THE SAVANNA ECOSYSTEM

An analysis of plant, soil and water relations in the northern Rupununi savannas of British Guiana as an aid to understanding their nature and origin.

by

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'Since it is clear that whether grasses and other herbaceous plants occupy an area alone or share it with trees and shrubs depends on the soil moisture regime it is necessary to go further than merely to obtain a useful and rational climatic classification. It is necessary to develop more fully the water balance approach, to determine the actual influence of soil moisture on climax vegetation formations and to make maps of these active controls of vegetation distribution.'

C.W. Thornthwaite & J.R. Mather, The Water Balance, 1955, p. 75.

TABLE OF CONTENTS

LIST OF APPENDICES

LIST OF FIGURES

LIST OF MAPS

LIST OF PLATES

LIST OF TABLES

PREFACE

McGill University Savanna Research Project

In May 1962 the McGill University Savanna Research Project was established and has been conducted since that date in the Department of Geography, McGill University and in the savannas of the Rupununi District, British Guiana and the Territorio do Rio Branco, Brazil.

It is generally recognised that although a very wide range of theory has been propounded to explain the nature and origin of savannas, no one has yet brought forward a single convincing viewpoint which has met with universal acceptance. One reason for this is that the majority of theories extant are based upon inadequate field data with almost a total lack of experimental evidence. The McGill University Savanna Research Project was set up for the purpose of initiating an experimental and observational field programme which it was hoped would shed light upon the ecological relations of the savanna, and would ultimately enable an explanation to be made of the nature and distribution of the savanna vegetation of the region.

Methodology of the Project

Many geographers and ecologists and other scientists concerned with landscape have put forward the view that such partial concepts as climate, vegetation, soil, environment and even landscape, though very useful for analytical purposes,are not especially conducive to synthetic thinking or integration. Their use frequently necessitates arbitrary and often artificial boundaries and definitions. A botanist, pedologist or geologist tends to seek solutions to his problems within the range of phenomena with which he normally deals, when a more adequate answer may be in a consideration of one or more related fields, or alternatively, he may borrow from fields with which he is less familiar because of his specialisation, and take the risk of drawing unwarranted conclusions.

Fundamental to the approach, therefore, of the McGill University Savanna Research Project has been the ecosystem concept. Such an holistic approach to the interpretation of landscape and environment is considered to provide a suitable framework for an interdisciplinary investigation of the savanna. In the sense in which the term 'interdisciplinary' is used here, it does not signify simply the idea of a number of approaches or disciplines being used in an attempt to investigate a single problem. The mere employment of a botanist, geologist or geomorphologist, and so forth, on the one problem of the origin of the savannas would constitute only a multidisciplinary approach. An interdisciplinary approach, on the other hand, is held to be one in which the relations between the various disciplines employed are of equal importance with substantive results obtained and are themselves the subject of investigation.

To this end, the present writer, during the period September 1962 - August 1964 has been employed as a research assistant by the Project, and has worked both in Montreal and British Guiana with a number of scientists from differing disciplines. The present thesis is a product of this work and a contribution to the Project investigations.

(Condensed from McGill University Savanna Research Project, Progress Report, 1964).

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ABSTRACT

Numerous theories have in the past been proposed to explain the nature and origin of savannas. In the northern Rupununi of British Guiana, ecosystematic studies indicate that the savanna vegetation, which is xeromorphically adapted, is associated with an ecoclimate of alternating wetness and drought, although in some areas, deep rooted woody species are able to tap perennial soil moisture supplies.

The present ecoclimate is a product of numerous interacting factors, principally: a seasonal rainfall regime, widely inferior soil conditions and an imbalanced regional drainage system, which exist within a region of low altitude and relief.

The origin of the present savanna is probably due to climatic fluctuations that have taken place during the Quaternary, which have induced, within the physical environment described, an ecoclimate favourable to the extension of savanna, possibly with secondary assistance from man in recent times, into an area that previously supported forest.

PART ONE: INTRODUCTION

CHAPTER 1

THE NATURE OF THE PROBLEM

(a) What is the Ecosystem?

In the words of J.S. Rowe an ecosystem is :-

> 'A topographic unit, a volume of land and air plus organic contents extended areally over a particular part of the earth's surface for a certain time.'
>
> J.S. Rowe, 1961, p. 422.

Since the inception of the term 'ecosystem' by Tansley in 1935, and even prior to this, when comparable thinking among earlier ecologists had led to the use of such terms as 'microcosm' (Forbes, 1887.) and 'biome' (Clements, 1916.) the concept of the 'ecosystem' has been an integral part of ecological thinking. Its value as a unit of study lies principally in the common emphasis it places on plants and the physical environment of the soil, air and water surrounding them, providing thereby a firm basis for an interpretation of the relations between them.

The ecosystem represents an integrated, volumetric unit of study and is distinct, for example, from the Clementian 'plant association' (Clements, 1905.) or the Curtisian 'plant community' (Curtis, 1959.), which refer to discrete phenomena, namely: plant species, growing in space within a given area. McMillan, following the latter concepts, emphasizes that :-

> 'Ecology, first and foremost, must deal with all individuals and with the problems relative to the position of those individuals in a particular habitat. Secondly ecology must deal with the occurrence of all individuals in populations ... and with the occurrence of individuals in communities.'
>
> C. McMillan, 1956, p. 602.

However, such implied rejection of the ecosystem as a primary unit of study by plant ecologists, who emphasize in the first instance floristic compositional studies, is based on a differing, and no less valuable, conception of the practical aims of plant ecology. At the same time the theoretical basis of the ecosystematic concept does not appear to have been questioned by such writers.

A second implication of the concept, which is of significance to the present thesis, is the decreased emphasis placed by many ecologists on marginal delimitation of the unit of study, and the resultant emphasis placed on establishing the nature of its core area. Rowe states :-

> 'To some people this subjectivity of boundary delineation is a stumbling block to acceptance of the ecosystem as an object of study, yet it need not be. A precise analogy is with soils, which have been made objects of study despite the fact that their boundaries are fixed only by definition. Obviously study can be focussed on geographic 'cores' though boundaries around them are elastic.'
>
> J.S. Rowe, 1961, p. 422.

In this case it is far from being a stumbling block; indeed, only by admission of such a limitation, can progress be made towards unravelling the complexity of the <u>internal</u> physical relations within the savanna.

For where an ultimate interpretation of the savanna in relation to the tropical forest is attempted, i.e., the external relations, the nature of the two extremes must be known before the dynamics of the margin can be understood. This is especially the case with the Rupununi savannas, where the nature of the savanna margin is dynamic and takes the form of a very abrupt change from savanna to forest, which is demonstrably a condition resulting from fire. Yet fire is not necessarily postulated as the pre-eminent control within the savanna as a whole. Beard, speaking of the savannas of northern tropical America, for example, asserts that :-

> 'The savannas do not ... depend on fire for their maintenance, and are an edaphic climax.'
>
> J.S. Beard, 1953, p. 203.

Thus, although Beard's assertion is not necessarily acceptable to all, its validity can be more easily assessed by treating the savanna, which is by definition a physiognomic unit, both in the light of a concept which has been developed by plant ecologists, and one which emphasizes the nature of the core area.

Equally relevant in this context is the fact that as yet geography has not evolved analytical techniques capable of treating biogeographical problems with the precision achieved by the plant ecologist. The approach of geographers to vegetation studies has remained more extensive and regional in character (see Cole, 1960, 1963) with the result that at this stage the biogeographer, at least to start with, must rely heavily on ecological techniques and methodology. Ultimately, of course, the aim of the geographer remains the understanding of the larger region, but he can valuably make intensive micro-regional or habitat studies a basis for subsequent regional interpretation. For this reason primarily the ecosystem is considered a valuable starting point for gaining a regional understanding of the northern Rupununi savannas.

(b) Definition of Savanna

The term 'savanna' appears to have been first mentioned in print by Oviedo in 1535, and is considered to be of Amerindian origin.

> 'This name 'savanna' is applied to land which is without trees, but with much grass either tall or short.'
>
> G.F. de Oviedo, translated by J.S. Beard, 1953, p. 150.

Numerous more refined definitions have subsequently been put forward, notably by Lanjouw (1936) and Robyns (1936). A more recent and widely cited definition is that of J.S. Beard :-

> 'Savannas are communities in tropical America comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present.'
>
> J.S. Beard, 1953, p. 189.

Here as in the definition of Oviedo, the dominance of the herb layer is stressed. Such, however, is unacceptable to some writers. Aubréville (1961), referring to the 'campo cerrado' of Brazil, which he describes as a wooded savanna, clearly states :-

> 'Dans les campos cerrados la strate arborée et arbustive est physionomiquement évidemment la plus importante par

son degré de recouvrement, sa densité et sa position structurale dominante.'

A. Aubréville, 1961, p. 102.

Similarly a number of writers in Surinam (Lanjouw, 1936; Lindeman, 1953, 1959; Heyligers, 1963) have used terms such as 'savanna forest' and 'savanna wood' to refer to formations which clearly fall outside Beard's definition.

In the face of such difference of opinion it is unwise at present to commit oneself too closely to any definition. The existing disagreements seem to reflect the fact that the savanna ecosystem is insufficiently understood to allow a widely acceptable genetic definition to be put forward, which, based on a deeper understanding of the general causes and origins of so-called savannas, would provide a firmer foundation for classifying any marginal formations.

Whether a savanna is a natural formation, and how far it is in equilibrium with adjacent formations, are questions therefore that must be asked, and answered more thoroughly than in the past, and these necessarily involve the question of the time element, for which valuable evidence is contained in disciplines other than ecology. The evolution of landforms and drainage patterns, and the evidence found in soil profiles can provide useful data on what has happened in the past, when the less durable floral evidence has, for the most part, been removed*.

Thus by widening the framework of the present study beyond, for example, the limits of the Clementian concept of the 'plant association' (Clements, 1905) where the primary focus is on the vegetation itself,

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* Pollen analysis is an exception to this, and some work has been undertaken in tropical South America (van der Hammen, 1961, 1963, 1964).

and using an ecological approach in its most literal sense, some headway can be made towards understanding the savanna environment, and hence defining it more accurately. Purely descriptive definition, based on physiognomic characteristics, therefore, must remain at this stage primarily an aid to further investigation of the savanna environment, and a definition such as that provided by Beard (1953) is a suitable starting point for this study.

(c) Earlier Treatments of the Savanna Environment

Numerous theories have been advanced in the past to explain the nature and origin of savannas. Four major directions of interpretative theorisation have appeared; they are related to climatic, pedologic, geomorphic and biotic influences or to a combination of these.

Climatic interpretations have generally stressed the importance of alternating wet and dry conditions during the year and have been advanced by Grisebach (1872), Schimper (1903), Bews (1929), Bouillenne (1930) and Troll (1956). Warming (1892) describes the joint influence of an alternating wet and dry climate in association with adverse soil conditions in the Lagoa Santa region of Brazil, although in a later paper (Warming, 1909) he stresses more strongly the climatic element. Myers (1936), writing of the Rupununi savannas, similarly emphasizes the alternating wetness and desiccation, but allies fire to this as a strongly modifying factor in the environment.

Pedologic interpretations have on the one hand stressed leaching and impoverishment of the soil as influential factors in the savanna environment. Pulle (1906) and Ijzerman (1931) in Dutch Guiana first postulated this view, which was later substantiated by Lanjouw (1936) and

Hardy (1945), although in the work of the latter two writers the secondary effect of fire, which operates more potently under inferior soil conditions, was emphasized.

Other pedologic interpretations have been put forward; Waibel (1948) attributes differences in vegetation in the Planalto Central of Brazil to differences in soil and ground water conditions; Bennett and Allison (1928) in Cuba relate impermeable subsoils to the occurrence of savanna through the effect they have on soil moisture relationships. Charter (1941) and Beard (1944, 1953) have reinforced this viewpoint and have gone a stage further by correlating such drainage impedance to a mature or senile stage in landscape evolution. Similarly, the pedologic - geomorphic approach has been stressed by Cole (1960, 1963), who has associated drainage impedance and flat senile land surfaces with savanna environments in parts of both the Old and New Worlds.

Finally, a number of writers have emphasized the anthropic factor and the effect clearing, burning and cultivation of forest have had on the evolution of savanna; Phillips (1930), Stebbing (1937), Clayton (1961) accord such factors an important place in the degradation of forest to savanna in various parts of Africa, while in the New World, Christoffel (1939), Rawitscher (1948), Ferri (1955) and Parsons (1955) reached similar conclusions.

A very considerable diversity of opinion is represented in the preceding paragraphs; the situation however is neither as conflicting nor confusing as it might at first appear. Firstly, no writer has studied all savannas, and many of the theories evolved are based on investigations in very limited areas and make no claim to be applicable in general; it is thus quite conceivable that in one region fire may be the prime reason for the existence of a savanna, while elsewhere drainage impedance may outweigh it in importance.

Secondly, the tendency in the present review to categorise tidily the various 'factors' is a convenience but a denial of reality. Within the ecosystem all factors are interacting, and any given condition reached in the ecosystem is a result of not one, but many factors adjusting in relation to each other. Thus when a single factor is isolated as pre-eminent, its pre-eminence may be exaggerated, being only very slight and achievable only within precise limits imposed by other secondary factors.

A third confusion springs from the emphasis placed in the theorisation on regional rather than ecological factors. If the causal relations between the habitat and plant growth, i.e., in terms of soil nutrients or soil moisture, were emphasized more and the correlations between a region and its vegetation, i.e., in terms of climatic seasonality or stages of landscape evolution, were emphasized less, a clearer understanding of the origin of the savannas as a whole might emerge and genetic interpretation and definition become more satisfactory.

To this end, therefore, the aim of the present thesis is the investigation, initially in ecological terms and subsequently on a regional basis, of a savanna environment in British Guiana; prior to this the bearing of earlier theorisation on the present analysis will be assessed under the following headings :-

(i) Climatic theorisation; is there a savanna climate?

(ii) Anthropic theorisation; the role of man in the savanna.

(iii) Pedologic theorisation; based on chemical deficiency in the soil.

(iv) Theorisation based on drainage impedance in old landscapes.

(d) Climatic Theorisation: Is there a Savanna Climate?

Early attempts at an interpretative classification of world vegetation, such as that of Köppen (1923), have been based on climatic data. This method has yielded useful, but by no means complete correlations, so that today more precise criteria are being applied to the work. Savanna formations, however, have proved less susceptible to this treatment than other types of vegetation. Many workers, including Schimper (1903) and Miller (1961) have spoken definitely of a 'savanna climate'. Thornthwaite and Mather (1955) also, basing their work in temperate latitudes, insist on the existence of a 'grassland climate', although at the same time they stress the need for more refined parameters than the purely climatic, which would take account of the soil climate as well as the climate of the air.

Miller, in discussing climate and the geomorphic cycle, uses the phrase 'savanna climate' and states :-

> 'The savanna is characteristic of a hot climate with a wet season and a dry, the latter increasing in length with increasing latitude until the desert boundary is reached.'
>
> A.A. Miller, 1961, p. 194.

Clearly climatic influences operate strongly within the savanna ecosystem, but to place primary emphasis on the relation between climate and vegetation, implied in the phrases 'savanna climate' or 'grassland climate' is in the tropics surely misleading. Mohr and Van Baren, for example, when discussing the tropics, state :-

> 'The present overhead climate is a much overestimated factor, while the significance of the soil climate has generally been neglected, or at least under rated.'
>
> E.C.J. Mohr & F.A. Van Baren, 1959, p. 118.

In extra-tropical parts of the world there is more justification for linking climate with vegetation regions, through the effect climate has on soil types. The concept of soil zonality put forward by Glinka*, also evolved in temperate latitudes, illustrates a wide dependence of soils on climate. Such a premise is less valid in the tropics, where soils reflect less directly the effects of contemporary climate, and where parent materials and past climatic conditions exert a correspondingly greater influence. (Mohr & Van Baren, 1959).

Thus in tropical regions, where links between climate and soil are less precise, even more tenuous is the link between climate and vegetation, implied in the concept of the 'savanna climate'. The problem is partly one of terminology (for neither Thornthwaite & Mather (1955) nor Miller (1961) deny the importance of soil conditions), and it is felt that the use of the phrase 'savanna ecoclimate' would cover more adequately what is here being discussed.

The 'ecoclimate' (literally: climate of the plant habitat) can be considered to take account not only of the atmospheric climate, but also the soil climate, whose principal elements are soil water and soil air, and whose character depends as much on the physical nature of the soil itself as on climate. Thereby a balanced and more precise approach is made to the study of plant growth.

The concept has been used by Aubréville (1961) in his work in Brazil, where by focusing attention on the soil climate he demonstrates a more detailed and realistic interpretation of tropical vegetation in that country than has hitherto been achieved; it is hoped that its application in the Rupununi will achieve similar results.

(e) Anthropic Theorisation: The Role of Man in the Savanna

Anthropic influences have undoubtedly played a significant role in

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* K.D. Glinka, translated by C.F. Marbut, 1927.

determining the nature of contemporary vegetation in the Rupununi savannas. It is only necessary to spend a short time in the savanna during the dry season to become aware of the destruction brought about by fire, which each year results in vast acreages of grass being burnt out. Such treatment at the hand of rancher and Amerindian cannot fail to modify plant communities in the region.

The prime question, however, is whether anthropic influences in general can be considered more than a secondary factor in the creation and maintenance of savanna. Waddell (1963), finding no evidence to the contrary, concludes that anthropic influences in the Rupununi may well only be marginal to the basic problem of how the savanna first appeared :-

> 'Thus the activities of man may merely accelerate locally an overall phenomenon of the waxing and waning of major vegetation patterns through climatic fluctuations.'
>
> E.W. Waddell, 1963, p. 193.

At present it is difficult to assess positively the anthropic influence in the Rupununi in more than qualitative terms, but the problem is aided by physical studies, for as a greater understanding of the physical relations in the savanna is acquired, it becomes easier to isolate deviations from the physical pattern that can be considered as potential anthropic disturbances.

Two major anthropic influences in the Rupununi are fire and cultivation. The latter is largely a savanna margin activity, and it has been possible in the present ecosystematic studies to avoid areas where cultivation has had a detectable influence. This was desirable as the first object of the study was to isolate and comprehend the natural interactions of the ecosystem. In the case of fire this was not possible, because of its widespread occurrence. How is it viewed in the present investigation?

The dominant plant species in the savanna, both among trees and grasses, are clearly fire-adapted, and at the species level, fire is as important a control as, for example, water conditions, although from place to place the limitations imposed by each may vary. Yet fire today is less obviously a determinant of vegetation formations in the Rupununi, in so far as it is evident that fire does not prevent tree growth in the savanna and indeed rarely kills savanna trees. On the other hand, observations along the margin of the savanna suggest that forest species are prevented by fire from growing into the savanna. Can one thus consider that the savanna is maintained by fire? Such an assumption implies that, given freedom from fire, forest would widely regenerate into the savanna, a conclusion at present open to question, although it is later argued that such would be the case.

Whether fire or cultivation can be considered significant in the creation of the savanna is even less certain, although the persistence of forest 'bush islands' in the savanna appears to diminish the possibility. Also the general coincidence of the savanna edge with a definite relief margin suggests physical rather than anthropic controls, although this may only signify a limit beyond which man cannot operate as a causal factor.

Ultimately, one must conclude that it is impossible to assess directly the significance of the anthropic factor without recourse to more detailed study of the physical factors, past and present, which are involved. The present thesis attempts to go some way towards doing this.

(f) Pedologic Theorisation: Based on Chemical Deficiency in the Soil

In Dutch Guiana, Pulle (1906) first postulated an edaphic origin for savannas. Basing his work on the fact that many savanna soils in that country were porous and strongly leached, he concluded a strong relation existed between infertile soils and the existence of savanna. A similar infertility exists in the highly weathered, alluvial soils of the Rupununi savannas, and according to Loxton, Rutherford & Spector, who sampled extensively in the area :-

> 'The soils have been found very deficient in all nutrients important to plant growth.'
>
> R.F. Loxton, G.K. Rutherford & J. Spector, 1958, p. 21.

However, in contrast to conditions in the Rupununi, and to Pulle's observations in Dutch Guiana, large areas of infertile soils in British Guiana, belonging principally to the Berbice White Sand Formation, are found supporting forest as well as savanna vegetation, although the majority of the area is under forest. The author, on a journey from Mackenzie to Atkinson in the Demerara Basin, a distance of some 43 miles, encountered virtually continuous forest occurring on the white sandy soils. Similarly Richards (1952) at Moraballi Creek describes stands of Wallaba forest occurring on sandy soils, which are :-

'excessively porous, and probably like other podzols, strongly leached and deficient in plant nutrients.'

P.W. Richards, 1952, p. 242.

By comparison with the Rupununi, however, these areas, although equally infertile, have a more favourable rainfall regime which clearly facilitates forest growth and thus reduces the degree of marginality wherein the chemical controls could significantly operate*. It is thus possible that in the more critical conditions of the Rupununi, where both water conditions and soil fertility are unfavourable, that the soil nutrient status may have played a greater role in the evolution of the landscape. For although the significance of soil fertility under tropical forest conditions is diminished, by comparison with other ecosystems, by the operation of a closed nutrient cycle which permits an established forest to support itself almost wholly on its own decayed organic matter rather than drawing on soil mineral reserves, nevertheless, poor chemical conditions, by contributing to an already marginal environment a slight but significantly greater degree of marginality, could have an effect on the landscape outweighing their normal importance.

Ultimately, one could thus conceive of chemical conditions being a co-determinant of savanna, when they are allied to other detrimental conditions, either physical or biotic. Evidence from other parts of British Guiana indicates that by itself a low nutrient status is unlikely to prevent forest growth, although it will have an effect on the floristic character of the stand, and the rates of forest growth and regeneration (Richards, 1952).

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* The mean annual rainfall for Mackenzie is 2,289 mm, and that for St. Ignatius, Rupununi 1,621 mm.

Although as simple a relationship as that postulated originally by Pulle (1906) and Ijzerman (1931), therefore, is unacceptable in the Rupununi savannas, secondary soil chemical effects have undoubtedly influenced the area, although to a degree not yet ascertained*.

(g) Theorisation Based on Drainage Impedance in Old Landscapes

A number of writers have remarked on the frequent coincidence that exists between savanna grasslands and level or very gently undulating landscape surfaces, often with impeded drainage and leached and highly mature soils. Beard, referring to savannas in northern tropical America, states :-

> 'Savannas occur upon ill-drained country of little relief, most generally a senile landscape such as an old alluvial plain or a reduced upland.'
>
> J.S. Beard, 1953, p. 213.

Similarly in speaking of the savannas of Northern Rhodesia, Cole concludes :-

> 'The savanna woodlands and grasslands are virtually coincident with the old pediplains recognised by Dixey, Cahen and Lepersonne, and other leading geomorphologists.'
>
> M.M. Cole, 1963, p. 296.

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* Pulle (1938) later extended his early conclusions by considering fire as the agent of destruction of the forest, which because of inferior soil conditions, subsequently failed to regenerate; with this view Lanjouw (1936) and Hardy (1945) concurred. Thus the more recent statements substantiate the view that soil infertility must be allied to other unfavourable conditions before it can be considered a potentially significant factor.

These conclusions, although approached from a macro- rather than a micro-regional standpoint, have much in common with the ideas formulated in the present thesis. Suffice to say at present, therefore, that the material collected in the Rupununi, although varying in detail from other areas that have been described, nevertheless appears to substantiate the concept of a savanna existing on a level and inadequately drained surface.

CHAPTER 2

THE PHYSICAL ENVIRONMENT

(a) The Rio Branco - Rupununi Lowland

Astride the political boundary that separates British Guiana from Brazil, there lies a belt of savanna, some 21,000 square miles in area, which forms an island amid the surrounding tropical forest. The eastern portion of the savanna, falling within the territory of British Guiana, is known as the Rupununi savannas, or more simply the Rupununi, although administratively the latter term includes a much larger hinterland of tropical forest.

The savannas as a whole are at a general level of 100-160 metres, rising somewhat towards the marginal watersheds. They form a gently undulating plain of monotonous appearance, wherein isolated peaks and low ridges occasionally rise to view above the tenuous lines of riparian forest that meander across the landscape.

The Rio Branco-Rupununi savannas are enclosed by a series of mountain ranges and elevated surfaces, which rise to 400-1,000 metres on their flanks, providing distant backdrops to the rolling savannas. Most prominent is the line of the Pacaraima Mountains, which encloses the basin to the north and north-west. Elsewhere the margin is lower and more dissected by lines of drainage, but even if here the savanna and relief boundaries do not coincide, one still associates savanna with the lowland tract, and forest with the steeper and more elevated terrain.

The physiographic margin is interrupted principally by two broad drainage outlets. In the north-east the Rupununi River, draining the eastern margin of the savannas, flows through the Essequibo system to the Atlantic coast, while to the south the broad alluvial plain of the Rio Branco leads waters from the remainder of the region into the Rio Negro and thence to the Amazon.

Climatically the savannas may be distinguished from the adjacent forest areas. Aubréville (1961) speaks of a 'climat haut brancosien', which by comparison with the forest, is notable for its lower rainfall, which totals from 1,400-1,650 mm. per annum, and the length and severity of the dry season, which lasts from seven to eight months each year.

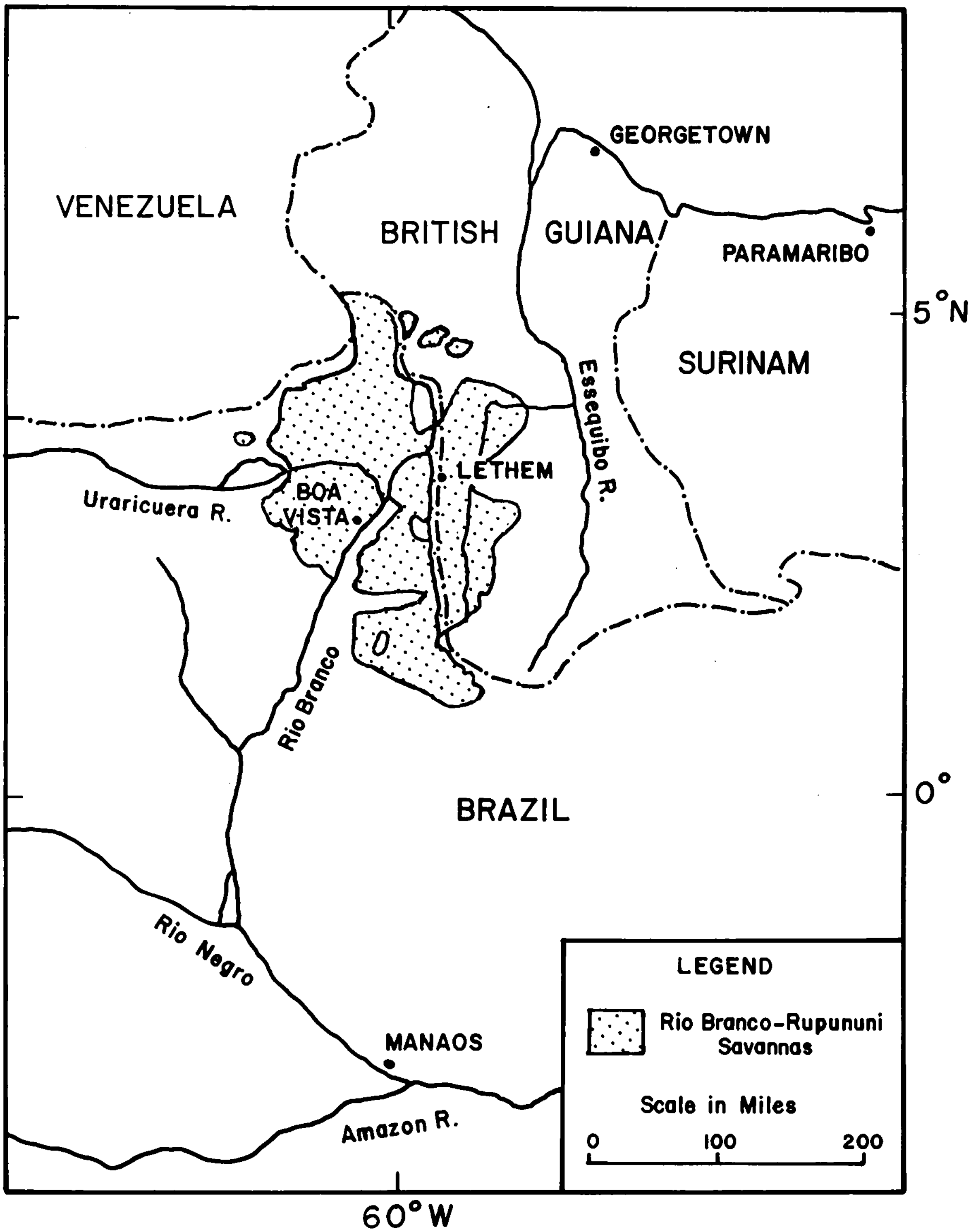
Temperatures in both areas are high and typical of a tropical regime; at St. Ignatius the mean annual temperature is 28.0°C, with a monthly range of 2.6°C, but the forest hinterland has an annual rainfall total of over 1,750 mm, which is more evenly distributed throughout the year.

The hydrological regime of the savannas is markedly affected not only by the drier climate, but also by the widespread occurrence of large tracts of elevated, highly porous sand and gravel soils, and equally extensive areas of flat, heavier textured deposits. The former retain little water, while the flats, uneasily drained in the wet season by the overloaded Amazon and Essiquibo systems, are readily inundated.

Within this environment there exists a savanna, ecologically dominated by grasses and sedges, but containing nonetheless large tracts of open wooded savanna. The trees differ markedly from the neighbouring forest species; they are lower, and their branches more stunted and gnarled than the forest counterparts, and their canopy never closes to shut out the light and inhibit the growth of a herbaceous layer.

The Brazilian language, richer in descriptive terminology, refers to the densest stands as 'campo cerrado' (literally: closed savanna). Here the trees may be as little as 5 metres apart, with mature species rising 3-6 metres in height, so that passage through them on horse or foot is not greatly impeded. After this there is recognised in the continuum the 'campo

MAP I
RIO BRANCO-RUPUNUNI SAVANNAS



coberto' (literally: covered savanna), which is described by Aubréville (1961) as a poor shrub savanna, dotted with small trees and bushes. The formation grades into the 'campo sujo' (literally: dirty savanna), where a sparser cover of low trees, 1-2 metres in height, is found. Finally, there exist large tracts, generally low-lying, of 'campo limpo' (literally: clean savanna), where trees are all but absent and only occasional shrubs and bushes break the uniformity of herbaceous growth.

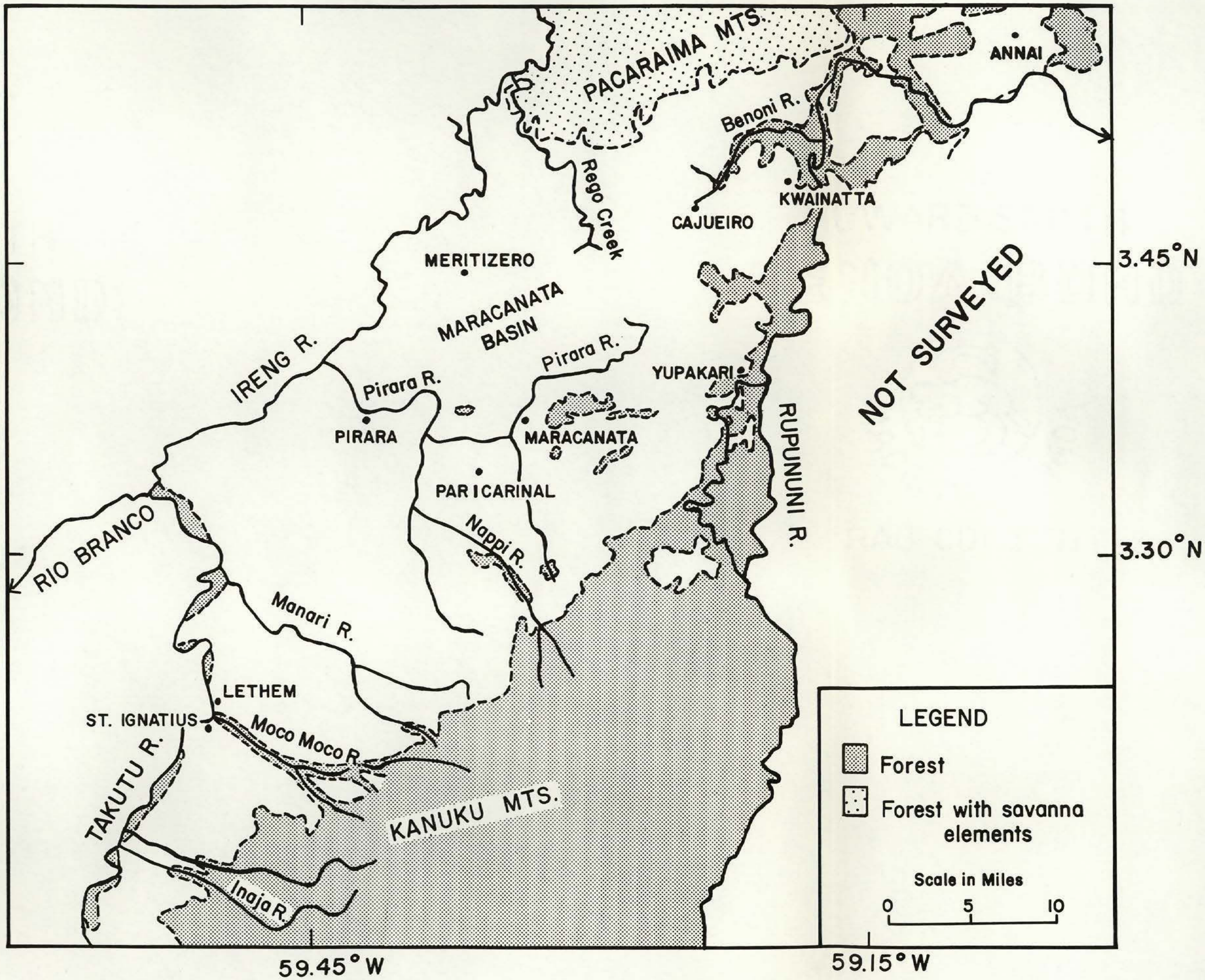
Within the savanna all stages in the continuum occur, and indeed occasional alien elements intrude, in the form of swamps, 'bush islands' and riparian forest tracts; but essentially the region remains a low, undulating plain of savanna with or without tree cover, which is distinctive in a number of physical attributes from the surrounding forest.

(b) The Rupununi Savannas, with particular reference to their northern section

The Rupununi savannas form the eastern margin of the larger savanna region, and are divided from the Brazilian sector by the Ireng and Takutu rivers, at whose confluence the united waters become, in Brazilian territory, the Rio Branco. Extending in a broad wedge to the east and rising some three miles from the Takutu River are the Kanuku Mountains, which divide the Rupununi into two halves.

To the south of the mountains the savannas gradually rise to the south and east. After first passing through a depositional zone, the approach to the savanna margin itself is marked by increasingly shallow soils, exposures of bedrock (chiefly quartz and granite) and more undulating relief. Finally, on the lithosolic margin of the region, at a height of 200-250 metres, rounded granite domes and broken tor-like features protrude from the savanna in large numbers. Beyond, a new relief level gradually establishes itself along the forest edge, rising to form a large forested surface at slightly under 300 metres.

MAP 2
NORTHERN RUPUNUNI SAVANNAS



One other feature peculiar to the southern savannas is the occurrence of isolated mountain blocks whose inselberg-like profiles, more commonly seen in drier climates, break the otherwise monotonous horizon.

In contrast to the south which can be considered, geomorphologically, to belong to the margin of the larger savanna region, the northern Rupununi savanna is part of the main lowland tract of the basin, lying between 100-140 metres above sea level. On the south it is enclosed by the youthful, forest-clad slopes of the Kanuku Mountains, which rise sharply from the lowland and climb to over 1,000 metres, terminating in their highest peaks in a series of rounded summits.

Skirting the mountain front are two broad, elevated erosion surfaces of undulating gravel ridges and long gentle sheetwash slopes, which extend northwards to Pirara in the west, and Kwainatta in the east. An isolated ridge west of Meritizero represents the only sizable outlier from the surfaces.

Northward of these features, there extends a broad, shallow trough, some 10-25 metres lower and infilled with recent, fluvio-lacustrine sediments, which reaches to the Pacaraima Mountains. Gently swelling ridges and elevated channels bear witness to a complexity of outwash and levée deposition and, amid the confusion of successive drainage alignments in the trough, basins and alluvial flats have gradually been built up. A few stream courses, flooded out of recognition in the wet season and reduced to mere trickles thereafter, meander among the earlier deposits, seeking an outlet, but more often than not ending in yet another enclosed basin from which they may seasonally overflow, but rarely force a permanent outlet.

Two outlets exist: one, the Pirara River, flowing westwards to the Ireng, drains the swamp collecting grounds at the foot of the elevated gravels around Maracanata and Paricarinal, carrying off wet season flood waters, which totally obscure its main channel, and maintaining its dry

PLATE 1: The forested Kanuku Mountains near Lethem, viewed across undulating, gravel terrain of the savanna.

PLATE 2: Typical open wooded savanna, on the Meritizero Ridge.

PLATE 3: Margin of the lowland trough: the seasonally inundated flood plain of the Pirara River, near Maracanata. (Photo by E. W. Waddell).

PLATE 4: The Pacaraima Mountains near Toka, with an extension of savanna onto the mountain slopes.

season flow with seepage waters. The other outlet is the Benoni, which flows north east to the Rupununi River. It too has a well marked channel, which leads back to the centre of the depression and links up with the seasonally-flowing Rego Creek. Like the Pirara, it passes through terrain, at times flat, level and treeless, and at others, amid gently undulating ridges and depressions, with occasional lines or clumps of trees marking the highest ground.

To the east, the country beyond the Rupununi River is less well known. Some areas of savanna are known to exist, and a recent report suggests that beyond these an ascent to an elevated erosion surface, cut in white and brown sands, occurs in a manner comparable to the eastern margin of the southern Rupununi savannas*.

The northern margin of the lowland is more abrupt than elsewhere. The outwash deposits of the Pacaraima Mountains are largely interbedded with the trough sediments, and the boulder strewn slopes, unlike the Kanukus, are a mosaic of forest and savanna growth. They rise to over 500 metres, and even beyond the first line of mountain, valleys and summits alike are shared by both forest and grassland, whose occurrence, inexplicable in terms of altitude or exposure, denies a precise coincidence of savanna with lowland plain.

(c) Landscape Evolution of the Northern Rupununi

The northern Rupununi savannas belong structurally to the Guiana Shield, an ancient pre-Cambrian mass that forms the nucleus of the northern part of the South American continent. Extending through the Guianas, Brazil and Venezuela, it is composed of granites, gneisses and schists, with

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* G.R. Suggett (Soil Survey Specialist, F.A.O.), private communication.

associated metamorphic and volcanic rocks, and it is predominantly of these that the Pacaraima and Kanuku mountains are formed (McConnell, 1959).

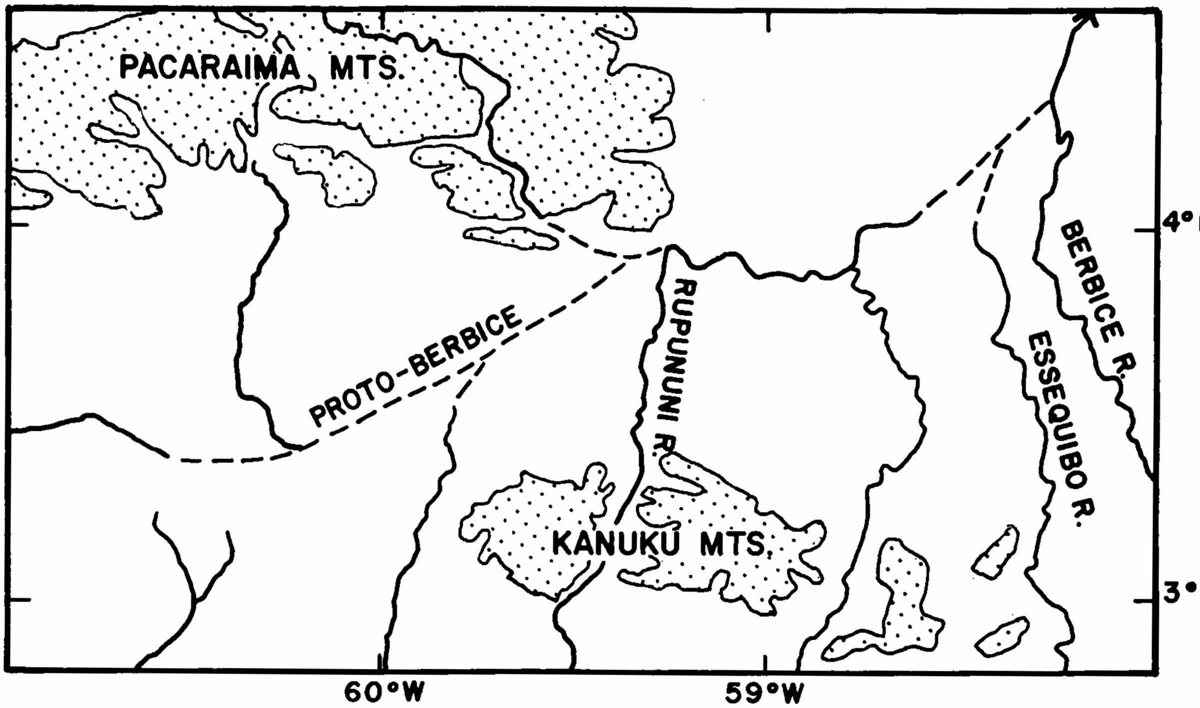
Lying between these mountains, and extending westwards into Brazil is the alluvial lowland, which includes the northern Rupununi savannas. The area is considered by McConnell (1962) to represent a planation surface, provisionally dated as end-Tertiary, which he describes as :-

> 'a very well-developed erosion bevel (which) occurs throughout the Guiana Shield at about 330-450 feet and is named the Rupununi Surface.'
>
> R.B. McConnell, 1962, p. 5.

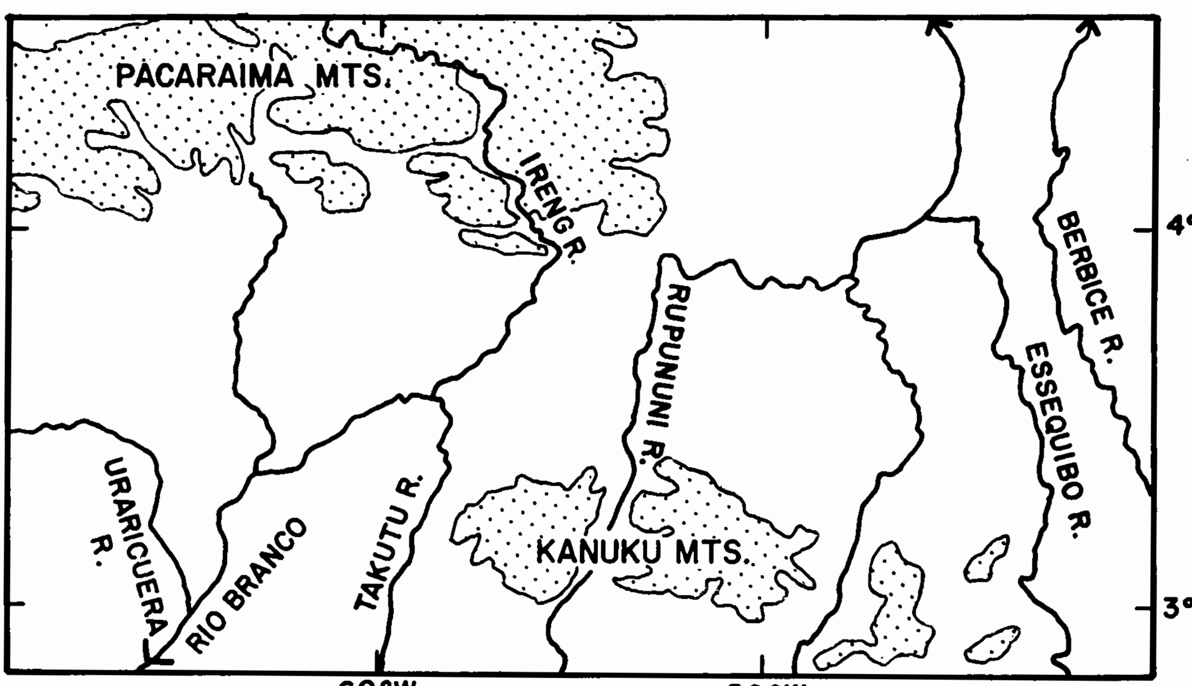
The northern Rupununi savannas themselves are believed to be underlaid by sedimentary rocks of the Takutu Formation of Permo-Triassic age, which consist of generally level beds of clay shales and mudstones. The contemporary landscape, however, has been fashioned by Quaternary alluvial deposition and erosion upon this bevelled surface, and the Takutu Formation outcrops only at depth along the major river banks (McConnell, 1959).

