	.	.	.	.	.	-
Doliocarpus calinea J. F. Gmel		.	.	.	.	.	.	.	±	+	80
Drosera capillaris Poir.		.	.	.	.	.	.	2.30	.	.	2
Elephantopus angustifolius Schwartz		.	.	0.01	0.05	0.10	.	.	.	.	5/60
Epidendrum nocturnum Jacq.		.	.	.	.	.	.	.	.	+	40
Eriosema crinitum (H. B. K.) G. Don.		.	0.01	0.01	0.05	0.07	.	.	.	.	40
Eriosema violaceum (Aubl.) G. Don.	X	.	.	.	0.53	0.74	.	.	.	.	-120
Eugenia punicifolia (H. B. K.) DC.	X	.	0.03	0.05	0.01	0.04	0.04	.	.	.	50
Eupatorium amygdalinum Lam.		.	0.01	0.20	0.04	0.03	.	.	.	.	60
Eupatorium odoratum L.		.	.	.	0.02	0.01	.	.	.	.	80
Euphorbia brasiliensis Lam.		.	.	.	0.04	0.07	.	.	.	.	30
Galactia jussieuana Kunth		.	.	.	0.26	4.40	.	.	.	.	60
Habenaria spec.		+	.	.	.	.	.	.	.	.	30
Heliconia psittacorum L. f.		.	.	.	0.01	6.40	.	.	.	.	60
Himatanthus articulatus (Vahl) Woods.		.	.	0.05	0.01	0.01	.	.	.	.	10
Humiria balsamifera St. Hil.	X	.	.	.	.	.	.	0.02	±	±	X
Hybanthus ipecacuanha (L.) Baill.		.	.	.	0.01	0.06	.	.	.	.	60
Hypolythrum pulchrum (Rudge) Pfeiff.		.	.	.	.	.	.	0.02	+	.	30
Hyptis atrorubens Poit.		0.01	0.05	0.40	0.29	0.40	.	.	.	.	40
Ilex jenmani Loesener		.	.	.	.	.	.	.	.	±	±300
Imperata brasiliensis Trin.		.	.	0.01	.	.	.	.	.	.	50
Lagenocarpus amazonicus (Clarke) Pfeiff.		.	.	.	.	.	.	.	±	.	20
Lagenocarpus tremulus Nees		.	.	.	.	.	.	0.10	+	.	60
Lagenocarpus weigeltii (Spreng.) Uitt.		.	.	.	.	.	.	.	.	±	30
Leptocorphium lanatum (H. B. K.) Nees	X	5.4	0.55	.	.	.	.	0.06	.	.	50
Licania divaricata Benth.		.	0.03	0.05	0.01	0.01	.	.	.	.	1000
Licania incana Aubl.	X	.	.	.	.	.	.	0.10	±	±	X
Lisianthus coerulecens Aubl.		.	.	.	.	.	.	0.02	.	.	30
Lisianthus uliginosus Griseb.		.	.	.	.	.	.	.	±	.	60
Mapouria chlorantha (Benth.) Brem.		.	.	.	.	.	.	.	.	+	-300
Maprounea guianensis Aubl.	X	.	.	0.05	0.01	0.01	.	.	.	.	400
Marlierea montana (Aubl.) Amsh.	X	.	.	.	.	.	.	.	±	.	100
Matayba opaca Radlk. var. fallax (Radlk.) Uitt.		.	.	.	.	.	.	.	.	+	sm
Mauritia flexuosa L. f.	X	.	.	.	.	.	.	.	.	.	1000
Mesosetum cayennense Steud.	X	37.3	38.5	.	.	.	.	.	.	.	20
Mesosetum loliiforme (Hochst.) Chase	X	.	.	.	.	.	23.6	1.80	.	.	10
Miconia ciliata (L. C. Rich.) DC.	X	.	.	.	.	.	.	.	+	.	50
Mitracarpus discolor Miq.		.	0.01	0.01	0.06	0.41	0.61	.	.	.	40
Mitracarpus microspermus K. Sch.		.	.	0.40	0.05	0.75	.	.	.	.	5
Myrcia sylvatica (Mey.) DC.		.	.	.	.	.	.	.	.	+	sm
Myrosma cannifolia L. f.	X	.	.	.	.	0.36	.	.	.	.	40
Ormosia costulata (Miq.) Kleinh.		.	.	.	.	.	.	.	.	+	700
Oxypetalum capitatum Mart. et Zucc.	X	.	.	.	0.03	0.04	.	.	.	.	50
Paepalanthus polytrichoides Kunth		.	.	.	.	.	.	2.50	.	.	10
Paepalanthus subtilis Miq.		.	.	.	0.02	.	1.13	.	.	.	10
Pagamea capitata Benth.		.	.	.	.	.	.	.	+	+	-300
Pagamea guianensis Aubl.		.	.	.	.	.	.	.	.	+	-600
Panicum micranthum H. B. K.	X	.	.	.	.	.	.	8.20	.	.	10
Panicum nervosum Lam.		0.20	.	.	.	.	.	.	+	.	50
Panicum rudgei Roem. et Sch.		.	.	.	0.01	2.50	.	.	.	.	80
Panicum stenodoides Hubbard		21.5	.	.	.	.	.	.	.	.	15
Paspalum plicatulum Michx.		.	.	.	.	2.10	.	.	.	.	60
Paspalum polychaetum Mez		.	.	.	.	.	.	0.70	.	.	20
Paspalum pulchellum Kunth	X	.	.	.	.	.	.	1.30	.	.	15
Pavonia speciosa H. B. K.		.	.	.	0.01	.	.	.	.	.	-60
Pectis elongata H. B. K.		.	.	.	0.01	.	.	.	.	.	30
Perama hirsuta Aubl.		.	.	.	.	.	.	1.30	.	.	20
Phaseolus longepedunculatus H. B. K.		.	.	0.01	0.03	0.03	.	.	.	.	±60
Phaseolus peduncularis H. B. K. var. clitorioides (Benth.) Hassl.		0.01	.	.	0.05	0.43	0.01	.	.	.	±60

