ABSTRACT .

GEOGRAPHY DEPT.

TREE GROWTH AND EDAPHIC CONTROL IN THE SOUTH RUPUNUNI SAVANNAS, GUYANA.

Ian Hutchinson, B. A.

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A pilot survey established:

a) Optimal quadrat size

b) The most efficient estimate of standing crop

c) Morphometry of root systems

Savanna vegetation was divided into four classes and a random sample was taken in each stratum (45 sites in all).

Because of inherent characteristics of data non-parametric methods were employed in the quantitative analysis. A Kruskal-Wallis analysis of variance showed that the depth to the water-table, available K^{\dagger} and exchange acidity of the soil were all significantly different between vegetation classes at the 1% significance level.

A principal components analysis with orthogonal rotation was performed on a rank correlation matrix and four factors were extracted, which explained 67% of the total variance.

These results indicate that seasonally high water-tables are a limiting factor to tree growth. In areas with deeper water-tables the availability of bases is closely linked to the standing crop of trees and shrubs.

M.Sc.

TREE GROWTH AND EDAPHIC CONTROL, SOUTH SAVANNAS, GUYANA

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TREE GROWTH AND EDAPHIC CONTROL IN THE SOUTH RUPUNUNI

SAVANNAS, GUYANA.

A thesis submitted to the Faculty of Graduate Studies of McGill University in July, 1970, in partial fulfillment of the requirements for the degree of Master of Science.

by

Ian Hutchinson, B.A.

1971

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CHAPTER ONE

THE SOUTH RUPUNUNI IN THE CONTEXT OF NEOTROPICAL SAVANNAS

Of the savannas north of the Amazon, those of the Rio Branco-Rupununi are the second largest in extent (Figure 1). They cover some 21,000 square miles in area, of which the South Rupununi savanna accounts for approximately 3,000 square miles.

During the last decade the McGill University Savanna Research Project (MUSRP) has investigated the 'savanna problem' in South America. Most of the research carried out by members of the project has been in the Northern Rupununi Savannas of Guyana (formerly British Guiana) and little attention has been paid to the area south of the Kanuku Mountains known as the South Savannas.

The South Rupununi savanna is located between $1^{\circ}N$ and $2^{\circ}N$ and between $59^{\circ}W$ and $60^{\circ}W$ and is drained by the headwaters of the Amazon (Takutu River), and the Essiquibo (Rupununi River).

Definition of Savannas

A serviceable definition of savanna vegetation was provided by 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.

Although Beard attempts to limit his definition to the Americas, 'savanna' is currently used to describe similar vegetation types elsewhere in the tropics.

Theories on the evolution and genesis of Neotropical savannas are divisible into a widely-cited fourfold division. Many of these theories are associated with a particular author or group of authors, but the proponents of these theories are not as assertive about the universality of their explanation as this simple division would make it appear.



Figure 1 SAVANNAS OF SOUTH AMERICA.

R = RUPUNUNI SAVANNAS

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Climatic Theories

The first ecological study of Neotropical savanna was made by Warming during his extensive stay at Lagoa Santa, Brazil. In the results of his researches, published many years later, (1892, 1909) he ascribed the presence of cerrado to a combination of a seasonal climate and soil conditions. In the latter paper he omitted the influence of the soil and wrote:

"The vegetation is xerophytic in many places because of the dry season that lasts for months...But the xerophylly is also due to the dry continental climate in general".

E. Warming, 1909; p. 296.

Grisebach (1872), considered that the climatic factor controlled the distribution of vegetation zones around the Amazon Basin. Schimper (1903), was more categorical than Grisebach, stating that the climate of the Venezuelan Llanos was "hostile to woodland".

Doubt was first thrown on the pre-eminence of atmospheric climate as a causal factor of savanna by the experiments and observations made by botanists of the University of Sao Paulo during the 1940's. It was observed that deeply-rooted, freely-transpiring trees rarely showed signs of wilting in an area where xerophytism was supposedly common and this led to the conclusion that water was not such a limiting factor as had first been thought. (Rawitscher, 1942; Ferri, 1943; Rawitscher, Ferri and Rachid, 1943; Rawitscher and Rachid, 1946).