The present drainage of the savanna is divided between the Amazon and Essequibo systems, but this has not always been the case. There is strong evidence to indicate that in the past the whole of the northern savannas, as well as the northern Rio Branco, were drained by a large river flowing from west to east, which debouched into the Atlantic at the mouth of the present Berbice River. (Barbosa & Ramos 1959; McConnell 1962). This river, named the Proto-Berbice, is considered to have been beheaded by more vigorous headwaters of the Amazon, the process having been initiated by westward tilting along the watershed margin (Loxton, Rutherford & Spector 1958). The pronounced gorges of the Takutu and Ireng rivers, some ten metres deep, bear witness to the more powerful rate of downcutting which is taking place in the Amazon Basin, and which has led to advance of the watershed.

MAP 3: PROBABLE DRAINAGE IN RIO BRANCO-RUPUNUNI SAVANNAS DURING PROTO-BERBICE PHASE



MAP 4: PRESENT DRAINAGE IN RIO BRANCO-RUPUNUNI SAVANNAS (RIO BRANCO PHASE)



The most prominent local indications of the previous drainage pattern are the frequent elbows of capture on the margin of the Amazon system, e.g., on the Rio Uraricuera above Boa Vista, and on the Pirara River west of Pirara Ranch, which suggest an earlier eastward flow; an old channel of the Ireng, which meanders eastwards across the northern savannas, finally joining the Rupununi River through the misfit Benoni River; and the remnants of sandy terrace deposits which occur within the northern savannas.

The present landscape of the northern savannas is considered to be a product of deposition and erosion during :-

(a) The Proto-Berbice Phase, when extensive sand and gravel deposits were laid down and partly re-eroded, the remnant today forming the more elevated parts of the northern savannas.

(b) The Rio Branco Phase, when the older sediments were further removed and resorted, and more recent fluvio-lacustrine deposits laid down in the lower areas.

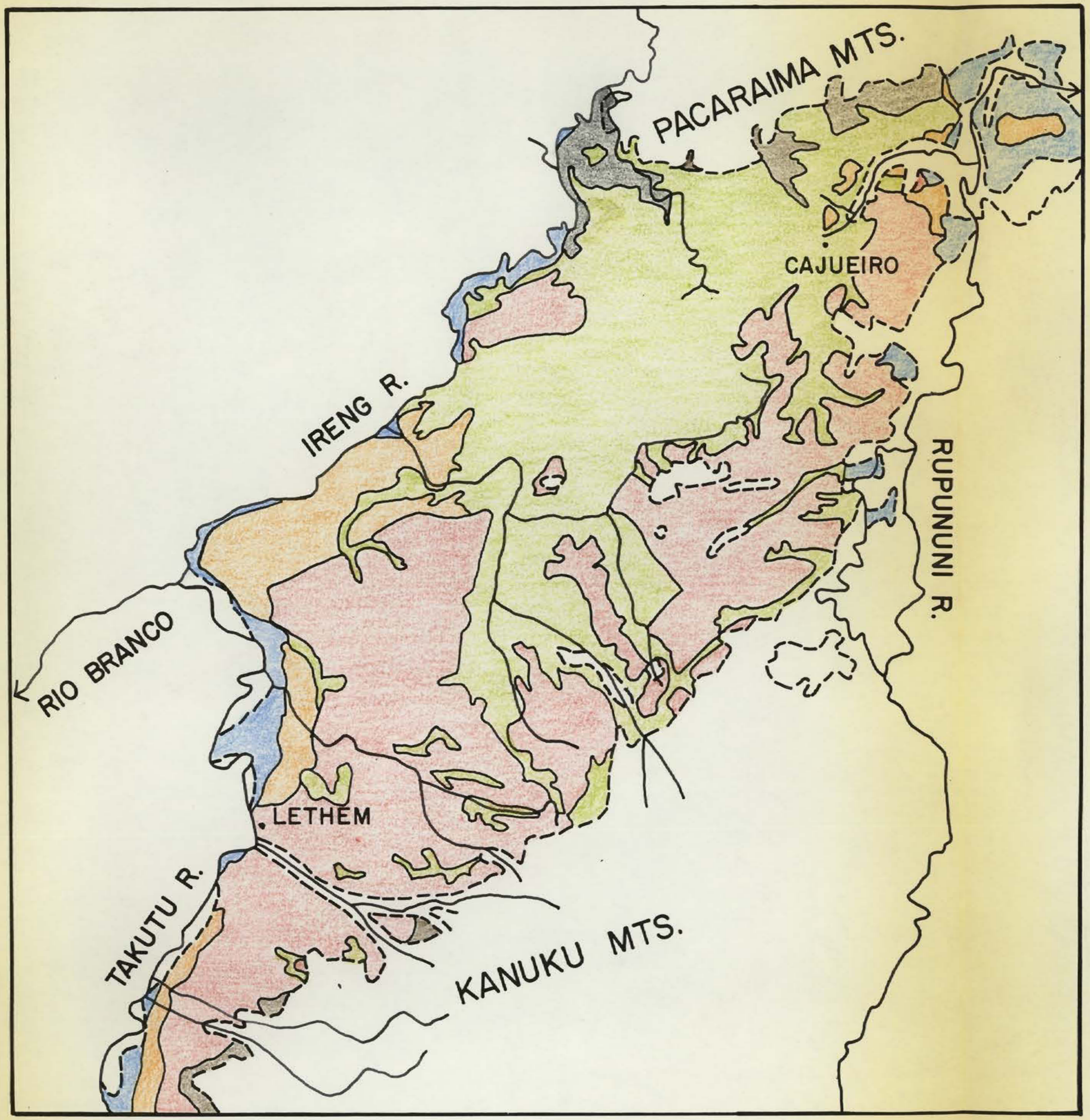
The following major land units are today recognisable as a result of the above processes :-

(a) Lethem-Yupakari land unit, of elevated secondary lateritic gravel deposits, laid down during the Proto-Berbice phase, which are currently being modified by sheetwash processes.

(b) Takutu - Proto-Berbice land unit, of elevated and moderately elevated sandy river terrace deposits, laid down during the Proto-Berbice phase.

(c) Proto-Ireng land unit, of moderately elevated, fine textured fluvio-lacustrine deposits, probably laid down during the late Proto-Berbice phase.

(d) Mountain Outwash land unit, laid down during the Rio Branco phase.



MAP 5
MAJOR LAND UNITS OF THE
NORTHERN RUPUNUNI SAVANNAS

LEGEND

Scale in Miles
0 5 10

Lethem-Yupakari unit

Takutu-Proto-Berbice unit

Proto-Ireng unit

Mountain outwash unit

Lowland unit

Flood plain unit

---- Savanna-forest boundary

(e) Lowland unit, of fluvio-lacustrine deposits, laid down during the Rio Branco phase.

(f) Flood Plain land unit, of recent origin, along the major rivers.

The Proto-Berbice Phase

Outcropping in many places through the layer of lateritic gravel deposits that extend south of a line from Kwainatta to Pirara, are blocks of massive lateritic pavement. This resistant material is considered to be the highly dissected remnant of an extensive and thick accumulation of primary laterite that formed on the Rupununi Surface, both in British Guiana and adjacent parts of Brazil, probably during late Tertiary times.

It is likely that the lateritic gravels in the northern savannas represent the secondary materials from this surface, which have been transported by the eastward-flowing Proto-Berbice from more distant parts of the basin*. Loxton, Rutherford and Spector (1958) suggest that the material represents detritus from the laterite cap of the Kanuku Mountains, but later writers, including Bleakley (1958), have doubted this, as does the present writer. Why, for example, is there no comparable deposition on the southern flank of the Kanuku Mountains, where erosion has continued in a similar manner?

Two levels, with different relief and drainage characteristics, are visible in these deposits, and represent different phases of Proto-Berbice activity. The existence of lateritic gravel outliers, principally the Meritizero Ridge, suggest that the material originally extended more completely over the northern savanna, only to have been eroded out of the northern half of the lowland by more aggressive downcutting during the latter part of the Proto-Berbice period.

Following the removal of this material, the Proto-Berbice river entered a further period of deposition, which is visible in a series of sandy materials

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* The existence of rounded quartz pebbles within the gravels suggests they are of secondary origin.

on the margin of the laterite, which from their configuration and textural uniformity appear to represent terrace materials. The remnants of this terrace, which are aligned in an east-north-easterly direction from the confluence of the Ireng and Takutu, extend towards Pirara Ranch; through the low-lying Maracanata Basin the sandy deposits are absent, but they reappear intermittently between Cajueiro and Kwainatta, reacquiring their former size and breadth along the Rupununi River near Annai. In addition, the terrace can be traced back along the Takutu for at least 50 miles south of its confluence with the Ireng, and a similar extension exists into Brazil.

At this time other fluvial sediments were probably deposited through the lower northern half of the northern savannas, but subsequent activity has either removed or covered them. Bleakley, referring to soil profiles visible in river gorges in the region, states :-

> 'Over thirty feet of sediments outcropping in the Takutu, Ireng and Rupununi fall into two groups, an upper silty and sandy loam series, and a lower coarse sand series with intercalated red and white clays.'
>
> D. Bleakley, 1958, p. 12.

The upper silty and sandy loam series, whose widespread presence was verified by surface borings in the lowland trough, clearly belongs to the Rio Branco phase of fluvio-lacustrine deposition. The lower sandy series with intercalated clays, and an absence of silty material, is more probably of fluvial origin, and may be contemporaneous with the elevated Proto-Berbice sandy terrace.

Also, probably towards the end of the Proto-Berbice phase, the Proto-Ireng River, still flowing east in a course roughly parallel to the Pacaraima Mountains, deposited a series of finer materials along its middle course, which today remains elevated above the more recent fluvio-lacustrine deposits.

Finally, before the end of the Proto-Berbice phase, the landscape appears to have undergone a further period of active erosion, during which the sandy terrace was dissected, e.g., by the flow of waters from the Nappi rivers into the Maracanata Basin, and the landscape generally lowered, prior to the start of the Rio Branco phase.

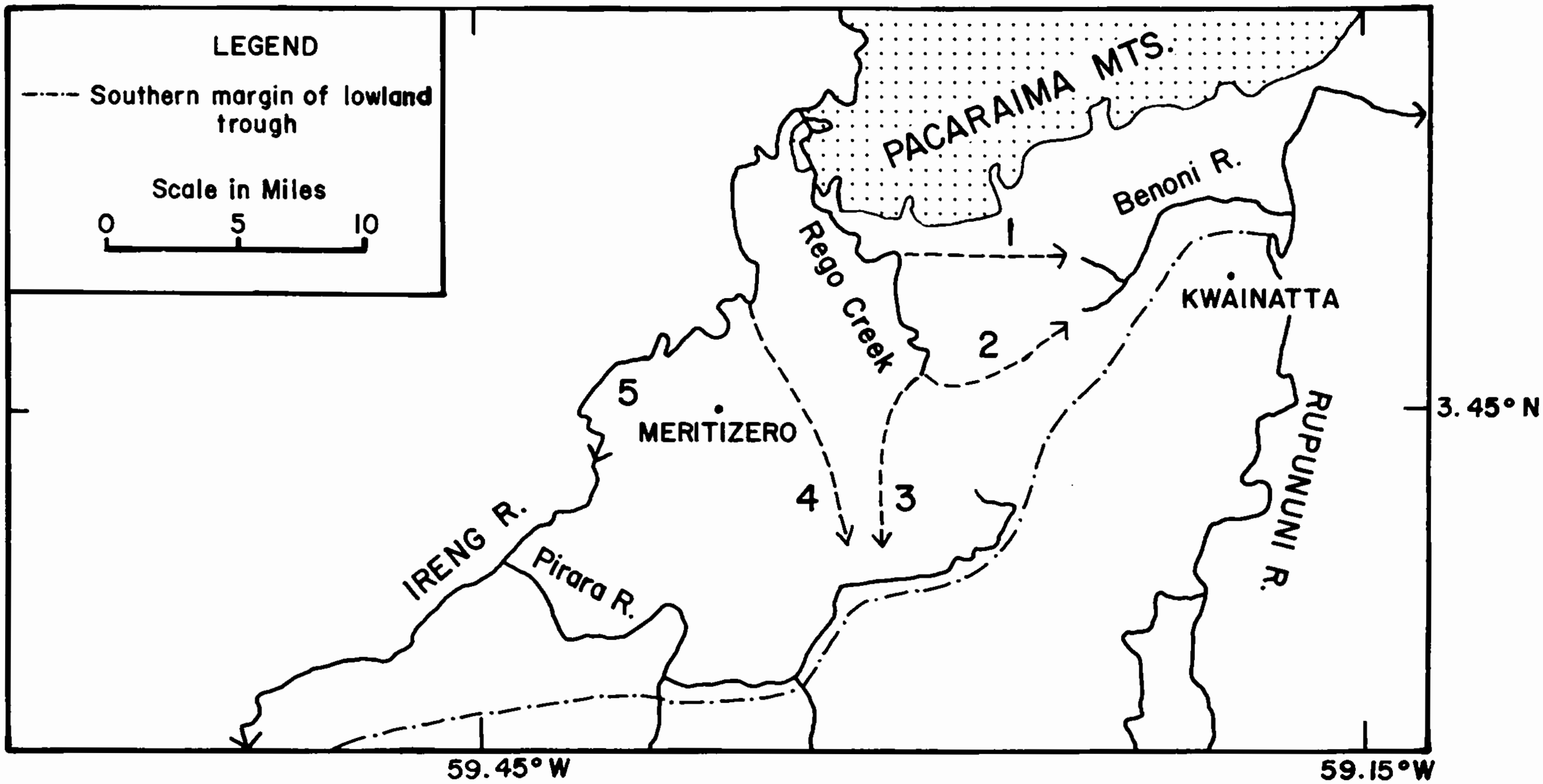
The Rio Branco Phase

The end of the Proto-Berbice phase of drainage coincided with a period of landscape rejuvenation to the west of the Amazon-Essequibo divide. The resultant extension by river capture of the watershed of this part of the Amazon Basin brought above the re-orientation of drainage in the northern savannas (McConnell, 1962).

The present disposition of sediments in the northern savannas suggests that in the early stages of rejuvenation a reduction in flow and carrying capacity of the Proto-Berbice River took place, due in the first instance to the westward tilting, but later aggravated by the progressive capture of the Proto-Berbice headwaters. As a result, siltation increased in the lowland trough and the outlet of waters to the east was impeded. The lower part of the northern savannas, through which the Proto-Berbice flowed, gradually infilled with fluvio-lacustrine deposits, until eventually the waters of the Takutu and the Proto-Berbice, which had hitherto flowed through the lowland to the east, were diverted to the west.

The Proto-Ireng River, whose headwaters were not affected by capture, and which had entered the Proto-Berbice further to the east, appears from the extensive sediments it has deposited to have maintained its flow for a longer period, until it too, having partly relied on the Proto-Berbice waters to assist in transporting its heavy load of mountain detritus through the lowland tract, was unable in the face of accumulating sediments and tilting, to maintain its flow to the east. During the transition period the Proto-

MAP 6 : SUCCESSIVE COURSES OF PROTO-IRENG RIVER DURING TRANSITION PERIOD OF DRAINAGE IN NORTHERN RUPUNUNI SAVANNAS



Ireng steadily debouched sediments into the northern savannas, its course moving progressively west as it blocked its easterly channels, until it also was linked with the Amazon system. Probably its final course was reached when a tributary of the Rio Branco, cutting back through the older deposits to the west of the Meritizero Ridge, captured the Ireng about five miles north of Meritizero Outstation.

(d) The Time Element

There remains the problem of time scale. The Rupununi Surface has been dated by McConnell (1962) as end-Tertiary. During the succeeding period of sedimentary activity, following the bevelling of the surface, a number of different levels were formed. Two levels are visible in the lateritic deposits, and a further one comprises the fluvio-lacustrine deposits in the lowest tract of the basin.

During the Quaternary, world-wide fluctuations in sea level and rainfall, and hence drainage regimes, took place as a result of Pleistocene temperature changes, and it is likely that the levels recorded in the northern savannas are attributable to such variations.

The landscape of the northern savannas is thus considered to belong to the Quaternary period, with the exception of occasional outcrops of primary massive laterite, which are relics of the late Tertiary; the two elevated surfaces of the Proto-Berbice phase are of Pleistocene origin, although in some areas they have been modified by recent sheetwash accumulation. The fluvio-lacustrine deposits, on the other hand, found on the lowest level and described as belonging to the Rio Branco phase, are almost entirely Holocene and represent accumulation that has taken place since the rise in sea level at the end of the Pleistocene glaciation, some nine to eleven thousand years ago.

PART TWO: ECOSYSTEMATIC STUDIES

CHAPTER 3

INTRODUCTION TO PLANT, SOIL AND WATER RELATIONS IN THE NORTHERN RUPUNUNI

In a region of the world that is normally considered to fall within the humid tropics, a newcomer to the Rupununi savannas in the month of February or March would find the region had acquired an appearance of extreme drought. Such is no illusion, for in spite of a mean annual rainfall of 1,621 mm. at St. Ignatius, northern Rupununi, the prevailing hydrological conditions for more than half the year are in keeping with an arid rather than a humid climate.

Two outstanding features characterize the hydrology of the northern Rupununi savannas; one is a plenitude, and in some places an excess of soil water during the wet season, the other a marked deficit of soil and surface water during the dry season. The imbalance is attributable to a combination of factors; it is primarily a response to seasonal rainfall, falling on a gently undulating and slow-draining landscape, large tracts of which are too low-lying to be adequately drained in the wet season, and whose widely inferior soils fail to retain an adequate supply of soil water to withstand the harsh desiccation of the dry season. While some of these features are inherent in the physical status of the region, others are secondary effects resulting from contemporary vegetational patterns.

The consequence of these conditions is that during the wet season, lasting from May to August, a large volume of rainwater runs off the land surface and accumulates in areas of low relief, causing extensive flooding

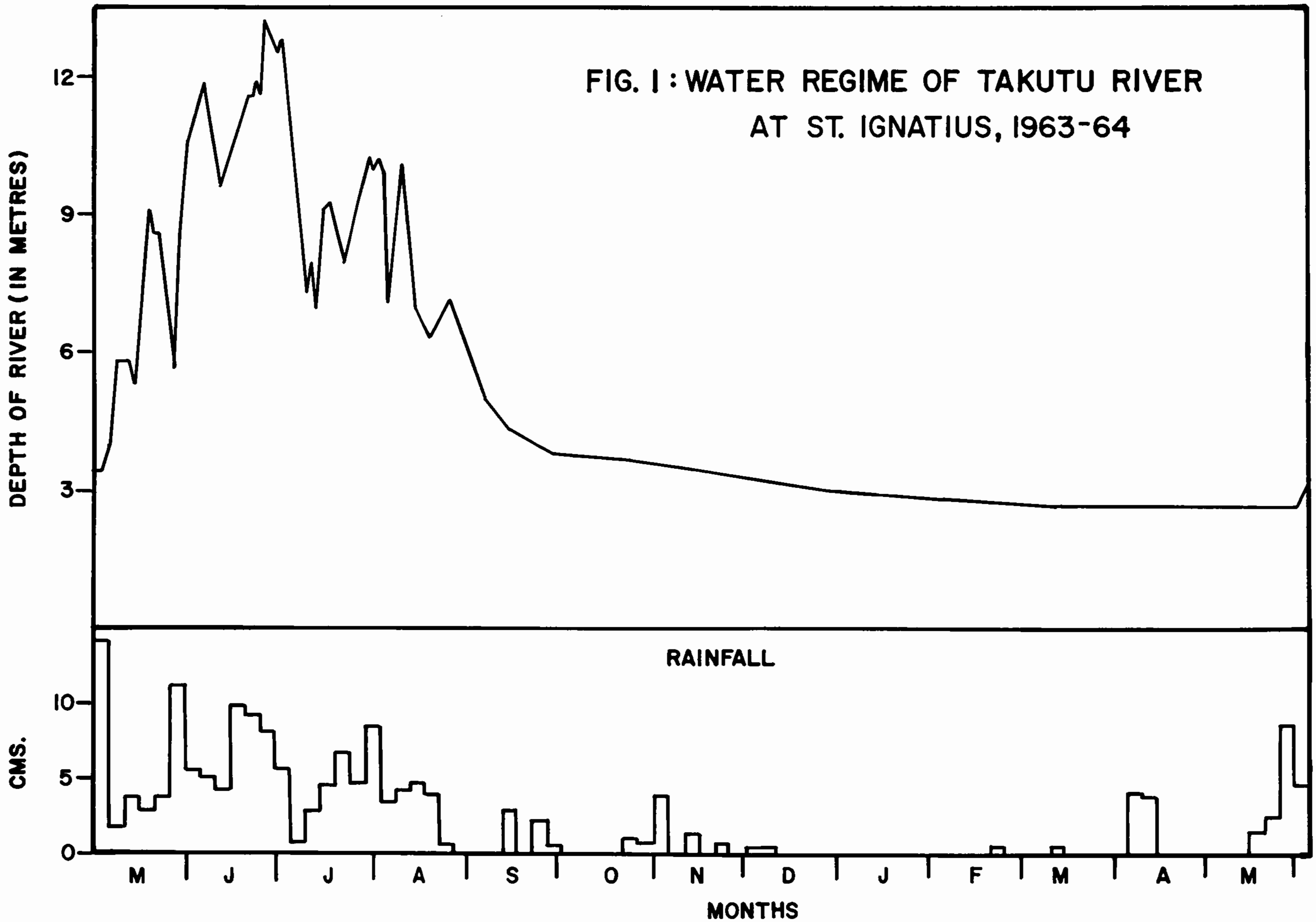


FIG. 1 : WATER REGIME OF TAKUTU RIVER AT ST. IGNATIUS, 1963-64

and waterlogging, while a limited amount is retained by the soils that are elevated enough to avoid inundation. In the dry season the surplus water is rapidly drained, ground water tables fall and soil moisture depletion continues apace, with the result that regional desiccation soon prevails.

During 1963/64 the Takutu River, one of the three major drainage channels in the Rupununi, rose and fell eleven metres. Thus, while raising the local base level and restricting drainage during the wet season, its rapid drop in August and early September drew off the bulk of the flood waters, and permitted rapid drainage of the region.

During the period June 1963 - May 1964, observations were made of soil water conditions at a number of sites adjacent to Lethem. The sites were intended to be representative of the range of water conditions found in the savanna; initially it was not possible to be sure that this was the case, but by selecting sites where marked variations in relief, soils and vegetation occurred, and by later inspection of a large number of individual sites in the area as a whole, it was confirmed that an adequate cross-section had been chosen. From these observations it was confirmed that an ecoclimate characterized by alternating wet and dry periods prevailed throughout the savanna.

From the point of view of plant growth there are two critical ecoclimatic phases in the regime. Firstly, in areas of low relief, the lack of soil aeration, due to flooding and waterlogging during the wet season, imposes severe restrictions on the growth of trees and grasses. The second critical phase is in the latter part of the dry season, when soil moisture through the profile is in short supply. At this time, with the virtual exhaustion of moisture in the upper layers of the soil, the shallow rooting grasses and sedges lie dormant, while tree growth remains closely dependent on the availability of deeper soil water reserves.

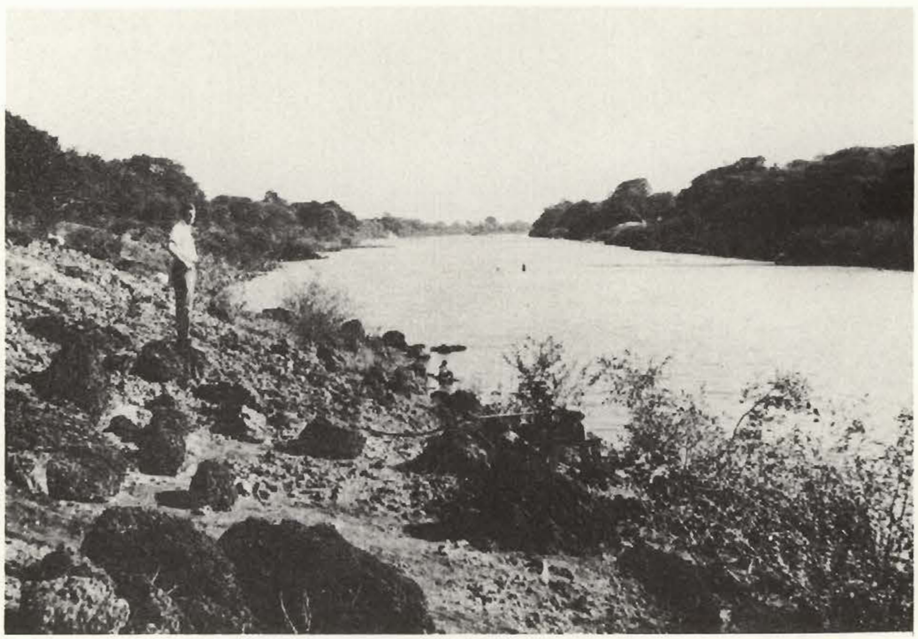


PLATE 5: The Takutu River at St. Ignatius at the end of the dry season. During the wet season, 1964, the river rose ten metres above the level shown, and in places overflowed its banks.

The first aim of the thesis is to explain the inter-relationships briefly described in the preceding paragraphs, and where possible provide quantitative data of phenomena. The following phases of field work were undertaken during a residence of 13 months at St. Ignatius.

Phase I — Reconnaissance of area and selection of representative sites for continuous observation of ecoclimatic conditions.

Phase 2 — Sample investigations throughout the area to examine plant, soil and water relations of a large number of individual sites.

Phase 3 — Regional investigations and mapping of terrain units, based on the findings of Phase 2, as a means of interpreting vegetation patterns through the area.

Phases I and 2 comprise an ecological investigation to determine, firstly, the principal factors affecting the ecoclimate, namely: climate (Chapter 4), soils (Chapter 5), and soil rooting conditions (Chapter 6); secondly, the nature of the ecoclimate itself (Chapter 7); and thirdly, the relations between plant growth and water conditions (Chapter 8).

Subsequently, in Phase 3, this information was used as a basis for regional interpretation of plant, soil and water relations (Chapter 9). In Chapter 10 an attempt is made to apply this, and any other available information, towards an interpretation of the origin and evolution of the savanna.

CHAPTER 4

SOIL WATER CONDITIONS: 1. CLIMATE

(a) Introduction

The climate of the northern Rupununi savannas, and indeed of the Rio Branco - Rupununi savannas as a whole, has an individuality that sets it apart from adjacent forest areas. Aubréville (1961) refers to a 'climat haut brancosien', recognizing as its main distinguishing feature a pronounced seasonality of rainfall, which at St. Ignatius, Rupununi results in 83% of the mean annual total of 1,621 mm. falling during the five months April to August.

By comparison, the rainy season in the central Amazon Basin to the south extends over a much longer period. Manaos, for example, with a mean annual rainfall of 1,846 mm., has eight wet months in the year with over 100 m. of rainfall, while at St. Ignatius there are only four. Similarly, to the west and north of the Rio Branco - Rupununi savannas the coastal margin of the Guianas experiences a second, subsidiary rainy season during the months of December and January, which greatly ameliorates ecoclimatic conditions at that time of year. A mild effect of the second rainy season is felt even at Annai on the north-west margin of the Rupununi savannas, where rainfall during December and January, the driest months at St. Ignatius, is slightly increased. Table 1 and Figure 2 illustrate seasonal rainfall conditions at selected stations.

FIG. 2 : MEAN RAINFALL CONDITIONS AT SELECTED STATIONS

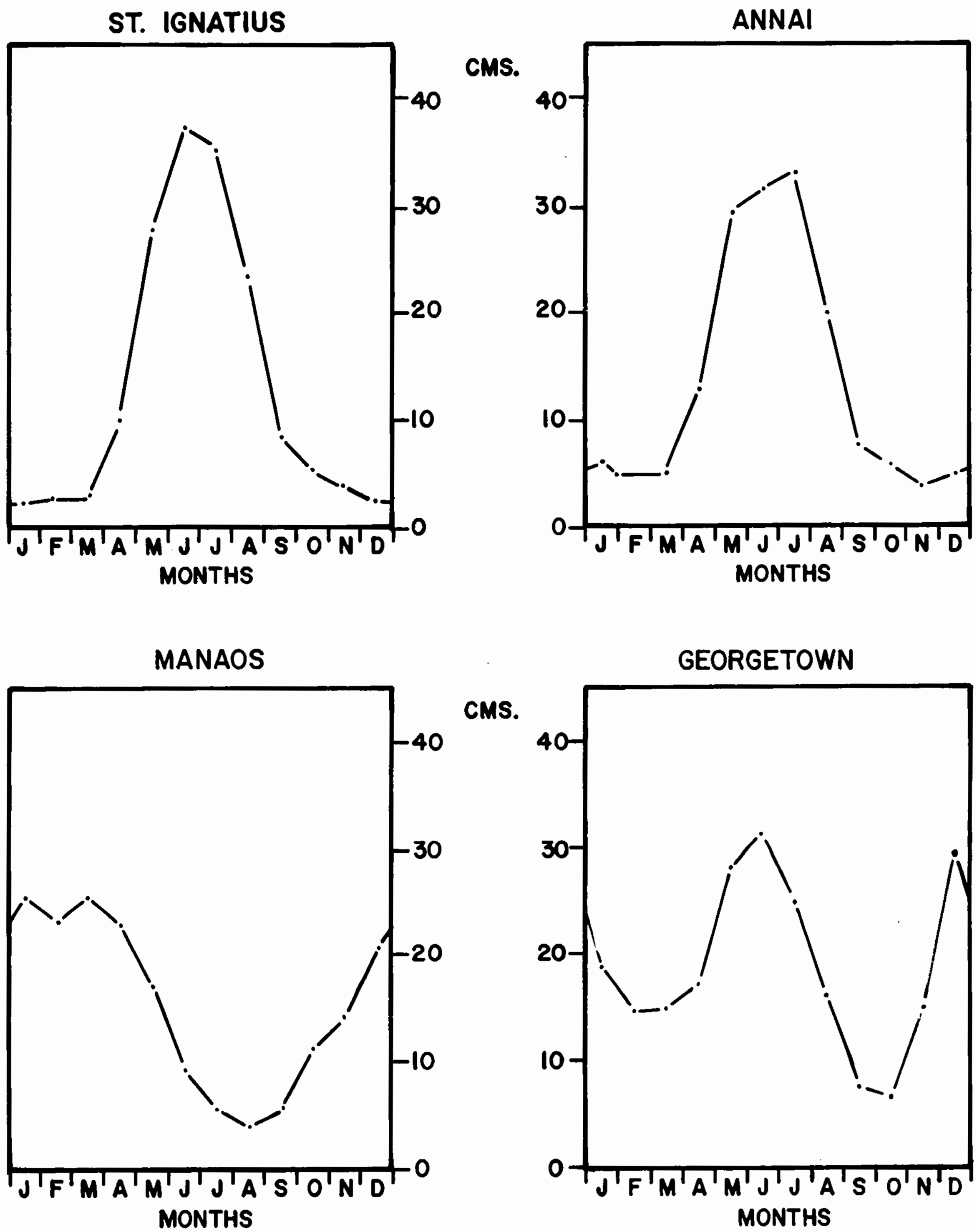


TABLE 1: Seasonal rainfall conditions at selected stations

	Mean annual rainfall (mm)	Highest monthly mean (mm)	Lowest monthly mean (mm)	No. of months with >100 mm	No. of months with 30-100 mm	No. of months with <30 mm
St. Ignatius, Rupununi	1,621	355	25	4	4	4
Annai, Rupununi	1,643	329	37	5	7	0
Manaos, Amazonas, Brazil.	1,846	255	39	8	4	0
Georgetown, Coastal B. Guiana	2,258	315	64	10	2	0

The seasonal transitions in the savannas are generally abrupt, and are associated with the passage of the inter-tropical frontal system, which in April or May moves northward across the Rupununi, bringing in its wake a period of intense rainfall, cloudy skies and moderate winds; three to four months later, in August or September, the front returns to the south, and clearer skies and dry weather come to the savanna. During the dry season which lasts from eight to nine months each year, strong north-easterly winds, drawn in by the low pressure area in the west centre of the continent, blow steadily across the savanna, and result in high evapotranspiration rates, and rapid soil moisture depletion.

The prolonged period of drought that occurs in the Rupununi has been attributed by Aubréville (1961) to a 'foehn' effect induced within the lowland of the Rio Branco - Rupununi savannas. He describes it thus :-

'Les masses d'air venant de l'Est ont un mouvement descendant qui a pour résultat de vaporiser les nuages venus de l'Est ou formés par les courants ascendants locaux. Le foehn est peut-être dû à la barrière des chaînes de montagnes qui entourent en grande partie ce territoire du Rio Branco sur les frontières de la Guyane anglaise.'

A. Aubréville, 1961, p. 161.

Such an explanation is confirmed by the rainfall and relief patterns in the region, although the seasonal drought conditions are also likely to be aggravated by the micro-climatic effect of the savanna vegetation itself.

It appears, however, that a belt of relatively lower rainfall, albeit less pronounced than in the savanna, extends north-north-eastwards from the Rupununi to the coast of British Guiana, where annual totals are less than in forest stations to the east and west. The annual total, for example, at Cayenne, 400 miles east-south-east of Georgetown, has an annual total of 3,011 mm. as against 2,258 mm. at Georgetown itself. Thus the 'foehn' effect, if indeed it operates, may only be a secondary factor within a broader regional pattern, whose causes are at present inadequately understood.

Mean monthly temperatures in the northern Rupununi remain constantly high throughout the year, although maximum temperatures are slightly greater during the less cloudy months of the dry season. Diurnal temperature variation similarly is greater in the dry season; in June the mean diurnal range is 7.3°C. by comparison with 8.8°C. in December. Table 2 illustrates mean temperature conditions at St. Ignatius, Rupununi :-

TABLE 2: Mean temperature conditions, St. Ignatius, Rupununi

	June (Wet season)	December (Dry season)	Annual
Mean temperature	26.7°C	28.5°C	28.0°C
Mean maximum temperature	30.3°C	32.8°C	32.1°C
Mean minimum temperature	23.0°C	24.0°C	23.5°C

Based on data for the period 1937-1943, 1948, 1957-1963.)

(b) Rainfall Seasonality and Water Regimes

The seasonality of rainfall in the Rupununi is pronounced, and the transition between the seasons generally abrupt. During the period 1960-1963, the rainy seasons lasted from 85 - 124 days, within the months April to September, during which time between 1,150 - 1,560 mm. of rainfall occurred. The showers during this period of the year are intense, and few days pass without a downpour. The remainder of the rainfall, representing 20-30% of the annual total in each year, falls during the dry season in isolated storms, or series of storms spread over several days. Their temporal distribution varies widely from year to year, but on the average December and January are the driest months at St. Ignatius. Table 3 illustrates the seasonal conditions at St. Ignatius during the period 1960-1964.

TABLE 3: Rainfall seasonality, St. Ignatius, Rupununi, 1960-1964

	Duration	Total days	Rainfall days	Rainfall (wet season) mm.	Rainfall (dry season) mm.
Wet Season, 1960	26 Apr-15 Aug	112	100	1,308	-
Dry Season				-	273
Wet Season, 1961	30 May-22 Aug	85	82	1,151	-
Dry Season				-	325
Wet Season, 1962	2 May-2 Sept	124	105	1,559	-
Dry Season				-	536
Wet Season, 1963	4 May-21 Aug	110	96	1,350	-
Dry Season*				-	190

The relation between rainfall and soil water conditions during the rainy season is direct. Soil moisture content and water table levels fluctuate from day to day in accordance with the immediate rainfall situation, and throughout this period there is an adequacy, and in places an excess of moisture for plant growth. During the dry season, ecoclimatic conditions are less direct, for however adverse the soil conditions, the capital of water retained in the soil at the end of the rains extends the 'wet season', from the point of view of plant growth, into the succeeding weeks. However, as will be illustrated later, the depletion of soil moisture capital in the Rupununi takes place rapidly under the high rates of evapotranspiration at the start of the dry season, and a relatively abrupt ecoclimatic transition exists between periods of water excess or adequacy, and water deficiency.

* The dry season, 1963/64, ended on May 18th.

(c) Rainfall Variability and Water Regimes

The mean annual deviation of rainfall at St. Ignatius is 269 mm. or 17% of the mean annual total of 1,621 mm. The effect on plant growth of this variability is felt most strongly during the dry season, at the time when the soil moisture capital is depleted and unable to compensate as readily for variations in the supply of moisture. Table 4 illustrates the annual variability of rainfall in the northern Rupununi :-

TABLE 4: Annual variability of rainfall, northern Rupununi

	Mean annual rainfall (mm.)	Mean annual deviation (mm.)	Deviation as % of mean annual rainfall	Absolute maximum annual rainfall (mm.)	Absolute minimum annual rainfall (mm.)
St. Ignatius	1,621	269	17%	2,139 (1943)	1,070 (1939)
Annai	1,643	238	15%	2,124 (1938)	1,047 (1939)

(Based on St. Ignatius data for 28 years between 1930-1963; on Annai data for 35 years between 1923-1961)

During the rainy season, even in the driest of years, rainfall deviation is not great enough to create any deficiency of moisture for plant growth, and on elevated sites where free draining conditions prevail, any excess of rainfall is readily removed from the soil. In contrast, in the low-lying areas of the northern Rupununi, variations in the degree of waterlogging and inundation will occur from year to year in accordance with rainfall patterns; but in an area already experiencing an extreme water regime, and where rates of drainage as much as rainfall determine the ecoclimate, the result of variable rainfall during the rainy season will be minimised by fluctuations in the amount of water removed from the area by surface and ground water drainage.

Rainfall variability has its greatest effect on the savanna ecoclimate during the dry season, when soil moisture capital is at a minimum and when plant growth is, therefore, more directly dependent on rainfall for its maintenance. The period from January to March is the driest phase of the ecoclimate, when even under normal climatic conditions the growth of savanna species is inhibited. Table 5 illustrates rainfall variability during this period of the year.

TABLE 5: Variability of rainfall, January to March, northern Rupununi

	Mean rainfall Jan-Mar (mm.)	Mean deviation Jan-Mar (mm.)	Deviation as % of mean rainfall	Absolute maximum rainfall Jan-Mar (mm.)	Absolute minimum rainfall Jan-Mar (mm.)
St. Ignatius	79	49	62%	301 (1950)	2 (1961)
Annai	157	76	48%	422 (1953)	7 (1926)

(Based on St. Ignatius data for 31 years between 1930-1963; on Annai data for 32 years between 1923-1961)

At this time rainfall is at its most unreliable and wide fluctuations in the volume and distribution of rainfall take place from year to year. The variability is most significant to tree species, which require perennial moisture supplies; during the dry season their growth will depend partly on intermittent moisture supplies from rainfall, and partly on deep soil moisture reserves, and failure of either will inhibit their growth. A shortage of rainfall, for example, may lead to an over-rapid use of the deep soil moisture supply, and consequent exhaustion of the moisture available for growth.

(d) Rainfall Intensity and Water Regimes

Rainfall intensity can be considered as a function of two variables, namely: the amount and the duration of rainfall, the intensity increasing as either or both of these variables increase. Visual observation of rainfall in the Rupununi indicates that a high proportion of falls, both during the rainy and the dry season, are of a highly intensive nature and that prolonged light rainfall, of a kind more common in temperate latitudes, is relatively rare. Making use of data obtained from a recording rain gauge at St. Ignatius, it was possible to analyse the intensity of rainfall at this site during the rainy season of 1963. During this period 216 falls of rain were recorded, falling on 96 out of a total of 110 days between May 4 and August 21. Table 6 illustrates rainfall intensity at St. Ignatius during this time :-

TABLE 6: Rainfall intensity, St. Ignatius, rainy season, 1963

	Size of falls	Total rainfall (mm.)	% Total rainfall during rainy season	No. of falls	Mean duration of falls	Mean rainfall per fall (mm.)	Mean intensity
1.	> 100 mm.	132	10%	1	490 mins.	132	16 mm. per hour
2.	10-100 mm.	642	48%	41	45 mins.	16	21 mm. per hour
3.	0.5-10.0 mm.	542	40%	130	-	-	-
4.	<0.5 mm.	34	2%	44	-	-	-

The most significant category in this chart is No. 2 (10-100 mm.), which accounted for 48% of the total rainfall during the rainy season. During each of these falls the volume and duration of rainfall was relatively great, and the intensity of rainfall high. In one storm, on July 31, 22 mm of water fell in less than fifteen minutes, and it is clear that even within downpours of this kind heavier rates are sustained for short periods.

Category No. 1 ($>$100 mm) refers to a single period of rainfall on the night of May 4-5, which heralded the northward passage of the Inter-tropical Front. On this occasion the overall rate of fall was less than in Category No. 2, but the sheer volume of water that descended resulted in highly intensive rainfall.

The lesser falls in Categories Nos. 3 and 4 ($<$ 10 mm) are less easily analysed from the data available, but at least 50 of the 130 falls in Category 3 fell at a rate comparable with Category 2, although the volume of water involved was less.

The principal effect of the high degree of rainfall intensity is the reduction in the amount of water that enters the soil. Infiltration rates are not high enough to accept the large volume of water falling on the soil, nor is there adequate sod development or accumulation of organic debris to hold moisture temporarily at the surface. As a result much rain water runs directly over the surface of the soil, and is lost through surface drainage rather than contributing to the capital of water retained in the soil and available for plant growth.

(e) Evapotranspiration and Water Regimes

During 1963-64 measurements of evaporation and transpiration were made at St. Ignatius with four lysimeters, two evaporation pans and an atmometer (See Appendix I). From observations it became apparent that rates of potential evapotranspiration (P. E. T.) vary greatly from season to season. During the rains potential evapotranspiration remains relatively low, but at the height of the dry season rates were more than double those of the rainy season. Table 7 illustrates potential evapotranspiration during this period.