Structure						Raunkiaer		Seasonal				Leaf					Rootsystem		
								asp		rhyt									
habit	shoots	branching	posture	foliage	woodiness	normal	fire	normal	fire		hydrotype	sklero morphy	size	shape	hairiness	shining	shape	distribution	litter area
h	1	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	Hx	skl	nano	gr	gl		disc	A	
sh	sv	bas	er	scat	lign	Phm	Ggp	Eg	Vb	WDwd	(Hx)	skl	meso	cp	gl	+	X	X	X
c.sh	1	bas	cl	scat	lign	Phn	Phn	Eg	D	WDwd	Hx	skl	micro	sp	gl	+	spec	A	under
h	1	no	er	ros	herb	Th	Th	S	S	(W wd)	(Hx	skl)	lepto	sp	d		-	-	
h	1	no	er	ros	herb	Hc	Ggp	Id	Vb	WDwd	Hx	skl	micro	sp	d+v		disc	A	
h	(sv)	no	er	scat	herb	(Phh)	-	-	-	-	-	skl	micro	sp	gl		-	-	under
sf	sv	no	er	scat	bas	Chs	Ggp	Sh	Vb	W -wd	Hx	skl	micro	cp	d+v		mush	C	
sf	sv	bas	er	scat	bas	Chs	Ggp	Id	Vb	WDwd	Hx	skl	micro	cp	d+v		mush	C	
sh	sv	bas	er	scat	lign	Phn	Ggp	Eg	Vb	WDwd	Eux	skl	micro	sp	gl	+	X	D	
sf	sv	bas	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	Hx	skl	micro	sp	gl		disc	A	
sf	sv	up	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	Hx	skl	micro	sp	d+v		mush	C	
h	1	no	er	scat	herb	Th	Th	S	S	W wd	Hx	skl	nano	sp	gl		-	-	
sh	sv	bas	er	scat	bas	Phn	Ggp	D	Vb	W wd	Hx	skl	micro	cp	d+v		cyl	D	
h	1	-	er	bas	herb	G	G	-	-	w	-	skl	-	sp	gl		-	-	
h	1	no	er	scat	herb	Phh	Grh	Eg	Vb	WDwd	Hx	skl	meso	sp	gl	+	show	A	
t	1	up	er	term	lign	Phmm	Phmm	Eg	D	WDwd	Hx	skl	meso	sp	gl	+	mush	C	
sh	sv	bas	pr	term	lign	Phn	Ggp	Eg	Vb	WDwd	X	skl	meso	sp	gl	+	spec	X	not
sf	sv	up	er	scat	bas	Chs	Ggp	Vb	S	W -wd	(Hx)	skl	micro	sp	d+v		-	-	
h	l	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	(Hx)	skl	micro	gr	gl		-	-	
sf	sv	bas	pr	scat	bas	Chs	Ggp	Id	Vb	WDwd	Hx	skl	micro	sp	d+v		mush	B	
sh	1	up	er	scat	lign	Phm	-	Eg	-	WDwd	Eux	skl	meso	sp	gl	+	mush	F	under
t	l	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	(Hx)	skl	meso	gr	gl		-	-	
t	l	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	Hx	skl	micro	gr	v		h.glob	A	both
t	t	no	er	bas	herb	Grh	Grh	Vs	Vs	W wd	Hx	skl	micro	gr	gl	+	h.glob	C	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	gl	+	h.glob	A	under
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	gl		X	D	
t	1	up	er	scat	lign	Phmm	Phmm	-	-	WDwd	-	skl	meso	sp	gl	+	-	-	
X	X	X	er	scat	lign	Ph	Ggp	Id	Vb	WDwd	Hx	skl	micro	sp	v		spec	X	both
h	1	bas	er	scat	herb	Th	Th	S	S	W wd	Hx	skl	lepto	sp	gl		-	-	
h	1	bas	er	scat	herb	Phh	(Th)	Eg	(S)	WDwd	Hx	skl	micro	sp	gl		spec	A	under
sh	1	-	er	term	lign	Phm	-	Eg	-	WDwd	-	mes	meso	sp	gl	+	-	-	-
sh	sv	up	er	scat	lign	Phm	Ggp	Eg	Vb	WDwd	Hx	skl	micro	sp	gl	+	mush	C	
sh	sv	bas	er	scat	lign	Phn	Ggp	Eg	Vb	WDwd	Hx	skl	micro	sp	gl	+	spec	D	both
t	1	up	er	term	lign	Phm	Ggp	Eg	-	WDwd	-	skl	meso	cp	gl	+	(R.gen	C)	under
t	1	no	er	ros	lign	Phmm	-	Eg	-	WDwd	-	-	-	-	-	+	disc		
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	d+v		X	X	
t	1	no	er	bas	herb	HCc	HCc	Vs	Vs	W wd	X	skl	nano	gr	d+v		X	X	
sh	sv	bas	er	scat	lign	Phn	Ggp	Eg	Vb	WDwd	Hx	skl	micro	sp	gl	+	spec	A	under
h	1	bas	er	scat	herb	Chs	Ggp	Sh	Vb	W wd	Hyg	hyg	nano	sp	d+v		com	B	
h	sv	bas	er	scat	herb	Th	Th	S	S	W	(Hx)	skl	lepto	sp	gl		-	-	
sh	sv	up	er	scat	lign	Phn	(Ggp)	Eg	(Vb)	WDwd	-	skl	nano	sp	gl	+	-	-	
h	1	no	er	scat	herb	Gb	Gb	Vb	Vb	X wd	Hx	skl	meso	sp	gl		cyl	A	
t	1	up	er	scat	lign	Phm	Phm	Eg	-	WDwd	Eux	skl	meso	cp	gl	+	mush	F	under
h	1	up	er	scat	bas	Ggp	Ggp	Vb	Vb	wd	Eux	mes	micro	sp	d+v		disc	A	
h	sv	up	er	scat	herb	Chh	(Ch)	Eg	-	WDwd	Hx	skl	lepto	gr	d+v		h.glob	A	
h	1	up	er	bas	herb	(Chh)	-	-	-	-	Hx	skl	lepto	gr	gl		-	-	
t	1	up	er	term	lign	Phm	-	Eg	-	WDwd	-	skl	micro	sp	gl	+	-	-	
t	1	up	er	term	lign	Phm	-	Eg	-	WDwd	-	skl	micro	sp	v		-	-	
t	t	no	er	scat	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	d+v		X	X	
h	l	no	er	scat	herb	Grh	Grh	Vb	Vb	W -wd	Hx	skl	micro	gr	gl		show	C	
(t	t)	no	er	scat	herb	Gc	Gc	Vb	VB	W wd	(Hx)	skl	meso	gr	d+v		-	-	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	d+v		h.tail	C	
h	l	no	er	scat	herb	Chg	Gc	Id	Vb	WDwd	(Hx)	skl	meso	gr	d		-	-	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	d+v		(h.glob	B)	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	d+v		h.tail	B	
sf	sv	bas	pt	scat	bas	Chs	Ggp	Id	Vb	WDwd	Hx	skl	micro	sp	d+v		mush	B	
h	1	up	er	scat	herb	(Th	Th)	S	S	(W wd)	-	skl	nano	sp	v		-	-	
sf	sv	bas	er	scat	bas	Chs	Ggp	Id	Vb	WDwd	Hx	skl	nano	sp	d+v		R.gen	A	
c.h	sv	bas	cl	scat	herb	Ggp	Ggp	Vb	Vb	W wd	Mes	mes	nano	cp	d+v		mush	B	
c.h	1	bas	cl	scat	herb	Gb	Gb	Vb	Vb	W wd	Hx	skl	micro	cp	gl		mush	C	

List of species (*continued*)