Waibel (1948), in a description of journeys made through some of the cerrados of Minas Gerais, found semi-deciduous forests, cerradoes, campo cerrado and campo sujo in juxtaposition in areas all presumably having the same general climate. He concluded that soil moisture, determined by local geology and physiography was the principal discriminating feature in this area.

More recently, researchers in Northern South America have tended to stress the soil climate rather than atmospheric climate as a determinant of savanna vegetation. Thus, Eden (1964) considered that the savannas of the Northern Rupununi could be divided into three 'ecoclimatic' types and van Donselaar, writing of the Guianese savannas as a whole, but more particularly of the coastal and Sipaliwini savanna areas of Surinam, writes: "The composition of savanna communities in general is primarily correlated with the hydrology of the soil".

J. van Donselaar, 1969, p. 306.

Geomorphological Theories

Cole (1959, 1960a, 1960b, 1963), working principally in the savannas of Brazil and East Africa, stresses the importance of the stage of landscape development. She considers that savannas are developed on peneplain or pediplain surfaces, associated with drainage impedance and 'senile' soils. On the forested slopes the "healthy balance of soil removal and renewal" leads to higher soil fertility and better moisture-retaining capacity. Virtually the same conclusions were reached by Feuer (1956) in a study of the vegetation and soil patterns in Goias, Brazil.

Biotic Theories

Under this heading it is proposed to consider the influence of fire, cultivation and grazing on savanna vegetation. Despite the assertion by Beard (1944), that "ecological problems are easier to elucidate in the Americas since many of the biotic factors are less important", the influence of these factors in Neotropical areas is still in dispute.

The Pleistocene extinction of ungulates in South America considerably reduced the effective grazing population. Wild animals which influence the vegetation in the Rupununi savannas today include small numbers of deer, (much reduced since the introduction of the gun into the area in the last centruy) and seed-eating rodents. Of much greater importance are the 30,000 head of bush cattle which are raised in the South Savannas.

Many South American savanna areas, it is claimed, owe their existence to fire. Rawitscher (1948) considered that the Brazilian cerrado was a fire climax, as did Myers (1936) in the Rupununi and Johannesson (1963) in Honduras. Although natural fires from a number of sources are theoretically possible - and lightning fires have been reported in tropical areas man's use of fire in savanna areas far outweight them in importance. Budowski is categorical about the effect of fire in tropical areas:

"It can be said that fire when used continuously will gradually replace forest by grassland."

"...together with the degradation towards a poor savanna (following on the use of fire) many other changes occur; the soil definitely deteriorates and lateritic iron pans are often formed..."

G. Budowski, 1959; p. 274.

The problem of whether forest would regenerate into savanna areas in South America if fire was excluded has never been satisfactorily answered. Experimental plots established in regularly-fired African savannas to answer this question indicate that regeneration of forest trees or an increase in the numbers of less-resistant savanna trees may result, depending upon the locality (Trapnell, 1959; Hopkins, 1965). Unfortunately no experiments of this type have been conducted in Neotropical savanna areas.

In a study of the anthropic factor in the Rupununi ecosystem Waddell does not propose that the savannas are induced by fire but suggests that:

"Given marginal environmental conditions, (such as would prevail in a savanna-forest ecotone), and therefore a state of 'potential imbalance' in the forest, the intervention of human agencies could cause a disruption through changes in the micro- and macro-climatic, hydrological and pedological conditions brought about by removal of the forest cover".

E. Waddell, 1963; p. 190.

Whilst in the Rupununi in the early dry season the author witnessed several small savanna fires, localised in extent, which consumed the ground layer of the vegetation, scorched the lower leaves of trees, and charred the bark. The savannas in this area are apparently fired so regularly that accumulation of ignitable material which would fuel a more severe fire is reduced. Indeed, this is one of the main reasons why the ranchers encourage the firing of the savannas. The other principal reason is that new grass growth is induced, especially in the early dry season.