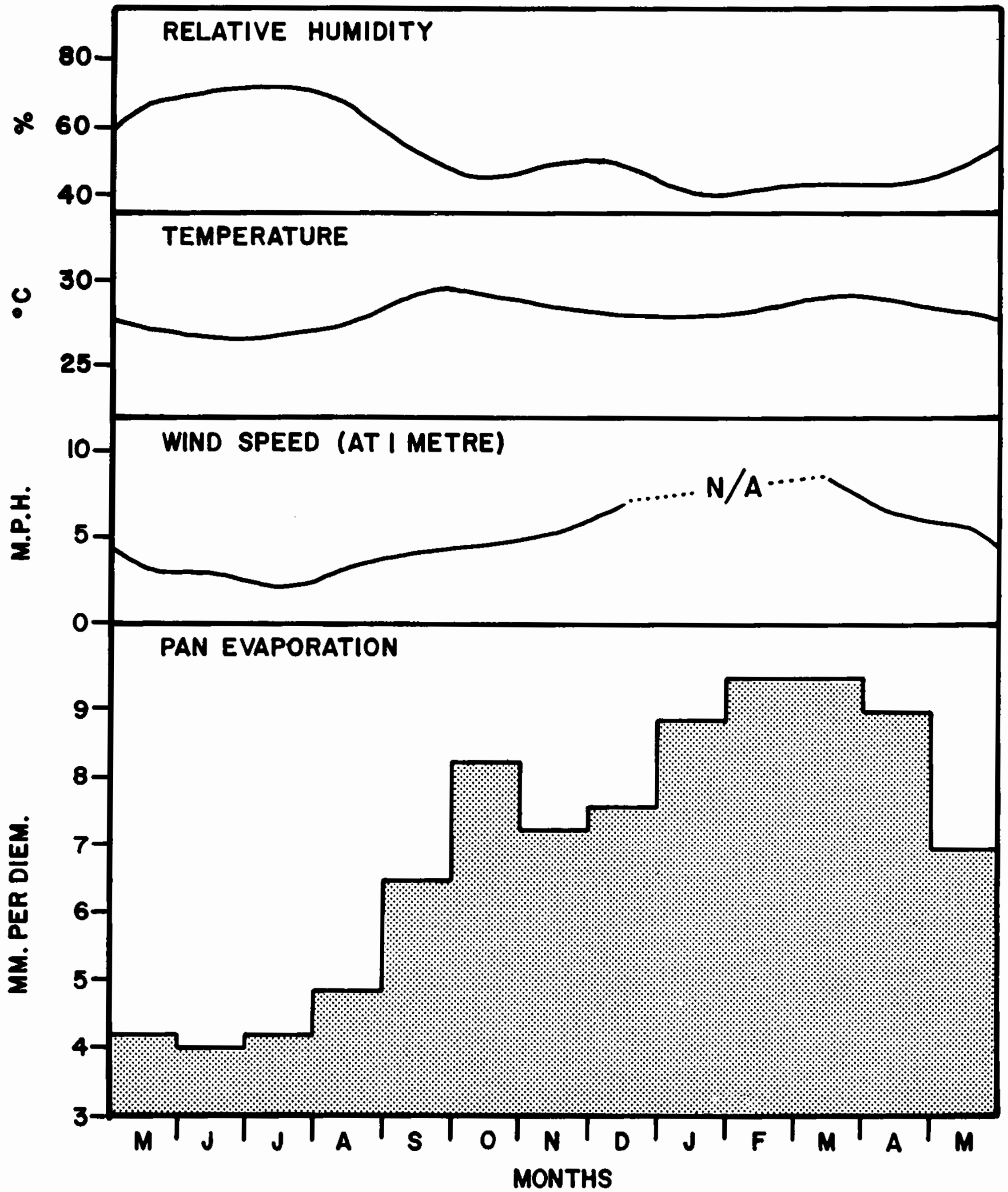
TABLE 7: Potential evapotranspiration, St. Ignatius, 1963/1964

	Mean daily pan evap. (mm.)	Mean daily lysimeter P.E.T.(mm.)	Mean daily atmometer evap. (mm.)
Rainy season (May 4 - Aug 21)	4.2	N/A	N/A
Early dry season (Sept - Dec)	7.3	7.1	7.6
Late dry season (Jan - Mar)	9.2	9.2	9.2

It is thus clear that the seasonality of the savanna ecoclimate, in the first instance a product of the rainfall regime, will be intensified by variations in potential evapotranspiration. In particular the rapid increase in potential evapotranspiration in the weeks immediately following the rainy season results in a rapid depletion of soil moisture capital and a relatively abrupt transition to a state of desiccation; similarly, the high rates throughout the dry season result in very rapid removal of the limited rain that does fall.

In Figure 3 pan evaporation during 1963/1964 is compared graphically with several meteorological factors. The effect of wind speed is particularly important; its potency can be illustrated by a comparison of the measured figures for potential evapotranspiration with those based on the Thornthwaite computation (Thornthwaite & Mather, 1957), which does not directly take account of variable wind speed. During the rainy season, when wind speeds were at a minimum, both measured and computed figures were relatively close and the monthly figures for mean daily evaporation fell within the range 4.2 - 4.7 mm; by contrast, in the dry season the measured figures rose to a mean monthly total of 9.4 mm per diem during March, while the computed Thornthwaite figure did not exceed 5.1 mm per diem in that or in any other month of the year.

FIG. 3 : PAN EVAPORATION AND SELECTED METEOROLOGICAL FACTORS, ST. IGNATIUS, 1963-64



Actual Evapotranspiration

Rates of actual evapotranspiration inevitably diverge from the potential figure. During the latter half of the rainy season (July 2 - August 21) actual rates were measured with three lysimeters under Pangola grass (Digitaria decumbens). The actual evapotranspiration over this period was 168 mm, or 3.3 mm per diem, which represents approximately three-quarters of the potential rate.

During the earlier part of the rains (May 4 - July 1) lysimeter readings were not available, but pan evaporation figures remained very similar, and the rate of actual evapotranspiration at this time is unlikely to have diverged greatly from 3.3 mm per diem.

Thus, an approximate estimate of water surplus can be made for this period :-

> Actual evapotranspiration during rainy season (May 4 - August 21) at 3.3 mm per diem = 363 mm
>
> ∴ Water surplus during rainy season, when 1,350 mm of rain fell = 987 mm*

This large water surplus in 1963, spread over a period of 110 days, was partly retained by the soil, a proportion going to make up the soil moisture deficiency at the end of the dry season, as well as contributing to the ground water reserves, but throughout the northern Rupununi an appreciable proportion of the surplus ran off the surface of the land and was a key factor in the widespread flooding and waterlogging of the lowland

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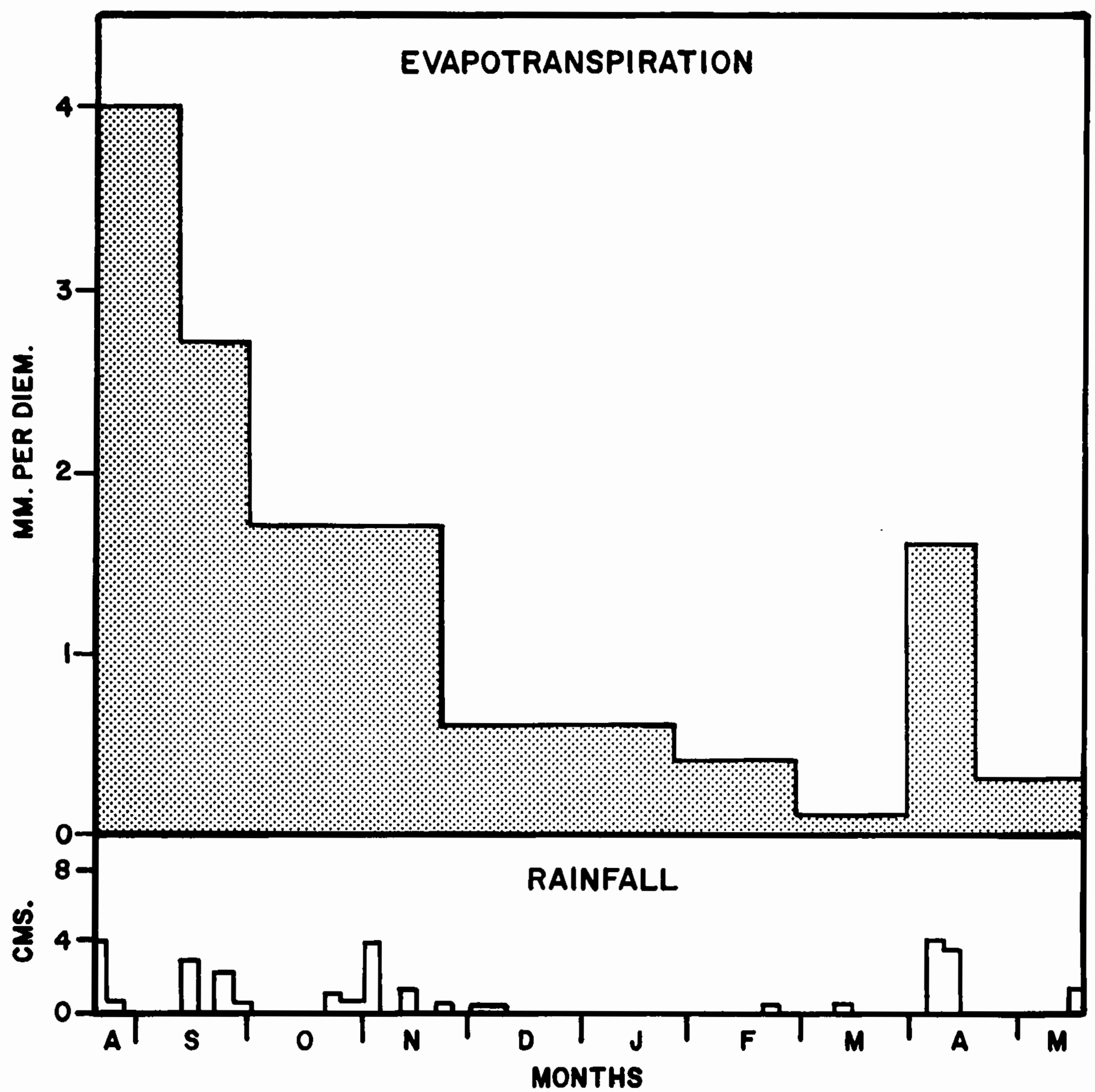
* How far the transpiration rate of the exotic Pangola grass (Digitaria decumbens) differs from native bunch grasses is not yet certain, but early comparative lysimeter results indicate no great discrepancy.

FIG. 4: ACTUAL EVAPOTRANSPIRATION AT SITE 24, NEAR ST. IGNATIUS, DRY SEASON, 1963-64



savanna during the months June to August; the effect is clearly visible in Figure I, which shows the extreme flooding of the Takutu River at this time.

In the dry season progressive moisture depletion of the soil took place, and actual evapotranspiration dropped well below the potential rate. No direct measurements of actual evapotranspiration were made during this period, but from soil moisture determinations it was possible to gain an idea of the rates at which water left the soil. Figure 4 illustrates actual evapotranspiration during the dry season, 1963/1964.

From this it is apparent that the period immediately after the rains had the highest rate of actual evapotranspiration; thereafter, under open grass savanna, a rapid reduction in evapotranspiration took place as the amount of water available in the soil was progressively reduced; under wooded savanna conditions, actual evapotranspiration would be maintained at a higher level during the dry season, as the trees draw on deeper moisture reserves, but only with the fresh onset of the rains and a resurgence of plant growth, would actual evapotranspiration on either site reach a high proportion of the potential.

One concludes, therefore, that although climatic influences on water use are pre-eminent during and immediately after the wet season, in the subsequent period, as ecoclimatic conditions become more acute, water use will reflect more directly the nature of plant growth and local soil conditions on any given site.

CHAPTER 5

SOIL WATER CONDITIONS: II. SOILS

(a) Introduction

Nowhere in the northern Rupununi, save in exposures along the major river banks, is bedrock visible, and the soils of the area are developed totally from alluvial materials, which have been deposited since Tertiary times in the northern Savanna trough. The soil profiles are for the most part mature, reflecting the powerful chemical and physical weathering forces that have acted upon them.

Eluviation of clay from the surface horizons, and oxidation and hydration of iron, and to a lesser extent manganese, have given rise to a pronounced sesquioxide content in the soil, while the leaching of organic matter and soluble bases through the acid profiles has reached an advanced stage. In the less well-drained sites translocation of iron has taken place under conditions of intense reduction, and has led in some sites to the accumulation of iron concretions within the zone of water table fluctuation.

Texturally, the zonal soils within the area have a high sand content, reflecting the arenaceous nature of their alluvial parent material. This is most marked in the eluviated A horizon, but continues into the B and C horizons, where loam and sandy clay loam textures are common. Among the more recent hydromorphic soils, developed chiefly on fluvio-lacustrine sediments, textures are heavier and there is some layering through the profile. Similar eluviation has taken place, but is less pronounced; silty clay and silty clay loam materials are commonly found, but may be occasionally interspersed with more sandy layers.

Differences in soil colour are pronounced between the zonal and intrazonal soils*. The former are predominantly yellow brown (Hue 10YR), red yellow (Hue 5YR), and red (Hue 2.5YR), with a few strong browns (Hue 7.5YR), and most display high chromatic values (Chroma 6-8). Topsoils have slight organic darkening, with colours becoming more red and brown in the B horizon, and paling again to yellow or grey as water effects become visible. In contrast, the hydromorphic soils, after a darker A horizon, rapidly turn to grey or light grey (Hue 5Y, 2.5Y, 10YR, with Chroma of 1), with variably coloured mottling, and in many places red (Hue 10R) iron concretions, as ground water effects become visible.

The soils are generally low in mineral nutrients and organic matter. The alluvial parent materials have been extensively reworked, and have undergone intensive weathering, and as a result are extremely impoverished. Their low organic content is attributable principally to the influence of fire and climate. The regular burning of the savanna destroys much of the organic debris, and only in very poorly drained swamp sites, where perennially moist conditions inhibit burning, is there any strong accumulation of humus in the topsoil. In addition, the high temperatures and heavy seasonal rainfall accelerate the processes of organic decomposition and leaching, with the result that rarely does the A_1 organic matter content in savanna soils exceed 2%, and in sandy topsoils is regularly below 1%. Table 8 illustrates the organic matter content of representative soils in the northern Rupununi.

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* Soil colours are described according to the Munsell soil colour notation (Munsell, 1954), and refer in all cases to samples in the moist state.

TABLE 8: Organic matter content of representative soils, northern Rupununi

Well drained savanna latosol		Moderately well drained savanna latosol		Very poorly drained swamp humic glei	
Sample depth (cm.)	Organic matter %	Sample depth (cm.)	Organic matter %	Sample depth (cm.)	Organic matter %
0-8	0.8	0-15	0.7	0-13	7.1
8-46	0.5	15-41	0.4	13-25	1.6
46-117	0.2	41-89	0.2	25-58	0.7
117-188	0.2	89-183	0.1	58-102	-

(Analyses from Loxton, Rutherford and Spector, 1958, and Stark, Rutherford and Spector, 1959)

As well as adversely affecting the chemical status of the soil, the low organic content influences strongly its physical nature. Humic material, with an adsorptive capacity far in excess of any mineral soil, and an ability to promote soil granulation, will under normal circumstances have a beneficial effect on the porosity of the soil. In the Rupununi this beneficial effect is largely absent, and as a result soil porosity and moisture retention are generally at a sub-normal level.

The only soils wherein structural characteristics are developed, and can be expected therefore to have a beneficial effect on porosity, are the finer textured, hydromorphic soils of the lowland trough. In the Maracanata Basin, for example, moderate to strong, fine platy structures are common in silty clay to silt loam textures in B and C horizons, resulting from the seasonal wetting and drying of the profile, and the aggregating effect of de-hydrated iron and aluminum oxides. In contrast, the elevated and better drained zonal soils display a singular absence of structure throughout the profile, and have lowered porosity.

(b) Soil Forming Processes

The zonal soils of the Rupununi conform most closely in their character to the latosolic great soil group*, although their latosolic characteristics are weakly developed. This is principally due to the nature of the soil parent materials, rather than to the operation of alternative soil forming processes.

The most prominent feature of latosolisation is the red and yellow colouration through profiles, indicating the presence of sesquioxides in the soil. A few sites display a tendency to bleaching of the A_2 horizon, more characteristic of podzolic soils, and it appears that the acidity of Rupununi profiles, generally between pH 4.0 - 5.5, will locally facilitate the partial leaching of sesquioxides from the A_2 horizon in a manner atypical of ortho-latosolic conditions. The tendency to leaching, however, is not widespread, and pronounced colouration is to be found throughout most profiles.

Under optimum conditions two other features are normally associated with the process of latosolisation, namely: an accumulation of hydrous oxide clays, and related to this, a granular structural development which promotes excellent internal drainage (Lyon, Buckman & Brady, 1952). In the Rupununi both these features are weakly developed on account of the inherently arenaceous nature of the parent materials of the zonal soils, which results in a high sand content throughout the profile. The condition may be partly due also to the high acidity of the soil which inhibits the mobilisation of silica, normally associated with the latosolic process.

* See Kellogg, C.E., 1949, 'Preliminary Suggestions for the Classification and Nomenclature of Great Soil Groups in Tropical and Equatorial Regions.' Commonwealth Bureau of Soil Sci., Tech. Comm. No. 46.

Table 9 illustrates the mineralogical composition of a moderately well drained, yellow latosolic profile with slight plinthite development in the lower C horizon, developed on sheetwash alluvium.

TABLE 9: Mineralogical composition of latosolic soil, northern Rupununi
Site 12 Location: Moco Moco

Depth (cm.)	Horizon	Texture	SiO_2 %	Al_2O_3 %	Fe_2O_3 %	Others %	pH
0-12	A	Loam	76.6	17.7	3.6	2.1	4.8
12-45	B	Loam	72.9	20.9	4.4	1.8	4.8
45-60*	C_{cn}	Gravelly loam	63.1	22.5	12.5	1.9	5.0
60-120	C_2	Silt loam	66.9	25.6	5.3	2.2	5.2
120-180	C_3	Silt loam	60.4	31.6	5.7	2.3	5.4

(Based on mineralogical analyses undertaken by the Geological Survey Dept., British Guiana).

The most significant features of the profile are :-

(i) The persistence of iron oxides through the profile, even though slight downward translocation of iron is apparently taking place under conditions of acidity.

(ii) The high SiO_2 content through the profile, which decreases with depth as clay is eluviated through the profile, and reflects the arenaceous nature of the parent materials.

These two features appear to be widely typical of the weakly developed latosolic soils of the northern Rupununi, wherein parent materials have modified, but not essentially changed, the normal soil forming processes.

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* The high iron content in this horizon is due to the presence of secondary ironstone gravel, laid down with the parent material, and is not a product of iron translocation within the profile; the colour and hardness of the gravel clearly distinguish it from the iron concretionary material which is currently forming within the C horizon.

Within the belt of well drained and moderately well drained zonal soils, extensive areas of gravel regosols also occur, developed on secondary lateritic gravel deposits. In spite of their azonal character, they too show evidence of latosolic processes. The red and yellow colourations are similar to adjacent latosols, and sesquioxides are prevalent throughout the profiles.

Finally, there is a large group of hydromorphic soils developed on low-lying, fluvio-lacustrine deposits in the northern part of the region. In these soils, which are modified by the occurrence of high seasonal water tables, translocation of iron has taken place under conditions of intense chemical weathering within the zone of water table fluctuation. The zone is characterised by the presence of ferrous iron, giving rise to pronounced mottling, and of neutral grey colours, which are a product of gleying under prolonged anaerobic conditions. In places plinthite has formed, although there is no tendency towards pan formation; such soils have been classified as ground water laterites. Where translocation of iron has resulted only in mottling and soft concretionary development, low-humic glei or humic glei soils have been recognised.

(c) Laterisation in Northern Rupununi Soils

The term 'laterisation' is used to refer to the pedogenic process whereby layers of aluminum-rich soil, associated with hardened iron concretions or plinthite, and incipient forms thereof, are formed. This process has been widely considered to take place under conditions where basic weathering leads to the preferential mobilisation of silica, and retarded mobilisation of iron and aluminum oxides. Under these conditions aluminum and iron hydroxides accumulate as residual features. (Carter & Pendleton, 1956; Mohr & Van Baren, 1959).

In the acid soils of the Rupununi, where ground water is frequently at or within a few metres of the surface during the wet season, iron concretionary materials occur in many soil profiles. The processes of laterisation, however, are somewhat different from those described above.

In the weakly developed latosolic soils concretionary materials occur at depth in the C horizon. This is mostly due to translocation of iron within the zone of water table fluctuation, but in some profiles a degree of vertical movement of iron also appears to be taking place (See Table 9); it is thus difficult to think in terms of a residual laterisation process.

Carter & Pendleton (1956), taking note of a similar movement of iron through tropical soil profiles described by Ellis (1952) and Nye (1955/1; 1955/2) in Africa, go so far as to suggest that a single pedogenic process operates in all humid environments, namely, a podzolic process, concluding that laterite is an illuvial phenomenon of iron accumulation in the B horizon, formed under processes closely akin to podzolisation, and differing markedly from the classic residual theory.

To a degree this is true in the acid zonal soils of the Rupununi, in that some vertical translocation of iron is taking place in the profile, and that iron accumulation is more an illuvial than a residual feature; but the principal translocation of iron appears to be associated more directly with ground water fluctuations than vertical water percolation, and is not specifically a feature of the B horizon. Also, as was noted in Section b, other apparently podzolic features observed in Rupununi soils are either very weakly developed, e.g., the bleached A_2 horizon, or are due, as in the case of the high SiO_2 content, more to the inherent characteristics of the parent materials than to the operation of podzolic processes.

In the hydromorphic soils a much higher degree of iron mobilisation has taken place through the profile. Most sites display a deep zone of mottling, extending from close to the surface to four or five metres in depth, through which are dispersed numerous iron concretions with varying degrees of hardness. Such an accumulation is scarcely a product of vertical movement of iron from the surface horizons as is suggested in the podzolic process. Not only do concretionary materials occur very close to the surface in many sites, but also the vertical movement of water through these soils, which are waterlogged for several months each year and under conditions of drought for much of the remainder, is in fact not very great, and is certainly less than in the free draining zonal soils where less, rather than more translocation of iron has taken place.

Conditions more akin to those prevailing in the Rupununi have been described by Marbut (1934) in the Amazon valley, where below the solum in vertical sequence there occur an iron oxide layer, a mottled zone and a grey zone. The mottled zone is coincident with the zone of water table fluctuation and is considered by Mohr & Van Baren (1959) to be a product of it.

Similarly, in the Rupununi the occurrence of mottling and iron concretions, although the latter are scattered within the mottled zone rather than forming an indurated iron oxide horizon above it, appears to be the result of precipitation of iron that may be partly derived from the surface horizons, but results principally from local translocation within the zone of water table fluctuation*.

There remains the question in the Rupununi of why iron concretions are dispersed through the permeable mottled zone, without any horizon of intense iron accumulation as described by Marbut (1934). The absence of an indurated iron layer may represent a youthful stage in the process

* In addition, it is possible that some iron may have entered the profile from the underlying grey zone, although the operation of such a process is repudiated by Nye (1955/1) in West African studies.

of laterisation; in one respect it can be argued that continuing landscape rejuvenation in the Rupununi will lead to regional lowering of water tables and ultimately to hardening of the upper part of the mottled zone to a comparably indurated condition. However, it appears that under present conditions factors other than 'youthfulness' have worked against the accumulation of a specific hardened iron horizon or pan within the profile.

Mohr & Van Baren (1959), when discussing conditions in the Amazon valley, state that :-

> 'The top of the mottled layer represents the top of the ground water for a considerable part of the year and the thickness of the layer is approximately the extent of the annual fluctuation of the ground water surface.'
>
> E.C.J. Mohr & F.A. Van Baren, 1959, pp. 366-7.

In the soils of the Rupununi, however, the ground water rarely remains at a constant level for any length of time. Three principal phases of ground water status are discernible :-

(a) A rapid rise of ground water at the start of the rainy season.

(b) A phase of short-period ground water fluctuation in accordance with immediate rainfall conditions, lasting for two to three months during the rainy season.

(c) A continuous and gradual lowering of ground water throughout the long dry season.

Assuming that iron is precipitated in a zone at or near to the water table, it is understandable, with a mobile ground water regime which fluctuates over several metres, for the precipitation to be dispersed through the mottled zone, rather than concentrated into an indurated horizon associated with a period of ground water stability. The situation is aggravated, moreover, by the annual variability of rainfall in the Rupununi, for even the temporary periods of water table stability that occur briefly each year are likely to take place at different levels in accordance with the rainfall regime of that particular year.

In conclusion, one may state that the laterisation processes, which normally lead to iron-rich and impermeable soil horizons, have not as yet advanced far enough in the Rupununi to cause drainage impedance. As will be later shown, the seasonal excess of water in the area is more due to inadequate surface drainage across the low-lying watershed zone of the Amazon and Essequibo river systems, although in the future the soils may well 'mature', as a result of drainage rejuvenation, into a condition where pedologic rather than hydrologic impedance prevails.

(d) Classification of Soils of the Northern Rupununi

A broad distinction has already been drawn between the better drained zonal and azonal soils, and the intrazonal soils which have been subjected to hydromorphism. Altogether 111 deep augur profiles (0-180 cm) and 50 shallow augur profiles (0-100 cm) were examined and described. These have been assigned to the following great soils groups :-

Zonal/Azonal Soils

i. Latosols

ii. Regosols

Intrazonal Soils

i. Ground water laterites

ii. Low-humic gleis

iii. Humic gleis

In order to refine these soil units, with special reference to plant growth, each site was allotted a drainage category. The categories used were based on the United States Department of Agriculture classification (USDA, 1951), but were modified and given more precise limits in accordance with local conditions. The following categories, which are defined in Appendix 2, were used :-

i. Excessively drained

ii. Well drained

iii. Moderately well drained

iv. Imperfectly drained

v. Poorly drained

vi. Very poorly drained

Using the above criteria it was possible to recognise the following major soil-drainage units in the region :-

i. Excessively drained regosols

ii. Well drained latosols

iii. Moderately well drained latosols

iv. Imperfectly drained ground water laterites

v. Poorly drained ground water laterites

vi. Poorly drained low-humic gleis

vii. Very poorly drained humic gleis

There was a number of exceptions to these units, but of local occurrence, and representing for the most part intermediate stages between groups. Three deserve mention :-

(a) Ground water laterite soils with moderately well drained profiles, in sites where ground water levels appear in the past to have been lowered, resulting in re-latosolisation of the profile, but with plinthite remaining in the C horizon.

(b) Poorly drained soils, where peaty topsoils have developed and humic, rather than low-humic glei soils formed under prolonged, but not perennially wet conditions.

(c) Very poorly drained soils, which have developed as humic gleis, but have been subsequently truncated by burning of the peaty horizon.

In the subsequent pages a typical profile is described within each soil-drainage unit*.

i. Excessively drained regosols

The excessively drained regosolic soils are developed on fine to medium secondary lateritic gravel deposits (Lethem-Yupakari land unit), aeolian materials (Lethem-Yupakari land unit) and on some mountain outwash sands and gravels. The gravel ridge terrain, which forms the largest proportion of the regosolic soils, is flanked marginally by an overburden of sheetwash derived from it. Ridge slopes vary from 2 - 20 degrees, and in many areas fossil laterite outcrops occur. By comparison, the relief of the aeolian and outwash materials is much less pronounced, and as a result surface water run-off somewhat reduced.

Range in characteristics

The soils range from gravels and sands to highly porous loams. Most of the profiles are texturally uniform, although in the mountain outwash deposits, silty horizons may be interbedded in the sands and gravels. All profiles are structureless. Colours are for the most part

* The United States Department of Agriculture 'Soil Survey Manual' (USDA, 1951) has been used as a basis for description of all soils.

red - yellow (Hue 7.5YR, 5YR), but paler hues are found.

Soil Profile

Site 15 Location: St. Ignatius

0 - 25 cm	Yellowish red (5YR4.6), fine gravelly loam. Structureless. Few roots. pH 4.6.
25 - 125 cm	Yellowish red (5YR5.6), fine gravelly loam. Structureless. Few roots. pH 4.8.
125 - 180 cm	Yellowish red (5YR5.6), fine gravelly sandy clay loam. Structureless. Few roots. pH 5.0.

Parent material: Secondary lateritic gravel.

Relief: Very gently undulating (less than 1 degree).

Soil surface: Slight crustal compaction, with a covering of very fine loose gravel.

Drainage: Excessively drained. Water table perennially below 200 cm.

Herbaceous root zone: 0-180 cm.

Vegetation: Wooded savanna (campo coberto), with bunch grass and sedges.

Dominant trees: Curatella americana, Plumeria inodora, Antonia ovata.

Sub-dominant trees: Byrsonima spp.

Dominant herbs: Trachypogon plumosus, Fimbristylis ferruginea.

Sub-dominant herbs: Mesosetum loliiforme, Buchnera elongata.

ii. Well drained latosols

The well drained latosolic soils are developed on sheetwash alluvium derived from adjacent secondary lateritic gravels (Lethem-Yupakari land unit), and to a lesser extent on sandy terrace deposits (Takutu - Proto-Berbice land unit). Sites are very gently to gently sloping, and on terrace deposits there is a tendency to undulation. Slopes rarely exceed 2 degrees. This unit grades downslope into the moderately well drained latosols from which it is distinguishable by lower ground water levels in the wet season. In many sites close to secondary lateritic ridges regosolic gravel materials appear as a D horizon beneath the sheetwash; where the sheetwash is 50 cm or more in depth, the site has been classified as latosolic.

Range in characteristics

Textures of the A horizon, which is commonly 20-40 cm thick, are sandy loam or loam changing in the B and C horizons to loam or sandy clay loam in the sheetwash, and sandy clay loam in the terrace deposits. The latter have a small but noticeable coarse sand content in many profiles, which increases slightly with depth. Structural development is negligible in nearly all sites. Colour differences exist; the terrace deposits are commonly brownish yellow or yellowish brown (Hue 10YR), while the sheetwash profiles are redder (Hue 2.5YR, 5YR, 7.5YR). A few iron concretions may occur below 150 cm in the C horizon of these soils.

Soil Profile

Site 24 Location: Manari

A_1	0 - 2 cm	Brown (10YR5.3), sandy loam, with few very fine secondary lateritic concretions. Structureless; very friable. Many roots. pH 4.8.
A_2	2 - 23 cm	Strong brown (7.5YR5.6), sandy loam, with few very fine secondary lateritic concretions. Structureless; very friable. Common roots. pH 4.8.
B	23 - 115 cm	Strong brown (7.5YR5.6), sandy clay loam, with few very fine secondary lateritic concretions. Structureless; friable. Common roots. pH 5.0.
C_1	115-150 cm	Reddish yellow (7.5YR6.6), loam, with few very fine secondary lateritic concretions. Structureless; very friable. Slight gleying. Few roots. pH 5.0.

C_2	150 - 190 cm	Strong brown (7.5YR5.6), loam, with frequent yellowish red (5YR5.8) mottles and abundant gleying; common incipient iron concretions. Structureless; common, medium to fine pores; very friable. Few roots. pH 5.4.
D	190 cm+	Medium secondary lateritic gravel.

Parent material: Sheetwash alluvium, from secondary lateritic gravels.

Relief: Very gently sloping (less than 1 degree).

Soil surface: Pronounced crustal compaction, partly covered by loose aeolian sandy material.

Drainage: Well drained; water table perennially below 150 cm, with estimated maximum depth of 4-5 metres in dry season.

Herbaceous root zone: 0-180 cm.

Vegetation: Wooded savanna (campo sujo), with bunch grass and few sedges.

Dominant trees: Curatella americana, Plumeria inodora.

Sub-dominant trees: Bowdichia virgilioides.

Dominant herbs: Trachypogon plumosus, Fimbristylis ferruginea, Mesosetum loliiforme.

Sub-dominant herbs: Bulbostylis conifera, Galactia jussieuana, Stenophyllus paradoxa.

iii. Moderately well drained latosols

The moderately well drained latosolic soils are developed on sandy terrace deposits (Takutu - Proto-Berbice land unit), levée and outwash deposits (Lowland unit), and to a lesser extent on sheetwash alluvium derived from secondary lateritic gravels (Lethem-Yupakari land unit). Sites are on slightly elevated ridges or gentle slopes, and frequently represent intermediate zones between well drained latosols and ground water laterites. Slopes rarely exceed 2 - 3 degrees.

Range in characteristics

Surface textures are commonly loamy sand to sandy loam, changing to loam or sandy clay loam in the B and C horizons. In some profiles platy and blocky structure is visible in the B and C horizons. Colours range from yellow browns (Hue 10YR) in the upper horizons to strongly grey-gleyed and mottled lower layers. A few iron concretions are likely to be found at depth in the profile.

Soil Profile

Site 05 Location: St. José

A_1	0 - 15 cm	Dark greyish brown (2.5Y4.2), loamy sand to sandy loam. Structureless; very friable. Many roots. pH 4.0
A_2	15 - 55 cm	Dark greyish brown (10YR4.2), sandy loam. Structureless; very friable. Common roots. pH 4.8.
B	55 - 135 cm	Greyish brown (2.5Y5.2), sandy clay loam. Structureless; friable. Few roots. pH 4.8.
C_1	135 - 175 cm	Light brownish grey (2.5Y6.2), sandy clay loam, with many, medium reddish yellow (7.5YR6.6) mottles and slight gleying. Structureless; firm. Very few roots. pH 4.9.
C_2	175 - 200 cm	Olive grey (5Y5.2), sandy clay loam, with few, medium reddish yellow (5YR6.6) mottles and slight gleying. Structureless; firm. Very few roots. pH 4.8.

Parent material: Sandy terrace deposits.

Relief: Very gently undulating (slope less than 1 degree).

Soil surface: Loose and sandy, with tendency to slight crustal compaction at about 5 mm.

Drainage: Moderately well drained; water table at approximately 100 cm during wet season, 1963. Lowest recorded water table: 537 cm (April 1, 1964).

Herbaceous root zone: 0-180 cm.

Vegetation: Wooded savanna (campo cerrado), with bunch grass and few sedges.

Dominant trees: Byrsonima spp.

Sub-dominant trees: Curatella americana, Bowdichia virgilioides, Plumeria inodora.

Dominant herbs: Trachypogon plumosus, Gymnopogon foliosus, Eragrostis glomerata, Fimbristylis ferruginea.

Sub-dominant herbs: Bulbostylis conifera, Aristida radiata.

iv. Imperfectly drained ground water laterites

The imperfectly drained ground water laterites are developed on a variety of parent materials, predominantly sheetwash alluvium, derived from secondary lateritic gravels (Lethem-Yupakari land unit), together with terrace and levée deposits, and fluvio-lacustrine alluvium. Texture and other profile characteristics vary considerably, but the sites are commonly at a relatively low relief level, and are characterised by level to gently sloping topography, which rarely exceeds 2 degrees in slope. This unit is distinguished from latosolic soils by the occurrence of plinthite and of more extensive mottling and gleying.

Range in characteristics

Surface textures are generally sandy loam, but heavier A horizons may occur. B and C horizons have loam, clay loam and sandy clay loam textures depending on the nature of the parent material. In the sites examined little structural development was found. Gleying and mottling may occur anywhere from the surface downwards, but between 50-100 cm they first become strongly developed. Plinthite occurs in the C horizon, most commonly commencing between 100-150 cm. A few sites have a thin, mucky A_1 horizon.

Soil Profile

Site 07 Location: St. Ignatius

A_1	0 - 7 cm	Dark grey (5Y4.1), sandy loam, with total gleying and mottled root channels. Structureless; very friable; few fine pores. Many roots. pH 4.6.
G_1	7 - 22 cm	Grey (5Y5.1), sandy loam, with total gleying and mottled root channels. Structureless; very friable; few fine pores. Many roots. pH 4.8.
G_2	22 - 90 cm	Grey (5Y5.1) to pale olive (5Y6.3), sandy clay loam, with common, medium yellowish red (5YR5.8) mottles; gleyed matrix. Structureless; firm; few fine pores. Few incipient iron concretions. Few roots. pH 5.0.
CG	90 - 200 cm	Grey (5Y6.1), loam, with common, medium strong brown (7.5YR5.8) mottles; gleyed matrix. Structureless; firm. Common plinthite. pH 5.2.

Parent material: Sheetwash alluvium, derived from secondary lateritic gravels.

Relief: Very gently sloping (less than 1 degree).

Soil surface: Firm and slightly compacted. Slight aeolian accumulation.

Drainage: Imperfectly drained; water table at or close to surface for 2 1/2 months during 1963. Lowest recorded water table: 350 cm (February 14, 1964), probably falling to 4-5 metres by end of dry season.

Herbaceous root zone: 0-90 cm.

Vegetation: Herbaceous savanna (campo limpo), with sedges and bunch grass.

Dominant herbs: Fimbristylis spp., Trachypogon plumosus, Aristida tincta.

Sub-dominant herbs: Byrsonima verbascifolia, Dichromena ciliata.

v. Poorly drained ground water laterites

The poorly drained ground water laterite soils are developed on fluvio-lacustrine deposits (Lowland unit), eroded sandy terrace deposits (Takutu - Proto-Berbice land unit) and on small areas of low-lying sheetwash alluvium (Lethem-Yupakari land unit). Sites are flat or very gently sloping, and the soils are characterised by the presence of a totally gleyed profile, with frequent mottling and iron concretions. They are distinguished from imperfectly drained soils by the greater intensity of chemical weathering, resulting from prolonged flooding and waterlogging, and from low-humic glei soils by the presence of plinthite in the profile.

Range in characteristics

Surface textures range from silty loam to sandy loam. Lower horizons are heavier, with sandy clay loam, clay loam, loam or silty clay loam textures, depending on the nature of parent materials. All profiles are totally gleyed below the A_1 horizon, which itself displays varying degrees of organic darkening. A number of profiles display platy or other structural development, usually associated with the finer textured horizons, but this is not well developed. Plinthite occurs anywhere below the A_1 horizon, but does not become common until the lower profile; there is no evidence of iron panning.

Soil profile

Site 90 Location: Maracanata

A_1	0 - 15 cm	Dark greyish brown (2.5Y4.2), loam, with many, medium yellowish red (5YR5.8) mottles. Structureless; firm; many fine pores. Many roots. pH 4.6.
G_1	15 - 100 cm	Light grey (2.5Y6.0), clay loam, with many, medium yellowish red (5YR5.8) mottles. Structureless; firm; many fine pores. Few roots. pH 4.8.

G_2 100 - 145 cm Light grey (2.5Y6.0), heavy clay loam, with many, medium yellowish red (5YR5.8) mottles. Structureless; firm; few fine pores. Few incipient iron concretions. Very few roots. pH 4.9.

CG 145 - 200 cm Light grey (2.5Y6.0), clay loam, with many, medium red (10R4.6) mottles. Structureless; firm. Much plinthite. pH 4.9.

Parent material: Flood plain alluvium.

Relief: Flat and level.

Soil surface: Very firm and uneven.

Drainage: Poorly drained; inundated for approximately 2 1/2 months during 1963. Lowest recorded water table: 420 cm (April 11, 1964).

Herbaceous root zone: 0-100 cm.

Vegetation: Herbaceous savanna (campo limpo), with sedges.

Dominant herbs: Fimbristylis spp., Scleria spp., Rhyncospora spp.

vi. Poorly drained low-humic gleis

The poorly drained low-humic glei soils are developed on fluvio-lacustrine deposits (Lowland unit), and occur in flats and very gently sloping depressions, which are seasonally inundated. Fine textured horizons in some profiles may impede drainage and prolong the period of inundation. They are distinguished from ground water laterites by the occurrence of somewhat heavier textures and by the absence of a plinthite zone, although soft iron concretionary development may occur in some profiles, and from humic glei soils by the absence of a thick organic A_1 horizon.

Range in characteristics

Textures are variable and layering is common. The commonest textures are clay, silty clay, silty clay loam and silty loam, with a few, more sandy horizons. In the finer textured horizons platy and blocky structure is common. Intense gleying (Hue 5Y, 2.5Y, 10YR) and mottling occur throughout the profiles, with very abundant mottling in many horizons.

Soil Profile

Site 76 Location: Rego Creek

G_1	0 - 15 cm	Grey (2.5Y6.0), silty loam, with many, medium yellowish brown (10YR5.8) mottles. Structureless; friable; very many pores. Common roots. pH 4.8.
G_2	15 - 115 cm	Grey (2.5Y6.0), silty clay loam, with almost total yellowish brown (10YR5.8) mottles. Structureless; firm; very many pores. Few roots. pH 4.9.
G_3	115 - 190 cm	Light grey (10YR7.1), loam, with almost total yellowish brown (10YR5.6) mottles. Moderate, fine sub-angular blocky structure; friable; few fine pores. pH 5.0.
G_4	190 - 200 cm	Light grey (10YR7.1), fine sandy loam, with almost total yellowish brown (10YR5.6) mottles. Structureless; very friable. pH 5.0.

Parent material: Fluvio-lacustrine alluvium.

Relief: Flat and level.

Soil surface: Very firm and uneven.

Drainage: Poorly drained. Probably inundated for at least three months, 1963. Water table below 200 cm by mid-October, 1963.

Herbaceous root zone: 0-110 cm.

Vegetation: Herbaceous savanna (campo limpo), with sedges.

Dominant herbs: Rhyncospora barbata, Fimbristylis spp.

Sub-dominant herbs: Aristida spp.

vii. Very poorly drained humic gleis

The very poorly drained humic glei soils are developed on fluvio-lacustrine and lacustrine sediments, and occur in flat, seasonally inundated seepage swamps, where water tables remain perennially at or close to the surface. The soils are characterised by intense chemical reduction, and are distinguished from the low-humic gleis and ground water laterites by the presence of an organic A_1 horizon at least 15 cm thick. There is an absence of any hardened iron concretionary material in the profile.

Range in characteristics

The A_1 horizon varies in thickness from site to site in accordance with local drainage conditions, and tends to thin out marginally. In places the A_1 horizon has been burnt out and truncated humic glei soils result. The commonest textures are clay, silty clay, silty clay loam and silty loam. The profiles are uniformly intensely gleyed with well developed mottling.

Soil Profile

Site 110 Location: Maracanata

A_1	0 - 18 cm	Black (2.5Y2.0), highly humic, silty loam. Weak, fine crumb structure; very friable; common pores. Many roots. pH 4.8.
A_1	18 - 25 cm	Black (10YR2.1), humic, silty loam. Structureless; very friable; few pores. Few roots. pH 4.9.
G_1	25 - 50 cm	Grey (2.5Y5.0), silty clay, with common, fine yellowish brown (10YR5.6) mottles. Moderate, fine crumb structure; very firm; few fine pores. Few roots. pH 5.2.
G_2	50 - 180 cm	Light grey (10YR7.1), clay loam, with common, small brownish yellow (10YR6.8) mottles. Weak, fine crumb structure to 110 cm, thereafter structureless; firm; few fine pores. Few roots. pH 5.2.

Parent material: Lacustrine alluvium within seepage swamp.

Relief: Very gently sloping (less than 1 degree).

<u>Soil surface</u>: Soft.

<u>Drainage</u>: Very poorly drained; negligible internal drainage. Site inundated for 7-8 months. Lowest recorded water table: 20 cm (April 11, 1964).

<u>Herbaceous root zone</u>: 0-75 cm.

<u>Vegetation</u>: Sedge swamp.

<u>Dominant herbs</u>: Cyperus articulata, Eleocharis geniculata.

CHAPTER 6

SOIL WATER CONDITIONS: III. THE NATURE OF THE ROOT ZONE AND THE WATER RELATIONS WITHIN IT

(a) The Herbaceous Root Zone

In soil studies concerned with the growth of plants, whether natural or cultivated, the depth of soil from which plants draw their water supply, i.e., the rooting zone, becomes of prime importance. G.R. Clarke, speaking of British soils, states :-

> 'The choice of a 30 in. profile is to some extent arbitrary, but repeated observations of profiles in arable soils of this country have shown that few visible roots of crops are normally to be found below this depth.'
>
> G.R. Clarke, 1961, p. 176.