		Community									
		Pan sten	Sch-Rhyn mes cay	Sch-Rhyn mitr	Pol-Trach cyper	Pol-Trach curat	Mes-Trach	Xyr-Pasp	Clus-Scl Com var.	Tern-Mat Hum var.	height in cm
Phyllanthus diffusus Klotzsch		.	.	.	0.04	0.03	0.02	.	.	.	30
Piriqueta cistoides (L.) Griseb.		.	.	.	0.03	0.03	.	.	.	.	40
Pithecellobium jupunba (Willd.) Urb.		.	.	0.03	0.01	0.01	.	.	.	.	600
Polycarpaea corymbosa (L.) Lam.		.	.	.	2.06	0.06	0.02	.	.	.	25
Polygala adenophora DC.		0.07	0.30	0.05	.	.	0.06	0.07	.	.	30
Polygala appressa Benth.		.	.	.	.	.	.	0.07	.	.	10
Polygala longicaulis H. B. K.		.	0.04	0.25	0.54	0.03	0.33	.	.	.	25
Polygala variabilis H. B. K.		.	.	.	.	.	0.02	.	.	.	40
Polystachya luteola (Sw.) Hook.		.	.	.	:	+	.	.	.	.	20
Protium heptaphyllum (Aubl.) March.	X	.	.	.	.	.	.	.	.	+	±200
Psidium guineense Sw.		.	.	.	0.01	0.04	.	.	.	.	-150
Pterolepis trichotoma (Rottb.) Cogn.		.	.	.	.	2.10	.	.	.	.	60
Retiniphyllum schomburgkii (Benth.) Müll. Arg.	X	.	.	.	.	.	.	.	±	±	150
Rhynchospora arenicola Uitt.		.	.	.	.	.	.	0.05	.	.	20
Rhynchospora barbata fo glabra Maury	X	.	.	.	.	.	0.28	0.06	.	.	5
Rhynchospora barbata fo barbata (Vahl) Kunth	X	21.1	28.5	10.5	0.01	.	.	.	.	.	15
Rhynchospora curvula Griseb.		.	.	.	.	.	.	0.04	.	.	3
Rhynchospora globosa (H. B. K.) Roem. et Sch.		37.3	.	.	.	.	.	.	.	.	40
Rhynchospora graminea Uitt.	X	.	.	.	.	.	.	2.30	.	.	10
Rhynchospora tenuis Link		:	.	.	.	.	.	0.05	.	.	15
Richardia scabra L.		.	.	.	0.02	0.04	.	.	.	.	50
Riencourtia glomerata Cass.		.	0.02	0.01	0.30	5.70	.	.	.	.	70
Rollinia exsucca (Dun.) A. DC.		.	0.01	.	.	.	.	.	.	.	sm
Sauvagesia sprengelii St. Hil.		.	.	.	.	.	.	1.10	.	.	30
Schizachyrium riedelii (Trin.) A. Camus	X	0.40	2.80	5.7	7.5	2.10	.	.	.	.	20
Schizaea incurvata Schkur		.	.	.	.	.	.	.	.	+	20
Schwenckia americana L.		.	.	.	.	.	0.02	.	.	.	40
Scleria bracteata Cav.		0.02	0.01	1.1	.	0.40	.	.	.	.	100
Scleria hirtella Sw.		.	0.01	.	.	.	.	.	.	.	20
Scleria micrococca (Liebm.) Steud.		.	0.04	0.20	0.02	0.01	0.29	.	.	.	20
Scleria pyramidalis Hochst.		.	.	.	.	.	.	.	±	.	-300
Sebastiana corniculata (Vahl) Müll. Arg.		.	.	.	0.01	0.03	0.01	.	.	.	40
Sipanea pratensis Aubl.	X	1.90	1.50	3.10	0.03	0.01	.	.	.	.	30
Stylosanthes guianensis (Aubl.) Sw. var. gracilis (H. B. K.) Vog.		.	.	.	0.04	0.10	.	.	.	.	60
Stylosanthes viscosa Sw.		.	.	.	.	.	0.34	.	.	.	40
Swartzia bannia Sandwith		.	.	.	.	.	.	.	.	+	sm
Symplocos guianensis (Aubl.) Gürke	X	.	.	0.01	.	0.01	.	.	.	.	150
Syngonanthus gracilis (Bong.) Ruhl.		.	.	.	.	.	.	0.04	.	.	2(5)
Syngonanthus umbellatus (Lam.) Ruhl.		.	.	.	.	.	.	0.07	.	.	40
Tapirira guianensis Aubl.		.	.	0.05	0.01	0.01	.	.	.	.	600
Tephrosia purpurea (L.) Pers.		.	.	.	0.05	0.40	.	.	.	.	40
Tephrosia sessiliflora (Poir.) Hassl.		.	.	.	2.54	2.20	.	.	.	.	40
Ternstroemia punctata (Aubl.) Sw.	X	.	.	.	.	.	.	0.02	±	±	-600
Tetracera asperula Miq.	X	.	.	.	.	.	0.02	0.03	+	+	80
Tibouchina aspera Aubl.	X	0.90	0.80	12.8	0.04	.	1.94	0.02	.	.	X
Trachypogon plumosus (Humb. et Bonpl.) Nees	X	0.40	11.8	25.2:	65.2	55.7	18.3	.	.	+	60
Trattinickia burserifolia Mart.		.	0.01	.	0.01	0.01	.	.	.	0.06	1000
Turnera ulmifolia L.		0.03	.	.	0.01	0.03	.	.	.	.	60
Utricularia fimbriata H. B. K.		.	.	.	.	.	.	2.30	.	.	20
Utricularia guianensis A. DC.		.	.	.	.	.	.	0.02	.	.	-
Waltheria americana L.		.	.	.	.	.	0.01	.	.	.	60
Xyris glabrata Griseb.		.	.	.	.	.	.	0.02	.	.	25
Xyris guianensis Steud.		.	.	.	.	.	.	9.00	.	.	5/20
Xyris longiceps Malme		.	.	.	.	.	.	0.02	.	.	5/20
Xyris subuniflora Malme		.	.	.	.	.	.	0.07	.	.	2/5
Xyris surinamensis Spreng.		.	.	.	.	.	.	1.30	.	.	20
Zornia diphylla (L.) Pers.	X	.	.	0.01	0.08	0.40	0.04	.	.	.	30

Structure						Raunkiaer		Seasonal			Leaf						Rootsystem		
								asp		rhyt									
habit	shoots	branching	posture	foliage	woodiness	normal	fire	normal	fire		hydrotype	skleromorphy	size	shape	hairiness	shining	shape	distribution	litter area
h	1	no	er	scat	herb	Th	Th	S	S	W wd	Hyg	hyg	lepto	sp	gl		-	-	
h	1	no	er	scat	bas	Th	Th	S	S	W wd	(Hyg)	hyg	nano	sp	d+v		-	-	
t	1	up	er	scat	lign	Phm	Phm	Eg	D	WDwd	Hx	skl	micro	cp	gl	+	mush	B	
h	1	up	er	scat	herb	Th	Th	S	S	(W w)	Hx	skl	lepto	gr	gl		gen	A	
h	1	no	er	scat	herb	Th	Th	S	S	Ww/d	Mes	mes	lepto	gr	gl		gen	A	
h	1	bas	er	scat	herb	Th	Th	S	S	W-wd	Hx	skl	lepto	gr	gl		-	-	
h	1	up	er	scat	herb	Th	Th	S	S	Ww/d	Hx	skl	lepto	gr	gl		gen	A	
sf	sv	bas	er	scat	bas	Chs	Ggp	Sh	Vb	W wd	-	skl	lepto	sp	gl		-	-	
e.h	1	no	er	bas	herb	-	-	-	-	-	-	-	micro	sp	gl		between		bark
sh	(sv)	up	er	scat	lign	Phm	Ggp	Eg	Vb	WDwd	(Hx)	skl	micro	cp	gl	+	(r.gen	B	under)
sh	sv	bas	er	scat	lign	Phn	Ggp	Eg	Vb	WDwd	Hx	skl	micro	sp	d+v	+	r.gen	D	
h	1	up	er	scat	bas	Th	Th	S	S	W wd	(Mes)	mes	nano	sp	d+v		-	-	
sh	1	bas	er	term	lign	Phn	(Th)	Eg	-	WDwd	X	skl	meso	sp	gl		spec	E	under
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	-	skl	nano	gr	d+v		-	-	
t	t	no	er	ros	herb	HCr	HCr	Vs	Vs	W wd	Hx	skl	nano	gr	gl		h.glob	A	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	v		h.glob	B	
t	t	no	er	ros	herb	HCr	HCr	Vs	Vs	W wd	(Hx)	skl	nano	gr	gl		-	-	
t	1	no	er	bas	herb	HCb	HCb	Vs	Vs	W wd	Hx	skl	micro	gr	gl		show	C	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	gl		X	X	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	nano	gr	gl		h.glob	A	
h	1	bas	er	scat	bas	Th	Th	S	S	W wd	(Mes)	mes	nano	sp	d+v		-	-	
h	sv	up	er	scat	herb	Ggp	Th	Vb	S	W d	Hx	skl	micro	sp	d+v		disc	A	
t	1	up	er	scat	lign	Phm	Phm	Eg	-	(WDwd)	-	skl	meso	sp	v	+	-	-	
sh	sv	bas	er	scat	lign	Chfr	Ggp	Eg	Vb	(WDwd)	Hx	skl	nano	sp	gl	+	spec	A	
t	t	no	er	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	micro	gr	gl		X	B	
h	1	no	er	bas	herb	Grh	Grh	Vb	Vb	W wd	Hx	skl	micro	gr	gl		h.glob	A	under
h	sv	no	er	scat	bas	Ggp	Ggp	Vb	Vb	W wd	(Hx)	skl	nano	sp	d+v		-	-	
h	1	no	er	scat	herb	Gb	Gb	Id	Vb	WDwd	Hx	skl	micro	gr	d+v		disc	A	
h	1	no	er	bas	herb	Grh	Grh	Vb	Vb	w	Hx	skl	nano	gr	d+v		disc	A	
t	t	no	er	bas	herb	Th	Th	S	S	W	Hx	skl	nano	gr	d+v		(disc)	(A)	
c.h	sv	(up)	cl	scat	herb	Phh	Gb	Eg	Vb	WDwd	Eux	skl	micro	gr	gl		disc	A	under
h	1	no	er	scat	bas	Th	Th	S	S	W wd	Hyg	hyg	nano	sp	d+v		-	-	
sf	sv	bas	pr	scat	bas	Chs	Ggp	Id	Vb	WDwd	Mes	mes	micro	sp	d+v		X	X	
h	1	up	er	scat	bas	Th	Th	S	S	W-wd	Hx	skl	nano	cp	v		com	B	
sf	sv	bas	er	scat	bas	Chs	Chs	Id	Sh	WDwd	Hx	skl	lepto	cp	d+v		mush	A	
t	1	up	er	scat	lign	Phm	-	Eg	-	WDwd	-	skl	micro	cp	gl	+	-	-	
sh	sv	bas	er	scat	lign	Phn	Ggp	Eg	Vb	WDwd	Hx	skl	meso	sp	v	+	R.gen	C	
t	t	no	er	ros	herb	-	-	-	-	-	Hx	skl	nano	gr	d+v		(h.glob	A)	
h	1	up	er	ros	herb	HCr	-	Eg	-	WDwd	(Hx)	skl	nano	gr	d+v		-	-	
t	1	up	er	scat	lign	Phm	Phm	Eg	D	WDwd	Hx	skl	meso	cp	gl		(spec	A)	
sf	1	bas	er	scat	bas	Chs	Th	Sh	S	W wd	Hx	skl	nano	cp	gl		-	-	
h	1	up	er	scat	bas	Th	Th	S	S	W-wd	Hx	skl	micro	cp	v		com	B	
sh	sv	bas	er	term	lign	Phm	Ggp	Eg	Vb	WDwd	X	skl	micro	sp	gl	+	X	X	X
c.sh	sv	up	cl	scat	lign	Phn	Ggp	(Eg)	Vb	WDwd	X	skl	meso	sp	gl	+	X	X	
sh	sv	bas	er	scat	lign	Phn	Ggp	Id	Vb	WDwd	X	skl	micro	sp	d+v	+	X	X	
t	t	no	er pt	bas	herb	Gc	Gc	Vb	Vb	W wd	Hx	skl	meso	gr	d+v		X	X	
t	1	up	er	scat	lign	Phm	-	Eg	-	WDwd	-	skl	meso	cp	gl	+	-	-	-
sf	sv	bas	er	scat	bas	Chs	Ggp	Sh	Vb	W-wd	Mes	mes	micro	sp	d+v		mush	C	
h	1	no	er	ros	herb	Th	Th	S	S	W	(Mes)	mes	lepto	gr	gl		-	-	
h	(1	no	er)	ros	herb	(Th	Th)	(S	S)	(W)	-	-	-	sp	-		-	-	
sf	1	bas	er	scat	bas	Chs	Chs	Id	Sh	WDwd	Eux	skl	meso	sp	d+v		mush	C	
t	t	no	er	bas	herb	-	-	-	-	-	-	skl	micro	gr	gl		-	-	
t	t	no	er	bas	herb	-	-	-	-	-	-	skl	nano	gr	gl		-	-	
t	t	no	er	bas	herb	-	-	-	-	-	-	skl	nano	gr	gl		(h.glob	A)	
t	t	no	er	bas	herb	(Th)	(Th)	(S	S)	(W wd)	(Hx)	skl	lepto	gr	gl		(h.glob	A)	
t	t	no	er	bas	herb	Gc	Gc	Id	Vb	WDwd	Hx	skl	micro	gr	gl		h.tail	C	
h	sv	bas	pt	scat	bas	Ggp	Ggp	Vb	Vb	W wd	Mes	mes	micro	cp	d+v		mush	C	