No data on the temperatures produced during fires in the Rupununi is available but analogues may be drawn from research in Africa and Australia. Pipot and Masson (1951) and Beadle (1940) working in Senegal and New South Wales respectively, recorded surface temperatures of 80-200°C. in fires in short-grass savanna. The 'cold' burns may be contrasted with temperatures recorded for severe burns in Nigeria (Hopkins, 1960) and the Sudan (Masson, quoted in Hopkins, ibid.). These fires occurred in tall-grass savanna and maximal temperatures of 850°C. were noted. In the Rupununi at the present-day, the regularly-fired short-grass savanna probably supports only 'cold' burns. Waddell (1963; p. 60) notes that

"fires of the severity described by Schomburgk¹ are probably a very unusual event today due to the much greater frequency of burning."

Cultivation of forest areas near the forest-savanna boundary, preceded by destruction of the forest by felling and firing is commonly given as a cause for the extension of savanna into forest areas. Taylor (1968) found evidence of this process occurring in the savannas of New Guinea, but Waddell (op. cit.) points out that this kind of process may only be an accompaniment to more general environmental change.

In one of the most comprehensive and thorough studies made in a savanna area, van Donselaar-Ten Bokkel Huinink summarises the effect of fires in the following perceptive remark:

"Thus, fire has the effect of a very severe drought. Most species do not die, but behave as if they were adapted to a more severe dry period."

> W. A. E. van Donselaar-Ten Bokkel Huinink 1966; p. 107.

Pedological Theories

The most comprehensive statement of this group of theories was made by Hardy (1960). Unfortunately his mimeographed paper has not achieved a wide distribution. Much of what follows is a restatement of his ideas.

¹Schomburgk, who travelled extensively in the Guianas, visited the Rupununi in the period 1840-1844.

Root Inhibition

Inhibition of the roots of trees may result from two causes; either from high water-tables or a mechanical barrier to growth, or from a combination of these. Drainage impedance as a primary cause of savanna vegetation was proposed by Charter (1941) in British Honduras and Beard (1953) for much of Northern Tropical America. Deficiency of oxygen in the soil is the chief limit ation to plant growth during periods when the water-table approaches the soil surface. A seasonally high water-table may be perched on an impermeable layer or may extend throughout the soil profile. In soils where this occurs roots will be confined to the superficial layers of the soil. Hardy (1960) considered that inhibition of forest growth by limitation on root development was the primary cause of four small savannas in Trinidad and was also an important causal factor in much of the Venezuelan Llanos. The controlling factor in the Trinidad savanna areas was either; a high perched water-table (Piarco Savanna), a fragipan layer (Aripo Savanna), a duripan (Erin Savanna) or bedrock close to the surface (St. Joseph Hill Savanna).

In Surinam, Heyligers (1963) postulated that the development of a duripan at 2-4 metres depth following removal of the forest cover by fire would prevent forest regeneration. In Venezuela, Bonnazi (1968) and Foldats (1968) found that an indurated or gravelly plinthite layer (arrecife), which covers large areas in the Llanos, is a barrier to root development:

"This barrier can only be penetrated by thin roots, not more than 1 cm. thick. When they are thicker they become deformed and finally die. The thicker roots run over the surface of the mechanical barrier adapting themselves to its relief".

Foldats 1968; p. 57.

In the forest 'matas' the arrecife layer is either absent or it is less compacted. Sarmiento and Monasterio (1969) used association analysis to show that the floristic composition of the ground layer is controlled by the depth to the indurated layer in the fields of the Estaçion Biologico do los Llanos, Venezuela. Ferri and Lamberti (1960) working in an area of putative cerrado in Pernambuco, found that a hardpan layer was not penetrated by tree roots. The largest area in South America subject to drainage impedance and consequent root inhibition is the Llanos de Mojos, Bolivia, described by Denevan (1966, 1968):

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"There is little doubt that many of the savanna/forest boundaries in the Mojos are drainage controlled through differences in microrelief.... Although the soils under poorly drained grassland and under the better drained forests do differ, particularly in depth to hardpans, neither the structure nor the fertility of the savanna soils seems capable of permanently preventing tree growth".