In the grassland environment of the Rupununi where grass species retain their root systems from year to year and where seasonal water deficiences occur in the upper layers of the soil, the plant rooting zone in many sites extends deeper than is described by Clarke.

In order to determine more precisely rooting conditions in the Rupununi, quantitative measurements were made of a number of herbaceous root profiles (See Appendix 3), which indicated that, although the majority of roots were in the upper 60 cm, plants in better drained sites were drawing a proportion of their water supply from as deep as 180 cm, and that a few roots descended to at least twice this depth.

Quantitative measurements were restricted to the zone 0-180 cm and it was concluded on the basis of these figures, and of visual observation of deeper samples, that the percentage of total roots below that depth was unlikely to exceed 5%, and in many cases would be much less.

The main purpose of the sampling was to determine herbaceous root distribution patterns within representative soil-drainage units. For ease of comparison and to avoid possible human variability in preparing the samples over a period of several months, the roots in each layer were described as a percentage of the total roots in the zone 0-180 cm, and the roots below this depth were ignored. A further distinction was made between :-

(a) Major root zone, which contained not less than 75% of the total roots in the zone 0-180 cm.

(b) Minor root zone, which contained up to 25% of the total roots in the zone 0-180 cm.

Together these form the 'effective herbaceous root zone'. A sub-division of the root zone is necessary to take account, in the lower layers of the soil where root density and permeation is at a minimum, of the inability of the plant roots to remove totally the available moisture in the soil mass before wilting commences. Hagan (1955), with reference to wilting conditions under Bermuda grass (Cynodon dactylon) in California, cites an example where more than 90% of the available moisture in the surface 2 feet (61 cm) of soil was used before wilting took place; where at 4 feet (122 cm) only 50-60% usage was maintained; and where at the base of the root profile at 6 feet (183 cm) less than 15% usage took place before wilting commenced*.

In Tables 10/11 the data collected on root distribution and on the nature of the root zones is illustrated.

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* To take account of these differences Hagan (1955) recognises a 'complete extraction zone', thoroughly permeated with fine roots, and a 'partial extraction zone', commencing in the example cited at about 2 feet (61 cm), where the proportion of moisture utilised is greatly reduced.

TABLE 10: Percentage herbaceous root distribution through sample profiles

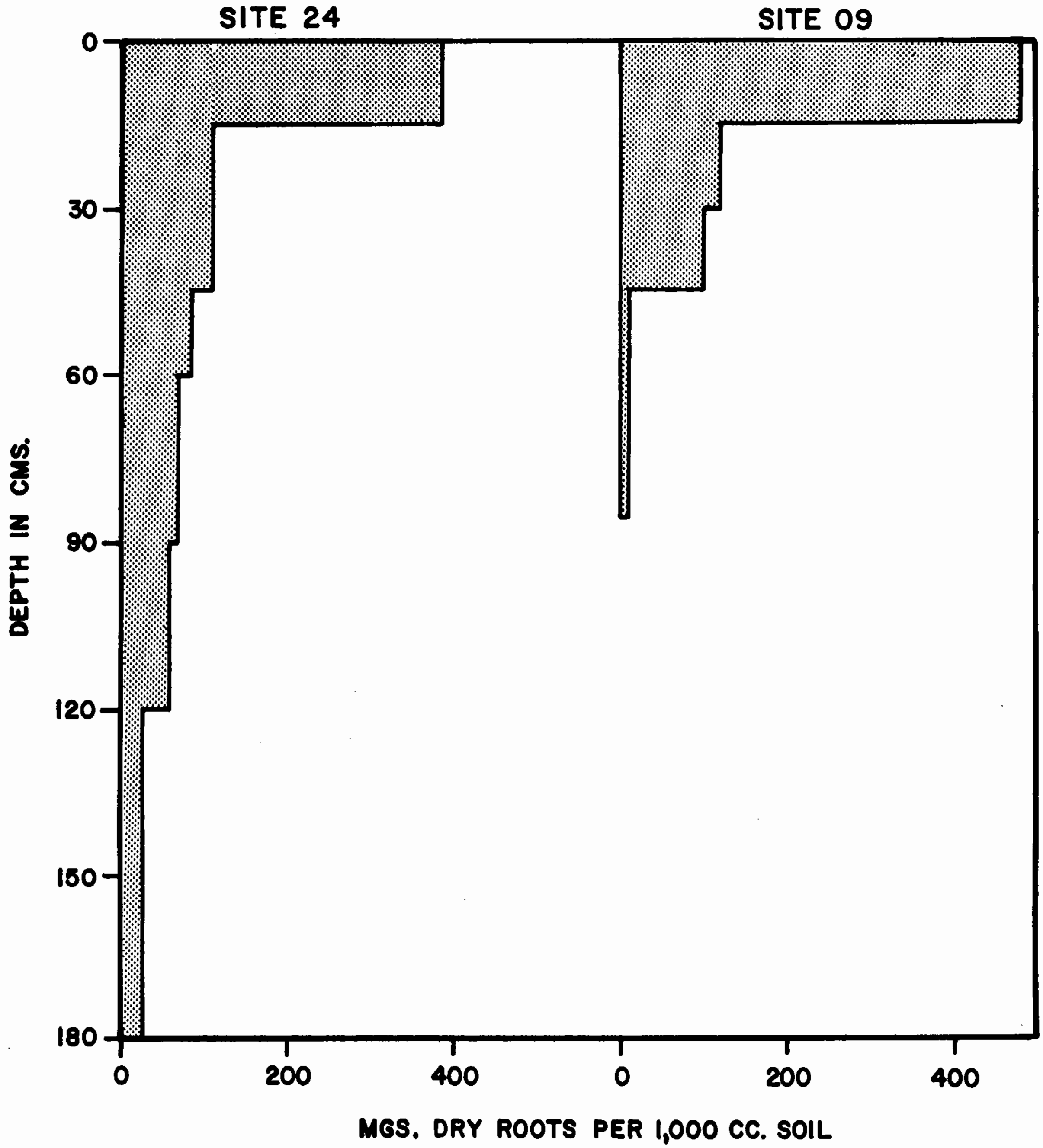
Depth of soil (cm)	Site No.						
	24	06	13	05	12	07	09
0-15	43	49	56	30	56	65	66
15-30	13	14	18	18	17	17	16
30-45	13	11	6	14	8	12	14
45-60	10	8	5	14	7	5	2
60-90	8	7	2	8	3	1	2
90-120	7	4	4	7	6	-	-
120-150	3	3	7	5	3	-	-
150-180	3	4	2	4	-	-	-
	100	100	100	100	100	100	100

TABLE 11: Root zones of sample profiles

Site	Effective root zone (cm)	Depth of major root zone (cm)	Depth of minor root zone (cm)	Drainage class	Herbaceous cover
24	0-180	60	120	Well drained	Bunch grass
06	0-180	60	120	Well drained	Pangola grass
13	0-180	45	135	Well drained	Bunch grass
05	0-180	60	120	Moderately well drained	Bunch grass
12	0-150	45	105	Moderately well drained	Bunch grass
07	0-90	30	60	Imperfectly drained	Mixed grass and sedge
09	0-85	30	55	Poorly drained	Mixed grass and sedge

(The soil profiles of Sites 24/05/07 are described in Chapter 5; those of the remainder in Appendix 4.)

FIG. 5: ROOT DISTRIBUTION OF HERBACEOUS PLANTS AT SELECTED SITES



From these figures the relation between drainage conditions and the root distribution of herbaceous plants becomes apparent. The principal control on root growth is soil waterlogging, which leads to inadequate aeration for plant growth, and possibly to side effects induced by the accumulation of carbon dioxide (Kramer, 1949); the depth of root penetration in seasonally waterlogged soils is thus greatly reduced. Roots, nevertheless, are able to survive in the upper zone of seasonal waterlogging which apparently still remains partially aerated in the wet season. Site 05, for example, whose profile was waterlogged below 100 cm for at least two months during 1963, differs little in root distribution at that depth from the better drained sites Nos. 24/13/06. Similarly, the imperfectly and poorly drained sites, which are more completely waterlogged in the wet season, have roots in the upper zone of waterlogging, but are virtually devoid of them below 90-100 cm, where saturation is more complete and prolonged.

Within the upper root zone of perennially free-draining soils, variations in root distribution also occur, which are unrelated to waterlogging. The reasons for this are not entirely clear, but a correlation does exist between higher porosity and deeper root penetration in these sites. Site 05, for example, where root penetration is appreciably greater than in other free-draining profiles, has a mean porosity of 41.7% in the zone 0-60 cm, by comparison with 37.1% in Site 13 and 37.9% in Site 24. It is possible, therefore, that higher porosity facilitates the penetration of roots through the upper soil layers.

In conclusion, it is possible to approximate the depth of soil, under differing drainage regimes, which comprises the moisture reservoir for the growth of herbaceous plants. Broadly speaking, a division of the herbaceous rooting zone into two categories is possible :-

(a) Excessively, well and moderately well drained zonal and azonal soils, where the majority of the roots occur in the zone 0-60 cm and the effective root zone extends to 150-180 cm.

(b) Imperfectly, poorly and very poorly drained intrazonal soils, where the majority of the roots occur in the zone 0-30 cm and the effective root zone rarely extends below 90-100 cm.

(b) The Nature of the Tree Root Zone

The roots of savanna tree species, which necessarily draw on moisture other than that in the herbaceous root zone, in order to survive the dry season, extend deeply into the soil. However, as with herbs, tree growth is affected by mal-aeration. In imperfectly drained sites, where the water table is seasonally at or close to the surface, savanna tree growth is commonly restricted in size and density, while, in most poorly drained sites, there is a complete absence of tree growth; the condition is due to the inability of tree roots, which in such sites would need to be several metres deep to acquire moisture in the dry season, to survive the seasonal mal-aeration of the lower profile. In mal-drained areas, therefore, it is only in certain perennially wet sites, where there is no need for deep tap roots and where shallow-rooted and water-tolerant palms occur, that extensive tree growth is possible.

Within the free draining soils, where tree growth is not thus restricted, the rooting habit of the trees reflects the demand for water both in the wet season and in the dry season when the upper soil moisture supplies are exhausted.

Surface excavations of tree roots were made; one specimen of *Plumeria inodora*, 35 cm high and growing on a well drained soil, showed the following features :-

PLATE 6: Plumeria inodora, growing on latosolic sheetwash soil. The shrub has been strongly retarded by fire, and one season's vegetative growth is seen springing from a rootstock that is several years old.

(a) A vertical tap root, 3 cm in diameter at ground level, which was excavated to a depth of 130 cm, where it had tapered to 1 cm in diameter.

(b) A series of lateral roots, frequent between 0-50 cm, but sparse below that depth.

This and other excavations suggest that during the rainy season moisture is drawn by trees from the surface layers of the soil in a manner similar to herbs. In the dry season the deeper tap roots must acquire water either from the ground water, the capillary zone above it or an intermediate zone beneath the grass roots, where available moisture persists into the dry season. It became apparent from field observations that the density and height of tree growth reflect the availability, in terms of root penetration, of these supplies.

Other observations, principally on the face of newly eroded river banks, indicate that mature savanna trees are capable, under favourable soil conditions, of root penetration to a depth of at least four metres, and it is thus probable that where tree growth does occur the roots are able to tap dry season ground water supplies; in most cases in the Rupununi these supplies are at a depth of between four and six metres by the end of the dry season. What the critical depth is below which tree roots cannot penetrate, whether by reason of seasonal anaerobism or because of uneconomic rates of moisture assimilation to the plant itself, is not known; there are sites, however, e.g., on the eastern part of the Meritizero Ridge, where the ground water in the dry season is exceptionally deep and tree growth is absent, presumably because of the seasonal inaccessibility of ground water in terms of root penetration.

(c) Water Holding Capacity of the Soil

The water retention characteristics of a particular soil depend on the total volume and individual size of the pores within it. It has already been indicated in Chapter 5 that, on account of the low organic content and compaction of many soils, inferior porosity conditions exist in the savanna. There are exceptions among the hydromorphic soils, but they are limited in area and have in many cases a prolonged saturated state, which exercises other strong controls over plant growth.

Under typically free draining conditions, however, soil porosity can be considered sub-optimum for plant growth. In Table 12 the porosity of two savanna soils is compared with that of a Marshall silt loam in the United States, which represents close to optimum conditions (Baver, 1956).

TABLE 12: Pore space relationships at field capacity in the A horizon of savanna soils and a Marshall silt loam

	Sandy loam (Rupununi)		Marshall silt loam
	Site 07	Site 05	
Soil volume	60%	62%	44%
Water volume	31%	33%	32%
Air volume	9%	5%	24%

In order to gain a fuller knowledge of porosity and soil moisture characteristics within the region, 65 soil samples were taken from the zone 0-180 cm in nine soil pits and the following determinations made (See Appendix 5) :-

(a) Saturation moisture capacity (as % dry weight).

(b) Field capacity (as % dry weight).

(c) Permanent wilting point (as % dry weight).

(d) Bulk density.

(e) Soil density.

Prior to the description of individual sites, these data have been generalised to indicate the principal characteristics of the soils. In Table 13, Categories 1-3 are representative of zonal soils and also many of the imperfectly drained intrazonal soils; within this group, which areally covers the largest part of the savanna, an unusually low gravitational water percentage and macroporosity is to be found. In general the condition results from the highly compacted nature of the soil parent materials and the minimal structural development that has taken place within them. The condition is particularly abnormal in the sandy loam soils, which under optimum conditions would have a much higher percentage of their pore space free draining; in this case, however, the occurrence of sandy loam most commonly as an A horizon, renders it liable to the added compaction effect of intense rainfall, while at the same time the relatively higher organic content in the horizon improves to a degree the amount of water retained at field capacity.

In this respect Baver has stated :-

> 'The impact of falling drops of water on exposed soil exerts a significant dispersing action on the aggregates. The dispersed particles are then carried into the soil pores, causing increased compaction and decreased porosity.'
>
> L. D. Baver, 1956, p. 168.

In Table 13 the structureless soils of Categories 1-3 have a low porosity by comparison with Categories 4-5, which are from the wettest part of the drainage continuum. In the latter soils, however, the porosity

TABLE 13: Porosity and moisture characteristics of soils of the northern Rupununi

Soil		Porosity %	Saturation %	Gravitational water %	Available moisture %	Wilting %	Height of available moisture per 10 cm. of soil
1.	Structureless sandy loam	37.8	22.4	2.5	14.5	5.4	2.46 cm
2.	Structureless, sandy clay loam	39.4	24.3	2.2	10.4	11.7	1.69 cm
3.	Structureless, loam/silt loam	43.6	28.9	2.0	10.1	16.8	1.52 cm
4.	Humic, silt loam/ silty clay loam	65.9	128.5	12.0	65.0	51.5	4.28 cm
5.	Silt loam, with many vesicular pores	61.0	124.5	12.0	72.5	40.0	4.42 cm

and moisture retention characteristics of the soil are of secondary importance in terms of plant growth. For seasonal waterlogging, through the malaeration it induces, not only demands of the plants that grow there a high degree of water tolerance, but also by concentrating the roots into the upper horizons of the soil, thereby reduces the depth of soil from which the plants draw their water.

(c) Surface and Ground Water Drainage

In addition to the water holding capacity of the soil, other soil factors affect the savanna ecoclimate. The principal of these is the adverse infiltration - run off ratio in many free draining soils which support bunch grass. This stems from surface compaction of the soil under intense seasonal rainfall, and is especially pronounced within the Lethem-Yupakari land unit, where a combination of compacted soil surfaces and gentle to moderate slopes has led to excessive surface drainage. In such areas the thin sheet of water flowing down gravel ridge slopes during heavy rain, the deposition of loose sandy material at the foot of many slopes, and indeed the existence of extensive sheetwash deposits bear witness to the process.

On a latosolic soil near Lethem, the compaction has been described as follows :-

> 'The crust is continuous, although it has been partly covered with loose, wind-blown sand, which has accumulated during the present dry season. The crust itself, about 2 mm thick, crumbles readily in the hand, but is a definitely hardened layer composed of soil minerals together with a limited amount

of ash and organic debris. The site supports an herbaceous layer of bunch grasses with a few sedges.'

M.J. Eden, Field Notes, November, 1963.

In other soils, surface compaction develops in a similar manner, but in general the infiltration elsewhere is higher because either the topsoil, by virtue of its texture, remains more permeable, or the terrain is more level. Such is the case with the very gently undulating relief of the more porous sandy terrace deposits of the Takutu - Proto-Berbice land unit. Table 14 compares infiltration rates, under experimental conditions, in this area with those of a sheetwash profile in the Lethem-Yupakari land unit.

TABLE 14: Relative infiltration rates of two savanna latosols, northern Rupununi

Soil	Site	Porosity of A_1 horizon	Infiltration rates		
			First minute	First five minutes	Hourly rate
Sandy terrace latosol	05	40.6%	1.5 cm	6.5 cm	23.3 cm
Sheetwash latosol	24	37.2%	0.9 cm	2.5 cm	7.0 cm

(See Appendix 6: 'Measurement of Soil Infiltration Rates.')

The principal regional effect of low infiltration rates is to reduce the amount of ground water drainage through latosolic and regosolic soils and to promote direct run off into rivers and low-lying areas. As a result a hydrologic imbalance is created, which leads during the rainy season, in a region where already low river gradients exist, firstly to flooding of the rivers and subsequently to backing up of the slowly escaping flood waters into the lower parts of the savanna. Once this process commences soil profiles in low-lying areas rapidly become waterlogged and internal

With the lowering of rainfall towards the end of the rainy season, most of the surface flood water rapidly disperses, and is accompanied by a regional drop in river levels. An increased ground water gradient is thus established, and internal drainage recommences in the poorly drained sites, facilitated by the highly porous sand and gravel substratum which prevails widely in the fluvio-lacustrine trough (Bleakley, 1958). In a few places, ground water drainage is impeded by heavy textured horizons, and ponds and small lakes may persist for several months, but there is at this time no general profile impedance, and ground water levels fall fairly rapidly with the lowering of the rivers.

In mid-November, 1963, three months after the end of the rains, water table measurements in the Maracanata Basin, in sites which had been previously flooded or waterlogged for several months, gave the following readings :-

TABLE 15: Ground water in the Maracanata Basin, mid-November, 1963.

Site drainage	Mean depth to ground water	Range in depths	No. of sites
Poorly drained	150 cm	99-205 cm	7

CHAPTER 7

ECOCLIMATES AND THE NATURE OF WATER REGIMES

(a) Water Regimes

In order to determine the nature of soil moisture regimes within the savanna, regular measurements were made of soil moisture in the herbaceous root zone and of the depth to ground water at a number of selected sites during the period June 1963 - May 1964.

Ground water tables were measured in augur borings at approximately 20 day intervals; no evidence of either perched water tables or artesian pressures were found. Soil moisture samples were similarly collected, and gravimetric determinations of moisture content made for the following layers of soil :-

0 - 15 cm	60 - 90 cm
15 - 30 cm	90 - 120 cm
30 - 45 cm	120 - 150 cm
45 - 60 cm	150 - 180 cm

From these data the height of available moisture and gravitational moisture in each layer was calculated, the data being presented graphically to illustrate the march of soil water in the herbaceous root zone during the period of observations. Seven sites, whose soil water characteristics are tabulated in Table 16, have been selected to represent the range of water regimes in the northern Rupununi. The only drainage unit not represented is the excessively drained category, in whose soils it was not possible to determine accurately the water holding capacity of the root zone;

the regime of this unit is discussed with that of the well drained latosols. In the following pages the water regime of each site is described, and from these data an attempt has been made to classify the regional ecoclimates.

TABLE 16: Soil water characteristics of the herbaceous root zone of representative profiles

Site	Soil	Drainage class	Effective root zone (cm)	Available moisture per 10 cm of soil	Total moisture available in root zone
15	Regosol	Excessive	180	N/A	N/A
24	Latosol	Well	180	1.72 cm	30.9 cm
05	Latosol	Moderately well	180	2.07 cm	37.3 cm
12	Latosol	Moderately well	150	1.63 cm	24.5 cm
07	Ground water laterite	Imperfect	90	1.80 cm	16.2 cm
09	Ground water laterite	Poor	85	3.65 cm	31.0 cm
110	Humic glei	Very poor	75	N/A	N/A

(Profile descriptions of Sites 15/24/05/07/110 are to be found in Chapter 5, and of Site 12 in Appendix 4)

i. Site 24. Well drained latosolic soil

In Site 24 free draining conditions were maintained in the herbaceous root zone throughout the year, except for brief periods during the rainy season when ground water rose temporarily into the lower part of the root zone after heavy rain. By mid-October, however, the ground water had fallen to 270 cm, although thereafter the rate of drainage slowed up, so that the maximum depth reached at the end of the dry season was probably 400 - 450 cm.

FIG. 6 : GROUND WATER REGIME OF SITE 24

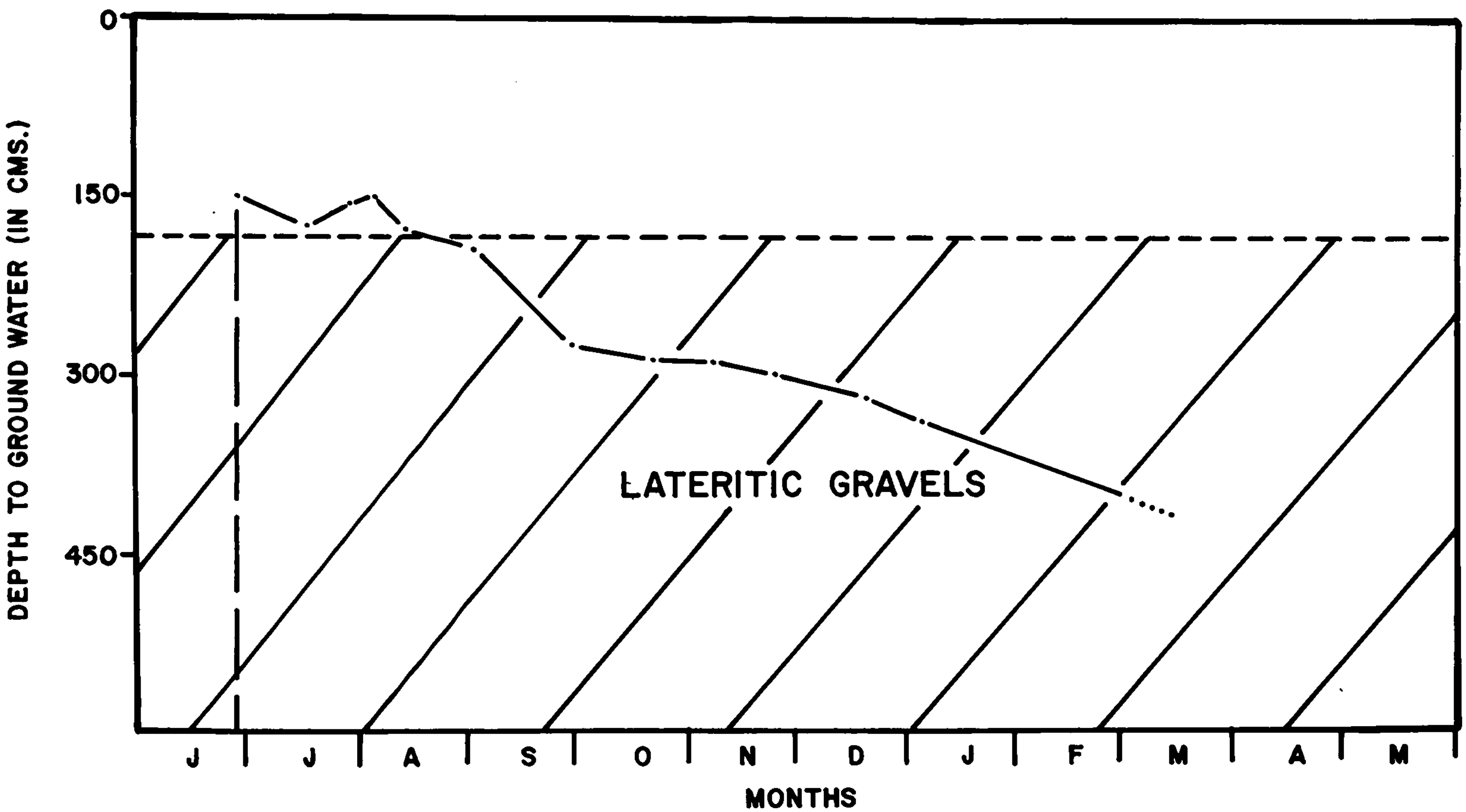
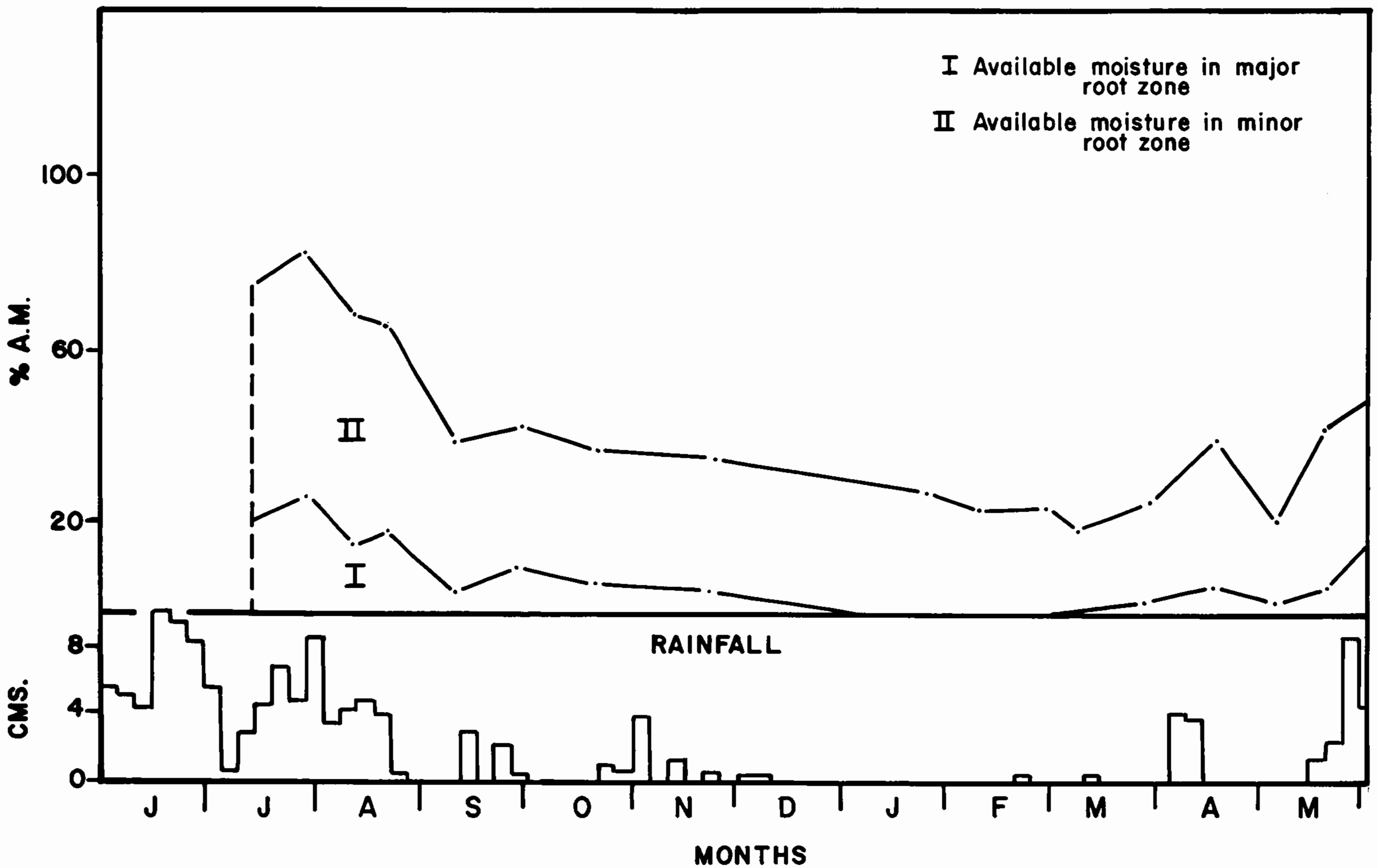


FIG. 7 : AVAILABLE MOISTURE REGIME OF ROOT ZONE (0-180 cm.) OF SITE 24



The available moisture capacity of the grass root zone of this site is 30.9 cm, of which 11.9 cm is retained within the major root zone. During the rainy season conditions were optimum for plant growth; throughout the latter part of the rains, and it can safely be assumed during late May and June also, the root zone held at least 65% of the available moisture potential. During August, however, there commenced a rapid depletion of soil moisture reserves, as rainfall diminished and finally ceased on 21 August.

During the first three weeks of the dry season up to mid-September, only 0.44 cm of rainfall occurred, during which time a third of the remaining available moisture was utilised, bringing the reserve down to 40% of the potential capacity. Thereafter, the rate of capital depletion dropped abruptly and water use in the succeeding 6 1/2 months, during which time 14.7 cm of rain fell, only reduced the soil moisture capital a further 20%, leaving the soil at the end of the dry season, at 20% capacity.

From these data, it became clear that much of the moisture in the root zone in mid-September was either inaccessible to plants, or only slowly becoming accessible with the gradual extension of root systems. Thus, from three weeks after the end of the wet season, a serious deficiency of moisture existed, which was reflected in a reduced rate of herbaceous growth; however, as late as December some grasses were still flowering and it is clear that plant growth continued intermittently up to this time, chiefly in response to isolated showers*. In the new year the herbaceous layer entered a period of dormancy, in spite of the moisture remaining in the root zone, and ultimately in early February the organic debris on the site was removed by fire, and no fresh growth appeared.

* The effectiveness of dry season rainfall, however, in terms of plant growth remains somewhat limited. Ignoring any run-off that might take place, one centimetre of rainfall at this time would raise less than 5 cm of dry topsoil to field capacity on most sites, from where it would be evapotranspired in less than 36 hours; during the entire dry season of 1963/1964 only four showers of this magnitude took place.

The period of dormancy lasted until early April when two heavy showers, bringing 7.6 cm of rain, re-awakened plant growth. The moisture added to the upper layers of the soil, however, was rapidly used, and it was only with the start of the rainy season on May 19 that sustained growth recommenced.

It was not possible to determine accurately the porosity and moisture characteristics of the herbaceous root zone of excessively drained soils. However, from the nature of the soil profiles it is clear that such sites experience a more acute regime in the grass root zone than the well drained soils, principally because of the low water retention capacity of the sand and gravel parent materials. For this reason they are likely to dry out more rapidly than the latosols at the start of the dry season, and experience a longer period of dormancy. The porous, loamy soils of the Meritizero Ridge are somewhat different, for their water retaining capacity is higher than that of the other regosols. But their exposed situation and higher evapotranspiration produce a water regime that is equally as acute as the other regosolic soils.

ii. Sites 05/12. Moderately well drained latosolic soils

The soil water regime of moderately well drained soils is similar in many respects to that of the well drained soils; the main contrast lies in the greater degree of waterlogging in the lower root zone of the former during the rainy season. At Site 05 the water table remained close to 100 cm from the commencement of observations in June until mid-August, and is likely to have been at least as high during the earlier part of the rains; at Site 12 a similar level was established at about 150 cm during the latter half of the rainy season. With the cessation of rainfall, however, both water tables dropped rapidly, and by the end of October they had reached a depth of more than 300 cm.

FIG. 8 : GROUND WATER REGIME OF SITE 05

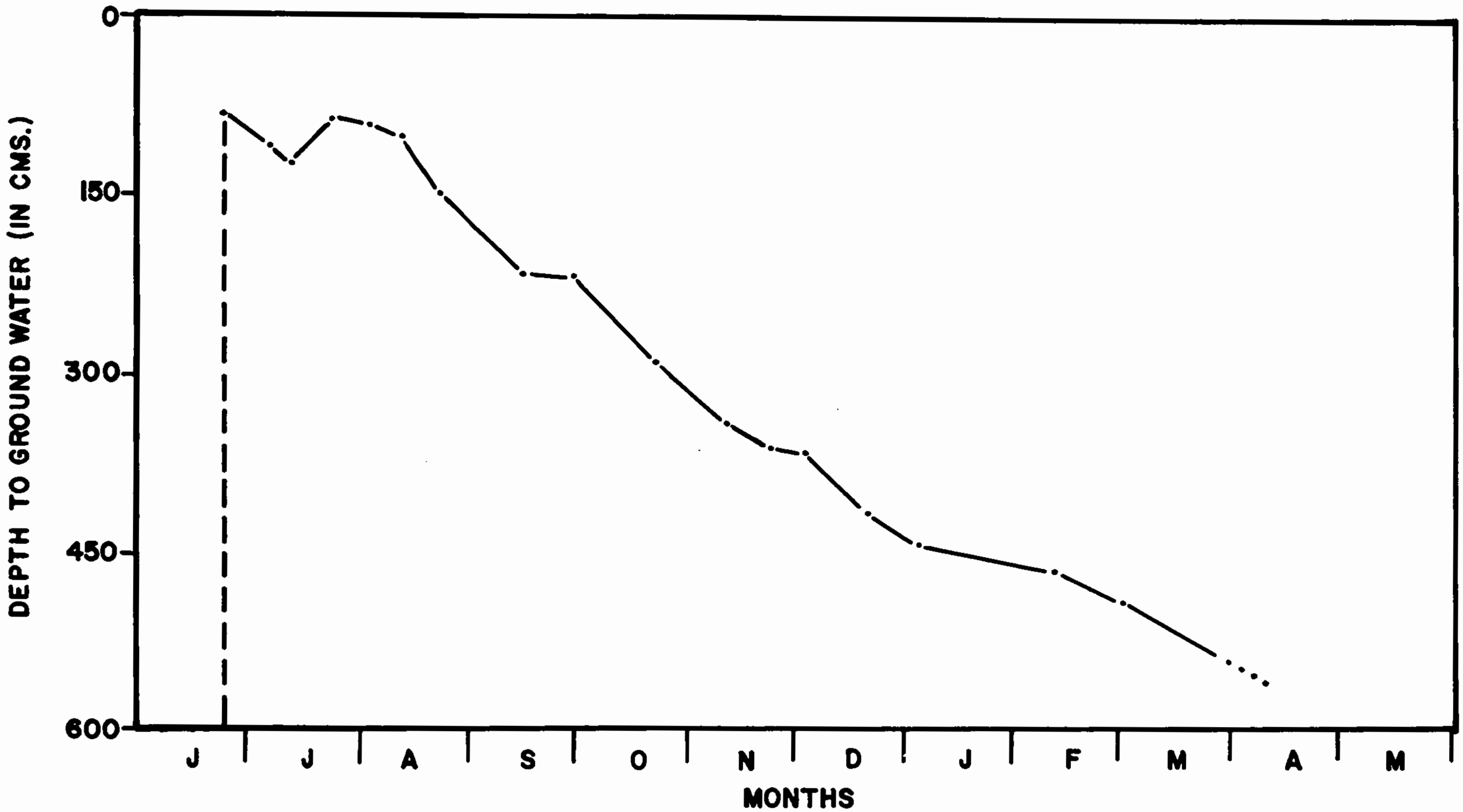


FIG. 9 : AVAILABLE MOISTURE REGIME OF ROOT ZONE (0-180 cm.) OF SITE 05

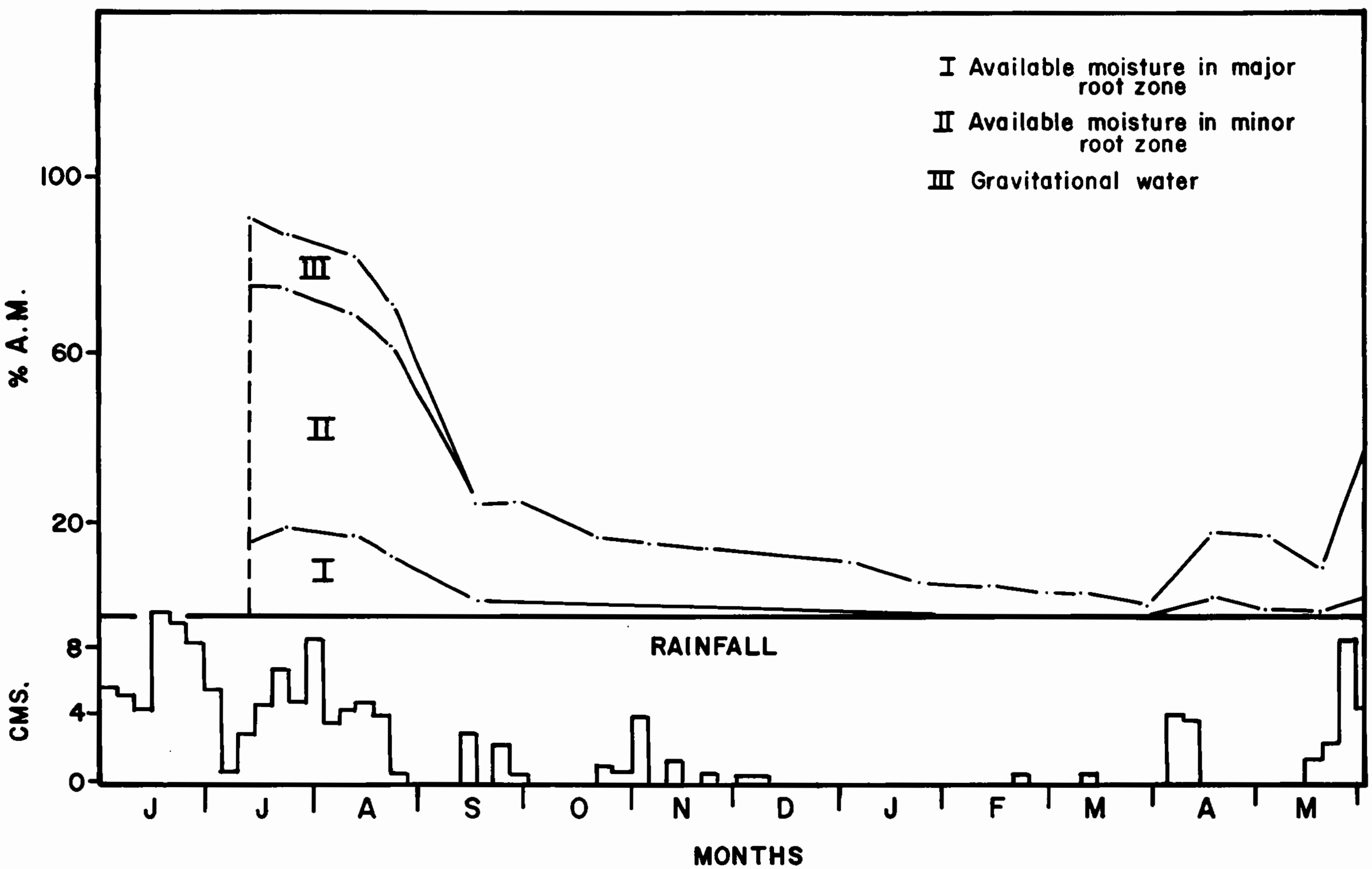
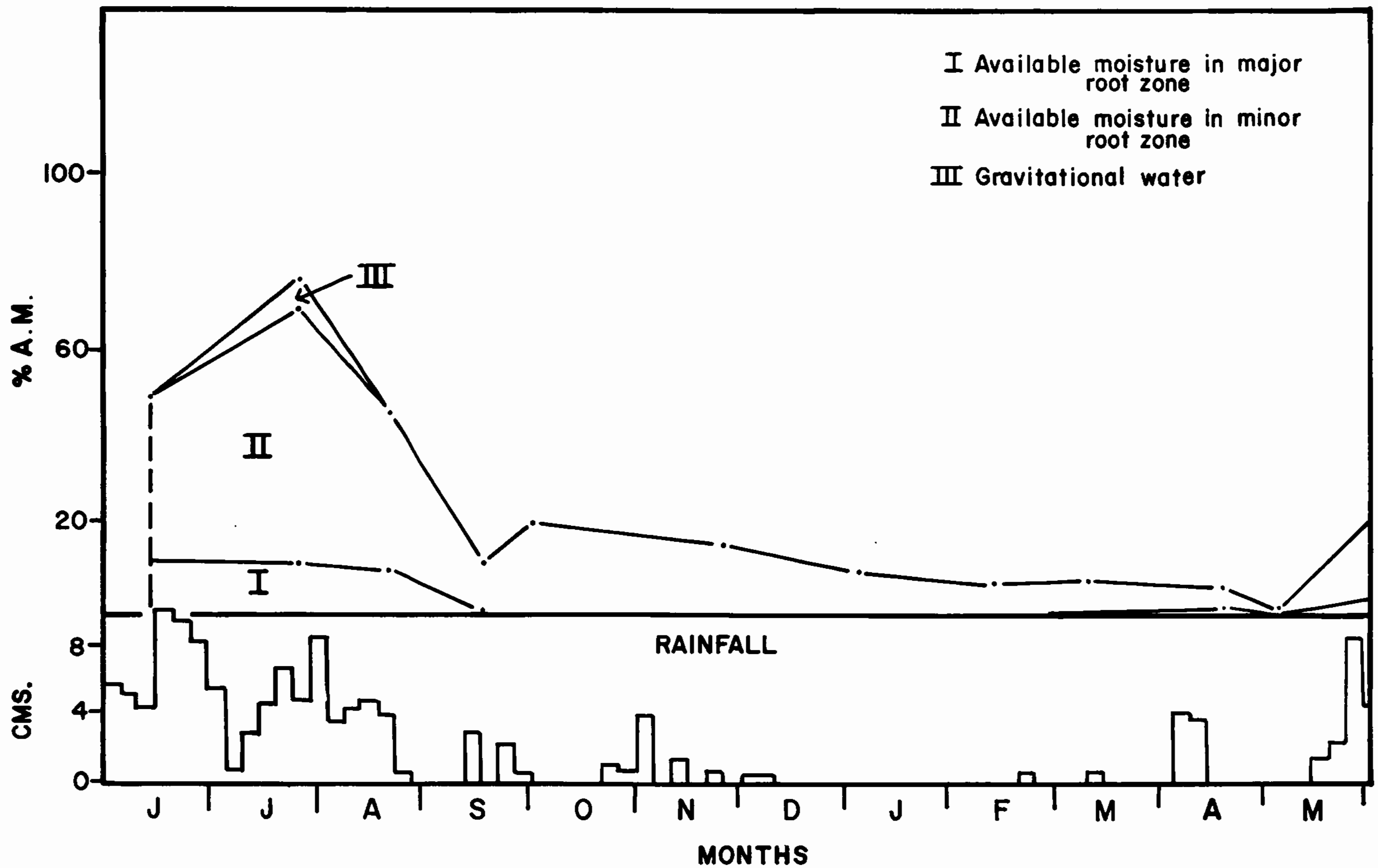


FIG. 10: AVAILABLE MOISTURE REGIME OF ROOT ZONE (0-150 cm.) OF SITE 12

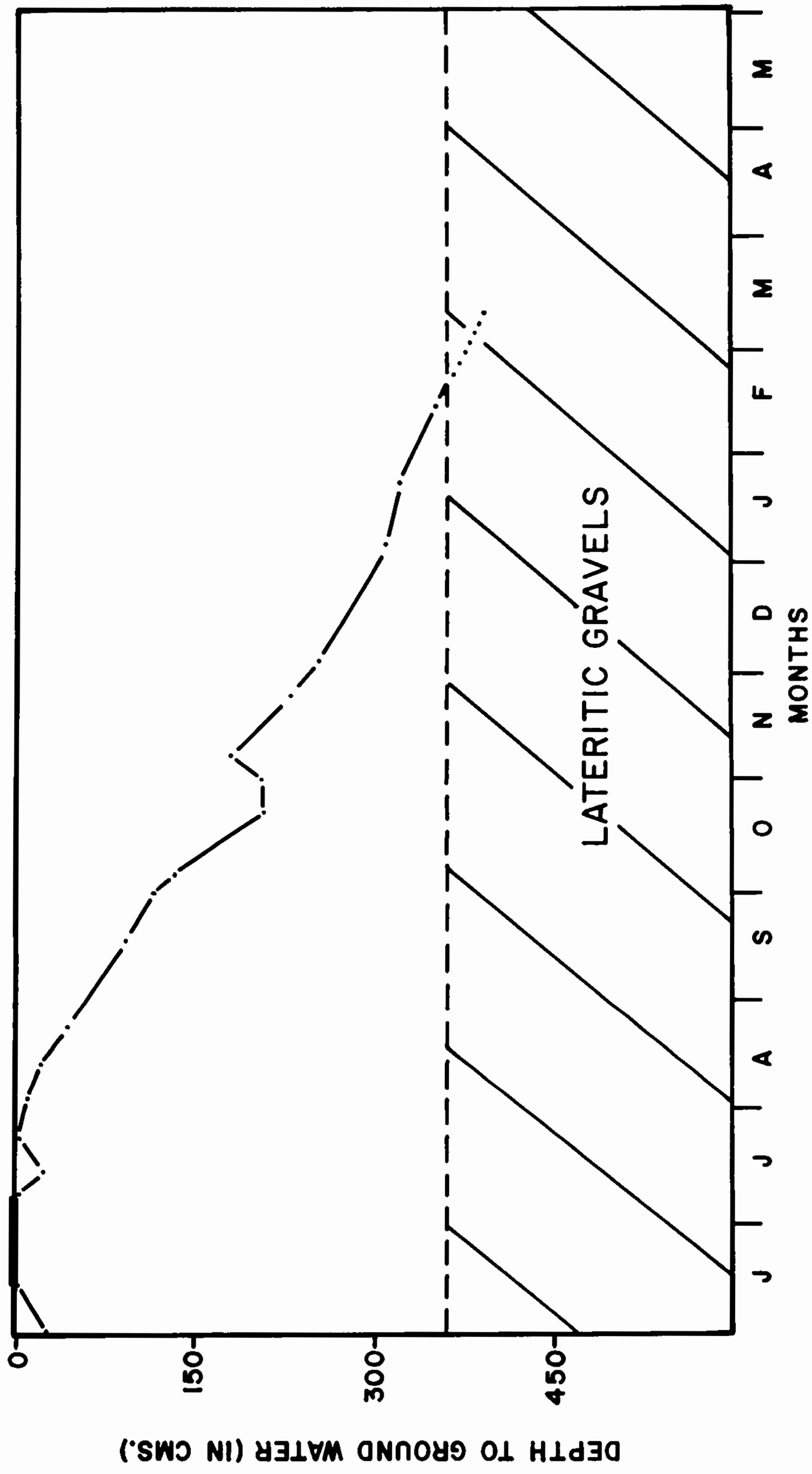


A marked contrast exists between Sites 05/12 in the nature of the substratum. In Site 12, developed on lateritic sheetwash materials, a D horizon of lateritic gravel commences at 305 cm; in Site 05, on sandy terrace deposits, the C horizon of sandy clay loam texture extends to at least six metres and probably much deeper. However, the rate of fall of water table in the early stages of the dry season was similar in both cases and presumably reflected the gradual lowering of the local drainage base level, i.e., the level of the main rivers, rather than any differential conditions in the substratum itself.