VIII. 3. Further data on some species whose characteristics are variable depending on vegetation units

Andropogon leucostachyus, Ch. III.3.11.1. and Table 3.

Root behaviour corresponds with the general picture of the vegetation unit.

In *Panicetum stenodoidis:* show and C.

In the *Schizachyrio-Rhynchosporetum mesosetosum:* h. glob and B.

Expected for *Schizachyrio-Rhynchosporetum mitracarpetosum:* h. glob and B.

Aristida tincta, Ch. III.3.11.1 and Table 3.

The root behaviour corresponds with the general picture of the vegetation unit.

In *Panicetum stenodoidis:* h. glob and C.

In *Schizachyrio-Rhynchosporetum mesosetosum* and *mitracarpetosum:* h. glob and B.

Axonopus pulcher, Ch. III.3.11.1 and Table 3.

The rooting behaviour in all units h. glob and B.

Depth of the roots increases in the *Panicetum stenodoidis*, where water supply is mainly from below. The length of horizontal roots is greater in soils where rain water is quickly absorbed.

Axonopus purpusii, Ch. III.3.11.1 and Table 3.

Root behaviour follows the general picture of the vegetation units.

In the *Schizachyrio-Rhynchosporetum mesosetosum:* h. glob and C.

In the *Schizachyrio-Rhynchosporetum mitracarpetosum:* h. glob and B.

The horizontal roots become longer than in the other subassociation.

Byrsonima crassifolia, Ch. IV.3.3

Byrsonima crassifolia occurs as a tall tree with well developed trunk, as orchard tree form, and as low shrub with xylopodium. The shrub form is found on white sand, the other two forms on heavier soils. The orchard tree form of *Byrsonima* was not encountered on the Lobin savanna, but is known elsewhere (Van Donselaar, 1965).

Root systems were dug out for a tree of 7 m in sandy clay loam, and for a shrub 1½ m tall in white sand. The primary root of both was bent horizontally at a depth of about 60 cm. The long horizontal roots were the most important part of the root system. The length of the latter was notably shorter in the shrub than in the tree. The longest roots were 8 and 26 m. respectively.

An interplay of fire and annual growth, determined by water supply and nutrient content of the soil, is probably responsible for the form.

Clusia fockeana, Ch. II.3.9 and Fig. 12.

Clusia fockeana is rooted in white sand both inside and outside the litter area. Ground water limits the extent of the roots. Vertical roots go down to within reach of the ground water, horizontal roots are forced into the upper cm of the soil by high water tables.

High temperatures during the long dry season probably limit the roots to the area of litter or to a depth of 20 to 30 cm below the surface.

The size of root and shoot systems increase as the environment becomes drier.

A specimen which was dug up in a bush on sandy clay loam, in vegetation belonging to the *Schizachyrio-Rhynchosporetum mitracarpetosum*, had both vertical and horizontal roots. The horizontal ones were very shallow at the boundary of litter and mineral soil, and were limited to the litter area of the bush.

Clusia fockeana may occur as a solitary shrub on white sand.

Comolia lythrarioides

Comolia lythrarioides was dug up in wet and in dry white sand. In the dry sand, the size of horizontal and vertical roots is much greater than in wet sand. The maximum depths were respectively 50 and 30 cm, the maximum horizontal length 70 and 20 cm.

Conomorpha magnoliifolia, Ch. III.3.9 and Table 2

Roots are limited to the litter area. Where ground water permits a small vertical primary root is present. The length of the horizontal roots increases with increasing drought of the soil.

Curatella americana (Photo 4)

The behaviour of root systems in different environments was treated in Ch. III.3.11.1. The habit is described in Ch. IV.3.2 under the heading "trees".

In the *Polycarpaeo-Trachypogonetum curatelletosum*, the ratio of roots to shoots is so large, that the species must be counted as one of Iversen's euxerophytes. In other units it is a scleromorphic hemicryptophyte.

Dimorphandra conjugata

The root systems of "dakama" were dug up twice, both from vegetation types which were not discussed.

In a bush on dry white sand (Fig. 14) an individual 5 m high only had two horizontal roots, which were strongly branched. They occurred in the litter layer or at the boundary of litter and sand. The roots were limited to the litter area. The terminal root branches in the litter had a coral-like appearance, indicative of mycorrhiza.

In a bush on moist white sand, where ground water reaches the surface during a part of the long rainy season, the root system of a shrub 3 m tall was exposed. At the time of excavation (April 14, 1959), ground water stood at 50 cm below the surface. Besides some horizontal roots, there was also a primary root going down to 60 cm. Horizontal roots also bent downwards at their tips to a depth of about 60 cm. The length of horizontal roots was 2 m; they occurred at some depth in the sand and were not limited to the litter area.

Eriosema violaceum

Eriosema violaceum makes the impression of benefiting from regularly occurring fires. In places that were not burned in previous years, depauperate specimens were found, which were 1.20 m tall and had only leaves on the youngest stem part. They had a minute root system.