Denevan, 1968; p. 47.

Denevan (ibid.) and Cole (1960) also consider the Pantanal of Southern Brazil to be a savanna caused by drainage impedance.

Nutrient Defiency

Many of the soils underlying Neotropical savannas are deep, highly leached, acid soils, low in exchangeable bases and possessing high levels of iron and aluminium oxides. Most of the work that has stressed these features as controlling influences on savanna genesis and development, has taken place in the cerrado of Brazil. In summarising the results of his research Hardy (1960) emphasises this nutrient control:

"The limiting factor to forest growth in the case of the Campo Cerrado is inadequacy of nutrient supply. Root room, water supply, and air supply are fully adequate. Perched water -tables cannot occur in this soil".

Hardy, 1960; p. 2.

It was the pedological researches of Alvim (1954) and Alvim and Araujo (1952), that demonstrated that the low nutrient status of the soil was probably a primary cause of the absence of forest. Arens (1958, 1963) furthered their work by propounding the theory of oligotrophic scleromorphism. Goodland (1969) sums up Arens' work as follows:

"This theory...says that as cerrado plants have plenty of light, air and water they can therefore synthesize carbohydrates and fats, and they do so - in excess. But as they are so deficient in minerals, the manufacture of protein and hence growth is more difficult".

Goodland, 1969; p. 32.

Perhaps the most conclusive work on the question of xerophytism was conducted by Ferri (1959, 1960) and Coutinho and Ferri (1960) on the campos of the Amazon varzea and marginal cerrado areas in Parana. In the former areas the plants had an abundance of water throughout the year but the soils were very deficient in nutrients. The tree flora, which had many species in common with the more extensive cerrado areas to the south, developed a very similar'xeric' physiognomy, thus supporting Arens' theory. Loveless (1961), working in the 'Evergreen Bushland' of South Jamaica found that the features associated with sclerophylly were, an increase in the weight of crude fibre and a decrease in protein and moisture in the leaf. He links this to the very low phosphate content of the soils on which this vegetation type is found. According to McClung and de Freitas (1957, 1958) and Hardy (1962) phosphate is the major limiting factor in cerrado soils. Acute sulphate, nitrogen, calcium and trace element deficiencies have also been reported by these authors.

In the Southern Rupununi Loxton, Rutherford and Spector (1958) stated that there was no difference in nutrient status between forest and savanna soils; however, further data collection led Rutherford and Hills (1968) to state that in this area "The summary results...indicate that all forest types are higher in nutrients than savannas".

Hardy (1960) proposed that nutrient deficiency was a secondary factor in the Berbice savannas of Guyana and destruction of the closed nutrient cycle in the forest ecosystem by fire, felling or erosion deflected the natural regeneration of the forest in an irreversible change to scrub or savanna.

Mineral Toxicity

Three possible sources of toxicity caused by excessive concentrations of minerals in the soil solution exist in savanna areas. These are respectively: aluminium, manganese and iron. As far as is known no publications have dealt with manganese or iron toxicity in savanna soils, but the possible importance of the former has been recognised, at least in Brazil (Goodland, 1970; personal communication). Aluminium

Hardy (1958, 1960) was the first to point out the possibility that toxic levels of aluminium might exist in highly leached acid to strongly acid savanna soils in South America. Most of the experimental work on aluminium toxicity has been conducted on field crops or temperate plants. The reaction is known to be species-dependent and plants may be divided into three broad classes; sensitive, tolerant or accumulative.

There is as yet no unambiguous evidence to prove that plants require aluminium (Hutchinson, 1943; Grime and Hodgson, 1969), but Hackett (1962) reported that aluminium had a stimulative effect on the growth of <u>Deschampsia flexuosa</u>. In a sensitive plant such as barley Clarkson (1966a, 1969) has shown that aluminium sulphate at concentrations of 10^{-3} M halts root elongation, and arrests cell division, probably by interfering with DNA synthesis in the S period of the mitotic cycle. Aluminium may also interfere with the phosphorus metabolism of the plant, resulting in a depression of respiration (Clarkson, ibid.). This fixation of phosphorus in the root cells may mean that it is not available for shoot growth.