In Site 05 the maximum depth to ground water recorded was 537 cm in early April, and this is considered to be a typical condition within the drainage unit, whatever the nature of the substratum.

The available moisture capacity of the grass root zone of Site 05 is 37.3 cm, with 14.3 cm in the major root zone; and of Site 12,24.5 cm, with 8.1 cm in the major root zone. During the rainy season an adequate supply of moisture was available for plant growth in the upper root zones, while the lower part in both instances remained saturated. Throughout July and early August, both sites held at least 50% of the available moisture potential, but with the reduction and subsequent cessation of rainfall, rapid moisture depletion took place in August, as had been the case in Site 24. By mid-September, three weeks after the end of the rains, only 26% of the available moisture remained in Site 05 and 13% in Site 12. The rainfall in the latter part of September (5.6 cm) checked this rapid loss, but thereafter a progressive but very gradual depletion took place as the remaining moisture slowly became accessible to plant roots. Thus, in late March and early April the available moisture was almost completely exhausted and did not exceed 8% in either site.

FIG. 11 : GROUND WATER REGIME OF SITE 07



Negligible herbaceous growth took place after December, and the period of dormancy was only ended by the showers in early April, with continuous growth commencing in mid-May with the start of the rainy season.

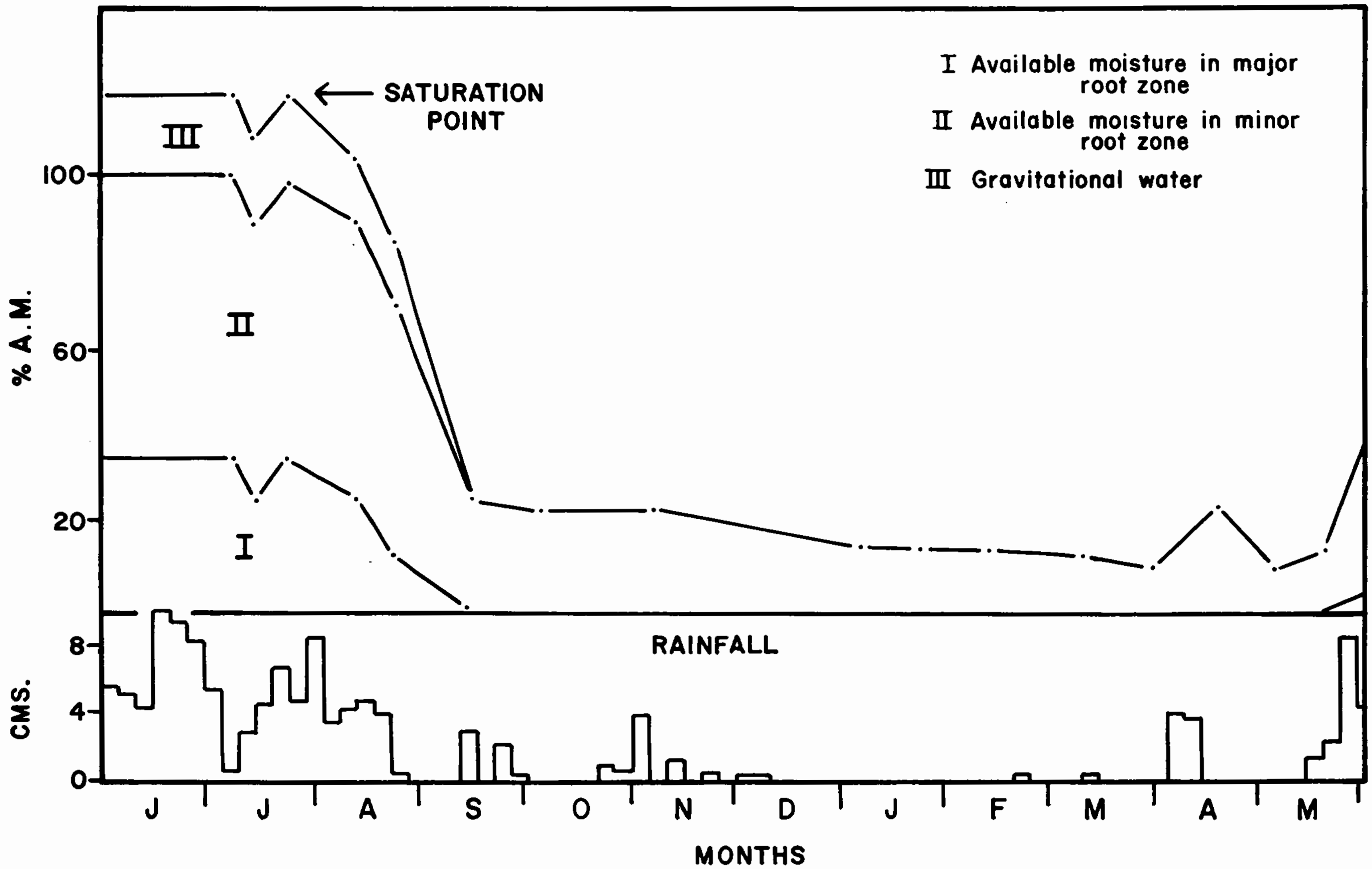
iii. Site 07. Imperfectly drained ground water laterite soil

Ground water observations were maintained at this site throughout the rainy season 1963, and during the month of May the water table rose from below 200 cm to the surface, where it remained with intermittent slight lowerings until mid-August. Thus, the grass root zone was almost continuously saturated for three months, although throughout this time vertical drainage was taking place. By late October, however, the ground water had again dropped below 200 cm; the maximum depth reached in 1964 is not known, but was probably between four and five metres.

The available moisture capacity of the grass root zone of Site 07 is 16.2 cm. From the end of the rains rapid depletion of the moisture took place. On August 21 there were more than 15 cm of gravitational and available moisture in the root zone; by mid-September this had been depleted by more than half, by evapotranspiration and vertical drainage, and all the available moisture in the major root zone (0-30 cm), which contained 82% of the roots, had been exhausted. Herbaceous growth was therefore greatly reduced at this time, and continued so in the succeeding months as the remaining water in the lower root zone only became slowly available, although intermittent rainfall in October and November gave temporary stimulation to growth.

Thus, during the 6 1/2 month period from mid-September to early April, the available moisture capital was only reduced from 26% to 9%, and the phase of dormancy in the herbaceous layer during the months January

FIG. 12: AVAILABLE MOISTURE REGIME OF ROOT ZONE (0-90cm.) OF SITE 07



to March was repeated. Again plant growth awakened with the showers in early April, and sustained growth commenced in mid-May.

iv. Site 09. Poorly drained ground water laterite soil

From the start of the rainy season, 1963, the water table in the site rose rapidly and by early June the area was inundated to a depth of approximately one metre. The site lies within an enclosed basin surrounded by elevated ridges and thus acted as a collecting ground for waters from the adjacent areas. The site remained inundated until late October, when ground water drainage became effective enough to remove the surplus water. By mid-February the water table had fallen to 215 cm, and it is likely that by the end of the dry season it reached 300-350 cm.

The available moisture capacity of the root zone of Site 09 is 31.0 cm of which 12.9 cm is in the major root zone. From November 2, when saturated conditions were last recorded at the site, utilisation of available moisture by fresh plant growth commenced. However, isolated rainfall during November and early December slowed up this process, and by mid-December more than 70% available moisture still remained in the profile; five weeks later, by January 20, this had been depleted to 25% and thereafter the accessibility of supplies was clearly reduced and water usage lowered.

By early March the moisture in the major root zone was exhausted, and during the remainder of that month a short period of dormancy prevailed, relieved as elsewhere by fresh supplies of rainfall in April and May.

v. Site 110. Very poorly drained humic glei soil

Site 110 remained at or close to saturation throughout the year. The following conditions were recorded :-

FIG.13: GROUND WATER REGIME OF SITE 09

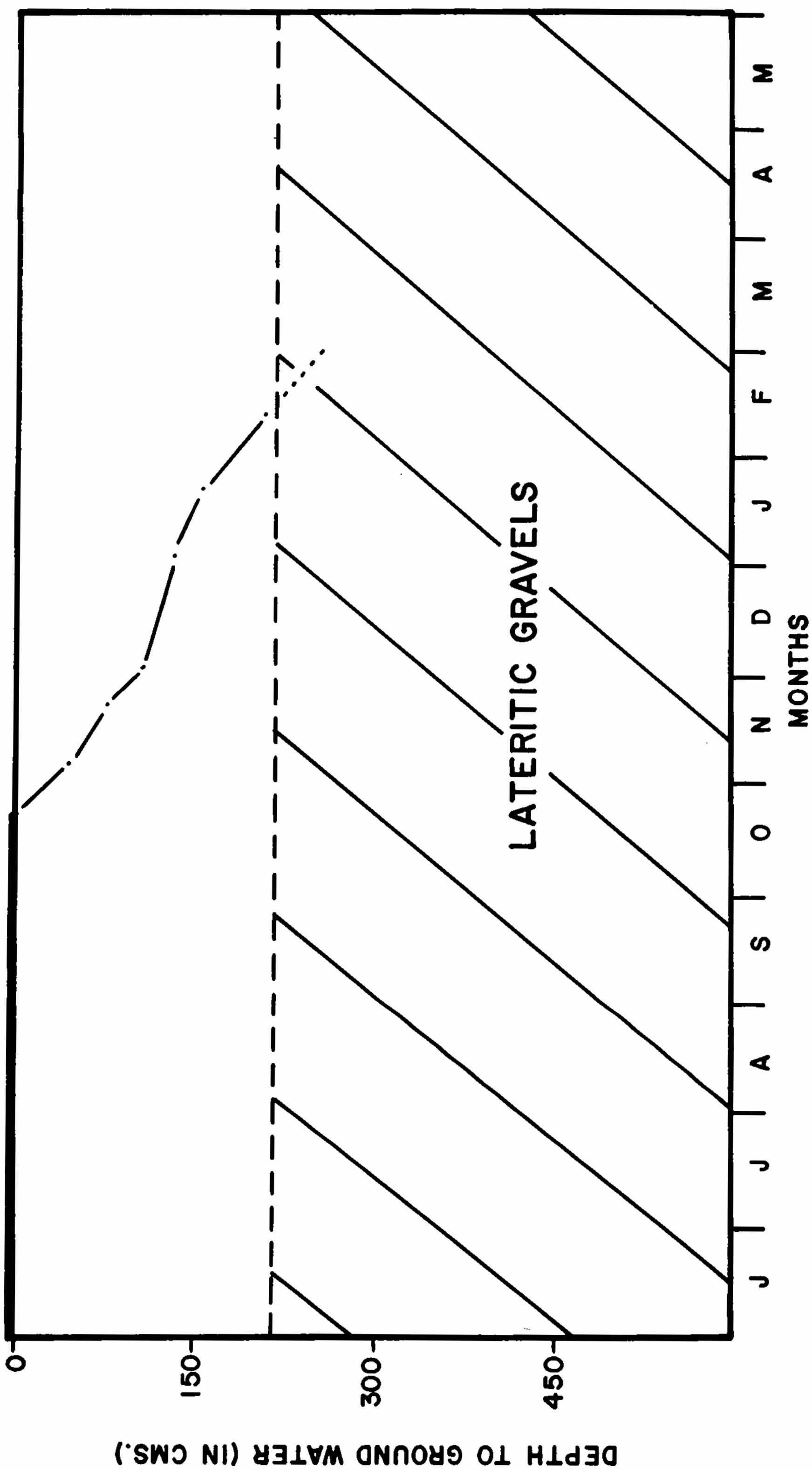
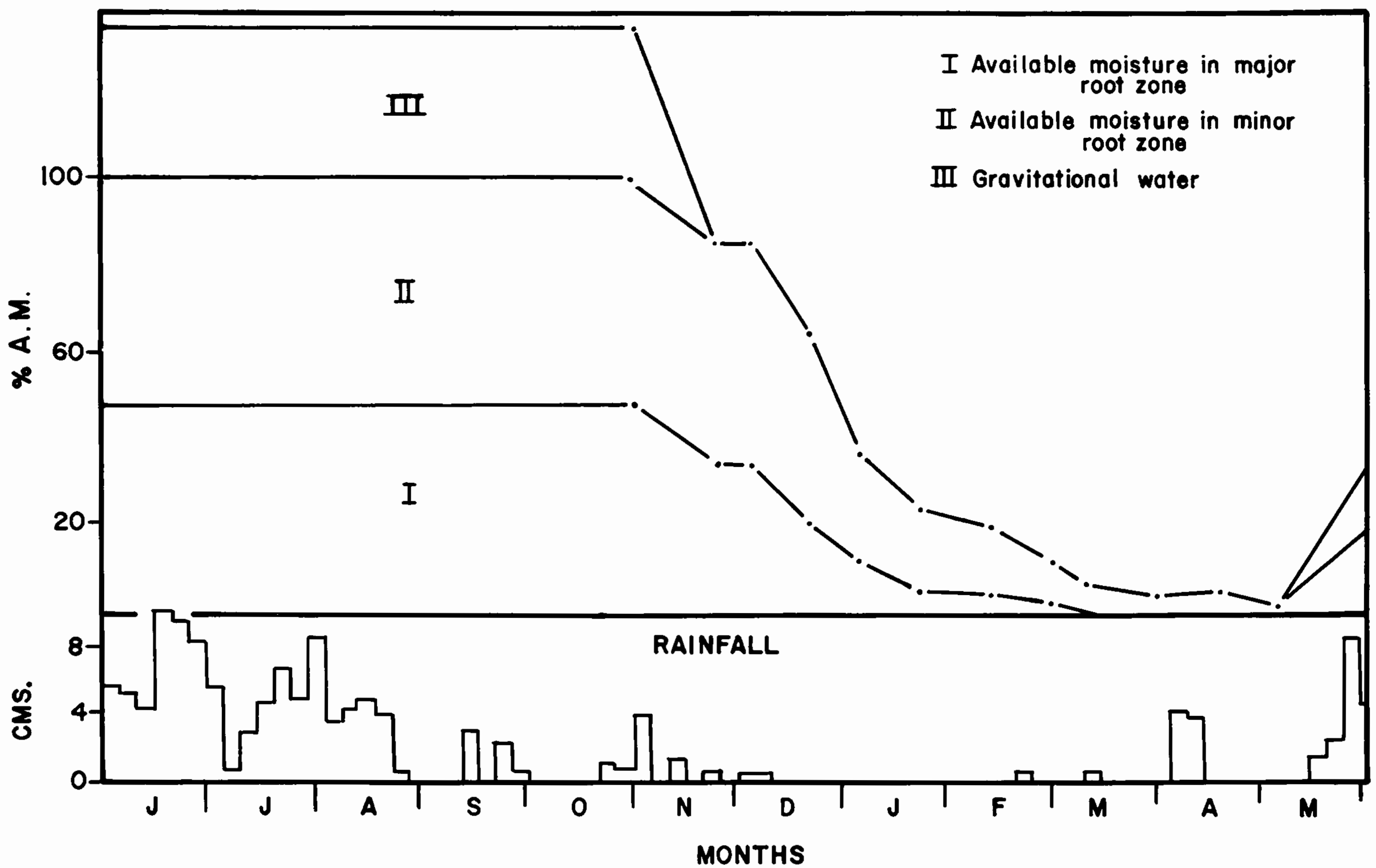


FIG. 14: AVAILABLE MOISTURE REGIME OF ROOT ZONE (0-85 cm.) OF SITE 09



October 14, 1963 - Site inundated to approximately one metre.

January 21, 1964 - Water table at 8 cm.

April 12, 1964 - Water table at 20 cm.

The site, which is situated on the lowland margin of the lateritic gravel and sheetwash deposits close to Maracanata, is perennially supplied with seepage waters from those deposits. It experiences a perennially wet water regime, and has been classified as a swamp habitat. No soil moisture determinations were made on this site.

(b) The Savanna Ecoclimate

The water regimes described hitherto experience, with the exception of the very poorly drained swamp site, an alternation of wet and dry conditions during the year, which is the principal feature of savanna ecoclimatic regime. Two savanna ecoclimates have been recognised in the Rupununi, and in addition there exists the distinctive swamp ecoclimate. They are defined as follows :-

1. Dry Savanna Ecoclimate, with alternating dry and wet phases

This ecoclimate prevails throughout the regosolic and latosolic soils, where excessively, well and moderately well drained conditions exist. It is characterised by an adequacy, but not an excess of water during the wet season, and a shortage of water during most of the dry season. Water tables in some sites rise into the lower grass root zone for a few months of the year, but in the long dry phase the sites are deeply draining, with water tables falling to four metres or below.

2. Wet Savanna Ecoclimate, with alternating dry and excessively wet phases

This ecoclimate prevails throughout most of the intrazonal soils, where imperfectly or poorly drained conditions exist. It is characterised by an excess of water during the wet season, which may be prolonged into the early part of the dry season, and a shortage of water during much of the dry season. Profiles are intermittently flooded or waterlogged for several months each year, but the sites are deeply drained in the dry phase, with water tables dropping below three or four metres.

3. Swamp Ecoclimate, with excessively wet conditions

This ecoclimate prevails in the very poorly drained soils. It is characterised by profile saturation or near saturation throughout the year, and represents conditions that are alien to the true savanna ecoclimate.

The above classification is based on observations over one twelve month period; it is thus desirable to consider how far the ecoclimates described are generally valid in a region where rainfall varies greatly from year to year. The rainfall during the twelve months of observations totalled 1,269 mm and displayed a deviation of 22%, by comparison with a mean deviation of 17%, from the mean annual total of 1,621 mm.

TABLE 17: Rainfall, 1963/1964 and mean conditions, St. Ignatius

	Rainfall (mm.)	
	1963/1964	Mean
June-August	976	963
September-November	87	177
December-February	13	77
March-May	193	404
TOTAL	1,269	1,621

Wet season conditions in 1963 were very close to the norm, but the dry season of 1963/64 was appreciably drier than in many years. But bearing in mind the relative ineffectiveness of scattered rainfall in the dry season, there is no reason to believe that any substantial deviation in the character of the dry season ecoclimate took place during 1963/1964, although as will inevitably be the case, the length of the wet and dry phases will have differed somewhat from other years.

(c) The Ecoclimatic Phases

Omitting for the moment the perennially wet swamp ecoclimate, an attempt will be made to analyse more precisely the phases of the savanna ecoclimate. During 1963/1964 four distinct phases were apparent; an ecologically wet or excessively wet phase, which lasted from the start of the rainy season to at least the end of the rains, and in some instances longer; two short ecologically intermediate phases, preceding and following the wet phase, and during which a rapid increase or decrease in soil moisture content was taking place; and an ecologically dry phase, when the soil moisture supply was at a minimum.

With the data at present available it is not possible to give a precise, quantitative definition to these phases in terms of available moisture or rates of growth, although this would ultimately be desirable. But, during the period 1963/1964, it was possible to isolate trends in plant growth that in general coincided with the different ecoclimatic phases.

The ecologically wet phase, during which time a high level of available moisture was retained in the soil, corresponded to the period of maximum plant growth; in excessively wet sites plant growth may have been limited by physiological drought for part of the phase, but it was apparent in many waterlogged soils that, provided vertical drainage was taking place and the topsoil was partially aerated, herbaceous growth could occur. When prolonged site inundation took place, however, plant growth only occurred with the lowering of the water in the latter part of the phase.

The first ecologically intermediate phase, during which rapid usage and limited replenishment of available moisture was taking place, corresponded to a period of reducing plant vigour. Because of the high rates of potential evapotranspiration during the dry season, this phase in most sites only lasted two to four weeks.

The ecologically dry phase, when a low rate of moisture usage was taking place from the limited and often inaccessible reserves in the soil, corresponded at first to a period of very limited growth, interspersed with short-lived responses to occasional rain showers during September and November, 1963, and finally to a period of complete dormancy.

The second ecologically intermediate phase, during which time intermittent replenishment of soil moisture took place, corresponded to a period of renewed herbaceous activity. The occasional showers during April, 1964, which occur in most years and herald the approach of the rains, served to initiate plant growth, which was only sustained, however, by the advent of the rainy season itself, and the recommencement of the ecologically wet phase in the following month.

In Tables 18/19 an attempt has been made to state the length of the respective phases in different sites.

TABLE 18: Ecoclimatic phases during the period June 1, 1963 - May 31, 1964 at selected sites in the northern Rupununi

Site	Wet Phase 1963	Weeks	Intermediate Phase (1)	Weeks	Dry Phase	Weeks	Intermediate Phase (2)	Weeks	Wet Phase 1964	Weeks
24	Jun 1 - Aug 21	11 1/2	Aug 22 - Sept 15*	3 1/2	Sept 16* - Apr 5	29	Apr 6 - May 18	6	May 19 - May 31	2
05	Jun 1 - Aug 21	11 1/2	Aug 22 - Sept 15*	3 1/2	Sept 16* - Apr 5	29	Apr 6 - May 18	6	May 19 - May 31	2
12	Jun 1 - Aug 21	11 1/2	Aug 22 - Sept 15*	3 1/2	Sept 16* - Apr 5	29	Apr 6 - May 18	6	May 19 - May 31	2
07	Jun 1 - Aug 31*	13	Sept 1* - Sept 15*	2	Sept 16* - Apr 5	29	Apr 6 - May 18	6	May 19 - May 31	2
09	Jun 1 - Nov 15*	24	Nov 16* - Jan 20*	9 1/2	Jan 21* - Apr 5	10 1/2	Apr 6 - May 18	6	May 19 - May 31	2
110	Perennially wet phase - 52 weeks									

* Approximate date.

TABLE 19: Duration of ecoclimatic phases in 1963/1964 at selected sites in the northern Rupununi

Site	Wet months	Intermediate months	Dry months	Ecoclimate
24	3	2 1/2	6 1/2	Dry savanna
05	3	2 1/2	6 1/2	Dry savanna
12	3	2 1/2	6 1/2	Dry savanna
07	3 1/2	2	6 1/2	Wet savanna
09	6	3 1/2	2 1/2	Wet savanna
110	12	-	-	Swamp

CHAPTER 8

PLANT GROWTH IN THE NORTHERN RUPUNUNI

The savanna plant communities of the northern Rupununi are dominated by a small number of herbaceous and woody species, which are adapted in their structure, and in the case of herbaceous plants in their life cycle to withstand drought and the seasonal assault of fire.

In the first instance, the savanna formations may be divided into :-

(a) Open wooded savanna

(b) Herbaceous savanna

Within this framework the system of nomenclature found most suitable to conditions in the Rupununi is one based on Brazilian terminology and used in areas that are floristically similar to the Rupununi. The following terms will be used :-

(a) Open wooded savanna

i. Campo cerrado

ii. Campo coberto

iii. Campo sujo

(b) Herbaceous savanna*

i. Campo limpo (grass-dominated)**

ii. Campo limpo (sedge-dominated)

In addition, the following alien elements are to be found within the northern Rupununi savanna :-

i. Sedge swamps

ii. Palm swamps

iii. Galeria forest

iv. Forest 'bush islands'

(a) Definition of Savanna Units

In the northern Rupununi the character of the savanna units is as follows :-

(a) Open wooded savanna

i. Campo cerrado. A wooded savanna, with an herbaceous layer dominated by bunch grasses with an underlying

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* The phrase 'herbaceous savanna' (c.f. 'savane herbeuse' used by French writers, e.g. Aubréville, 1961) is preferable to 'savanna grassland', commonly used by English writers, e.g. Cole, 1963/2, as the latter clearly cannot refer to sedge-dominated 'campo limpo' communities such as occur in the Rupununi. There is no doubt, however, that these sedge communities belong to the savanna ecosystem, for, typically dominated by such species as Rhyncospora barbata and Fimbristylis ferruginea, they experience an ecoclimate of alternating wetness and drought, exhibit seasonal growth and display xeromorphic structure etc., which are characteristic of the savanna ecosystem. Moreover, within the 'campo limpo' there are a number of herbaceous species common to both grass and sedge-dominated communities, a condition which is in marked contrast to the abrupt specific boundary existing between the sedge-dominated 'campo limpo' and perennially wet sedge swamps.

** The word 'dominance' is used to refer to the size, i.e., height, width, breadth of plants; 'density', when used, refers to the number of occurrences.

substratum of sedges, and a few forbs. The tree cover is dense, but not continuous; individual trees are from five to ten metres apart, and mature specimens normally grow to a height of three to six metres.

ii. Campo coberto. A less densely wooded savanna, with an herbaceous layer dominated by bunch grasses, with an underlying substratum of sedges, and a few forbs. Tree growth may be lower and is more sparsely distributed than in the above; individual trees are more than ten metres apart, and the height of mature specimens is generally two to four metres.

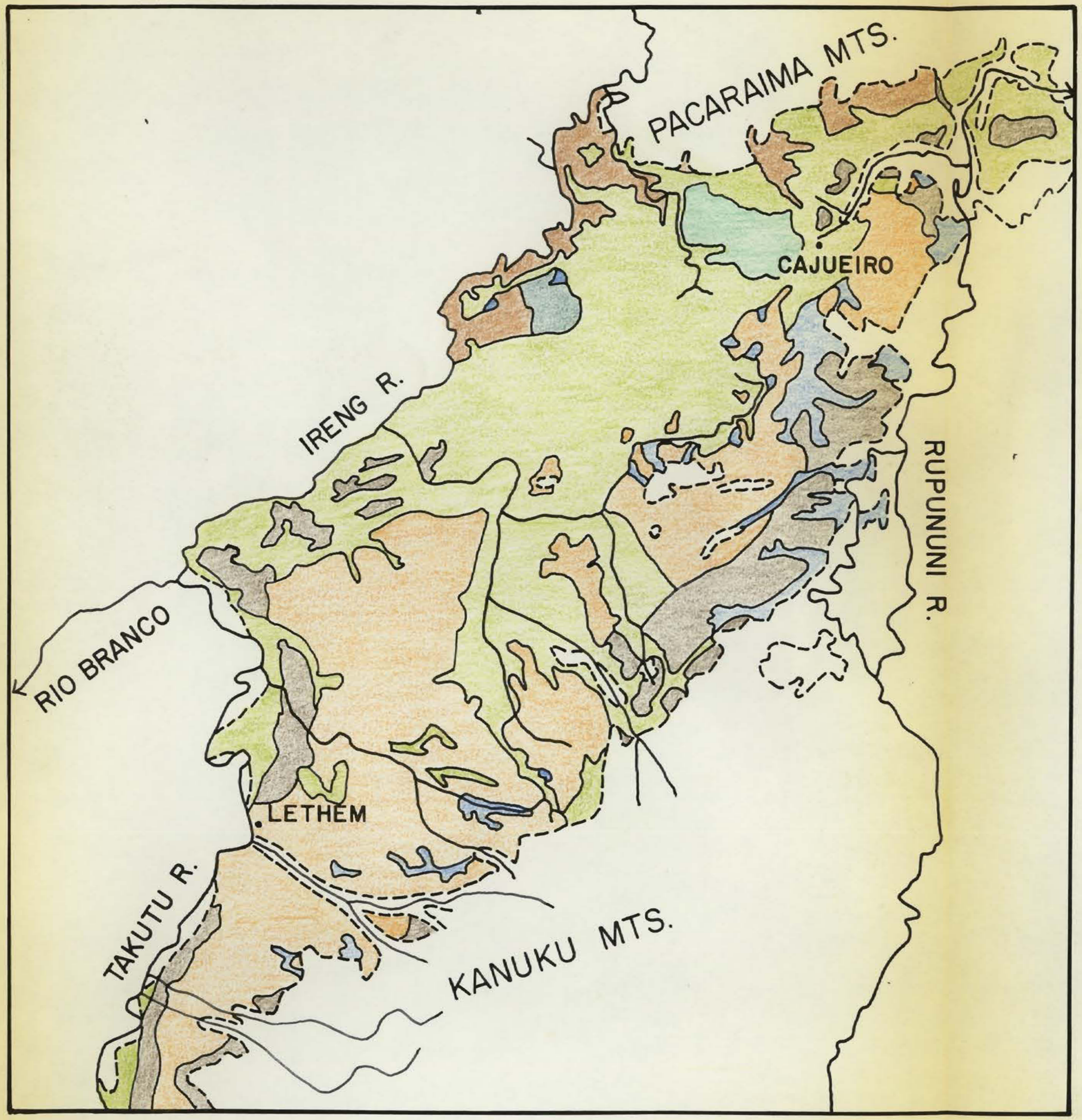
iii. Campo sujo. A sparsely wooded savanna, with an herbaceous layer generally dominated by bunch grasses, with an underlying substratum of sedges, and a few forbs. Woody growth consists of sparse and stunted low trees and shrubs; they are widely scattered, and individuals rarely exceed one to two metres in height.

(b) <u>Herbaceous savanna</u>

i. Campo limpo (grass-dominated). A treeless savanna with an herbaceous layer dominated by bunch grasses, with an underlying substratum of sedges, and a few forbs.

In places communities with mixed grasses and sedges as co-dominants occur; this stage is transitional to :-

ii. Campo limpo (sedge-dominated). A treeless savanna with an herbaceous layer dominated by sedges. A few grasses and forbs may occur, but in places almost pure sedge communities are found.



MAP 7
VEGETATION OF THE
NORTHERN RUPUNUNI SAVANNAS

LEGEND

Scale in Miles
0 5 10

Campo cerrado

Campo coberto

Campo coberto/sujo

Campo limpo (grass-dominated)

Campo limpo (mixed)

Campo limpo (sedge-dominated)

Swamp

---- Savanna-forest boundary

PLATE 7: 'Campo cerrado' on lateritic gravel terrain, near Yupakari. The dominant trees are Curatella americana and Byrsonima spp., with Trachypogon plumosus the principal herb.

PLATE 8: 'Campo coberto' on the western margin of the Meritizero Ridge. The site, which has been recently burnt, has a grass-dominated herbaceous layer, with Trachypogon plumosus commonly occurring, and a tree layer dominated by Curatella americana.

PLATE 9: 'Campo sujo' on latosolic sheetwash soil, near Lethem. In the foreground, low stunted Curatella americana and Plumeria inodora grow little above the herbaceous layer which is dominated by Trachypogon plumosus. In the background, the savanna gives way to galeria forest.

PLATE 10: Grass-dominated 'campo limpo' on eastern flank of the Meritizero Ridge. Deep, loamy soils support an herbaceous community dominated by Trachypogon plumosus, Fimbristylis ferruginea and Stenophyllus paradoxa.

PLATE 11: Sedge-dominated 'campo limpo' in the Maracanata Basin. The foreground, which has been recently burnt, is inundated in the wet season. The principal sedges are Rhyncospora barbata and Fimbristylis spp.

PLATE 12: Palms (Mauritia minor) surrounding a very poorly drained swamp, near Manari.

PLATE 13: Forest 'bush island' in open savanna near Maracanata; the forest is located under site conditions comparable with the adjacent savanna.

PLATE 14: Galeria forest along the Ireng River. In the foreground, the river bank is undergoing erosion, and no tree growth has established itself; elsewhere the forest extends 30-60 metres from the river.

(b) Tree Growth

Tree growth in the savanna is dominated by four genera: Curatella, Byrsonima, Bowdichia and Plumeria. Other less commonly occurring genera are: Anacardium, Antonia, Hirtella, Pavonia, Psidium, Randia, and Roupala, together with a few succulents of the genus Cereus.

The height and density of tree growth varies greatly from site to site; Curatella americana, the commonest shrub, may grow 8-10 metres in height, but is commonly between 2-5 metres in the Rupununi, with a gnarled and twisted form, and limbs often spreading as far laterally as vertically. Its leaves are coarse, rough and brittle, and its bark thick and corrugated. The shrub is able to withstand very considerable burning and stripped to its bare skeleton, will readily recover provided adequate moisture is available. The species, like other savanna shrubs, is considered evergreen by Beard (1953), and although individual leaves are shed annually, the only general leaf shedding occurs as a result of fire (See Plate 17).

Byrsonima spp. (B. coccolobiaefolia; B. coriacea; B. crassifolia; B. stipulaceae) are of smaller size, and commonly attain 2-3 metres in height. The leaves are smaller and less coarse, and have a waxy surface, and the bark is thinner and more smooth than Curatella sp. Bowdichia virgilioides and Plumeria inodora are less abundant, but are usually prominent by virtue of their greater height which commonly reaches one and a half times that of adjacent shrubs.

(c) Herbaceous Growth

The grasses of the savanna are perennial bunch grass species, which remain in a state of dormancy during the driest phase of the ecoclimate and survive thereby seasonal desiccation. The grasses grow in slender tufts at intervals of 15-30 cm between which other herbs are dispersed. The grasses grow to heights of 50-100 cm, although during the flowering season the spikes may reach 100-150 cm. The tufts are formed of a bunch of stems springing from a common rootstock; the leaf material is coarse, rolled and frequently pubescent.

Throughout the rainy season herbaceous growth is vigorous and little of the bare soil is visible from above; in the dry season the vegetative material dies off or is burnt, and a high proportion of the ground surface is exposed.

The principal genera to which savanna grasses belong are: Andropogon, Aristida, Axonopus, Eragrostis, Gymnopogon, Mesosetum, Panicum, Paspalum and Trachypogon.

Where sedges grow in profusion in the savanna, the herb stratum is lower than in the grass-dominated areas; the sedges are less strongly tufted and grow more closely together, covering a higher proportion of the ground surface. They may reach a height of 20-50 cm, with their inflorescences attaining twice this height, but much of the growth is under 30 cm.

The savanna sedges, like the grasses, are xeromorphic in character, and have thin, narrow leaves, in contrast to the broad pith-filled stems characteristic of swamp sedges. The principal sedge genera in the savanna are: Bulbostylis, Cyperus, Dichromena, Fimbristylis, Rhyncospora, Scleria and Stenophyllus.

The forbs in the savanna represent a small percentage of the population of almost all communities; the commonest genera are: Borreria, Buchnera, Cassia, Galactia, Phaseolus, Polygala and Sida.

There is, finally, one miniature shrub which occurs commonly in the herbaceous layer under imperfectly drained conditions, namely: Byrsonima verbascifolia. This plant rarely grows above 25-30 cm.

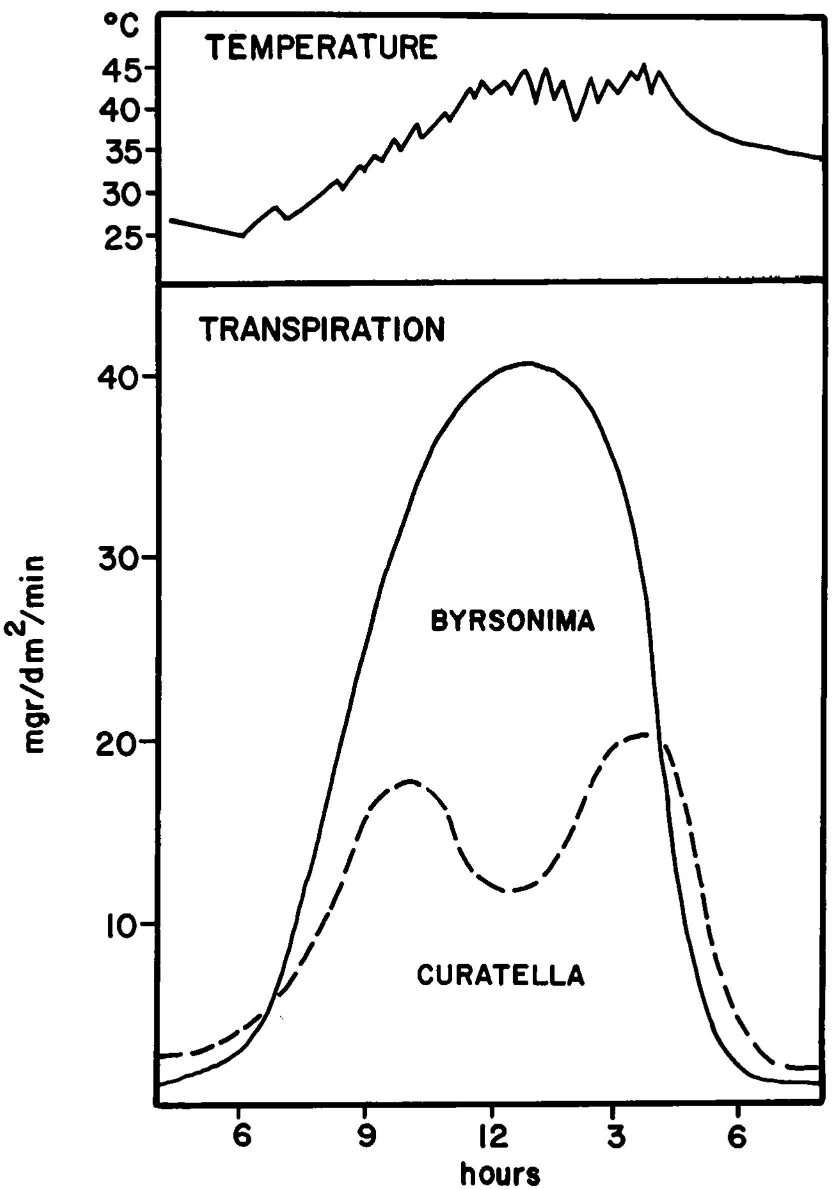
(d) The Adaptation of Savanna Species

The plant species of the savanna are adapted in various ways to withstand the dual attack of drought and fire in the dry season. The dormant habit of herbaceous growth permits survival during this time, while the thin narrow leaves, often pubescent, rolled and clustered tightly together, of the grasses and sedges reduce transpiration at critical periods of growth. Tree leaves are similarly xeromorphic, being pubescent, waxy or of a coarse, brittle texture. Beard (1953) describes also the drooping habit of tree leaves which protects them from the direct rays of the sun.

The degree of xeromorphism, however, varies from species to species. Experiments in the llanos of Venezuela (Vareschi, 1960) have shown, for example, that during the hottest part of the day there is an abrupt reduction in the rate of transpiration from Curatella americana, by comparison with Byrsonima crassifolia which experiences its highest rate at this time (See Figure 15); both species apparently have access to ground water, and as yet no explanation of the phenomenon is possible. Vareschi (1960) states :-

> 'If this economization of Curatella at midday is due to a shutting of the stomates or to a temporal breaking-down of the assimilation ... cannot be answered still.'
>
> V. Vareschi, 1960, p. 45.

FIG. 15: TRANSPIRATION RATES OF CURATELLA AMERICANA AND BYRSONIMA CRASSIFOLIA



The transpiration curves represent water loss from upper leaf surfaces of Curatella americana and Byrsonima crassifolia during a typical day in the dry season, at Calabozo, Venezuela. Included also are shade temperatures. (After Vareschi, 1960).

Further measurements were made of the rate of transpiration of trees which occur in forest communities, e.g., Cecropia sp., Inga sp., Roystonia regia, and it was found that the transpiration maximum of the savanna shrubs was appreciably greater than of the forest trees. It thus appears that both Curatella americana and Byrsonima crassifolia are, by comparison, only moderately xeromorphic, and that their abundant occurrence in the savanna reflects more their ability to withstand fire than to combat drought.

The principal fire adaptation of the woody species in the Rupununi savannas is their thick, corky and corrugated bark, which is especially pronounced in Curatella americana, mature species of which may have a bark up to 2-3 cm thick. Byrsonima spp. are less protected in this respect and appear to be the trees that are most commonly destroyed by savanna fires. The tree is also considered suitable firewood for domestic purposes!

In addition, the tuberous rootstock of both herbaceous and shrub species assists survival during fire; the rootstock is not destroyed by burning and from it after fire fresh growth can develop. It is for this reason that many apparently youthful shrubs have an anomalously large rootstock indicative of the periodic setbacks they suffer at the hands of fire in the early stages of growth.

(e) Ecological Relations of Plant Growth

The broad distinction between the elevated and the lowland parts of the northern Rupununi, which is already apparent in soil and drainage patterns, is repeated in the vegetation formations of the region. Table 20 illustrates these broad ecological relations.