Where vegetation had been burned, the xylopodium gave rise to several stems leafy along their entire length. Their height was 40 to 50 cm. The root system was well developed with a primary root down to 60 or 70 cm and lateral roots to 1.20 m in length in the sod layer.

Apparently the fire is the stimulus for the formation of new shoots. A drought alone is not drastic enough. The aerial parts remain alive, although languishing, and no new basal shoots are formed.

Eugenia punicifolia

The rooting behaviour is discussed in Ch. III.3.11.1.

The root system is so extensive in relation to the aerial portion, that *Eugenia punicifolia* must be counted as a euxerophyte sensu Iversen.

Depending on the height of the surrounding vegetation the species is counted as a nano-phanerophyte or frutescent chamaephyte.

Humiria balsamifera

A revision of the genus *Humiria* by CUATRECASAS (1961) makes all species identifications done in the course of this study uncertain. According to the new classification, all *Humirias* in the vegetations studied belong to *Humiria balsamifera*. A determination of the varieties after the termination of the field work proved to be impossible.

Humiria balsamifera appears in many forms (HEYLIGERS, page 84 and 95): from low shrubs with creeping branches to a tall tree with well developed trunk and heavy crown (1 specimen on the Coesewijne savanna).

In the present study only the shrubby form with creeping branches was investigated, in bushes on wet and dry white sand. In the bushes on dry white sand of the *Ternstroemia-Matayba* scrub, *Humiria* variant, *Humiria* forms the lowest zone in the dome-shaped canopy.

The height of the shrubs is correlated, through the available rooting space, with the ground-water level. The higher the ground water during the rainy season, the smaller the soil layer without water surplus, and the lower the shrubs.

In the *Comolia* variant of the *Clusia-Scleria* scrub, the shrubs reach a height of 40 to 60 cm; in the *Ternstroemia-Matayba* scrub, *Humiria* variant, they reach 1.50 to 2 m in the margins.

The aerial parts sprout from trunks which traverse great distances in the soil, within the litter area. In the *Clusia-Scleria* scrub one specimen was dug up with a 3½ m underground stem with many scars of old branches. Only the tip produced aerial parts.

For the root system see Ch. III.3.9. The thin shallow roots in wet white sand die off in the long dry season, probably by desiccation and high temperature. In the dry white sand the roots are not inhibited by ground water in the deeper soil layers (20 to 30 cm below the surface) where they are protected against high temperatures and desiccation. These roots grow in thickness and have a protective cork layer.

In accordance with the difference in rooting, the species is counted as a scleromorphic euxerophyte in the *Ternstroemia Matayba* scrub; in the *Clusia-Scleria* scrub it is a scleromorphic hemixerophyte.

The leaves, found on the tips of short lateral shoots, are alternately small and large. The large ones are formed in the growing season, the short ones at the end of the growing season or perhaps during the long dry season.

Leptocoryphium lanatum, see Tables 1 and 3

The manner of rooting in the various vegetation units is discussed in Ch. III.3.11.1.

Licania incana

The manner of rooting is discussed in Ch. III.3.9, the habit of the aerial portions in Ch. IV.3.3.

This species occurs as an isolated shrub on white sand, both wet and dry.

Maprounea guianensis

Underground this species often has a xylopodium, giving rise to several stems. Following fires it can obviously regenerate from below ground. Following a light fire it may also sprout from stems above the ground.

Marlierea montana

In the units investigated *Marlierea* only occurs in the *Clusia-Scleria* scrub. The species was found also and dug up from a bush on dry white sand and a bush on white sand and intermediate type of water economy.

A description of the manner of rooting is found in Ch. III.3.9.

The height of the shrubs increases with increasing drought of the environment. With increasing drought the plant needs a larger root system to provide the water. In this low-nutrient environment a larger root system, i.e., a larger volume of soil containing the roots, is correlated with larger size above the ground. Ground water in the wetter environment does not force the roots upwards into the upper centimeters.

In accordance with the size of the root system, the Iversen hydrotype varies with the environment. In wet environments *Marlierea montana* is a scleromorphic hemixerophyte, in both other habitats a scleromorphic euxerophyte.

Mauritia flexuosa, see Fig. 17

Mauritia flexuosa grows in the creek valleys of the savannas. The vegetation of these areas is not included in the present study. The root system of one specimen 7 m tall was dug out. There were many

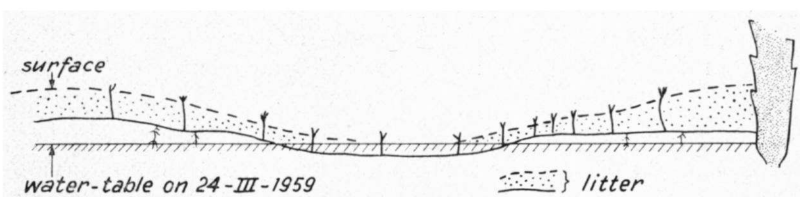

Fig. 17. *Mauritia flexuosa.* 1/80 ×

horizontal roots, two of which were followed to the end. They were 8 and 5 m long. Their depth was dependent upon the ground water. The roots ran about 20 cm above the ground water table at the time (at the beginning of the long wet season). The maximum depth below the surface was 40 cm. Where the ground water reached the surface, the root remained 1 dm below the surface. A few lateral roots grew down into the ground water. Besides, there were many roots which grew straight up and branched above the surface: air roots.

An additional peculiarity are the many roots which are found in and between the old leaf sheaths of the trunk itself, up to about 1.50 m.

The high level of the ground water prevented an investigation of any vertical roots below the trunk.

Mesosetum cayennense, see Table 3 and Ch. III.3.11.1.

The manner of rooting corresponds with the general picture of the vegetation.

In the *Panicetum stenodoidis:* horsetail type and C.

In the *Schizachyrio-Rhynchosporetum mesosetosum:* hemispherical and B.

Mesosetum loliiforme, see Table 1.

The method of rooting is mentioned in Ch. III.3.6. Due to the large root system in relation to the aerial size, the species belongs to the scleromorphic euxerophytes in the *Mesoseto-Trachypogonetum*. In other units the root system is less extensive, so that the species is counted as a scleromorphic hemixerophyte. The size of the root system and therefore the hydrotype depends upon the water economy of the environment.

The habit is always the same: a stoloniferous tussock, from which new individuals arise. Is it accidental that this growth form, characteristic of moving sandy substrates, also occurs on this rather bare sandy soil?

In contrast to most of the other tussock forming species, *Mesosetum loliiforme* has the transition from shoots to roots right at the surface. Hence the species is Vs and hemicryptophyte.

Miconia ciliata

This species was dug up both in the *Comolia* variant of *Clusia-Scleria* scrub on wet white sand, and in a bush on sandy clay loam, in a vegetation belonging to the *Schizachyrio-Rhynchosporetum mitracarpetosum*. In both environments there were only horizontal roots in the sod layer and within the litter area. The number and length of the roots (about 70 cm) were also similar.

The shrubs were taller on the sandy loam than on the white sand, 1.30 m and 0.50 m respectively. The difference must be correlated with the nutrition in the two soil types.

Myrosma cannifolia

Myrosma cannifolia was found only after fire on the Lobin savanna. The species was not in evidence either during the dry season or the long rainy season.

Oxypetalum capitatum

Oxypetalum capitatum is present only during the short wet and short dry seasons.

The root system consists of very many horizontal roots in the upper 5 cm, which become 30 to 40 cm long. With this extensive superficial root system the species should be able to benefit from every rain shower.

On the basis of the large number of roots, the species is counted as a euxerophyte. The leaf is mesomorphic. *Oxypetalum capitatum* is therefore a mesomorphic euxerophyte.

Panicum micranthum, see Table 1.

The method of rooting is discussed in Ch. III.3.6 in correlation with habitat.

Paspalum pulchellum, see Table 1

The method of rooting is discussed in Ch. III.3.6 in correlation with habitat.

Protium heptaphyllum is common only in the *Ternstroemia-Matayba* scrub, *Humiria* variant, of all the units of vegetation studied in this investigation. No specimen was dug up in this unit of vegetation, but a study was made in a bush on sandy clay loam, in a vegetation belonging to the *Schizachyrio-Rhynchosporetum mitracarpetosum*. The primary root of this 2 m tall shrub bends horizontally at a depth of 20 cm, while a thin lateral root penetrates to 1.70 m. There are further lateral roots in the sod layer, of which one was followed to the end. It bend downwards at 2 m from its origin, and reached 2.40 m below the surface. The roots remain within the litter area.