Goodland (1969), working in the Triangulo Miniero of Brazil, concluded that the high level of aluminium saturation of the soil exchange-complex, linked with the low base status of the cerrado soil was the primary cause in determining the presence of cerrado vegetation:

"The increase in xeromorphy of the vegetation from cerradao through campo sujo is related to an increase in the aluminium saturation of the soil. The gradient from cerradao to campo sujo, the change in physiognomy, the decrease in biomass, the decrease in the number of tree species, the decrease in the canopy and the change in floristic composition may all be related to an increase in aluminium saturation".

Goodland, 1969; p. 199.

As well as these conclusions, based on high inter-correlations between the above variables, Goodland cited the importance in the tree flora of a number of 'accumulator' families (Rubiaceae, Malpighiaceae, Vochysiaceae); indicative of high levels of exchangeable aluminium. Manganese

Manganese toxicity may also be an important problem in savanna soils. Unlike aluminium, manganese chlorosis results in particular symptoms; for example, brown spotting on leaves. Manganese may also accumulate to a significant extent in the plant shoots and is not so readily trapped in the root cortex. Morris (1949) shows that the concentration of manganese in the soil solution increases rapidly from 2 - 15 μ g/ml. at pH 5.0 to 40 - 80 μ g/ml. at pH 4.5. Reeve and Sumner (1970), working on oxisols in Natal, found no decrease in the yield of sorghum with Mn levels of 5 - 30 μ g/ml. Some crops (barley, soybeans) may suffer yield depression at 1 - 4 μ g/ml. but <u>Deschampsia flexuosa</u> can tolerate over 60 μ g. (Olsen, 1936).

Unlike aluminium, manganese does not interfere with the phosphorus metabolism of the plant.

Ferrous Iron

Toxic concentrations of ferrous iron may be found in many savanna soils subject to waterlogging. Under these anaerobic conditions the pH of a soil rises and exchangeable Al^{+++} is replaced by Fe⁺⁺. Plants growing in these conditions may have to be tolerant of seasonal deficiency of oxygen and toxic levels of iron, and dessication and toxic levels of aluminium or manganese in the dry season.

It is obvious from what has been said above that these pedological factors may operate singly or in unison. Particular combinations that are probably common in savanna areas are nutrient deficiency and Al+++/Mn++ toxicity; and drainage impedance and Fe⁺⁺ toxicity.

Premises and Hypotheses

This report is an ecological reconnaissance of the South Savannas and attempts to lay a groundwork of knowledge for future research in the area. The problems investigated include a floristic comparison of the woody vegetation of the North and South Savannas; a quantitative description of tree and shrub physiognomy, and relationships between root and shoot development for a number of species. Previous knowledge of South Rupununi soils is correlated with data taken from a sample survey and a tentative classification is outlined. The central problem in this thesis is to determine which, if any of the afore-mentioned factors are responsible for the changes in physiognomy and biomass of the trees and shrubs of the South Rupununi Savannas.

Variation in the density and size of the woody vegetation is the most commonly used classification system for savannas and so the establishment of the reasons for this variation in any area must be one of the primary tasks of the savanna ecologist.

The search for principles and causes in ecological research, centres around three techniques. These are the approaches of the natural historian, the statistician and the laboratory worker. Each of these attempts to rationalise a set of complex environmental interactions in order to discover the nexus of the problem that is being dealt with. In most synecological problems the richness of the flora and the large numbers of variables of possible significance and of disparate origin produce a system which it is impossible for the laboratory worker to reproduce or control. The statistician on the other hand has available a variety of techniques which enable him to assess the independence of interrelationships and to test the significance is not necessarily synonymous with ecological significance.