TABLE 20: Broad ecological relations within the northern Rupununi

<table>
<tr><td>Drainage class</td><td>Excessive</td><td>Well</td><td>Moderately Well</td><td>Imperfect</td><td>Poor</td><td colspan="2">Very Poor</td></tr>
<tr><td>Soils</td><td>Azonal</td><td colspan="2">Zonal</td><td colspan="4">Intrazonal</td></tr>
<tr><td>Ecoclimate</td><td colspan="3">Dry savanna ecoclimate</td><td colspan="2">Wet savanna ecoclimate</td><td colspan="2">Swamp eco-climate</td></tr>
<tr><td rowspan="2">Vegetation formation</td><td colspan="3" rowspan="2">Wooded or herbaceous savanna (Campo cerrado > C. limpo: grass-dominated)</td><td rowspan="2">Savanna (transition zone)</td><td rowspan="2">Herbaceous savanna (C. limpo: sedge-dominated)</td><td colspan="2">Swamp</td></tr>
<tr><td>Palm</td><td>Sedge</td></tr>
<tr><td>Herbaceous growth</td><td colspan="3">Grasses, with substratum of sedges</td><td>Grasses & sedges</td><td>Sedges & few grasses</td><td colspan="2">Sedges</td></tr>
</table>

In the more elevated areas, where a dry savanna ecoclimate prevails, the terrain supports a wooded savanna or, in a few areas, grass-dominated herbaceous savanna. In this zone, where there is never a ground water saturation problem in the upper soil, other factors determine the nature and distribution of woody growth; these are principally the accessibility of perennial moisture supplies, and fire. In the zone as a whole grass species remain dominant in the herbaceous layer, although their composition varies in accordance with the moisture regime in the solum.

In less elevated areas, under a wet savanna ecoclimate, the imperfectly drained soils, which are intermittently waterlogged during the rainy season, represent the transition zone wherein the restrictive effect of seasonal mal-aeration on plant growth becomes apparent, and where woody formations gradually disappear and give way to sedge-dominated communities.

Within the poorly drained areas there exist only the sedge-dominated formations, with or without grass species, and only very rarely are shrubs to be found under the excessively wet seasonal conditions. Beyond this is the abrupt transition from poorly drained savanna to perennially wet swamp.

(f) Margins of Savanna Growth

The margin of the savanna, where it abuts onto swamp, is frequently marked by palms, of which the principal species are *Mauritia minor* (Ite palm), *Maximiliana regia* (Cocorite palm) and *Astrocaryum jauri* (Jauri palm). In a few places extensive areas of palm swamp are to be found, but the trees, which prefer slightly drier conditions than the sedge swamp, more commonly form a narrow transition belt between it and the savanna.

The transition from savanna to galeria forest or bush islands is equally abrupt, although it does not always coincide with as precise a 'macro-ecoclimatic' divide. More often it appears that a sharp floristic break is established upon an ecoclimatic continuum by burning. In many places, for example, it is possible to move from beneath a forest canopy into the open savanna in a distance of three or four metres. How is this sharp break maintained?

Firstly, it appears that savanna tree species are intolerant of shaded conditions, and thus do not grow into the forest; nor are they able to achieve more than an open stand in the savanna. Secondly, the forest trees, individually mal-adapted to withstand the advent of fire, particularly in the sapling stage, are unable to regenerate easily into the savanna. Thus an abrupt floristic and physiognomic divide is maintained (See Plates 15-16).

In especially dry periods the forest may burn marginally, but in most cases, where there is no shifting cultivation to aid the spread of savanna, it will regenerate rapidly enough to maintain itself and prevent the establishment of a gradual savanna-forest transition*.

(g) Analysis of Herbaceous Savanna Communities

On sites in the savanna where soil profiles were examined a qualitative description was made of the density and dominance of plant growth. The data on herbaceous species have been analysed and are herein tabulated according to site drainage characteristics.

The excessively, well and moderately well drained sites in the Rupununi are dominated by the single species *Trachypogon plumosus*, which

* The situation is discussed more fully in Chapter 10; see also E.W. Waddell (1963), Chapter 5.

PLATE 15: The anthropic influence: a typical burn at ground level, which will effectively prevent any forest saplings growing in the savanna.

PLATE 16: The anthropic influence: an abrupt savanna-forest boundary, near Moco Moco.

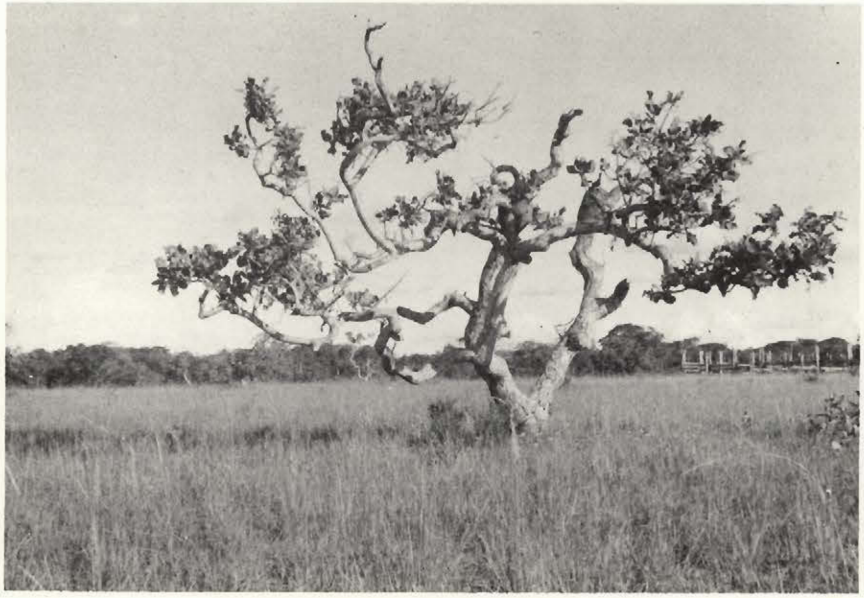


PLATE 17: Mature specimen of Curatella americana, showing signs of past fire-damage (Photo by T.L. Hills)

PLATE 18: Herbaceous layer, on fine gravelly soil, dominated by Trachypogon plumosus, with a few forbs and sedges visible (Photo by T.L. Hills).

appears as the primary grass in density and dominance in virtually every site. Its leaves grow 50-80 cm in height and overtop most other herbaceous plants. It is a strongly tufted species with coarse, frequently pubescent leaves, and provides much of the raw material for savanna fires. It has a wide amplitude of tolerance within the better drained sites, and appears in association with a variety of other grasses and sedges (See Plate 18).

The number of sedge species is small in the drier sites, and although they achieve a high density, they are strongly dominated by the taller grasses which during periods of growth overshade them. After Trachypogon plumosus, the three sedges Bulbostylis conifera, Stenophyllus paradoxa and Fimbristylis ferruginea are the commonest herbs and display a similar wide tolerance within the better drained sites. Several other grasses also appear widely here, principally Axonopus spp. (A. aureus, A. chrysites) and Aristida spp. (A. radiata, A. tincta, A. setifolia), but they everywhere remain secondary in importance to Trachypogon plumosus. More selective in their distribution are Mesosetum spp. (M. loliiforme, M. tenuifolium) found most commonly on the excessively drained sites, and Andropogon angustatus and Gymnopogon foliosus, which are both prominent species in moderately well drained soils.

Within the transition zone of mixed grasses and sedges, where imperfectly drained soils exist, the most prominent species, both in dominance and density are Trachypogon plumosus, Fimbristylis ferruginea, and Bulbostylis conifera. In addition, within this zone there frequently occurs the diminutive herbaceous shrub Byrsonima verbascifolia.

The number of individual species attaining prominence in sedge-dominated, poorly drained sites is smaller than in the bunch grass savanna. Fimbristylis ferruginea and Rhyncospora barbata are most common and on occasions form almost pure stands. The widely tolerant grasses Aristida spp. appear regularly here together with a few Trachypogon plumosus, but their overall dominance is secondary to that of the sedges.

The herbaceous species occurring within each drainage class have been analysed and are detailed as follows :-

(a) Number of site occurrences of species displaying high density.

(b) Number of site occurrences of species displaying moderate density.

On each site between one and four herbaceous species were normally recorded within each of the two categories specified above. In order to obtain an expression of the overall occurrence of individual species within each drainage class, a value of two was allotted to each high density site occurrence, and a value of one to each moderately dense site occurrence; the total value for each species was then calculated, and an index of density (c) expressed finally as a percentage of the total value within each drainage unit.

Finally other recurring species are listed (d).

The results for the five savanna drainage classes are to be found in the following pages. Subsequently in Table 21, the index of density data for the five classes are compared, and an indication given of the amplitude of tolerance to variable moisture conditions of the savanna herbs.

i. Excessively drained sites (Sites: 10)

(a) High density occurrence

Trachypogon plumosus	9
Bulbostylis conifera	5
Mesosetum spp.	3
Fimbristylis ferruginea	2
Andropogon angustatus	1
Aristida spp.	1
Galactia jussieuana	1
Stenophyllus paradoxa	1

(b) Moderate density occurrence

Bulbostylis conifera	4
Aristida spp.	3
Stenophyllus paradoxa	3
Andropogon angustatus	2
Axonopus spp.	2
Buchnera elongata	2
Fimbristylis ferruginea	2
Cassia flexuosa	1
Galactia jussieuana	1
Mesosetum spp.	1
Trachypogon plumosus	1

(c) Index of density

Index of density	Value	% Value
Trachypogon plumosus	19	28
Bulbostylis conifera	14	21
Mesosetum spp.	7	10
Fimbristylis ferruginea	6	9
Aristida spp.	5	7
Stenophyllus paradoxa	5	7
Andropogon angustatus	4	6
Galactia jussieuana	3	5
Axonopus spp.	2	3
Buchnera elongata	2	3
Cassia flexuosa	1	1
		100

(d) Other recurring species

Evolvulus sericeus

Tree Growth:		
	Campo cerrado	- 3 sites
	Campo coberto	- 6 sites
	Campo sujo	- 1 site
	Campo limpo	- Nil

ii. Well drained sites (Sites: 14)

(a) High density occurrence

Trachypogon plumosus	13
Stenophyllus paradoxa	8
Fimbristylis ferruginea	7
Bulbostylis conifera	5
Aristida spp.	2
Axonopus spp.	2
Cassia flexuosa	2
Dichromena ciliata	1
Mesosetum spp.	1

(b) Moderate density occurrence

Aristida spp.	7
Andropogon angustatus	4
Borreria spp.	4
Fimbristylis ferruginea	4
Axonopus spp.	3
Mesosetum spp.	3
Galactia jussieuana	2
Bulbostylis conifera	1
Byrsonima verbascifolia	1
Cassia flexuosa	1
Evolvulus sericeus	1
Stenophyllus paradoxa	1

(c)

Index of density	Value	% Value
Trachypogon plumosus	26	23
Fimbristylis ferruginea	18	16
Stenophyllus paradoxa	17	15
Aristida spp.	11	10
Bulbostylis conifera	11	10
Axonopus spp.	7	6
Cassia flexuosa	5	4
Mesosetum spp.	5	4
Andropogon angustatus	4	4
Borreria spp.	4	4
Dichromena ciliata	2	1
Galactia jussieuana	2	1
Byrsonima verbascifolia	1	1
Evolvulus sericeus	1	1
		100

(d) Other recurring species

Buchnera elongata
Bulbostylis lanata
Hyptis sp.
Paepalanthus capillaceus
Ruellia spp.
Zornia diphylla

Tree Growth:

Campo cerrado	-	6
Campo coberto	-	5
Campo sujo	-	2
Campo limpo	-	1

iii. Moderately well drained sites (Sites: 13)

(a) High density occurrence

Trachypogon plumosus	12
Andropogon angustatus	6
Fimbristylis ferruginea	3
Bulbostylis conifera	2
Byrsonima verbascifolia	2
Eragrostis hypnoides	2
Gymnopogon foliosus	2
Stenophyllus paradoxa	2
Axonopus spp.	1
Dichromena ciliata	1
Paspalum spp.	1

(b) Moderate density occurrence

Axonopus spp.	7
Fimbristylis ferruginea	7
Bulbostylis conifera	5
Aristida spp.	4
Stenophyllus paradoxa	4
Andropogon angustatus	3
Borreria spp.	3
Galactia jussieuana	3
Byrsonima verbascifolia	2
Paspalum spp.	2
Cassia flexuosa	1
Eragrostis hypnoides	1
Mesosetum spp.	1
Trachypogon plumosus	1

(c)

Index of density	Value	% Value
Trachypogon plumosus	25	22
Andropogon angustatus	15	13
Fimbristylis ferruginea	13	11
Axonopus spp.	9	8
Bulbostylis conifera	9	8
Stenophyllus paradoxa	8	7
Byrsonima verbascifolia	6	5
Eragrostis hypnoides	5	4
Aristida spp.	4	4
Gymnopogon foliosus	4	4
Paspalum spp.	4	4
Borreria spp.	3	3
Galactia jussieuana	3	3
Dichromena ciliata	2	2
Cassia flexuosa	1	1
Mesosetum spp.	1	1
		100

(d) Other recurring species

Evolvulus becasanus
Paepalanthus capillaceus
Phyllanthus stipularia
Ruellia spp.

Tree Growth:

Campo cerrado	-	4
Campo coberto	-	6
Campo sujo	-	2
Campo limpo	-	1

iv. Imperfectly drained sites (Sites: 20)

(a) High density occurrence

Trachypogon plumosus	18
Fimbristylis ferruginea	10
Byrsonima verbascifolia	9
Bulbostylis conifera	6
Rhyncospora barbata	4
Aristida spp.	3
Andropogon angustatus	2
Galactia jussieuana	1
Paepalanthus capillaceus	1
Paspalum spp.	1

(b) Moderate density occurrence

Dichromena ciliata	8
Aristida spp.	7
Borreria ferruginea	7
Fimbristylis ferruginea	6
Byrsonima verbascifolia	5
Axonopus spp.	4
Andropogon angustatus	3
Bulbostylis conifera	3
Paspalum spp.	3
Rhyncospora barbata	3
Galactia jussieuana	2
Trachypogon plumosus	2
Cassia flexuosa	1
Mesosetum spp.	1

(c)

Index of density	Value	% Value
Trachypogon plumosus	38	23
Fimbristylis ferruginea	26	16
Byrsonima verbascifolia	23	14
Bulbostylis conifera	15	9
Aristida spp.	13	8
Rhyncospora barbata	11	7
Dichromena ciliata	8	5
Andropogon angustatus	7	4
Borreria ferruginea	7	4
Paspalum spp.	5	3
Axonopus spp.	4	2
Galactia jussieuana	4	2
Paepalanthus capillaceus	2	1
Cassia flexuosa	1	1
Mesosetum spp.	1	1
		100

(d) Other recurring species

Eragrostis hypnoides
Ruellia spp.
Schieckia orinocoensis
Scleria sp.
Tibouchina aspera

Tree Growth:			
	Campo cerrado	-	3
	Campo coberto	-	6
	Campo sujo	-	5
	Campo limpo	-	6

v. Poorly drained sites (Sites: 28)

(a) High density occurrence

Rhyncospora barbata	16
Fimbristylis ferruginea	15
Aristida spp.	8
Trachypogon plumosus	5
Cyperus spp.	4
Scleria sp.	3
Coutoubea racemosa	2
Others	11

(b) Moderate density occurrence

Aristida spp.	8
Trachypogon plumosus	8
Dichromena ciliata	5
Byrsonima verbascifolia	3
Rhyncospora barbata	3
Borreria ferruginea	2
Fimbristylis ferruginea	2
Others	6

(c)

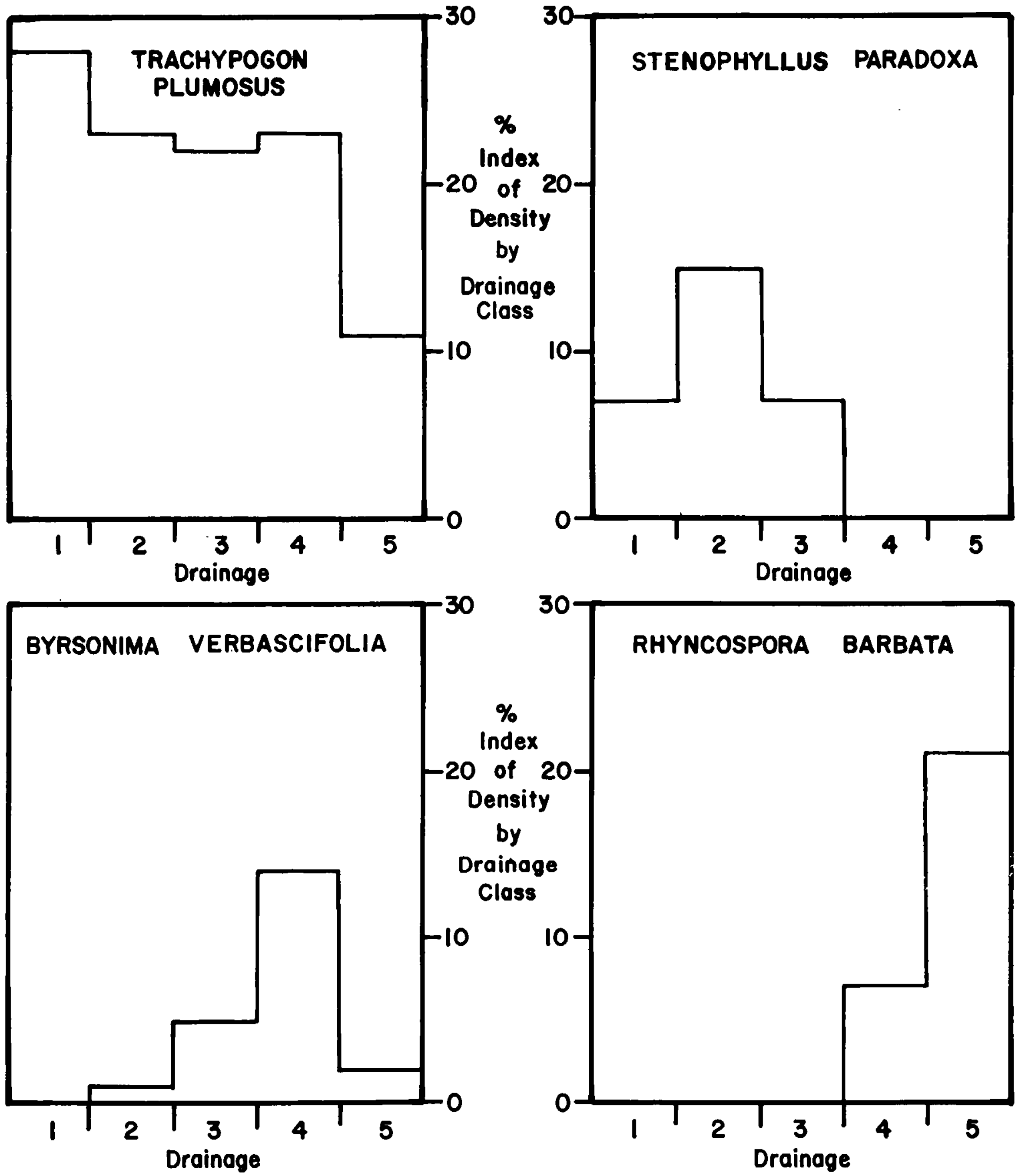
Index of density	Value	% Value
Rhyncospora barbata	35	21
Fimbristylis ferruginea	32	19
Aristida spp.	24	15
Trachypogon plumosus	18	11
Cyperus spp.	8	5
Scleria sp.	6	4
Dichromena ciliata	5	3
Coutoubea racemosa	4	2
Byrsonima verbascifolia	3	2
Borreria ferruginea	2	1
Others	28	17
		100

(d) Other recurring species

Andropogon angustatus
Axonopus spp.
Bulbostylis conifera
Eragrostis spp.
Mesosetum spp.
Mimosa spp.
Paepalanthus capillaceus
Paspalum spp.
Polygala spp.
Rhyncospora longispicata
R. tenuis

Tree Growth			
	Campo cerrado	-	1
	Campo coberto	-	1
	Campo sujo	-	Nil
	Campo limpo	-	26

FIG. 16 : AMPLITUDE OF TOLERANCE TO VARIABLE DRAINAGE OF SELECTED SPECIES



KEY

1 = Excessively drained
2 = Well drained
3 = Moderately well drained
4 = Imperfectly drained
5 = Poorly drained

TABLE 21: Amplitude of tolerance of savanna herbs to moisture variation, expressed as % density within each drainage class.

	Drainage Class				
	Excessive	Well	Moderately Well	Imperfect	Poor
Andropogon angustatus	6	4	13	4	2
Aristida spp.	7	10	4	8	15
Axonopus spp.	3	6	8	2	1
Borreria spp.	-	4	3	4	1
Buchnera elongata	3	-	-	-	-
Bulbostylis conifera	21	10	8	9	2
Byrsonima verbascifolia	-	1	5	14	2
Cassia flexuosa	1	4	1	1	-
Coutoubea racemosa	-	-	-	-	2
Cyperus spp.	-	-	-	-	5
Dichromena ciliata	-	1	2	5	3
Eragrostis hypnoides	-	-	4	-	1
Evolvulus sericeus	-	1	-	-	-
Fimbristylis ferruginea	9	16	11	16	19
Galactia jussieuana	5	1	3	2	-
Gymnopogon foliosus	-	-	4	-	-
Mesosetum spp.	10	4	1	1	1
Paepalanthus capillaceus	-	-	-	1	1
Paspalum spp.	-	-	4	3	2
Rhyncospora barbata	-	-	-	7	21
Scleria sp.	-	-	-	-	4
Stenophyllus paradoxa	7	15	7	-	-
Trachypogon plumosus	28	23	22	23	11
Others	-	-	-	-	7
TOTAL	100	100	100	100	100

(h) Analysis of Wooded Savanna Communities

The species Curatella americana and Byrsonima spp. form a large proportion of tree growth in all wooded savanna communities. Curatella americana is generally the more common of the two and may on occasions form almost pure stands. However, in dense tree communities Byrsonima spp. appear more frequently and may outnumber Curatella americana.

Tree growth in the savannas is limited to areas where aerated soil conditions exist throughout the year. Herein tree growth displays the effects of other factors, principally water accessibility in the dry season and burning*. Thus, in some sites, in well aerated soils, tree growth is entirely absent because of water deficiency in the dry season. Elsewhere compacted, and in the dry season, hardened soils hinder root penetration and often result in low and stunted growth that is highly susceptible to damage from grass fires. Especially is this the case on the lateritic sheetwash soils where large tracts of 'campo sujo' are to be found.

The extent to which fire is responsible for the distribution patterns of tree growth is difficult to assess. Although savanna trees generally survive fire, the periodic burning of their vegetative material will have a restrictive effect on growth; a number of small shrubs that were examined displayed an anomalously large rootstock, suggesting that particularly in the early stages of life, vegetative growth can be set back or temporarily halted by burning, but this only appears to take place, to any degree, in sites where physical limitations already inhibit growth.

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* 'Water accessibility' is a function of two variables; firstly, the amount of water in the soil, and secondly, the penetrability of the soil, i.e., how effectively the roots can reach the water.

The composition of the three wooded savanna formations, whose variable density is thus principally a function of water accessibility, has been analysed and is detailed as follows :-

(a) Number of site occurrences of species displaying high density.

(b) Number of site occurrences of species displaying moderate density.

In order to obtain an expression of the overall occurrence of individual species within the different woody formations, a value of two was allotted to each high density site occurrence, and a value of one to each moderately dense site occurrence; the total value for each species was then calculated, and an index of density (c) expressed finally as a percentage of the total value within each unit.

(d) Finally other recurring species are listed.

The results for the three formations are as follows :-

i. Campo cerrado (Sites: 14)

(a) High density occurrence

Byrsonima spp.	9
Curatella americana	9
Plumeria inodora	3
Pavonia speciosa	1

(b) Moderate density occurrence

Plumeria inodora	8
Bowdichia virgilioides	5
Byrsonima spp.	5
Curatella americana	5
Pavonia speciosa	1

(c)

Index of density	Value	% Value
Byrsonima spp.	23	34
Curatella americana	23	34
Plumeria inodora	14	21
Bowdichia virgilioides	5	7
Pavonia speciosa	3	4
		100

(d) Other recurring species

Antonia ovata
Hirtella racemosa
Psidium sp.

ii. Campo coberto (Sites: 24)

(a) High density occurrence

Curatella americana	18
Byrsonima spp.	10
Plumeria inodora	5
Antonia ovata	1
Randia formosa	1

(b) Moderate density occurrence

Byrsonima spp.	10
Bowdichia virgilioides	7
Plumeria inodora	6
Curatella americana	3
Psidium sp.	2
Randia formosa	1

(c)

Index of density	Value	% Value
Curatella americana	39	40
Byrsonima spp.	30	30
Plumeria inodora	16	16
Bowdichia virgilioides	7	7
Randia formosa	3	3
Antonia ovata	2	2
Psidium sp.	2	2
		100

(d) Other recurring species

Cereus sp.

iii. Campo sujo (Sites: 6)

(a) High density occurrence

Curatella americana	8
Byrsonima spp.	5
Plumeria inodora	3

(b) Moderate density occurrence

Byrsonima spp.	3
Bowdichia virgilioides	2
Plumeria inodora	1

(c)

Index of density	Value	% Value
Curatella americana	16	42
Byrsonima spp.	13	34
Plumeria inodora	7	19
Bowdichia virgilioides	2	5
		100

(j) Swamp Communities

The ecoclimatic individuality of the swamp habitats within the savanna is reflected in flora that has little in common with the adjacent savanna. The physical transition is generally abrupt, and there is little intermingling of savanna and swamp species, a condition which is in marked contrast to the gradual transition between different savanna formations, and which emphasizes the separateness of the two ecosystems.

The swamp plants are strongly adapted to the excessively wet conditions. A number of species in the permanently flooded areas are floating plants, while on the waterlogged margins, a dense growth of pithy-stemmed herbs is found in addition to the palms.

The following species are prominent :-

Cyperus articulatus

Eichornia crassipes

Eleocharis geniculata

Eriocaulon tenuiifolium

Nitella sp.

Nymphaea sp.

PART THREE: REGIONAL STUDIES

CHAPTER 9

REGIONAL DISTRIBUTION OF SAVANNA FORMATIONS

Within the northern Rupununi, six major land units have been recognised and delimited on the basis of geomorphic and pedologic characteristics; they are as follows :-

(a) Lethem-Yupakari land unit, of elevated secondary lateritic gravel deposits, which are currently being modified by sheetwash processes.

(b) Takutu - Proto-Berbice land unit, of elevated and moderately elevated sandy river terrace deposits.

(c) Proto-Ireng land unit, of moderately elevated, fine textured fluvio-lacustrine deposits.

(d) Mountain Outwash land unit, of material deposited at the foot of the Pacaraima and Kanuku mountains.

(e) Lowland unit, of fluvio-lacustrine deposits.

(f) Flood Plain land unit, along the major rivers.

The six major land units have been sub-divided into thirteen 'terrain units', each of which comprises an area wherein a general uniformity of vegetation and ecological controls are to be found and which may be considered as subsidiary ecosystems within the greater savanna ecosystem. Map 7 (endflap), compiled with the aid of aerial photographs, illustrates the distribution of these units*.

In the following pages an attempt has been made to describe the nature of each terrain unit. Table 22, by way of introduction, illustrates the broad ecological relations of the respective units.

1. Lethem-Yupakari Land Unit

Skirting the northern face of the Kanuku Mountains, and extending across half the northern Rupununi, to Pirara in the west and Kwainatta in the north, is a region of undulating gravel ridges and gently sloping sheetwash deposits of lateritically-derived materials, through which exposures of massive laterite occasionally protrude. The northern margin of the area, dipping to the fluvio-lacustrine deposits of the Proto-Berbice depression, is marked by a number of outliers of the unit, of which the largest is the ridge to the west of Meritizero.

The localized outcrops of hard, pavement-like slabs of massive laterite occur widely in lower and mid-slope positions and are relict of a late Tertiary laterite surface, from which the present parent materials of the unit have been derived. Remnants of the massive laterite surface extend far into the Rio Branco savannas, and it is from the more distant parts of the basin that the secondary lateritic gravels, found in the Rupununi, have in the past been transported by the Proto-Berbice River.

The landscape is partly composed of the dissected gravel topography, but in lower areas the troughs of the gravel ridges have been infilled, and in places the old gravel surface completely buried beneath a mantle of recent sheetwash alluvium of loam or sandy clay loam texture. In addition, a few very gently sloping depressions and flats have been formed within the area, where the finest sheetwash alluvium has been laid down

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* Aerial photographs by Hunting Aerosurveys, Ltd., England.

TABLE 22: Ecological relations of terrain units in the northern Rupununi

Terrain unit	Ecoclimate*	Texture of solum	Texture of substratum	Vegetation	Herbaceous formation
1. Lethem-Yupakari land unit					
Yupakari	D	Gravelly L/SCL		C. cerrado/ coberto	Grasses
Lethem	D	SL-SCL	Gravel	C. coberto/ sujo	Grasses
Meritizero	D	Loam	Loam over gravel	C. limpo	Grasses
2. Takutu - Proto-Berbice land unit					
Inaja	D	LS-SCL	SCL	C. cerrado	Grasses
Pirara	W	SL-SCL	SCL	C. limpo	Sedges
3. Proto-Ireng land unit					
Rego	D/W	SIC/SCL-C	?	C. coberto	Mixed
4. Mountain Outwash land unit					
Toka	D	Sand, with silty horizons		C. coberto	Grasses
5. Lowland unit					
Maracanata	W	Silt/clay	Silt/clay over sands	C. limpo	Sedges
Nappi	W	Silt/clay	Silt/clay over sands	C. limpo	Sedges
Qatata	S	Silt/clay	?	Swamp	Sedges
Bella Vista	D	SL-SCL	?	Variable	Grasses
Cajueiro	D	SL-SCL	Sand/gravel	C. limpo	Mixed
6. Flood Plain land unit					
Mirichy	D/W	Highly variable			

* D = Dry savanna ecoclimate
W = Wet savanna ecoclimate
S = Swamp ecoclimate

under semi-lacustrine conditions. Elsewhere, on the Meritizero Ridge, there is evidence of aeolian accumulations in association with the lateritically derived parent materials.

The Lethem-Yupakari land unit covers the majority of the elevated part of the northern Rupununi savannas; it experiences a dry savanna ecoclimate and is, for the most part, covered by open wooded savanna, except for the eastern margin of the Meritizero Ridge, where tree growth is absent.

Tree density and size vary from area to area but throughout the unit the dominant species, both woody and herbaceous, change little.

Within the contemporary landscape three terrain units have been recognised :-

(a) Yupakari terrain, consisting of the gravel ridge deposits.
(b) Lethem terrain, consisting of the sheetwash deposits.
(c) Meritizero terrain, consisting of aeolian deposits laid down against lateritically-derived sediments.

(a) Yupakari Terrain

The secondary lateritic gravel topography, which supports a dense to moderately dense open wooded savanna, has been designated the Yupakari terrain. Within the unit two distinct erosion levels are visible; the higher of these, consisting of a fine pisolithic gravel surface at 140 metres, extends along the Rupununi River and the northern face of the Kanuku Mountains between Karanambo and Nappi, with lower transitional remnants extending to the north-west.

Near Yupakari, where tree growth is most dense, the surface is strongly dissected by tributaries of the Rupununi River; the convex ridges rise abruptly from the adjacent swamps and riverine flats, with slopes of up to 20 degrees, and in this younger landscape gullying rather than

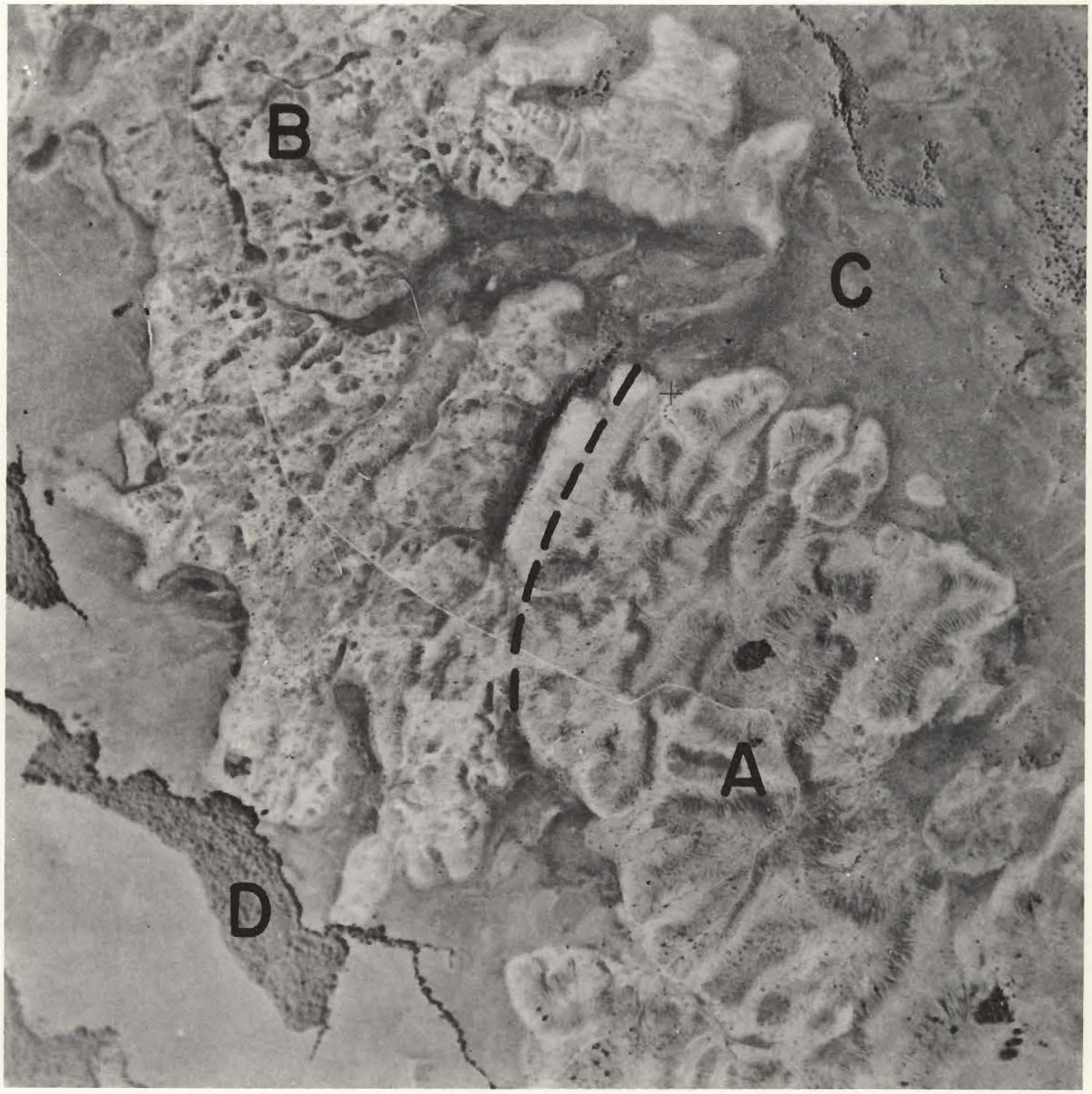

PLATE 19: The Lethem-Yupakari land unit, north of Hawkins Mission. The elevated gravel surface of the Yupakari terrain (A) has steep slopes and pronounced gullying. The area is covered by 'campo cerrado', but two small 'bush islands' are also visible. Northwards, gentler relief has led to sheetwash accumulation (B) over much of the gravel terrain.

Also represented are the Nappi terrain (C) of the Lowland unit, galeria forest (D), and, in the north-east corner of the photograph, a margin of palm swamp (Photo by Hunting Aerosurveys, Ltd.).

sheetwash erosion has predominated. The gravel deposits are less dissected around Nappi, where an undulating surface with local sheetwash infilling, extends northwards to Hawkins Mission; marginally, however, where the gravels abut onto the flood plain of the Nappi River, steep slopes and gullying reappear.

Thence, the surface gradually falls away to the north and west, although the fine pisolithic gravels persist. The terrain is moderately dissected, with slopes of 5 - 10 degrees, and sheetwash accumulation between the ridges gradually increases with lower relief.

To the south and west of Manari, the fine pisolithic gravel gives way to medium to fine gravels of sub-angular and blocky structure, associated with occasional rounded quartz pebbles. The material comprises the lower of the two erosion surfaces, at approximately 120 metres, and extends southwards to the western extremity of the Kanuku Mountains, with only very slight occurrences beyond that point*.

The lower gravel terrain has been moderately dissected in the past, but sheetwash erosion has overlain much of the area and today only the upper parts of the ridges, rising only a few metres, protrude from the surrounding alluvial mantle.

The gravel soils have been classified as regosolic; they are generally loose and unconsolidated, although in a few places there are signs of slight reconsolidation in the substratum (See Plate 20). Physical analysis of samples from the zone 0-100 cm gave the following results :-

(a) <u>Fine gravel regosol (140 metre surface)</u>

Site 64 Location: near Nappi

Coarse gravel	-
Medium gravel	7% (by weight)
Fine gravel	59% (by weight)
Loam/clay loam	34% (by weight)

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* The elevation of the two surfaces has been determined by N.K.P. Sinha.

PLATE 20: Medium gravel surface of the Yupakari terrain.

PLATE 21: Outcropping, primary laterite to the south of Pirara, supporting a dense growth of savanna trees and shrubs, with Plumeria inodora and Curatella americana prominent.

(b) Medium gravel regosol (120 metre surface)

Site 81 Location: Maracanata

Coarse gravel	-
Medium gravel	48% (by weight)
Fine gravel	23% (by weight)
Loam	29% (by weight)

The Yupakari terrain supports a wooded bunch grass savanna, with 'campo cerrado' commonly found on the fine textured gravels, and 'campo coberto' on the medium textured. Throughout the area tree growth is often stunted, which may be partly attributable to the infertility of the soil, but at the same time, the variable water retention capacity of the gravel soils has had an effect on tree growth, which explains contrasts in tree density between areas that are uniformly infertile.

Throughout the terrain unit the herbaceous layer is dominated by bunch grasses, principally *Trachypogon plumosus*, although they are usually in association with a well developed understorey of sedges, principally *Bulbostylis conifera*, *Fimbristylis ferruginea* and *Stenophyllus paradoxa*.

(Site 15, described in Chapter 5, represents a typical site within this unit).

Effect of primary laterite on plant growth

Throughout the lateritically-derived terrain local exposures of primary laterite occur, forming pavement-like slabs or blocks of hard rock which protrude above ground level. The laterite forms part of a highly dissected, but deep and extensive relict surface beneath the gravel and sheetwash deposits; at the Maracanata water hole, for example, a vertical exposure of massive laterite measuring eighteen metres is visible.

Perennial seepage waters emerge from at or close to the base of the laterite in a number of springs between Maracanata and Yupakari and indicate the pervious nature of the rock. However, where exposures of primary laterite are found at the surface, they frequently coincide with a dense growth of woody savanna species, which appear to be a response to local moisture supplies retained in the upper layers of the creviced and dissected laterite (See Plate 21). At the same time, there is also a sparser herbaceous growth within such sites and thus a less destructive fire effect, which may benefit tree growth.

(b) Lethem Terrain

The sheetwash deposits of the Lethem terrain which, for the most part, experience a dry savanna ecoclimate, are strongly developed in association with the lower gravel surface at 120 metres. Here finer materials have been sorted and carried by sheetwash processes from adjacent gravel ridges, and deposited as a mantle up to several metres in depth, over the lower parts of the gravel terrain. The sheetwash soils are compacted, and form very gently undulating or sloping surfaces, of rarely more than 2 degrees, amid the ridge topography.

The soils, underlain by the poorly water-retaining gravels, support 'campo sujo', and less frequently 'campo coberto'. On a few imperfectly drained sites seasonal waterlogging may exclude tree growth altogether, but where better drained conditions exist and, especially where the sheetwash mantle is deep, a uniformly stunted and sparse tree cover prevails.

It is apparent that in such areas, in addition to the low water retention in the gravel substratum, the solum itself creates an unfavourable medium for tree growth, for the compaction and resultant poor aeration of the surface layers of the soil greatly hinder the establishment of young saplings, by restricting the development of their root systems.

In Site 24, for example, near Lethem, the upper layers of the soil (0-60 cm) have a porosity of 37.9% and a macroporosity of less than 5%; rapid and effective root penetration is hard to achieve through such a soil and initial tree growth is slow. As a result the low shrubs are highly susceptible to burning each year and by comparison with better developed trees spend more of their growth potential in replacement than extension of vegetative material. Many of the trees never grow above 1-2 metres; a smaller proportion may effectively penetrate to the porous underlying gravel, and grow to a considerable size, but on the deeper sheetwash deposits and in the more elevated sites where ground water is less accessible stunted and sparse growth is to be expected (See Plates 9/22).

Conversely, where the subterranean gravel is only covered by a shallow mantle of sheetwash, or in lower sites, where ground water is more readily available, a denser 'campo coberto' is found.

As in the Yupakari terrain the dominant tree species vary little, with <u>Curatella americana</u> and <u>Byrsonima spp.</u> prominent throughout. In most areas the terrain supports an herbaceous cover dominated by <u>Trachypogon plumosus</u>, with an understory of sedges; in a few sites, where imperfectly drained conditions persist, a mixed bunch grass and sedge community is found.

(Site 24, described in Chapter 5, represents a typical site within this unit).

(c) <u>Meritizero Terrain</u>

The Meritizero Ridge extends a distance of eight miles from the Ireng River in the west to the Meritizero Outstation in the east. It is

PLATE 22: Stunted Curatella americana, restricted to the herbaceous layer by annual burning, but displaying a well developed root stock.

PLATE 23: Succulent (Cereus sp.) growing on the exposed Meritizero Ridge.

between two and three miles in width, and rises some twenty metres above the level of the lowland trough. The ridge has a core of massive laterite, capped with secondary lateritic gravels, and is an outlier from the main Lethem-Yupakari land unit.

The western end of the ridge forms part of the Lethem terrain, but to the east deposits of aeolian origin have been laid down against the lateritic material. This part of the ridge has been designated the Meritizero terrain and comprises a broad, very gently undulating summit level from which gentle convex slopes descend to the floor of the lowland trough.

The occurrence of the deposits at the eastern and, at the present time, windward end of the ridge suggest that in the past strong winds blowing along the trough from the east have deposited the loessal material against the elevated lateritic core of the ridge.

Plant growth on the western end of the ridge, is typical of the Lethem terrain; the Meritizero terrain to the east, however, experiencing a similar dry savanna ecoclimate, supports a bunch grass savanna which is devoid of tree growth and dominated by _Trachypogon plumosus_, with a few secondary grasses and an herbaceous understorey of sedges, principally _Fimbristylis spp._ and _Stenophyllus paradoxa._ (See Plate 10).

There does not appear to be any peculiar anthropic condition associated with the Meritizero terrain, and the unusual occurrence of 'campo limpo' under well drained soil conditions appears to reflect an especially severe ecoclimate during the dry season. In the first instance, it is likely that lateral ground water drainage in the deep porous soils is more rapid in the upstanding and relatively narrow ridge, and that the depth to ground water in the dry season is greater than in the broad expanses of the sheetwash deposition.

In addition, the loess which owes its existence to an exposed situation suffers also the extreme desiccation of that exposure; the occurrence, for example, of a number of succulents in the area indicates that problems of water conservation are particularly acute on the eastern margin of the ridge (See Plate 23). Also, the exposed location results in fiercer and more destructive burning on the eastern flanks of the ridge, which further hinders the establishment of woody saplings.

Thus, although the moisture retention characteristics of the aeolian loams are better than within the sheetwash or the gravel materials, the conditions described above result in inaccessible ground water and very rapid depletion of soil moisture during the dry season, and apparently provide an ecoclimate that is sufficiently acute to prevent the growth of trees.

(Site 42, described in Appendix 4, represents a typical site within this unit).