On the basis of these facts we may suppose that the root system of this species in the *Ternstroemia-Matayba* scrub will have long horizontal lateral roots within the litter area. The root tips will certainly reach below the sod layer.

Retiniphyllum schomburgkii, see Table 2 and Ch. III.3.9

The roots are exclusively in the litter layer. The tips have a coral-like appearance, indicative of mycorrhiza. The length and number of the roots vary according to environment. In dry habitats there are more and longer roots (3 m), and the shrubs become taller (1.50 m) than in wet environments, where the roots reach 1 m in length and the shrub is 1 m tall. The roots are branched repeatedly.

In the *Ternstroemia-Matayba* scrub, *Humiria* variant, *Retiniphyllum schomburgkii* belongs to the scleromorphic euxerophytes, in the *Clusia-Scleria* scrub, *Comolia* variant, to the scleromorphic hemixerophytes.

Rhynchospora barbata var. *barbata*, see Table 3

The method of rooting is discussed in Ch. III.3.9.

Rhynchospora barbata, var. *glabra*, see Table 1

The method of rooting is discussed in Ch. III.3.6 in connection with the habitat. With increasing importance of rain for the water supply the spread of the root system increases.

Rhynchospora graminea, see Table 1

The method of rooting is discussed in Ch. III.3.6 in connection with the water regime of the soil.

Schizachyrium riedelii, see Table 3

For a description of the root system see Ch. III.3.11.1.

When no fires occur, a few flowering stems survive the long dry season. With the advent of new rainfall these stems, then prostrate, sprout from the nodes. It was not ascertained whether these new shoots also take root.

Sipanea pratensis

The method of rooting in the various environments is described in Ch. III.3.11.1.

Sipanea pratensis does not lose all its leaves during the long dry season. It belongs to the incompletely deciduous category of seasonal aspects. This is remarkable since the leaf is mesomorphic, and the root system is not extremely large. In individuals which are not destroyed by fires, new stems arise after the long dry season on the woody old stem bases. In spite of the seasonal rhythm W*D*wd, it is a real half-shrub. The slight coverage in the *Polycarpaeo-Trachypogonetum* is probably due to the diminished light intensity under the tall *Trachypogon* tussocks.

Ternstroemia punctata, see Table 2

In Ch. III.3.9 the root systems from different habitats are described, and the factors influencing the root system are discussed. The principal ones are water surplus, drought and probably high temperatures. The water surplus in the wet habitat forces the roots into the most superficial layers.

Drought in the habitat is correlated with a larger root system. High temperatures force the roots down to the level of 20 to 30 cm below the surface or if this is not possible, restrict them to the litter area.

In dry white sand shrubs of *Ternstroemia* may be isolated.

The extensive root system in dry white sand is a reason for counting the species in the *Ternstroemia-Matayba* scrub to the euxerophytes; in the *Clusia-Scleria* scrub, *Ternstroemia punctata* belongs to the hemixerophytes.

Tetracera asperula

In the *Mesoseto-Trachypogonetum* the method of rooting may be described as R. generalized form and distribution type C. The roots become 6 m long horizontally, while the greatest depth depends on the ground water. In the specimen that was dug up it was 1.20 m.

In the *Clusia-Scleria* scrub *Comolia* variant, the root type is specialized and the distribution A. The greatest length is 3 m, while the roots do not go deeper than 10 cm. Here the ground water also limits the depth of roots.

Horizontal roots produce many small laterals.

In *Mesoseto-Trachypogonetum*, *Tetracera asperula* is a scleromorphic euxerophyte, in the wet habitat a scleromorphic hemixerophyte. On the basis of similarity in water economy of the soil it is assumed that the species behaves in the *Ternstroemia-Matayba* scrub as it does in the *Mesoseto-Trachypogonetum*, and in the *Clusia-Scleria* scrub as in the *Xyrido-Paspaletum*.

Tibouchina aspera, see Fig. 16.

The different methods of rooting in the various vegetation units are discussed in Ch. III.3.11.1. There is a clear correlation with the water economy of the soil.

The extent of the root system in the *Mesoseto-Trachypogonetum* is a reason for calling *Tibouchina* a scleromorphic euxerophyte.

The height of the shrubs, which burn annually, is mostly 30 to 50 cm. In places where the fire misses a year, some specimens become 1.50 m tall. The two large individuals which were dug up both have large root systems compared with smaller individuals. On the basis of the available information it cannot be decided whether this is accidental or whether a causal relationship exists.

Trachypogon plumosus, see Tables 1 and 3

The root systems in various vegetation units are described in Ch. III.3.6 and 3.11.1, and correlated with the various habitats. There is a clear relationship between water economy of the soil and method of rooting. In contrast to most grasses of these units, *Trachypogon plumosus* does not tolerate water surplus.

Individuals which were not burned produced green leaves from the tips of old culms. The tussock appears dry and not very vigorous; new sprouts appear from below the surface. *Trachypogon* makes the impression of benefiting from drought and fires.

Zornia diphylla

Zornia diphylla appears in the best condition after the long dry season. One gathers the impression, that the species benefits from the total clearing of the vegetation by fires. Later in the growing season, when the vegetation has regenerated and closed in over the lower species, the vitality of *Zornia* declines.

CHAPTER IX

CONCLUSION

Much has been written about the origin and permanence of savannas. BEARD (1953) and VAN DONSELAAR (1965) offer detailed discussions of the various conditions which may be responsible.

On the basis of correlations which were made in the preceding chapters, between characteristics of species and vegetation units on the one hand and the environment on the other hand, the following assertions may be made as a contribution towards solving the problems of savannas.

Relationships between trees and tall shrubs and the environment

1) The roots of trees and shrubs (dicotyledons in general) will not tolerate an alternation of water surplus and desiccation. They avoid the layers which are saturated with water. This means that in most cases the ground water limits the growth in depth.

The growth of trees is possible even on permanently saturated soils. BEARD (1953) 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 only trees which seem able to tolerate such conditions (alternation of saturation and drought) are the few oddly gnarled species found in savannas, where as the xeromorphic herbs, particularly the bunch grasses, seem to be well adapted to the site". The supposition that most trees will not tolerate this alternation, appears to be confirmed by the behaviour of roots of the woody species. Only the supposition concerning the "gnarled trees" as a generalization appears incorrect. Of the two species with such a growth form (*Curatella americana* and *Byrsonima crassifolia*) the root system was investigated. The occurrence of both species is again limited by ground water. *Curatella* appears to have a slightly better tolerance for water surplus. In habitats where the ground water reaches the surface the roots ran through the upper decimeter of the soil.

It seems probable that occurrence in a water saturated soil is only possible when there is a special system of aeration to supply the roots with oxygen. It may be readily assumed that roots with such a system are not well protected against drying out. This explains why roots will tolerate only one or the other of these conditions. Where periods of desiccated soil occur, roots with aeration systems are lacking and other roots are limited in their distribution in the soil by ground water.

2) All species which are studied, that occur in savanna vegetation are adapted to drought.

The root system consists of few to many very long superficial roots, practically without ramification and with a thick bark. Although this was not proved, it seems probable that such roots may form new young functional rootlets rapidly, which perish again without damage to the plant (see citation of KUTSCHERA, 1960, in Ch. III.1.7). Only a portion of the species has a generally insignificant primary root which penetrates to depth within reach of ground water.

The leaves are without exception scleromorphic and most species have a glossy upper surface. In the dry environment (those with excessive drainage) leaves are generally smaller.

3) All tall woody species retain the leaves during the long dry season without exception. Some are at most incompletely deciduous. The long dry season usually consists of less than two months with precipitation below 60 mm. From the campos in Brazil, with 3 to 5 months precipitation below 60 mm, no complete deciduousness has been reported either (RAWITSCHER, 1952; HUECK, 1959). Nor do the

savanna trees lose the leaves in the Rupununi savannas of British Guiana, where the dry season consists of at least five months with less than 60 mm precipitation (LOXTON, 1958).