2. Takutu - Proto-Berbice Land Unit

Extending in a north-easterly direction across the northern Rupununi, and following the Takutu River southwards from its conjunction with the Ireng River are remnants of the Proto-Berbice sandy terrace. Once continuous, the dissected remnants today consist, on the one hand, of a series of isolated ridges with broad, gently undulating surfaces and, on the other, a lower and more monotonous terrain with little relief variation.

The higher ridges are well or moderately well drained, with a few poorly drained depressions on their broader surfaces, and have been designated the Inaja terrain (See Plate 24). The soils of the lower remnant of the terrace, which is most extensive to the west of Pirara, have been strongly eroded and locally re-sorted. The area is imperfectly or poorly drained and has been designated the Pirara terrain.

(a) Inaja Terrain

The soils of the Inaja terrain are maturely developed; the upper horizons consist of deep loamy sand and sandy loam materials, often 100 cm in depth, underlain by sandy clay loam which becomes gradually heavier and more compacted with depth. Weak laterisation occurs in the zone of water table fluctuation, but there is no evidence of panning or drainage impedance.

The Inaja terrain experiences a dry savanna ecoclimate, and supports a well developed 'campo cerrado' formation. The latosolic soils have higher porosity and less compaction in the surface horizons than the sheetwash latosols, and in addition are favoured by a sandy clay loam substratum with a relatively high water retaining capacity. In general, therefore, the penetration of tree roots in the early stages of growth is facilitated, and the chances of young trees extending their roots to the point where they may consistently draw on deep ground water supplies in the dry season, are correspondingly greater.

The herbaceous layer within the terrain unit is dominated by bunch grass species, principally *Trachypogon plumosus*, although several other genera are widely found, notably: *Andropogon*, *Eragrostis* and *Gymnopogon*; in general, sedges are less common than in other grass-dominated herbaceous layers.

(Site 05, described in Chapter 5, represents a typical site within this unit).

(b) Pirara Terrain

The Pirara terrain consists of imperfectly or poorly drained remnants of the sandy terrace deposition. Soils are less maturely developed than in the Inaja terrain, and there is some accumulation of fine sheetwash material. The profiles are predominantly sandy clay loam in texture, with shallow, sandy loam topsoils and poorly developed B horizons.

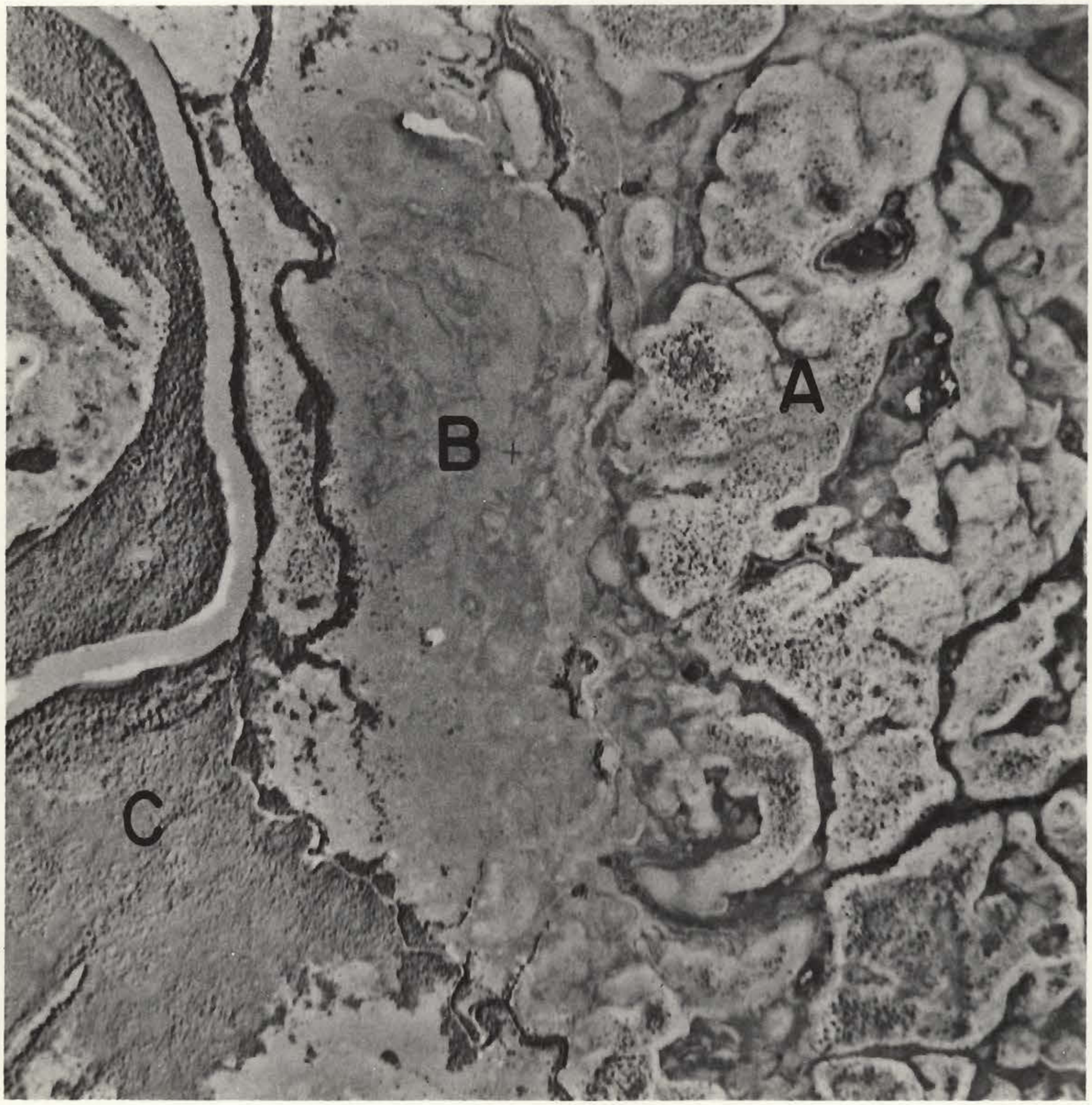

PLATE 24: Flood Plain and Takutu - Proto-Berbice land units, near Manari. The Inaja terrain (A) is strongly dissected, but supports dense 'campo cerrado' on the summit areas.

To the west, the seasonally inundated flood plain of the Takutu River is covered by sedge-dominated 'campo limpo' of the Mirichy terrain (B) and forest (C) (Photo by Hunting Aerosurveys Ltd.).

The Pirara terrain experiences a wet savanna ecoclimate and is largely devoid of tree growth; the 'campo limpo' supports an herbaceous cover of sedges or mixed sedges and grasses, in which Fimbristylis ferruginea and Rhyncospora barbata are prominent, with Aristida spp. and Trachypogon plumosus of local importance.

(Site 62, described in Appendix 4, represents a typical site within this unit).

3. Proto-Ireng Land Unit: Rego Terrain

Adjacent to the foot of the Pacaraima Mountains in the north-western part of the savannas, a zone of fine textured deposits occurs along and between the Ireng River and the Rego Creek. These deposits, within which a series of terrace levels are visible (Bleakley, 1957), have been laid down by the Ireng/Proto-Ireng outflow into the lowland trough.

The area, which has been designated the Rego terrain, is flat with minimal surface undulation, and has been little dissected by drainage channels in spite of the slightly elevated position it occupies in relation to the main lowland trough. The parent material of the terrain is similar to that of the lowland trough, and consists of fine materials with occasional admixtures of sand; commonly found are clay and silty clay, with a few sandy clay and sandy clay loam horizons. In places well structured soils have developed.

Vertical drainage in the area is slow and, after heavy rain, water may remain on the surface for many hours. But the elevation of the area results in constant, albeit slow, drainage through the profile, and although temporary saturation has led to mottling and gleying of profiles, the soil remains sufficiently aerated to support tree growth.

The density of tree growth is not high, and the area has been classified as 'campo coberto'; individual trees, however, are less stunted

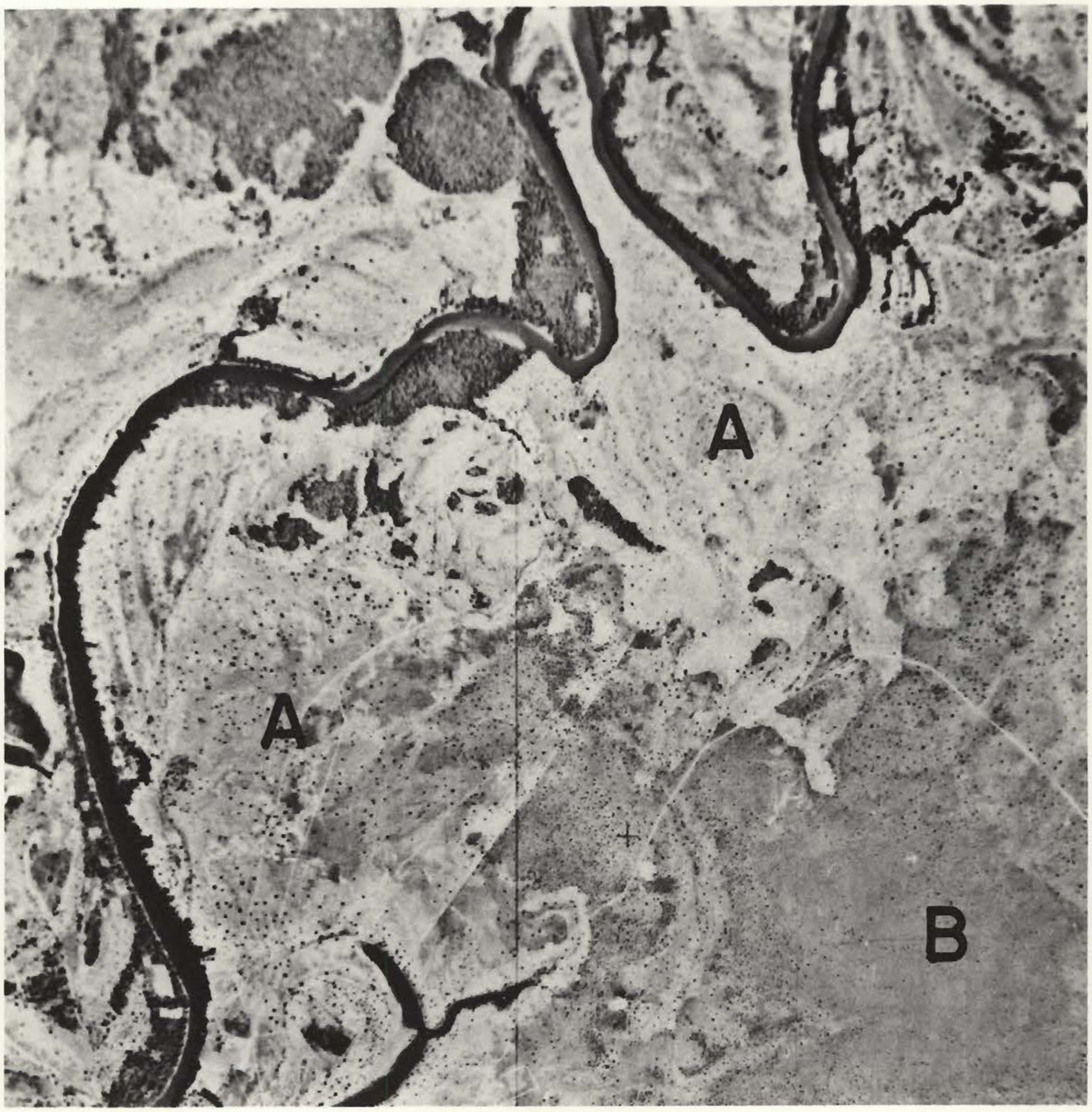

PLATE 25: The Proto-Ireng land unit. On the eastern side of the Ireng River lies the Rego terrain (A), which is sufficiently elevated above the deeply-incised Ireng to escape seasonal inundation. In the south-east of the photograph, the land drops away gently to a poorly drained depression (B) of the Nappi terrain (Photo by Hunting Aerosurveys, Ltd.).

and taller than in many other areas. The herbaceous cover is composed of both grass and sedge-dominated communities, whose distribution is related in many instances to slight micro-relief variations and local profile drainage.

(Site 103, described in Appendix 4, represents a typical site within this unit).

4. Mountain Outwash Land Unit - Toka Terrain

Along the foot of the Pacaraima and Kanuku mountains a series of gently sloping outwash deposits, carried down from the mountain slopes by seasonally flowing waters, extend onto the margin of the savanna surface.

On the Kanuku front, the deposits are restricted to the western end of the range, and are generally under forest or secondary bush, only rarely supporting savanna vegetation.

Along the Pacaraima front, the outwash alluvium is more extensive and has in places been carried several miles into the lowland by seasonally flowing streams. Yet, considering the size of the mountain front, there is a relatively small accumulation of outwash debris along its foot, and it seems that the present material represents only the recent accumulation of a more extensive deposition that has, in the past, been interbedded with, and buried, by fluvio-lacustrine sediments accumulating in the lowland trough (Stark, Rutherford & Spector, 1959).

The examination of soil profiles along the mountain foot indicates the periodic mobility of the outwash deposition; many profiles are strongly layered, with textures ranging from loam to fine gravel materials with, in a few places, finer textured horizons which represent temporary incursions of fluvio-lacustrine deposits.

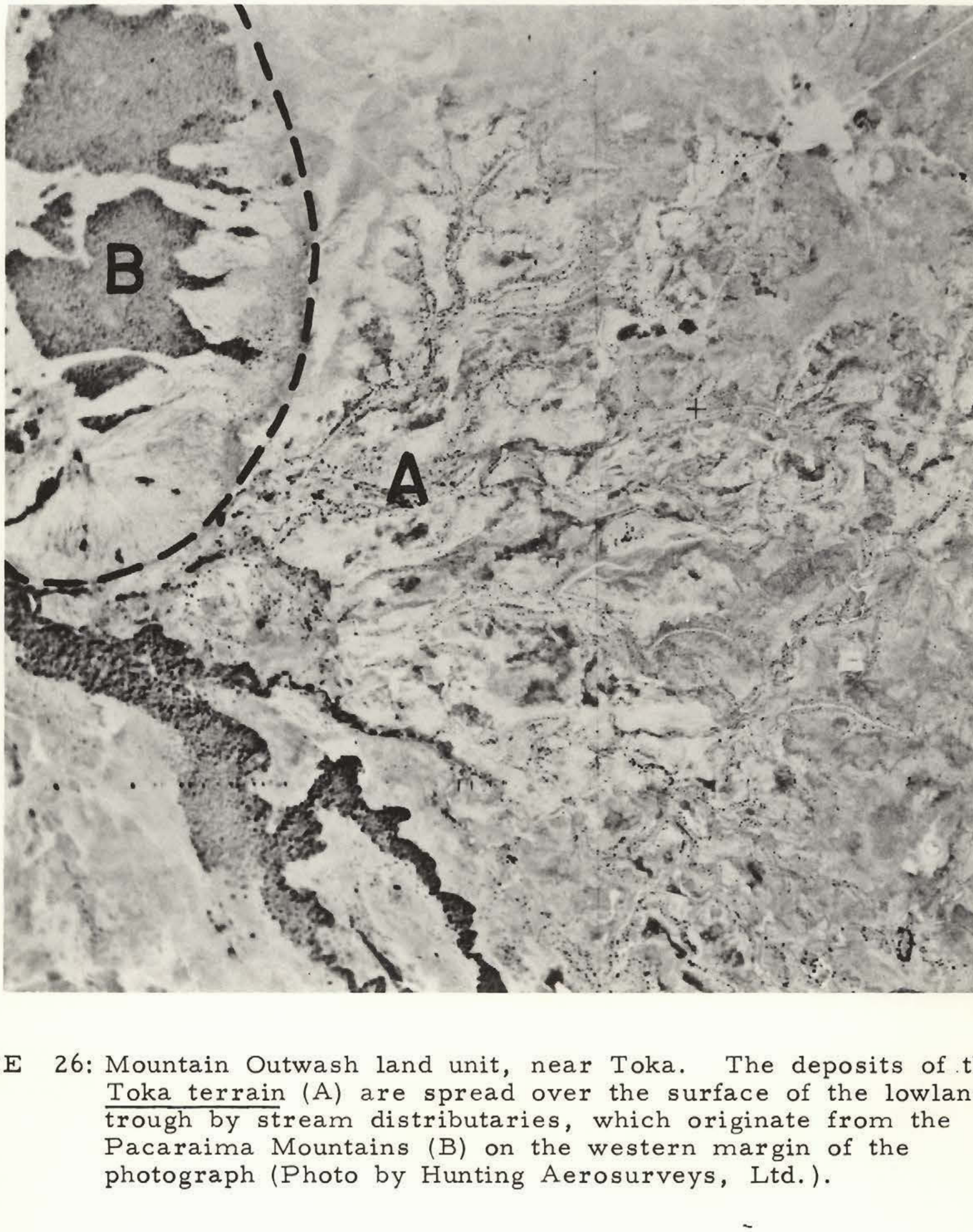

PLATE 26: Mountain Outwash land unit, near Toka. The deposits of the Toka terrain (A) are spread over the surface of the lowland trough by stream distributaries, which originate from the Pacaraima Mountains (B) on the western margin of the photograph (Photo by Hunting Aerosurveys, Ltd.).

Although much of the outwash deposition is only slightly above the level of the lowland, it is sufficiently elevated to avoid complete seasonal waterlogging, and a dry savanna ecoclimate prevails. The terrain supports a tall woody growth dominated by Curatella americana, which grows to heights of 3-5 metres in open 'campo coberto' formation, with occasional denser tracts of 'campo cerrado'.

The herbaceous layer is dominated by the bunch grass Trachypogon plumosus, with a subsidiary layer of sedges, although in a few lower sites, where imperfectly drained conditions exist, mixed bunch grass and sedge communities are more common.

(Site 87, described in Appendix 4, represents a typical site within this unit).

5. Lowland Unit

The Lowland unit comprises an area of predominantly hydromorphic soils, which have developed on recent deposits of fluvio-lacustrine alluvium. Ecoclimatic conditions vary within the unit, but seasonal water-logging or inundation and a wet savanna ecoclimate prevail in much of the area.

The largest part of the unit, which has been designated the Maracanata terrain, consists of a gently undulating landscape of broad depressions and low intervening swells. Across the area meander a number of longitudinal sandy ridges, which represent old stream courses and which, in their passage, cut off or enclose basins and small ponds; the ridge areas have been designated the Bella Vista terrain.

A third element in the landscape is the extensive flats that have formed along the courses of the main contemporary drainage outlets of the region, where ponding back of seasonal flood waters has led to deep and uniform alluvial deposition. This unit is referred to as the Nappi terrain.

A fourth and smaller area, designated the Cajueiro terrain, and stretching between the Rego Creek and the Cajueiro Outstation, comprises a zone of more elevated outwash deposition, laid down by the Proto-Ireng River at a time when it followed a direct outlet course to the east.

Finally, in a number of sites adjacent to the Lethem-Yupakari land unit, the flat and swampy habitats of the Qatata terrain are found, where perennial seepage waters emerge from the margin of the higher ground.

(a) Maracanata and Nappi Terrain

The Maracanata and Nappi terrain units are distinguished by their relief. The Nappi terrain, comprising the contemporary flood plains of the Pirara, Nappi and Benoni rivers, and to a lesser extent, the Manari, is relatively flat and level, and is gradually encroaching on the landscape of the Maracanata terrain. The Nappi terrain is totally inundated for lengthy periods during the rainy season, but the water rapidly disperses with the cessation of the rains and the water table drops to 3-5 metres by the end of the dry season (See Plate 27).

The Maracanata terrain is an older landscape, formed by alluvial deposition from successive courses of the Proto-Ireng, a process which is still being continued today by the Rego Creek. The terrain is gently undulating and consists of shallow basins and depressions with intervening slight domes and elevated ridges. Most of the area is waterlogged or flooded during the rainy season, but the soils, as in the Nappi terrain, dry out after the rains. Ground water usually falls to three or four metres during the dry season, but in places ponds and small lakes persist for much of the year.

The soils of both units are undergoing processes of laterisation, and display mottling and iron concentration, but no evidence of iron panning was found. Texturally the units are similar, with loams, clay loams and silty loams commonly found, and many of the profiles are layered.

PLATE 27: The Nappi terrain: Sedge-dominated 'campo limpo' adjacent to the Rego Creek (The micro-relief features in the photograph are worm mounds).

PLATE 28: The Cajueiro terrain: a uniform landscape of 'campo limpo' with mixed grasses and sedges, extending towards the Pacaraima Mountains.

Both areas, which experience a wet savanna ecoclimate, support a 'campo limpo' formation; the terrain is dominated by herbaceous sedge communities, with a slight admixture of grasses on some sites. Fimbristylis ferruginea and Rhyncospora barbata are most commonly found.

(Site 97, described in Appendix 4, and Site 76, described in Chapter 5, represent typical sites within these units).

(b) Qatata Terrain

The swamps of the Qatata terrain, which form alien elements within the savanna ecosystem, consist of low-lying lacustrine flats, located at the foot of the lateritic gravel deposits, principally between Maracanata and Karanambo. These sedge swamps, which are maintained by the perennial flow of seepage waters from the adjacent Lethem-Yupakari unit, are very poorly drained and are inundated for much of the year, but may drain superficially towards the end of the dry season as the flow of seepage water is reduced.

The swamp soils are fine textured and, displaying a thick, peaty surface horizon, have been classified as humic gleis.

Along the swamp margin, palm species commonly mark the transition from savanna to swamp, the principal species being Mauritia minor. Within the swamp itself a distinct herbaceous community exists, which floristically has very little in common with the adjacent savanna. Pithy sedges of the genera Cyperus and Eleocharis, together with a variety of floating plants, are commonly found.

Other swamp areas are scattered widely through the savannas, although in places, where the degree of waterlogging is less acute, palm rather than sedge swamps occur, which are again dominated by Mauritia minor. Several of these communities occur along the foot of the Kanuku Mountains, a notable example being at Kuma.

(Site 110, described in Chapter 5, represents a typical site within this unit).

(c) Bella Vista Terrain

Amid the lacustrine alluvium of the Maracanata terrain a number of longitudinal sandy ridges, designated the Bella Vista terrain, extend for distances of several miles across the low-lying, fine textured deposits. The ridges rise abruptly one to two metres above the general level of the lowland and are typically 10-25 metres in breadth. The topsoils are sandy loam or fine sandy loam in texture, changing gradually to sandy clay loam with depth; in most sites the soils are latosolic, although there are signs of incipient laterisation in the lower profile.

The ridges, which frequently have an initial point of contact with the Ireng or Rego river courses, and subsequently disperse into small outwash fans at their termination, represent old drainage distributaries that have in the past carried waters from the Ireng/Proto-Ireng headwaters into the lowland trough. The sandy materials may represent stream bed deposits which have survived a general erosional lowering of the trough surface, although present interpretation of the landscape suggests a depositional rather than an erosional evolution in recent times*. Alternatively, they may represent the remnants of levée deposition.

The terrain, which experiences a dry savanna ecoclimate, is moderately to imperfectly drained and the surface layers of the soil remain free draining throughout the year. The area is thus able to support tree growth on the ridge summits; most commonly a series of small bush islands are scattered at intervals along the ridges, often centred around one or two large trees, while between the islands low savanna scrub and herbaceous communities are found.

Most of the trees present are widely distributed in the savanna, but a number of less common species, including succulents of the families Cactaceae

* Oral discussion, J.B. Bird.

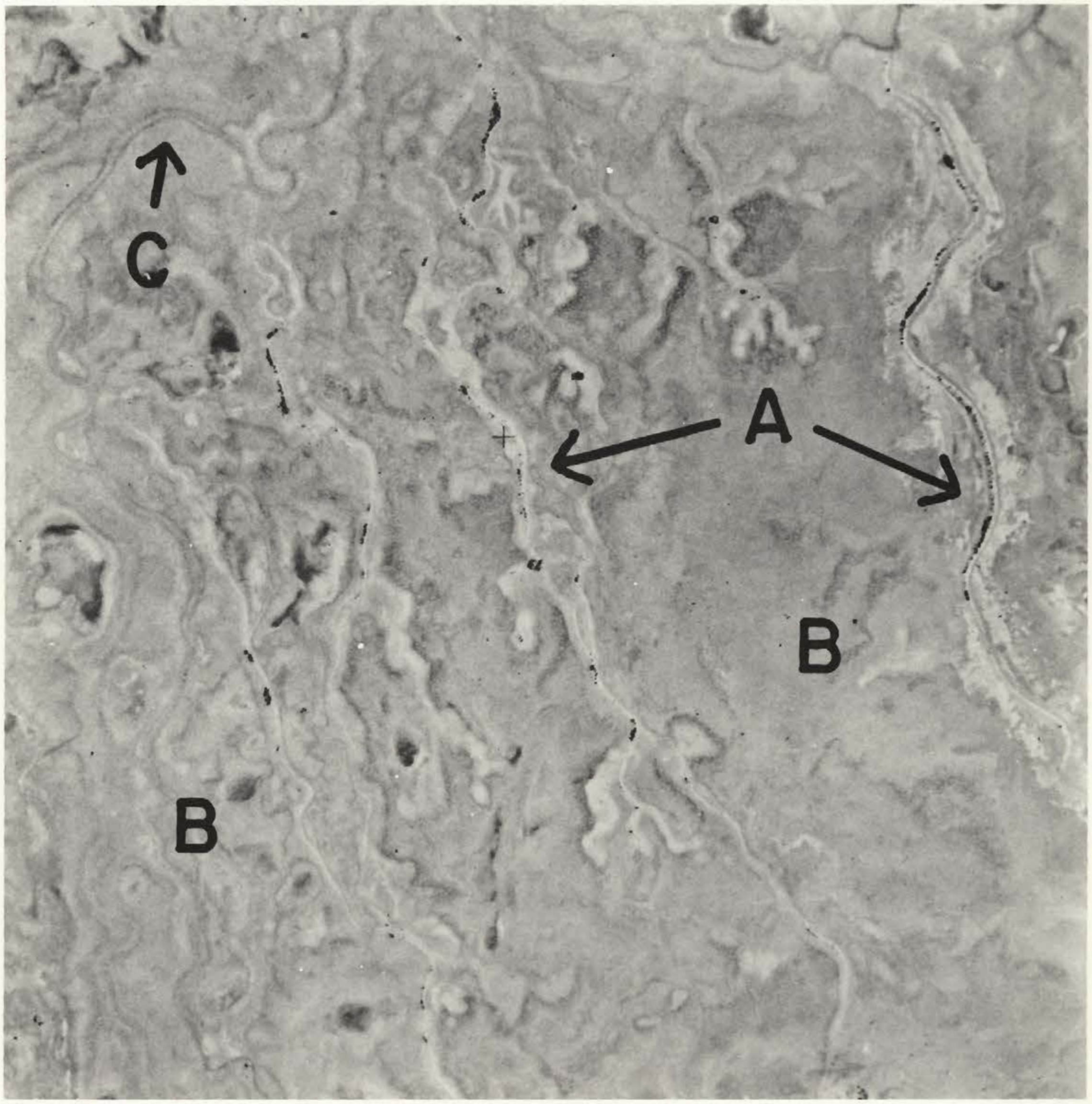

PLATE 29: The Lowland unit, to the east of Meritizero. Across the sedge-dominated 'campo limpo' of the Maracanata terrain (B) extend the longitudinal sandy ridges of the Bella Vista terrain (A), which support 'bush islands' and low shrub growth. Along the western margin of the photograph, a contemporary, seasonal drainage channel is visible (C). (Photo by Hunting Aerosurveys, Ltd.).

and _Agave_, are found. An herbaceous formation of bunch grass or mixed bunch grasses and sedges is typical, with the following species most commonly occurring: _Aristida spp._, _Trachypogon plumosus_, _Fimbristylis spp._

(Site 40, described in Appendix 4, represents a typical site within this unit).

(d) Cajueiro Terrain

The fluvio-lacustrine deposits of the Cajueiro terrain extend in an east-west direction from the Rego Creek to the Cajueiro Outstation, forming a slightly elevated surface above the surrounding Nappi terrain. The deposits consist of sandy, river-borne alluvium carried by the original Proto Ireng and deposited as outwash material, probably under semi-lacustrine conditions, within the lowland trough. The deposition, which must have effectively blocked the direct eastward outlet of the Proto-Ireng, appears to have deflected the river southward, and been responsible for the change in direction in the mid-course of the present Rego-Creek; the process is thus an early stage in the westward reorientation of the Ireng/Proto-Ireng drainage within the lowland trough.

The deposits form an area of broad sandy ridges, which fan out eastwards in a dendritic pattern from two points of contact with the Rego Creek. Between the domed ridges the shallow intervening troughs are infilled with finer textured materials, and the resultant gently undulating topography, which has been modified by sheetwash processes, is relatively uniform in character over large areas (See Plate 28).

Soils are normally latosolic in character with incipient iron concretions in their lower layers, but grade gently into ground water laterites on the lower slopes. The upper part of the solum is sandy loam or fine sandy loam in texture, but the clay content gradually increases with depth; in the

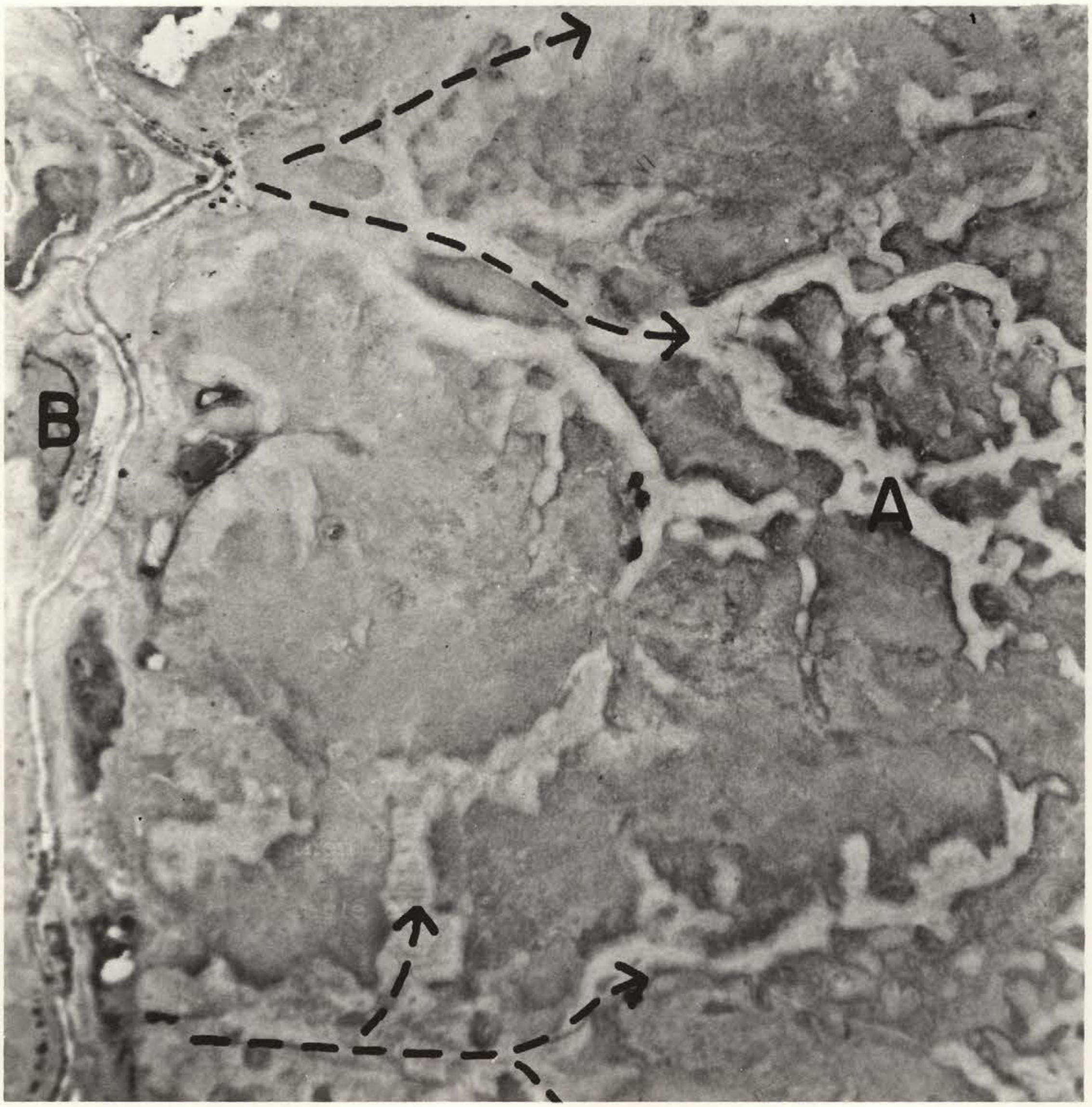

PLATE 30: The Lowland unit: the outwash deposition of the Cajueiro terrain (A) extends eastwards across the photograph from the Rego Creek; the area is widely overlain by sandy materials, with the younger and more elevated deposits clearly visible in the photograph by virtue of their better drainage. Along the flood plain of the creek a number of inundated areas are visible (Photo by Hunting Aerosurveys, Ltd.).

substratum coarser sand and gravel materials appear, and reflect an earlier phase of purely fluvial deposition when the Proto-Ireng flowed directly to the east.

The terrain is moderately well, or imperfectly drained and, except on the lower margins, experiences a dry savanna ecoclimate. The area, however, is devoid of tree growth with the exception of a few, low shrub communities of fire-stunted Curatella americana and Byrsonima spp., which scarcely exceed 50 cm. in height.

The absence of tree growth is not readily explained; the upper layers of the soil remain free draining throughout the year, and are not hard or compacted enough to inhibit greatly root penetration. Nor is the ground water very deep - on one site the depth in April 1964 was only 380 cm. In addition, there is no evidence of peculiar anthropic influence within the area; grazing practices are the same as elsewhere, nor is the local population distribution in any way abnormal.

The absence of tree growth might be a product of adverse chemical conditions, but in an area of uniformly low nutrient content in the soil such an explanation does not appear likely. Soil chemical analyses have not yet been undertaken.

Alternatively, it may be that the relatively smooth terrain surface, which lies in an exposed position along the mountain front and facing the Rupununi River outlet to the east, whence blow the prevailing winds, experiences higher wind speeds at ground level, which increase evapo-transpiration and fire intensity, and result in conditions unfavourable to tree growth within this environment. However, if the wind factor is invoked as an abnormally potent ecoclimatic factor in the Cajueiro terrain, one must ask why its effect does not extend to the equally exposed sandy ridges of the Bella Vista terrain, where soils and ground water conditions are to a large extent similar.

No explanation is evident, although it is apparent that on the ridges of the Bella Vista terrain the problem of water conservation is especially acute, a fact indicated by the presence of highly xeromorphic succulents, which are found here more frequently than anywhere else in the northern Rupununi.

The Cajueiro terrain thus presents an area of unbroken 'campo limpo', which is dominated by mixed bunch grass and sedge communities.

(Site 112, described in Appendix 4, represents a typical site within this unit).

6. Flood Plain Land Unit: Mirichy Terrain

The flood plains of the Takutu, Ireng and Rupununi rivers vary widely in nature and extent. Extending to more than a mile in breadth in some places, they may be covered with dense galeria forest or swamp forest, while elsewhere tracts of both woody and herbaceous savanna prevail (See Plate 24).

A major contrast exists between the Rupununi flood plain and that of the Takutu and Ireng. The latter rivers normally inundate their flood plains at the height of the rainy season, but during the dry season, with the large fall in river levels, the flood plain soils readily dry out, and a savanna ecoclimate prevails widely. In most places a thin band of galeria forest, commonly 20-40 metres broad, lines the river bank; elsewhere, the forest may extend in a broad tract across the flood plain, but the majority of the Takutu and Ireng flood plains display a complex of savanna vegetation.

By contrast the Rupununi River, which is little incised in its channel, has a broader and less well drained flood plain; ox-bow lakes and braided streams are more common, and the flood plain does not experience the same degree of seasonal desiccation as is the case with the western rivers.

As a result, forest and swamp communities are more prominent, and fewer tracts of savanna are found on the flood plain.

(Site 43A, described in Appendix 4, is from this unit).

PART FOUR: GENETIC STUDIES

CHAPTER 10

EVOLUTION OF THE SAVANNA ECOSYSTEM

To determine the place of the savanna ecosystem in relation to the adjacent tropical forest requires more than a understanding of the contemporary ecoclimate. The ecoclimates described herein are a product of existing conditions in the savanna and, as such, they can provide an adequate explanation of how the vegetation formations today exist, and how they are adapted to the environment.

They cannot explain why the savanna exists or why it evolved, for the ecoclimate is not a genetic concept, but merely a descriptive interpretation of a number of differentially varying causes. But knowing precisely these causes, and studying their evolution, both with the aid of data collected in the field and with relevant information from other areas and sources, an attempt can be made to reconstruct the past evolution of the ecoclimate, and hence that of vegetational patterns in the area. In short, a knowledge of how the savanna exists today is a prerequisite to postulating why it originated at some time in the past. What information is there of past evolution in the Rupununi?

(a) Evidence from the Vegetation

The main forest vegetation surrounding the Rupununi today commences along the physiographic margin of the late Tertiary lowland surface (McConnell, 1962), wherein the savanna currently exists. Locally, savanna may transgress into the mountains and forest extend into the savanna, but there is a general coincidence of forest with the elevated terrain. This formation, described by Myers (1936) as 'fringing forest', but including also the fingers of galeria forest that extend along rivers and creeks into the savanna, contains many deciduous species. Myers likens it to a Monsoon forest, but because the rainfall of the Rupununi is lower than in a true Monsoon climate, prefers to describe it as semi-deciduous. He states :-

> 'At the height of the dry season a considerable proportion of the trees and bushes are leafless, though the general aspect of the fringe is green'.
>
> J.G. Myers, 1936, p. 170.

Along the river flood plains, the galeria forest may extend up to a mile from the river, while elsewhere only a narrow ribbon of tree growth is found. The trees are tall with a dense, tangled understorey of lianes and small shrubs, and in wetter sites palms occur. According to Myers (1936), where the galeria forest merges into the mountain forest it retains its semi-deciduous characteristics on the lower slopes, but gradually changes to rain forest with greater height and penetration into the mountains; along the Pacaraima front the transition takes place at about 300 metres.

Within the savanna itself there remains a number of other forest communities, described by Myers (1936) as 'bush islands'. Distinct from the small groves of cashew (Anacardium occidentale) and mango (Mangifera indica), which mark human habitations, the bush islands are isolated from the fringing forest, and vary from small patches 10-20 metres in diameter to stands a mile or more in width. In all cases the margin with the savanna is abrupt. The formation, 'consists of a curious kind of forest, difficult to classify, of a dryish type, but less deciduous than the larger leaved monsoon-like forest of the Pakaraima foothills ... (it) is made up of a great mixture of shrubs, many small trees and lianes, including a strong representation of Myrtaceae, and many Leguminosae.'

J.G. Myers, 1936, p. 169.

These bush islands may be associated with locally favourable site conditions - the large island to the east of Maracanata has, centrally at least, perennial seepage water supplies - but many other islands in the northern Rupununi, often on porous gravel soils, enjoy site conditions no more favourable than the adjacent savanna.

The present restrictive effect of savanna fires on tree growth, and the isolated occurrence of the bush islands make it difficult to consider the islands as recent extensions of forest into the savanna, and indeed their floristic individuality clearly sets them apart from the surrounding fringing forest. It appears more likely that the scattered bush islands represent relics of an older forest formation, which existed in the Rupununi before the present savanna. One queries why they exist today. They may simply be the final, retreating remnants of the old forest cover which will soon disappear naturally. Alternatively, and this is more likely, they may be 'frozen' relics, which are today ecoclimatically adapted to the environment. If this is the case, it implies that the savanna, by contrast, is in a state of ecoclimatic disequilibrium and that its present existence may be due to man's activity. (This does not necessarily imply that man created the savanna, but only that he may be responsible for its maintenance).

That the savanna may presently be in a state of ecoclimatic disequilibrium is indicated by a comparison of forest and savanna trees. As has been shown by Vareschi (1960), the transpiration rate of many bush island species is much less than that of Curatella and Byrsonima, whose principal adaptation is to fire. Were fire eliminated in the savanna, and forest given the opportunity to extend onto the lowland surface, the lower rate of transpiration of the forest species would compensate for the greater number of forest trees that would draw on water supplies, so that the forest might well advance. Also, the widespread deciduous habit of the forest trees is an additional and highly effective means of water conservation in the dry season and is in marked contrast to the evergreen habit of existing savanna trees. In addition other micro-climatic and 'micro-ecoclimatic' advantages would progressively accrue with the growth of forest. The hypothesis, moreover, is supported in the field by observations that in part of the southern Rupununi, where no cultivation is currently taking place, the forest is actively advancing (Waddell, 1963).

Before however an effective interpretation of the vegetational patterns can be attempted, it is necessary to evaluate in greater detail the respective influences of man and evolving physical conditions within the savanna region. Two main questions require to be answered; when was the earlier forest cover replaced by savanna, and what factors were responsible for the change?

The possible causes appear to be as follows :-

(i) That climatic and geomorphological changes have taken place in the region, which introduced an ecoclimatic regime conducive to the replacement of forest by savanna.

(ii) That fire and cultivation have led to the replacement of forest by savanna.

(iii) That against a background of changing ecoclimatic conditions, fire and cultivation have effected or accelerated the conversion of forest to savanna.

(b) Ecoclimatic Change as a Causal Factor in the Savanna

During the late Pleistocene and the Holocene, major changes in temperature and sea level are known to have taken place in many parts of the world; in higher latitudes the changes are relatively well documented, but their influence in the tropics is less clearly understood.

In some sub-tropical areas, however, e.g., North Africa, climatic chronologies have been established for the Quaternary which relate 'pluvial' phases to known periods of low temperature and glaciation in higher latitudes (Büdel, 1963). The assumption of similar 'pluvial' conditions in the tropics however is, as Büdel indicates, open to question, although some workers in East Africa confirm the relationship between 'pluvial' phases and high latitude glaciation (Nilsson, 1949, et alii)

In tropical South America, palynological data from Columbia and coastal British Guiana indicate that pronounced fluctuations in the extent of savanna and forest have taken place since the late Pleistocene (van der Hammen, 1963, 1964), and in a number of instances the vegetational changes coincide with known climatic fluctuations in higher latitudes, whose effects were presumably extended to the tropics as well. The viewpoint is substantiated by paleotemperature analysis of core samples from the Caribbean area by Emiliani (1964). It is assumed, therefore, that a comparable sequence of climatic and associated vegetational changes have taken place in the interior of British Guiana since the latter part of the Pleistocene. If so, the present vegetation of the Rupununi area is unlikely to be older than 10,000 - 12,000 years. What relevant information is there regarding this period?

In general, one might assume that in marginal areas in the tropics wetter conditions would be associated with the growth of forest, and drier conditions with savanna. In many cases this would be so, but the present ecoclimatic studies have shown that, provided a degree of seasonality exists, tree growth may be inhibited by an excess of water as well as by a lack of it, so that, in areas of impeded drainage, an increase in rainfall need not necessarily imply an expansion of forest. However, in the elevated and free draining parts of the Rupununi it is probable that during any wetter climatic phases a forest cover similar to that found in the relict bush islands would have existed, and indeed would probably have extended into parts of the lowland trough as well. Conversely, a return to drier conditions in the region would result in a retreat of the forest across the elevated and free-draining terrain and a general extension of savanna from the lowland trough.

In the period under review, the earliest major climatic change which is likely to have affected the Rupununi is associated with the increase of temperature at the end of the Würm-Wisconsin glaciation, approximately 11,000 - 9,000 years before the present (B.P.). This brought about a rise in sea level and probably modified tropical rainfall regimes. The nature of the rainfall changes, however, which hold the key to understanding the savanna evolution, are open to question.

Palynological evidence from the Pleistocene in Bogota, Colombia indicates the presence of wetter forest communities, and presumably a wetter climate, contemporaneous with high latitude glacial periods, and drier forest communities with interglacial periods*. This would suggest that, in this area at least, the end of the final glacial stage coincided with a transition from wetter to drier climatic conditions and a general retreat of forest and extension of savanna.

Similar investigations in British Guiana also show changes in vegetation at this time (van der Hammen, 1963); the latter part of the last glacial stage is characterised in coastal areas by herbaceous savanna, which is followed in the early Holocene by swamp and swamp forest communities.

* van der Hammen, oral communication.

Unfortunately, the latter vegetation is situated near the shoreline, and reflects post-glacial marine transgression rather than any specific rainfall regime; the herbaceous savanna, however, which existed prior to it during the latter part of the Würm glacial, developed over an elevated clay surface, exposed by regression, which van der Hammen concludes would have become impermeable. He states finally that the rainfall at the time may have been heavier than at present, and suggests, in effect, that a wet savanna eco-climate prevailed in the area and maintained a purely herbaceous vegetation. The data thus conform with his Colombian findings of a wetter period in tropical South America during the latter part of the Würm-Wisconsin glaciation, and is in keeping with the East African conclusions of Nilsson (1949).

Further support for this viewpoint comes from Heyligers (1963) in Surinam; from an examination of sedimentary deposits he found evidence of variable climatic conditions during the Pleistocene, and concludes that a drier phase existed during the Riss-Würm interglacial, and was followed by 'one or more pluvial periods' during the Würm glacial itself, although he makes no mention of the climate during the succeeding Holocene.

The Holocene Period

Following the period of transition at the end of the Würm-Wisconsin glaciation, a more stable period of higher temperature prevailed in extra-tropical latitudes, and is referred to as the 'post glacial climatic optimum' (Zeuner, 1952); the period of greatest heat - the Altithermal - is considered by Antevs (1955) to have lasted from 7,000 - 4,000 B.P.

In the tropics at this time, pollen data from British Guiana show the persistence of coastal swamp and swamp forest communities under estuarine or tidal conditions, and give little indication of prevailing climatic conditions. However, an excellent pollen profile from Laguna de Agua Sucia, Colombia probably covers most of the Holocene (van der Hammen, 1964). Extending to a depth of 500 cm, it has dates of :-

2,340 $\pm$ 90 B.P. at 55 cm.

4,110 $\pm$ 70 B.P. at 285 cm.

In the pollen profile, herbaceous elements dominate from 435 - 235 cm during what was probably the tropical equivalent of the Altithermal; thereafter from 235 - 25 cm there is a dominance of woody elements, with Byrsonima initially prominent but gradually giving way to other tree species; towards the end of the period two minor increases in herbaceous elements occur, although forest trees remain dominant. Finally, in the upper 25 cm there is a rapid return to herbaceous dominance.

The question remains as to what these vegetational conditions indicate in terms of the climate of tropical South America. The rapid increase in herbaceous elements in the upper 25 cm of the Laguna de Agua Sucia profile may well reflect anthropic as well as climatic activity, but the change from savanna to forest at 235 cm (circa 4,000 - 3,750 B.P.), coincident with the end of the Altithermal, is almost certainly a function of climate. Does it reflect increasingly wetter or drier conditions? The temporal continuum at Laguna de Agua Sucia is from herbaceous savanna to Byrsonima-dominated woody growth, to forest species, which conforms most closely, by comparison with contemporary areal continua in the Rupununi, to increasing availability of ground water. Such may well be a function of increasing rainfall, and would support the hypothesis of a wetter period in the latter part of the Würm-Wisconsin glaciation, followed by drier conditions in the early Holocene and, at 4,000 B.P., a second onset of wetter conditions.

However, although the available evidence points to such a hypothesis, conclusions based on investigations in only a few areas in tropical South America, and reached in spite of a lack of adequate information on the past status of other ecoclimatic factors, i.e., soil, relief and drainage, remain somewhat speculative. As far as the Rupununi is concerned, it can only be reliably stated that there is indirect evidence of major climatic change, firstly, at about 11,000 - 9,000 B.P., associated with the end of the Würm-Wisconsin glacial, and, secondly, at about 4,000 - 3,750 B.P. or coincident with the end of the Altithermal. Both are likely to have substantially affected savanna/forest distributions in the region.

Since 4,000 B.P., further climatic fluctuations have taken place in extra-tropical latitudes, although in general the character of the period has been somewhat cooler than during the Altithermal (Ahlmann, 1953). Comparable changes would be expected in the tropics and, in spite of the more obvious anthropic impact in recent centuries, climatic fluctuation must still be considered a potential influence on vegetational evolution in the Rupununi.

There is however some evidence to suggest that savanna has existed in the Rupununi for at least a large part of the last 4,000 years, so that one may assume that the climatic fluctuations that have taken place during this time have been inadequate, under prevailing ecological conditions, to alter significantly the nature of vegetation in the region. The evidence concerns the occurrence of sheetwash deposition. The deposits of the Lethem terrain, which show no internal unconformities and are currently accumulating, have attained several metres in thickness in many areas, and in places have covered much of the original gravel parent material; such, for example, is the case in the middle valley of the Moco Moco, where the gravel terrain has been completely overlain by a mantle of sheetwash. The sheetwash process could not have taken place to any great extent under a forest cover, and the present depth and extent of the deposits indicate that the process has continued for a lengthy period, which is likely to have extended over much of the last 4,000 years and possibly longer.

During this period, therefore, the importance of climatic change has been reduced, either because the change itself was less, or because other ecological factors have assumed greater importance. At this stage, therefore, it is relevant to evaluate, as far as is possible, the influence of man as an ecological factor affecting the savanna-forest boundary.

(c) The Role of Man in the Savanna Environment

It is presently impossible to date accurately the antiquity of man in South America, although some data are available. Human skulls found in Chile have been dated, by radiocarbon methods, as 6,500 - 9,000 years old (Libby, 1955), while other remains in the Lagoa Santa region of Brazil, dating from a pluvial period, are considered by their investigators to be 'a few thousands of years' old (Walter, Cathoud & Mattos, 1937).

Within the Rupununi, very limited archaeological investigation has been undertaken, and it is only possible to substantiate the existence of man in the area for a few hundred years, although Waddell (1963) has concluded that pre-Colomban tribal movements occurred in South America that probably influenced the Rio Branco-Rupununi area. For the present, one can do more than admit the possibility that man has been a factor in the region for a significant period of recent millennia.

The advent of man in the Rupununi introduced the destructive agencies of forest cultivation and artificial burning of vegetation, both of which must be considered as potential causes of forest retreat. How powerful is their impact under contemporary climatic conditions?

In the Rupununi today a very large proportion of the savanna is burnt each year during the dry season and, on occasions, fire extends into bush islands and the fringing forest. The extension, however, is restricted to periods when the forest is exceptionally dry, and normally forest regeneration rapidly occurs with the onset of the rainy season. In the dry season of 1960/1961, for example, when the Kanuku Mountains were burnt, reportedly in places up to their summits, only 1.9 cm of rainfall occurred in the six month period November 1960 - April 1961, yet regeneration took place in the succeeding rains*.

It is also doubtful whether savanna fires initiated by man could result in the large scale retreat of forest. Waddell (1963) considers that after a succession of dry years the ecological conditions in the forest might be permanently disturbed, and savanna grasses given a chance to become established. Yet the chances of this are not very great. In the first instance, forest fires by no means completely clear the ground; even if a mass of organic debris is burnt, a skeletal forest of branches and trunks will remain and partially protect the land, and a root system will still exist as a stabilising factor in the soil.

Moreover, the initial vegetative regeneration in areas of burnt forest in the Rupununi takes place very rapidly with the start of the rains, and the period when rapid soil deterioration might take place is relatively short. Even if several successive 'dry' years occur, the intervening wet seasons are always sufficiently pronounced and of long enough duration, to allow protective secondary growth to re-establish itself.

If fire is to be considered a cause of forest destruction, it is infinitely more likely to have taken place in association with forest cultivation - in which case the antiquity of man in the region is less important than the antiquity of cultivating man, in assessing the anthropic role. It is indeed possible that by clearing and burning fields within the forest, and by exposing the soil to physical and chemical deterioration man has in the past caused the retreat of forest.

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* Prior to the arrival of man, natural fires, initiated by lightning, may well have been a feature of the environment. Such fires are reported to take place today, but bearing in mind the conditions of forest regeneration described above, and the general coincidence in the Rupununi of lightning with periods of rainfall, which ensures that natural fires will generally occur when the vegetation is not especially dry, it is difficult to envisage natural burning under present climatic conditions as the cause of large scale forest destruction.

PLATE 31: The anthropic influence: the destruction of forest for shifting cultivation.

PLATE 32: Semi-deciduous 'bush island' to the south of Pirara.

Under present conditions, Waddell (1963) has concluded, and field observations of the author confirm, that along parts of the forest edge in the southern Rupununi, where a high density of cultivation exists, the forest is locally in retreat. Similarly, in bush islands in the northern Rupununi, local retreat appears to be taking place. In the Maracanata bush island the irregular, angular margin of the forest, the lack of conformity of the margin with any inherent soil or relief factors, and the group of smaller peripheral islands, which in the face of yearly burning of the adjacent savanna, cannot be considered as regenerative growth, all point to anthropic agents at work.

During the recent past, however, profound changes in anthropic conditions have occurred, in response to increased contact with more advanced cultures, which are likely to have accentuated the impact of man. During the present century a more nucleated pattern of settlement within the savanna has replaced the traditional dispersion of the shifting cultivators, with resultant local intensification of agricultural activity along the forest edge. In addition, marked fluctuations of population have taken place, culminating, in the period since 1945, in a very rapid increase in response to the provision of extended government health services. In addition the introduction of steel axes in place of stone has greatly increased the destructive power of man (Waddell, 1963).

A further complication arises in trying to assess man's role in the past, in that the present savanna-forest margin coincides with a physiographic and macro-climatic boundary. Thus the present ecological interactions are not necessarily similar to those which occurred within the more uniform lowland surface, currently occupied by the savanna, and across which the forest retreat under consideration actually took place.

However, the continued persistence of bush islands within the savanna appears to suggest that a savanna-forest boundary traversing the lowland surface would not be exceptionally vulnerable to anthropic destruction by comparison with the present fringing forest, in spite of the more favourable climatic and pedologic condition pertaining in the latter. For if the forest in the lowland were more vulnerable, the present bush islands would probably have already been destroyed by man. Alternatively, it could be maintained that an original differential resistance between the present forest boundary and one that existed in the lowland has been reduced by a change to a wetter climate during the process of forest retreat across the lowland.

From present conditions, therefore, it remains difficult to assess the destructive influence of man in the past. There is, however, no reason to doubt that his influence is as great today, as it has been under similar climatic conditions in the past, and indeed in many places it may be much more.

If this conclusion is accepted, in order to attribute the present Rio Branco-Rupununi savanna purely to anthropic causes, one must envisage the destruction of approximately 20,000 square miles of forest by a population of shifting cultivators, whose principal tool of destruction, prior to the present century, has been the stone axe. Such a process is feasible, but is difficult to visualise in the short period of time available since the last climatic changes took place, i.e., within the last four thousand years. Under these conditions it is hard to credit the origin of the savanna to purely anthropic influences.

Conclusion

During 1964 palynological investigations have been undertaken in the Rupununi by van der Hammen, but as yet no findings are available. In view of this, it is premature, and somewhat unwise to go beyond a statement of the more likely alternatives in the evolution of the savanna landscape.

The first alternative is the assumption of a wetter climate in tropical South America during the latter part of the Würm-Wisconsin glaciation, followed by a relatively dry period in the early Holocene and a return to wetter conditions at approximately 4,000 B.P. Under these conditions one would envisage the advance and establishment of savanna in the Rupununi during the early Holocene, with a subsequent tendency towards the re-establishment of forest at approximately 4,000 B.P. If man were present at the time, even in small numbers, he could have restricted the natural advance of forest by burning the savanna and preventing the growth of forest species into it. In this case, one must postulate the dominance of savanna within the Rupununi throughout the Holocene.

Alternatively, if man were not present four thousand years ago, a natural advance of forest could have taken place into the Rupununi at that time, with the proviso that some areas of savanna, under wet ecoclimatic conditions, might have persisted in the lowland trough. Under these conditions one assumes a second retreat of forest to the present condition at some time since then. It has been argued that cultivating man alone is unlikely to have been responsible for large-scale destruction of forest in such a period. Thus since 4,000 - 3,000 B.P., one assumes further ecoclimatic change towards drier conditions as the prime cause of the savanna, although the process may have been aided or accelerated by man, and the savanna, once established, maintained by him in the face of any continuing climatic fluctuation, such as is indicated in East Africa (See Table 23). Such an interpretation would conform to the vegetational evolution in the Laguna de Agua Sucia region of Colombia.

A third alternative, for which there is no positive evidence, but which in the present state of knowledge, cannot be entirely discounted, is based on

TABLE 23: Probable sequence of climatic and vegetational evolution in the Rupununi since the latter part of the Pleistocene.

	Climate			Vegetation		
	High latitudes	East Africa*	Tropical South America	Laguna de Agua Sucia, Colombia**	Ogle, coastal Br. Guiana**	Rupununi, Br. Guiana
	Cold (Final glacial phase)	Wet (Gamblian phase)	Cool & wet		Herbaceous savanna (drainage impedance)	Forest
C. 10,000 years B.P.	Warm (Post-glacial climatic optimum)	Dry	Warm & dry	? Savanna ↓	Swamp (shoreline conditions) ↓	Savanna ↓
C. 4,000 years B.P. C. 2,000 years B.P.	Cooler with minor fluctuations	Wetter ↓ Dry ↓ Wetter	Wetter ? 	Forest ↓ Savanna ↓	Increase in herbs ↓ Savanna	(Forest) ↓ Savanna ↓

* After Clark (1962)

** After van der Hammen (1963, 1964)

the opposite occurrence of a wetter climate during the Altithermal, with forest extended over at least the free draining parts of the Rupununi. This would presumably have been followed by a return to drier conditions at approximately 4,000 B.P., and associated with it, a natural evolution of savanna, which has persisted until the present day.

Of the three alternatives the last conforms least satisfactorily to the present interpretation of the climatic evolution of the region. In an assessment of the merits of the former alternatives, the antiquity of man becomes important, and of this there are currently few data, although the advanced stage of sheetwash deposition in the area would appear to be more compatible with the appearance of savanna in the early Holocene than in the last two to four thousand years.

PART 5

CHAPTER 11

CONCLUSIONS

In the examination of the savanna ecosystem, attention has been focused initially on the concept of the ecoclimate. This concept provides a means of expressing the influence on plant growth, in terms of moisture availability, of many elements in the ecosystem, principally climate, relief, drainage and the physical condition of the soil.

Nevertheless, the ecoclimatic concept is only of indirect value in genetic studies, for as well as reflecting factors which are determinants of the vegetation, it is itself partly a product of that vegetation. Its real value lies in the understanding it can give of the way in which causal elements in the ecosystem currently affect, and more importantly, would affect, were they to change, the ecoclimate and hence the vegetation.

Of the factors examined, climatic fluctuations during the last 12,000 years have been considered the most significant, and in Chapter 10 an attempt has been made to relate these to the evolution of the present savanna landscape. But, although climatic fluctuations have been postulated as the dynamic element responsible for the present savanna, this single factor must not be overemphasized, for it has only operated under specific conditions imposed on the ecosystem by other factors.

In the first instance, the processes of climatic and vegetational change have taken place within an area of low soil fertility; thus, although it has been maintained that the chemical status of the soil cannot alone induce savanna, it is highly likely that soil infertility would accelerate any initial climatic tendency towards savanna. Equally, such a tendency would be increased by the presence of man to a degree commensurate with his destructive activity.

In addition to considerations of climatic, pedologic and anthropic factors in the ecosystem, attention was paid in Chapter 1 to correlations that have been drawn, by some writers, between older landscape surfaces and savannas. Such an interpretation represents a broader, regional approach to a problem that has, in the present thesis, been given more detailed ecological treatment.

In some respects, however, the findings of the two approaches are compatible, in that both mal-drainage and impoverished soil conditions, which are commonly associated with old landscape surfaces, are to be found in the Rupununi, although in that region their causes are very different, and not directly a result of prolonged landscape evolution.

In the first instance, the Rupununi is a recent depositional landscape, where mal-drainage is a function of recent drainage evolution and low elevation, rather than pedologic impedance in senile soils. Similarly, soil infertility is a product of impoverished, alluvial parent materials, rather than of pedologic processes during the present cycle. From this, it is apparent that ecological conditions favourable to the existence of savanna can be reproduced under a variety of conditions, and are not necessarily associated with a late stage in landscape evolution.

A final problem remains that of the present status of the savanna. For within a dynamic ecosystem, the stability of the savanna must always remain in doubt; it is quite possible, therefore, that the natural conditions that originally induced the savanna may have been subsequently altered or subdued by more powerful ecological influences.

In this respect, it has been argued in Chapter 10 that physical conditions in the Rupununi are today improved to the point where they are capable of supporting forest, but that the savanna is maintained, against this natural tendency, by man-made fires. If this is so, the savanna is currently in a state of physical disequilibrium and man must now be considered the ecological dominant. Yet again this dominance has only been achieved within a physically adverse environment, and is not generally operative, for example, in the elevated and forested areas surrounding the Rupununi lowland.

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APPENDICES

APPENDIX I

EVAPORATION AND TRANSPIRATION MEASUREMENTS AT ST. IGNATIUS, RUPUNUNI, 1963/1964

(a) Lysimeters

Three lysimeters were installed on the meteorological site at St. Ignatius and commenced operation in July 1963. They were located on an open site, with a tree belt three to four metres high, 75 metres to the east. Each lysimeter consisted of a steel drum, 56 cm in diameter and 76 cm deep, sunk into the ground with a 7 cm rim projecting above the surface. At the base of each drum an outlet pipe was installed and led off a distance of eight metres to a collecting chamber. The bottom of each drum was filled with a layer of gravel to a depth of 10 cm, and then filled with soil of sandy clay loam texture. An A_1 soil horizon with Pangola grass (Digitaria decumbens) growing on it was transplanted into the drum and, when the grass had become established, readings were commenced. The grass cover was approximately 75% over the period of observations, and was maintained at the same height as the surrounding grass.

All evapotranspiration data quoted represents the mean figure of the three instruments.

A fourth lysimeter of similar design was set up, in December 1963, on an exposed lateritic gravel ridge, approximately 400 metres from the meteorological site. The drum was filled with gravelly loam and gravelly clay loam materials and had a sparse cover of bunch grass (Trachypogon plumosus), which covered approximately 15% of the surface.

(b) Evaporation pans

Two pans were in use at St. Ignatius during 1963-1964. The first was of standard Class A design, 121 cm (47.5 ins) in diameter and 25 cm (10 ins) deep, but installed as a sunken pan with the rim projecting 7 cm above ground level. The water level in the pan was maintained between 5.0 - 7.5 cm below the rim. Measurements were made on the side of the pan with a measuring rod.

A second smaller pan was similarly installed and operated; its dimensions are as follows :- diameter 56 cm; depth 47 cm. Faulty readings were obtained from this pan during the early part of 1964, and figures quoted are for the larger Class A pan.

The situation of the instruments is similar to that of the three lysimeters.

(c) Atmometers

A standard black porous disc atmometer was installed in July 1963 at St. Ignatius, at a height of 120 cm above the ground.

APPENDIX 2

SOIL DRAINAGE CLASSES

(a) Excessively drained

Water is removed from the soil very rapidly, and the water table remains permanently below 200 cm. No gleying or mottling is visible in the profile.

(b) Well drained

Water is removed readily from the soil. The water table remains below 150 cm in the wet season, falling well below the grass root zone in the dry season. Gleying and mottling may be present below 150 cm.

(c) Moderately well drained

Water is removed readily from the upper profile, but the ground water table may rise as high as 100 cm for several months in the wet season, dropping below the grass root zone early in the dry season. Slight gleying and mottling may occur as high as 50-75 cm.

(d) Imperfectly drained

Water is removed slowly in the wet season, with the ground water table at or close to the surface for 2-3 months, dropping to a depth of several metres during the dry season.. The profile is usually gleyed throughout, with associated mottling.

(e) Poorly drained

Water is removed slowly from the soil, and the site is waterlogged and intermittently flooded for 3-6 months each year. The ground water table drops several metres during the dry season. The profile is gleyed throughout, with mottling prominent.

(f) <u>Very poorly drained</u>

Water is removed slowly from the soil, and the site is waterlogged or inundated for the greater part of the year; the water table rarely drops below 50 cm. The profile is totally gleyed, with mottling prominent in the upper layers.

APPENDIX 3

DETERMINATION OF HERBACEOUS ROOT DISTRIBUTION IN SOIL PROFILES

The method employed to determine the nature of herbaceous root distribution was as follows :- samples of undisturbed soil, weighing 5-10 kg, were removed from the face of a soil pit at the following depths:-

0 - 15 cm	60 - 90 cm
15 - 30 cm	90 - 120 cm
30 - 45 cm	120 - 150 cm
45 - 60 cm	150 - 180 cm

In the laboratory, the eight samples were oven dried, and weighed. Each block of soil was then placed on a board, measuring 30 x 80 cm, tilted lengthways at an angle of approximately 10 degrees, and through which projected a 3 cm grid distribution of nails 2.5 cm in height.

The soil block, placed on the board, was then hosed down at a slow and constant rate, and the soil allowed to disintegrate and be washed away, leaving the root network, virtually complete, enmeshed in the nails. Each operation took from one to three hours depending upon the nature of the soil, and all samples were treated by the same person.

Finally, the roots were collected, oven dried and weighed, and the root weight in each layer expressed in terms of mg of root material per 1,000 cc of soil.

Several alternative methods were tried before that described above was selected. They involved the use of augur samples, and soil-root separation based on sieving and flotation. Although faster, none proved acceptably accurate.

APPENDIX 4

SOIL PROFILE DESCRIPTIONS

(a) Site 06 Location: St. Ignatius (Lethem terrain)

A_1	0 - 12 cm	Dark grey (10YR4.1), sandy loam. Structureless; very friable. Many roots.
A_2	12 - 25 cm	Dark brown (10YR4.3), sandy loam, with few faint mottles. Structureless; very friable. Many roots.
B	25 - 120 cm	Yellowish brown (10YR5.4), sandy clay loam, with few faint mottles. Structureless; firm. Few roots.
C	120 - 200 cm	Light brown (7.5YR6.4), sandy clay loam, with common yellowish red (5YR5.8) mottles; few incipient iron concretions. Moderate, fine crumb structure; firm. Few roots.

Soil: Latosol

Parent material: Sheetwash alluvium, from secondary lateritic gravels

Relief: Very gently sloping (less than 1 degree)

Soil surface: Slight surface compaction

Drainage: Well drained; water table perennially below 150 cm.

Herbaceous root zone: 0 - 180 cm.

Vegetation: Maintained pasture, under Pangola grass (Digitaria decumbens).

(b) Site 09 Location: St. Ignatius

A_1	0 - 15 cm	Black (5Y2.1), silty loam, with high humic content. Weak, fine crumb structure; very friable; many fine pores. Many roots.
A_2	15 - 30 cm	Dark grey (5Y4.1), silty loam, with moderate humic content. Structureless; very friable; many fine pores. Many roots.
G	30 - 70 cm	Pale olive (5Y6.3), silty loam, with faint mottling and gleying. Structureless; very friable; many pores. Few roots.

G	70 - 85 cm	Light grey (5Y7.2), loam, with many, medium yellow (2.5Y7.6) mottles and occasional plinthite. Moderate fine crumb structure; very friable; many pores. Few roots.
DG	85 - 120 cm	Light grey (5Y7.1), clay loam, with many, medium brownish yellow (10YR6.6) mottles and plinthite. Moderate, fine crumb structure; firm; few pores. No roots.
D_2	120 cm +	Medium, secondary lateritic gravel.

Soil: Humic glei

Parent material: Lacustrine alluvium, overlying sheetwash alluvium and lateritic gravels

Relief: Flat and level

Drainage: Poorly drained; inundated for 5 1/2 months during 1963. Lowest recorded water table: 212 cm (14 February 1964)

Herbaceous root zone: 0-85 cm.

Vegetation: Herbaceous savanna (campo limpo), with grasses and sedges.

Dominant herbs: Cyperus sp., Coutoubea racemosa,(unknown grass).

(c) Site 12 Location: Moco Moco (Lethem terrain)

A	0 - 12 cm	Dark olive grey (5Y3.2), loam, with few, fine secondary lateritic concretions. Moderate, fine crumb structure; friable. Many roots.
B	12 - 45 cm	Yellowish brown (10YR5.4), loam, with few, fine secondary lateritic concretions. Weak, fine crumb structure; friable. Common roots.
C_{cn}	45 - 60 cm	Yellowish brown (10YR5.4), gravelly loam, with many secondary lateritic concretions. Structureless; friable. Few roots.
C_2	60 - 120 cm	Light yellowish brown (10YR6.4), silt loam, with few, fine secondary lateritic concretions. Structureless; very friable. Few roots.
C_3	120 - 180 cm	Light yellowish brown (10YR6.4), silt loam, with mottling and few iron concretions forming in situ. Structureless; very friable. Few roots.

Soil: Latosol

Parent material: Sheetwash alluvium, from secondary lateritic gravel

Relief: Very gently sloping (less than 1 degree)

(d) Site 13 Location: St. Ignatius (Lethem terrain)

A_1	0 - 10 cm	Dark greyish brown (10YR4.2), sandy loam, with many, fine secondary lateritic concretions. Structureless; few fine pores; very friable. Many roots.
A_2	10 - 47 cm	Reddish yellow (7.5YR6.6), sandy loam, with many, fine secondary lateritic concretions. Structureless; few fine pores; very friable. Many roots.
B	47 - 75 cm	Strong brown (7.5YR5.6), sandy clay loam, with many, fine secondary lateritic concretions. Structureless; few fine pores; friable. Few roots.
C	75 - 135 cm	Strong brown (7.5YR5.6), loam, with many, fine secondary lateritic concretions. Structureless; few fine pores; friable. Few roots.
D	135 cm +	Medium, secondary lateritic gravel.

Soil: Latosol

Parent material: Sheetwash alluvium, from secondary lateritic gravel

Relief: Gently sloping (less than 2 degrees)

Soil surface: Firm and compacted

Drainage: Well drained

Herbaceous root zone: 0 - 165 cm

Vegetation: Wooded savanna (campo sujo), with dominant grasses

Dominant trees: Curatella americana, Plumeria inodora

Dominant herbs: Trachypogon plumosus, Fimbristylis ferruginea, Cassia flexuosa.

(e) Site 40 Location: Maracanata Basin (Bella Vista terrain)

A_1	0 - 15 cm	Dark greyish brown (10YR4.2), loamy sand. Structureless; loose. Many roots.
A_2	15 - 75 cm	Yellowish brown (10YR5.4), loamy sand. Structureless; very friable. Few roots.
B_1	75 - 105 cm	Yellowish brown (10YR5.6), sandy loam. Structureless; very friable. Few roots.
B_2	105 - 140 cm	Yellowish brown (10YR5.6), sandy clay loam, with slight mottling. Structureless; firm. Few roots.

Soil: Latosol

Parent material: Riverine alluvium

Relief: Level ridge summit

Soil surface: Loose and sandy

Drainage: Moderately well drained

Herbaceous root zone: 0 - 140 cm +

Vegetation: Low wooded savanna, on margin of 'bush island'

Dominant trees: Byrsonima spp., Curatella americana. Bush Island: Anacardium occidentale, Cereus sp., Mangifera indica.

Dominant herbs: Trachypogon plumosus, Paspalum spp.

Sub-dominant herbs: Aristida spp., Cassia flexuosa

(f) Site 42 Location: Meritizero (Meritizero terrain)

0 -15 cm	Light reddish brown (5YR6.4), fine sandy loam. Structureless; very friable. Common roots.
15 - 50 cm	Reddish yellow (5YR6.8), loam, with few, very fine quartz gravel fragments. Structureless; friable; many pores. Few roots.
50 - 220 cm	Yellowish red (5YR5.8), loam, with few, very fine quartz gravel fragments. Structureless; friable; many pores. Few roots.

Soil: Regosol

Parent material: Aeolian alluvium

Relief: Very gently undulating

Soil surface: Slight compaction, with some loose sandy material

Drainage: Excessively drained

Herbaceous root zone: 0-200 cm.

Vegetation: Herbaceous savanna (campo limpo), dominated by grasses

Dominant herbs: Trachypogon plumosus, Cassia spp., Fimbristylis spp.

Sub-dominant herbs: Stenophyllus paradoxa, Aristida spp., Axonopus spp.

(g) Site 43a Location: Bella Vista (Mirichy terrain)

A	0 - 20 cm	Brown (10YR4.3), loam. Weak, very fine sub-angular blocky structure; friable; few pores. Many roots.
B	20 - 45 cm	Light yellowish brown (10YR6.4), silty clay loam. Weak, very fine sub-angular blocky structure; firm; few pores. Common roots.
G_1	45 - 165 cm	Light grey (5Y6.1), silty clay loam, with many, medium strong brown (7.5YR5.6) mottles. Moderate, very fine sub-angular blocky structure; firm; few pores. Few roots.
G_2	165 - 220 cm	Light grey (5Y7.1), silty clay, with many, medium strong brown mottles. Moderate, very fine sub-angular blocky structure; very firm.

Soil: Latosol to low-humic glei

Parent material: Riverine flood plain alluvium

Relief: Flat and level

Soil surface: Very hard and compacted; slight cracking

Drainage: Moderately to imperfectly drained

Herbaceous root zone: 0 - 120 cm

Vegetation: Wooded savanna (campo coberto), with grasses and sedges

Dominant trees: Curatella americana, Byrsonima spp.

Sub-dominant trees: Plumeria inodora

Dominant herbs: Trachypogon plumosus, Dichromena ciliata

Sub-dominant herbs: Andropogon angustatus, Fimbristylis spp.

(h) Site 62 Location: San José (Pirara terrain)

A	0 - 20 cm	Dark greyish brown (10YR4.2), sandy loam. Structureless; very friable; few pores. Many roots.
B	20 - 70 cm	Dark greyish brown (2.5Y4.2), sandy clay loam, with few, faint mottles. Structureless, friable; few pores. Few roots.
G_1	70 - 110 cm	Light brownish grey (2.5Y6.2), sandy clay loam, with few faint mottles. Structureless; firm. Few roots.

G_2	110 - 210 cm	Light olive grey (5Y6. 2), loam, with many, medium reddish yellow (5Y6. 6) mottles; incipient iron concretions and plinthite. Structureless; friable.

Soil: Latosol to ground water laterite

Parent material: Riverine terrace alluvium

Relief: Flat and level

Soil surface: Firm and compact

Drainage: Imperfectly drained

Herbaceous root zone: 0 - 110 cm

Vegetation: Wooded savanna (campo sujo), with sedges and grasses

Dominant trees: Byrsonima spp., Plumeria inodora

Dominant herbs: Fimbristylis spp., Trachypogon plumosus

Sub-dominant herbs: Stenophyllus paradoxa, Byrsonima verbascifolia, Dichromena ciliata, Axonopus spp.

(j) Site 87 Location: Toka (Toka terrain)

0 - 20 cm	Dark greyish brown (2.5Y4.2), coarse loamy sand. Structureless; loose. Common roots.
20 - 75 cm	Strong brown (7.5YR5.8), coarse sand. Structureless; loose. Common roots.
75 - 100 cm	Grey (7.5YR6.0), silt loam, with many, medium strong brown (7.5YR5.8) mottles. Structureless; friable. Few roots.
100 - 120 cm	Strong brown (7.5YR5.8), coarse sand and gravel. Structureless; loose. Few roots.
120 - 130 cm	Yellowish brown (10YR5.8), loam. Structureless; friable. Few roots.
130 cm +	Dark grey (7.5YR4.0), silt loam. Structureless; friable. Few roots.

Soil: Regosol

Parent material: Mountain outwash

Relief: Gently sloping

Soil surface: Slightly compacted

Drainage: Moderately well drained

Herbaceous root zone: 130 cm +

Vegetation: Wooded savanna (campo cerrado), with grasses and sedges

Dominant trees: Curatella americana

Sub-dominant trees: Byrsonima spp.

Dominant herbs: Trachypogon plumosus, Rhyncospora barbata

Sub-dominant herbs: Fimbristylis spp., Bulbostylis conifera, Axonopus spp.

(k) Site 97 Location: near Pirara (Maracanata terrain)

A_1	0 - 15 cm	Dark greyish brown (2.5Y4.2), silty clay loam. Structureless; firm; few pores. Many roots.
G_1	15 - 85 cm	Light grey (5Y7.1), silty clay loam, with many, medium reddish yellow (7.5YR6.8) mottles. Structureless; firm; few pores. Few roots.
G_2	85 - 145 cm	Light grey (5Y7.1), silty clay loam, with very many, coarse red (2.5YR4.6) mottles. Structureless; very firm.
G_3	145 - 200 cm	Light grey (10YR7.1), sandy loam, with many medium brownish yellow (10YR6.6) mottles. Structureless; very friable.

Soil: Low-humic glei

Parent material: Fluvio-lacustrine alluvium

Relief: Gently sloping

Soil surface: Dry and firm. No cracking

Drainage: Poorly drained

Herbaceous root zone: 0 - 100 cm

Vegetation: Herbaceous savanna (campo limpo), with dominant sedges

Dominant herbs: Fimbristylis spp.

Sub-dominant herbs: Aristida tincta

(l) Site 103 Location: near Rego Creek (Rego terrain)

A_g	0 - 25 cm	Grey (5Y6.1), silty clay loam, with many medium mottles. Structureless; very firm; few pores. Common roots.
B	25 - 65 cm	Pale brown (10YR6.3), silty clay, with many, medium yellowish red (5YR5.8) mottles. Structureless; extremely firm. Few roots.
G_1	65 - 85 cm	Light grey (5Y7.1), silty clay, with many, medium yellowish red (5YR5.8) mottles. Structureless; extremely firm. Few roots.
G_2	85 - 170 cm	Light grey (5Y7.1), silty clay, with very many, medium, weak red (10R5.4) to strong brown (7.5YR5.6) mottles. Structureless; extremely firm.
G_3	170 - 200 cm	Light grey (5Y7.1), sandy clay loam, with very many, medium strong brown (7.5YR5.6) mottles. Structureless; firm.

Soil: Latosol to low-humic glei

Parent material: Fluvio-lacustrine alluvium

Relief: Flat and level

Soil surface: Dry and hard. Cracked

Drainage: Moderately well to imperfectly drained

Herbaceous root zone: 0 - 85 cm

Vegetation: Wooded savanna (campo coberto), with dominant grasses

Dominant trees: Curatella americana

Sub-dominant trees: Byrsonima spp.

Dominant herbs: Trachypogon plumosus, Aristida spp.

Sub-dominant herbs: Fimbristylis spp.

(m) Site 112 Location: Cajueiro (Cajueiro terrain)

A_1	0 - 5 cm	Dark grey (10YR4.1), sandy loam. Structureless; very friable. Many roots.
A_2	5 - 15 cm	Greyish brown (10YR5.2), sandy loam. Structureless; very friable. Many roots.

B	15 - 55 cm	Light yellowish brown (10YR6.4), loam. Structureless; friable. Few roots.
C_1	55 - 110 cm	Pale brown (10YR6.3), with few, medium yellowish red (5YR5.8) mottles. Structureless; friable. Few roots.
C_2	110 - 180 cm	Brown (10YR5.3), sandy loam, with many, medium yellowish red (5YR5.8) mottles. Structureless; very friable. Few roots.

Soil: Latosol

Parent material: Fluvial outwash alluvium

Relief: Very gently sloping

Soil surface: Slightly compacted

Drainage: Moderately well drained

Herbaceous root zone: 0 - 180 cm

Vegetation: Herbaceous savanna (campo limpo), with dominant grasses.

Dominant herbs: Trachypogon plumosus, Bulbostylis conifera; Aristida spp.

Sub-dominant herbs: Byrsonima verbascifolia, Galactia jussieuana

APPENDIX 5

FIELD AND LABORATORY TECHNIQUES TO DETERMINE POROSITY AND WATER HOLDING CHARACTERISTICS OF RUPUNUNI SOILS

In order to determine porosity and moisture holding characteristics of representative soils, 65 undisturbed core samples were taken from nine soil pits. From six to eight samples were collected at each site, at least four of which came from the zone 0-60 cm.

The samplers, consisting of short lengths of iron piping, which were sharpened at their driving end to facilitate entry into the soil, had the following dimensions :-

Length	:	6.2 cm
Internal diameter	:	5.2 cm
External diameter	:	7.0 cm
Internal volume	:	131 cc

The samplers were driven horizontally into the face of the soil pit, and subsequently removed containing a sample.

In the laboratory the soil, still in the sampler, was saturated from below and weighed. Each sample was then placed on a saturated cotton surface and in contact with it, and allowed to drain for 24 hours, or until such time as a constant weight was attained; during this period no evaporation from the soil was permitted. The samples were then re-weighed at field capacity, and subsequently oven dried, and the dry weight also obtained.

From these data, the bulk density, soil density and porosity were determined; also the moisture content at saturation point and field capacity was calculated. Finally, having obtained data on permanent wilting percentages*, the height of available moisture at field capacity in individual soil horizons, and in the herbaceous root zone as a whole was calculated for a number of sites.

* Wilting percentages were determined with pressure membrane apparatus by Booker's Sugar Estates, Ltd., Georgetown, British Guiana.

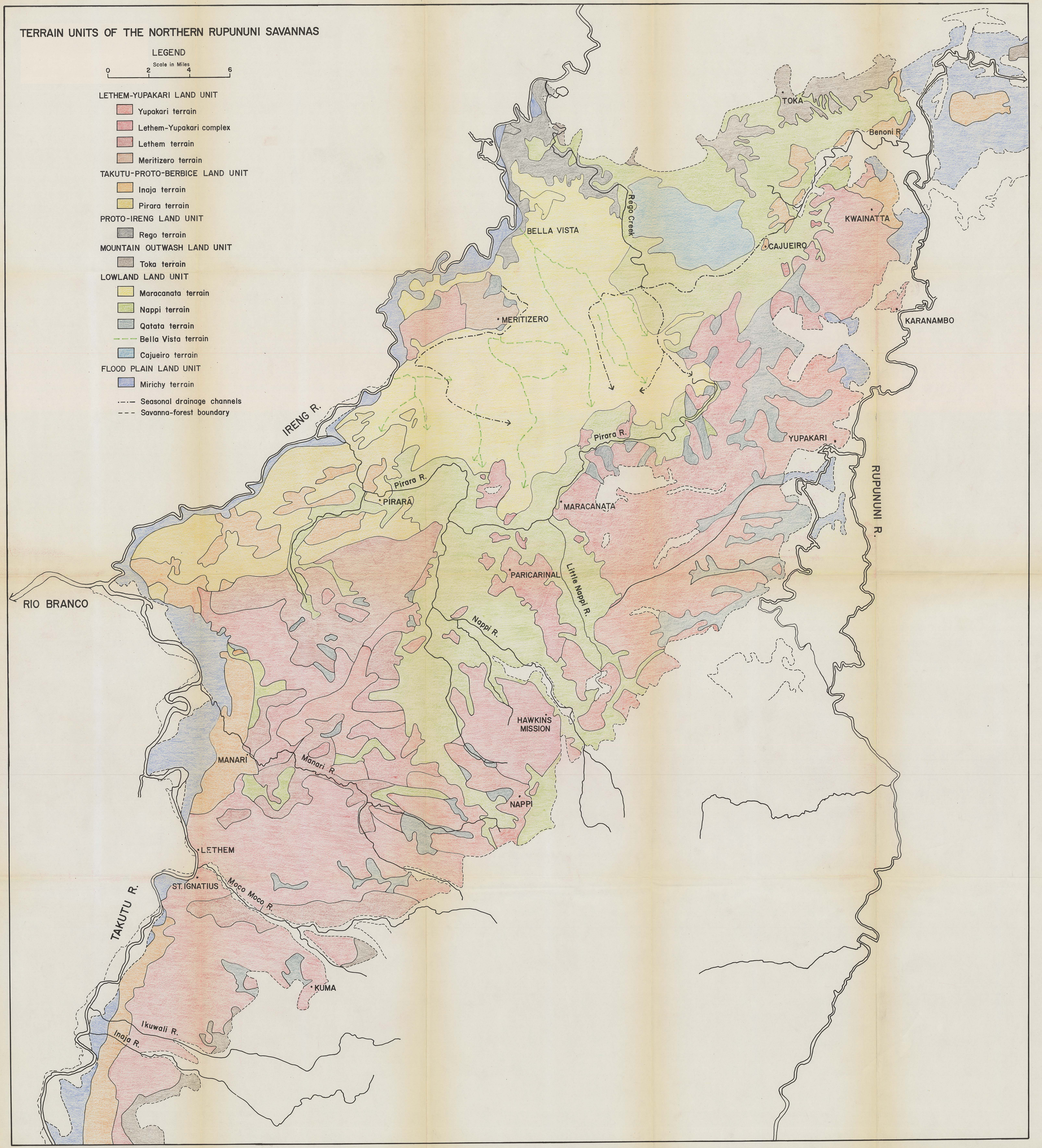
APPENDIX 6

MEASUREMENT OF SOIL INFILTRATION RATES

The determination of soil infiltration rates was undertaken as follows: two open-ended cylinders, 24 cm and 56 cm in diameter, were sunk into the ground, one within the other, to a depth of 12 cm, and both cylinders were filled with water to a depth of 10 cm. The rate of percolation through the inner cyliner was measured, the cylinder being topped up each time the water level fell 3 cm. Throughout the experiment the water in the outer cylinder was maintained at a similar level to the inner, with the aim of ensuring that only vertical percolation occurred in the inner cylinder.

The vegetation cover on both sites consisted of savanna bunch grass, principally *Trachypogon plumosus*.

In Table 14, the rates of infiltration over the first minute and the first five minutes are specified. At the time of field tests the surface soil moisture of the sites varied; as soil moisture content strongly affects initial rates of infiltration, the hourly rate, measured after the initial accelerated infiltration had ceased and a constant rate had been obtained, provides a better comparative figure. It is stressed that the rates are useful on a comparative basis, but are an over-estimate of actual rates under rainfall.


TERRAIN UNITS OF THE NORTHERN RUPUNUNI SAVANNAS
LEGEND
Scale in Miles
0
2
4
6
LETHEM-YUPAKARI LAND UNIT
Yupakari terrain
Lethem-Yupakari complex
Lethem terrain
Meritizero terrain
TAKUTU-PROTO-BERBICE LAND UNIT
Inaja terrain
Pirara terrain
PROTO-IRENG LAND UNIT
Rego terrain
MOUNTAIN OUTWASH LAND UNIT
Toka terrain
LOWLAND LAND UNIT
Maracanata terrain
Nappi terrain
Qatata terrain
Bella Vista terrain
Cajueiro terrain
FLOOD PLAIN LAND UNIT
Mirichy terrain
Seasonal drainage channels
Savanna-forest boundary
TOKA
Benoni R.
Rego Creek
KWAINATTA
BELLA VISTA
CAJUEIRO
KARANAMBO
MERITIZERO
IRENG R.
Pirara R.
YUPAKARI
Pirara R.
PIRARA
MARACANATA
RUPUNUNI R.
PARICARINAL
Little Nappi R.
RIO BRANCO
Nappi R.
HAWKINS MISSION
MANARI
Manari R.
NAPPI
LETHEM
ST. IGNATIUS
Moco Moco R.
TAKUTU R.
KUMA
Ikuwali R.
Inaja R.