The terminal buds of many species are killed by drought, so that the lower buds will develop.

4) In habitats with excessive drainage, which exaggerates the drought, the shrubs are lower but still evergreen. It seems justified to suppose that shrubs will remain low even on other soil types in areas that are climatically drier.

5) Greater rooting space, at least on white sandy soil, is accompanied by greater height of shrubs.

6) Annual growth is probably correlated with the hydrology of the soil.

7) Fires will destroy rejuvenation buds up to 2 to 4 m above ground level. Many plants which remain within this zone, will sprout from below the surface after a fire. Above 2 to 4 m the influence is less, so that buds may stay alive above this height.

8) Seedlings of trees and tall shrubs were not found in the open savanna during ¾ of a year of this investigation. They only occurred in bushes surrounded by the open savanna vegetation.

Relationships of tussock forming *Gramineae* and *Cyperaceae* to the environment

1) The behaviour patterns of root systems in relation to water surplus and drought are different for different species. The roots of savanna species will not tolerate permanent or long lasting water surplus. They limit themselves to layers in which this surplus is of short duration. The tolerance for the duration of the excess differs according to species. A long period of drought is also fatal for the roots. The critical length of the dry period also differs according to species.

2) All species are adapted to drought by means of a resting stage. The aerial portions dry out completely. After the dry season they sprout, several centimeters below the surface.

3) All species have additional adaptations to drought, by means of which dry periods during the growing season may be survived (the short dry season may be considered as such). They all have scleromorphic leaves, which are pubescent in many species. The leaves are able to reduce transpiration by rolling up or folding along the mid-rib.

The tussock form itself has the same effect.

4) Grasses and *Cyperaceae* are able to regenerate quickly after being damaged, by forming new shoots and roots.

5) Fires which almost always occur during the resting stage have therefore no damaging effect. On the contrary, many species appear to benefit from fires. The formation of new shoots is stimulated and many species flower as a reaction to fires.

SWEENEY (1956) reviews the literature concerning the influence of fire on the soil. The following may be cited: the burning of dried plants releases soluble Ca, P and K, which temporarily increase the amount of mineral nutrients in the soil. They are quickly leached out (Daubenmire). Fires cause a slight pH increase. This stimulates microbial activity in the soil, resulting in a temporarily increased nitrate content.

PILGER (1900) and LEBRUN (1937) also ascribe to this factor the "springtime effect" following fires in the savanna.

6) Seedlings are encountered regularly.

Relationships between other herbs and half-shrubs and the environment

1) For the reactions of roots to drought and water excess, the reasoning used for trees and shrubs is also valid.

2) Herbaceous stems are not drought resistant. They die off during the long dry season.

The stems of many species are woody towards the base, even in species that are not counted as half-shrubs.

Drought during the growing season (including the short dry season) is probably difficult to survive, in view of the fact that there are more species with herbaceous stems in those habitats, where the water economy makes drought during the growing season less effective.

3) Therophytes are limited as to season and habitat in such a way that there is the least chance of exposure to drought.

Environmental types and their potential vegetation

a) In an environment with water tables permanently at the surface one encounters shrubs and trees as well as grasses and *Cyperaceae*. Half-shrubs are lacking. This type of vegetation cannot be called savanna.

b) An environment in which the ground water is at the surface for a part of the year, while the upper soil layers dry out during the rest of the year, is unsuited for trees and tall shrubs, as well as smaller dicotyledons. If there are any shrubs at all, they are low and their roots are limited to the upper centimeters of soil. As a result the roots are exposed to drought and high temperatures during the long dry season.

On heavier soils, *Curatella americana* has the greatest tolerance for water surplus. A few species will tolerate some surplus on white sand.

Gramineae and *Cyperaceae* are well adapted to this environment.

c) In habitats where rainwater disappears quickly from the root layers even in the rainy season, due to excessive drainage, only low shrubs of a few species can occur.

Grasses and *Cyperaceae* are poorly represented.

d) In all habitats which are intermediate between these extremes, with alternating periods of desiccation and wetting of the soil, trees and shrubs as well as grasses and *Cyperaceae* may occur.

The species composition of the *Gramineae* and *Cyperaceae* depends upon the relative duration of the dry and wet conditions. The height of the herbaceous vegetation is correlated with the depth of the moist soil layer, in other words with the rooting volume.

Where trees and shrubs reduce the light intensity, grasses and *Cyperaceae* disappear. Non-tussock forming herbs and half-shrubs have better opportunity, probably due to the reduced insolation and transpiration.

e) Habitats with annual fires are unsuited for tree and shrub growth, while grasses and *Cyperaceae* thrive. Trees and tall shrubs occur only where the water economy of the soil is favourable enough to allow for rapid growth of the species to a level above the fire zone.

Most trees and shrubs are able to regenerate from a xylopodium below the surface, following the destruction of aerial parts.

f) In a habitat which is on the borderline of the ecological range, either on the wet or dry side, the vegetation will be destroyed during extreme years. On the wet extreme both abnormally wet and abnormally dry years are critical, for the dry extreme only the abnormally dry years.

Regeneration of the vegetation is then only possible by seedlings.

Possible succession following the omission of annual fires in savannas which are not edaphically controlled (d), or following the destruction of woody vegetation

The survival chances of seedlings of trees and shrubs are slight in all environments which feature a severe dry period. The establishment of a tree or shrub is a rare event.

A tree or shrub once established, improves the environment. The crown layer reduces insolation and evaporation, the litter layer improves the soil. The result is that new species can establish themselves under tree and shrub canopies, both herbs and woody species, while the heliophilous grasses and *Cyperaceae* decline. A bush is formed. A closed scrub may form as a result of the fusion of bushes. As long as the environment remains marginal for the survival of this vegetation, an extreme year may kill off the vegetation (see f). A bare soil results, on which the process is repeated. A single fire does not always have a destructive influence on woody vegetation; many species regenerate from below the surface.

In this way the occurrence of moeri-bushes (*Ternstroemia-Matayba* scrub) may be explained without fire.

With these data it is possible to explain the existence of many savannas on an ecological basis. The existence of a definite savanna environment is in most cases a problem that lies in the realm of soil science.

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SUMMARY

From July 1958 to May 1959 an investigation was carried out of the relation between physiognomic characteristics of the vegetation and the habitat on some savannas in the vicinity of Zanderij, Surinam. Root systems, structure, periodicity and characteristics of the leaves were considered, both of the species separately and of the vegetation types.

Nine vegetation types were studied which were described floristically by Heyligers (1963) and Van Donselaar (1965). The vegetation types differ in structure. The available types of structure are: low and sparse vegetation of tussocks of grasses and sedges; dense vegetation of both low and high tussocks of grasses and sedges; high and closed vegetation of tussocks of grasses and sedges, with or without a continuous but sparse tree layer; bushes with a more or less closed canopy. In the herb layers, apart from the tussocks, some perennial herbs and therophytes, rather many half-shrubs and few shrubs occur.

In the area of the investigation the climate shows a long rainy season, a long dry season, a short rainy season and a short dry season.

The different vegetation types occupy soil types differing in texture and hydrology.

It appears that principally the following factors influence the characteristics of the vegetations mentioned: the alternation of rainy and dry periods in combination with the hydrology of the soil; fires; tree layer with more or less closed canopy; layer of litter.

The hydrology of all soil types under consideration is characterised by the alternation of the moist and the bone-dry condition of the upper layers. The moisture content of the upper layers is determined by the rain water taken in by the soil, whether or not in combination with the ground water; the upper level of the latter varies according to the seasons. The run-off and the percolation velocity of the rain water strongly influence the hydrology.

The growing of the roots is determined by two mutually opposite factors: desiccation and saturation with water of the soil. In general the roots of the monocotyledons in the studied vegetation types tolerate the water-saturated condition of the soil, but they are not able to protect themselves against the influence of extended drought. The roots of the dicotyledons, on the other hand, do not tolerate a waterlogged soil, but they can withstand extended drought, probably because their corky bark protects them. There are few exceptions, among which the common grass *Trachypogon plumosus* that behaves just like a dicotyledon species.

If the water supply comes from beneath, the root systems of the monocotyledons are narrow and penetrate deeply. If the rain water is the main water source, the root systems spread, both of monocotyledons and dicotyledons. The quicker the rain water penetrates into the soil and sinks down, the larger the horizontal dimensions of the root systems are.

In consequence of the demands of the roots and the hydrology of the soil the roots have a certain soil volume at their disposal. This volume may be different for monocotyledons and dicotyledons in the same soil. In soils with a high water table during a part of the year the monocotyledons have narrow and deeply penetrating root systems, whereas those of the dicotyledons are superficial. In soils with a deep water table and above it a layer that is dry for a long time, both monocotyledons and dicotyledons develop their root systems in the uppermost layer which is wetted by the rain water. A few dicotyledon species have a primary root reaching down to the water table, where oxygen becomes the limiting factor.

Vegetation structure above ground level is related to the available rooting volume. If the rooting volume is larger, the dimensions of the aerial parts are larger too. Then there are more trees and shrubs, the differentiation in layers is greater and the dominating grass layer is higher.

It is hard to determine the role of the nutrient content, for this factor and the hydrology of the various soil types show parallel differences, so that their influence on the vegetation can not be distinguished separately. On white sand many species have a root system that is large in comparison with the aerial parts (more euxerophytes than on the other soil types).

The distance between the tussocks is correlated with root competition, except on white-sandy soils. If the root systems are narrow and penetrate deeply, the

tussocks stand close together, but if the root systems spread in the superficial layers, the bases of the tussocks stand far apart. On white sand, the vegetation is thin, though the layer of roots is not closed.

The dry seasons are the cause of a resting period for all species that are not completely woody. Grasses, sedges and perennial forbs survive only underground. Half-shrubs persist with their short, woody stem bases. All completely woody species, however, are evergreen. Only in a more favourable habitat, under a (thin) canopy, or on white sand with ground water available for long periods, non-woody species occur that function throughout the long dry season. Therophytes are present in all vegetation types, but they prefer habitats where the chance of drying up during the growing season is least, i.e. under a canopy or on white sand with ground water available during the greater part of the year.

The annual fires destroy completely the aerial dry parts of the plants. Grasses and sedges do not suffer from this, for the fire occurs during their resting period. On the contrary, they seem to profit by it. The aerial parts of half-shrubs are destroyed, but in the soil, a few centimeters below the surface, rejuvenation buds survive on a xylopodium. Shrubs and trees also may have a thickened xylopodium. Such a xylopodium is developed as a result of the repeated forming of new stems after the old ones have been burned. In many cases shrubs have several stems as a result of the fires.

The fire does not kill all rejuvenation buds above 2 to 4 m, so that part of the buds of higher trees and shrubs may sprout after the fire. As a result, trees and shrubs are found only in places where the fire has held off for one or several years, or where a period between two subsequent annual fires was long enough for them to grow above the upper limit of the dangerous zone. This last possibility is realised in the vegetation unit with the most favourable hydrology and consequently the largest available rooting volume, i.e. the *Polycarpaeo-Trachypogonetum*. Trees and high shrubs are observed in all vegetation types, except in those on wet white sand, where the small available rooting volume and the low nutrient content are probably the limiting factors.

Even under a thin canopy transpiration may be less in consequence of reduced insolation. Accordingly, characteristics indicating less severe drought are more frequently found here, and the species with these characteristics have a higher degree of cover than elsewhere. There occur more forbs, in particular therophytes (indicating more favourable conditions during the growing season), more species with mesomorphic and hygromorphic leaves and more species that function more or less normally during the long dry season.

The decreased amount of light diminishes the role of the grasses.

A layer of litter improves the soil: the organic content is higher, evaporation may be less; the temperature of the underlying soil may be lower. As a result, places with a layer of litter are occupied by many shrub species of which the roots restrict themselves to the litter-area.

The leaves are scleromorphic as a rule. Species with mesomorphic or hygromorphic leaves are found only in habitats with a continuous water supply during the growing period (wet white sand) or with less evaporation under a canopy.

In tussocks with basal leaves the leaf size is related to the height of the stratum. The height is related to the rooting volume. Also the leaves of non-tussock forming species in the herb layers are larger if the layer is higher. Therophytes have small leaves (lepto- and nanophyll). This can be considered in connection with the absence of sclerenchyma. Trees and shrubs usually are micro- and mesophyll. As a rule the size of the leaves is smaller in vegetation types on white sand.

Most woody species have leaves with a shiny upper surface, but most other species have more or less hairy leaves.

On the basis of these findings the following brief interpretation can be given of the relation between the different vegetation types and their habitats:

Panicetum stenodoidis. Silty clay; ground water in the surface during the long rainy season; cracks during the long dry season, so that at the beginning of the rains the soil is wetted quickly and down to a rather great depth. Consequently the rooting volume is comparatively large. The root systems of the monocotyledons are narrow and penetrate deeply, the plants are standing close together and the vegetation is moderately high. Few dicotyledons are present; their roots run very superficially. The annual fire destroys completely the desiccated aerial part of the vegetation. Only a few specimens of treelike *Curatella americana* were found.

Schizachyrio-Rhynchosporetum barbatae. Sandy clay loam; influence of the ground water up to 40 cm below the surface at most; poor percolation; strong run-off; the rain water does not wet the soil further down than 20 to 30 cm. Consequently there is a layer that is dry permanently or at least so for a long time between the ascending capillary ground water and the water in the top layer. The available rooting volume is small for both dicotyledons and monocotyledons; the vegetation is low. The roots spread beyond the projection of the aerial parts (rain water the main water source); above the surface the vegetation is not closed. Few dicotyledons have a primary root penetrating down to the zone influenced by the ground water, where the saturation of the soil with water is restrictive. Trees and high shrubs are rare. The annual fire destroys the vegetation up to 3 m above the surface. Probably trees and shrubs are present only on places where the fire held of for some time.

Polycarpaeo-Trachypogonetum. Loamy sand; water table not higher than 80 cm below the surface; no run-off; large available rooting volume; high grass vegetation, with or without a thin tree layer consisting of *Curatella americana.* All rain water is taken up quickly; the roots spread strongly; at their bases the tussocks stand far apart. In spite of the fierce annual fires in the high and dry tussocks, there may be a tree layer. Probably *Curatella* is able to outgrow the influence between two of them on this soil type with its relatively favourable hydrologic conditions. Under the tree layer conditions are better; there occur more therophytes and other forbs; more non-woody species without a resting period; more species with mesomorphic and hygromorphic leaves.

In the pure white sandy soils the vegetation is not closed, neither above nor below the surface. Quick percolation and ample aeration make the drought extremely effective. It is supposed that because of this situation seedlings have so little chance for survival that the vegetation remains open.

Mesoseto-Trachypogonetum. Dry white sand. The roots spread widely, both of monocotyledons and dicotyledons. Only few dicotyledon roots reach down to the layer influenced by the ground water. The root systems are completely arranged so as to catch the water of every shower that may occur occasionally even during the long dry season. In this connection it may be considered that relatively many species are completely woody (dwarf-shrubs) and function normally during the long dry season. The vegetation consists of low and high tussocks and here and there a low shrub.

Xyrido-Paspaletum pulchelli. Wet white sand; during the greater part of the year the ground water reaches the surface, but during the long dry season the upper decimeters are bone-dry. The alternation of long lasting saturation with water and periodical desiccation of the soil results in a small available rooting volume, also for the monocotyledons. Most dicotyledons have roots that run very near to the surface so that they are subject to extreme drought and high temperatures; the plants remain low.

Ternstroemia-Matayba bushes and *Clusia-Scleria bushes.* The shrubs of some species are able to establish themselves in open, purely sandy soil. They produce a layer of litter that improves the soil. Shrubs of other species that settle themselves now restrict their root systems to the area of the litter layer. The roots of some species are restricted to the area of the litter layer in wet sand, but in dry sand they go beyond this area at a deeper level. This may be caused by the high temperatures of the upper decimeters.

Because of the decreased light intensity underneath the canopy the grasses and sedges are limited.

On white sands only the vegetations of the *Mesoseto-Trachypogonetum* burn every year. The other vegetation types often escape the fires because they are either too thin or do not dry up in the long dry season.

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