It is obvious from what has been said above that there already exists a body of well-formulated opinion concerning the origin of Neotropical savannas which covers a diversity of causal and limiting factors. In the South Rupununi the inter-relationships between the vegetation and the environment (apart from the qualitative analysis of the anthropic factor by Waddell (1963)) are virtually unknown. Analogues may be drawn from the available work on the co-terminous savannas of the North Rupununi (particularly Eden, 1964; and Goodland, 1964) and the Rio Branco savannas (Takeuchi, 1960) but as will be shown the recent geological and geomorphological evolution of these areas is considerably different and wholesale application of the conclusions formulated in one area to the South Rupununi would be unwise.

In this investigation, which deals with a large system of variables of mixed origin, (biological, chemical and physical), representative of the contemporary environment over a study area of some 2000 square miles,

the initial problem is to 'collapse' the complexity of interactions into a few factors. Only a first approximation to a solution can be gained in this fashion but, as Fraser Darling noted in 1967, "Ecological reconnaissance can be developed further to give a fairly accurate, reasonably quick answer to specific problems."

No formal statistical design is used to tackle this problem, and to reduce the effect of 'a <u>priori</u>' knowledge all possible variables are considered in the system so as not to bias the study. This type of 'shotgun analysis' (Miller and Kahn, 1962), produces several difficulties in its application. These are divisible into two groups. Quantification

To analyse the system statistically the variables need to be expressed quantitatively, preferably on a ratio or frequency scale. Some important environmental influences are very difficult to quantify; for instance the random and periodic effects of fire and grazing at a site. The recent burning history of a site will be obvious but the frequency and intensity of fires in previous dry seasons is much more difficult to assess. Consequently these variables were omitted from the analysis and only sites which did not show signs of recent burning were sampled. Seasonality

Many of the variables undergo periodic (generally annual), cycles and data collected at one instant in time is only representative of a short time-span. Variables such as water-table depth come under this heading. It is assumed that the fluctuations of this particular variable during the field season were probably not as great at a site as variations between sites. However the most important omissions from the data set are in the field of atmospheric climate, which shows both diurnal and annual variation. Consequently a blanket assumption of uniformity in climate for the sites had to be made.

The Data

Three physical, ten chemical and three biological variables were measured over a total of forty-five sites as indicated in Table 1.1. TABLE 1.1

II.

- I. Physical Variables Water-Table Depth Slope Angle Infiltration Capacity
 - Chemical Variables. Soil pH % Carbon % Nitrogen P₂O₅ Exchange Acidity (H⁺) Exchangeable K Exchangeable Na Exchangeable Ca Exchangeable Mg Exchangeable Al
- III. Biological Variables.

Species Shoot Height Crown Area In the next chapter, (Chapter Two) the methods of data collection in the field and the analytical methods employed in the laboratory are described, and in Chapter Three background information on the physical environment and evolution of the Rupununi area is given.

Chapter Four is devoted to a brief description of the flora of the area and then deals with tree physiognomy, the morphometry of root and shoot systems and their development. In Chapter Five the soils of the Rupununi are described in terms of their physical and chemical characteristics and a tentative classificatory scheme is presented.

The penultimate chapter deals with the statistical methods used to analyse the variables and an ecological interpretation of these results then follows, with a summary of the results of the investigation in Chapter Seven.

FIELD METHODS AND DATA COLLECTION

Stratification of Sample

The working hypotheses and the variables for which data was to be collected were listed in Chapter One. The independent variable in this study is the amount of tree growth in each stand; in most savanna research projects, stratification of the sample is by the visual appearance of the vegetation, and no attempt is made to quantitatively discriminate between strata. In this research four classes of savanna (Figure 2) were established on the following criteria:-

- a) Herbaceous savanna¹ no shrubs or trees
- b) Shrub savanna shrubs (woody plants one to three metres high) and canopy cover of less than 2%.
- c) Open savanna woodland shrubs and trees (woody plants over three metres high) and canopy cover of 2 20%.

d) Savanna woodland - mainly trees and canopy cover of over 20%. These class limits were based on a pilot survey in which a stand was allocated to a nominal category based on <u>a priori</u> judgement and the canopy cover and tree height of the stand were measured.

Quadrat Size

The size of the quadrat to be employed for vegetation sampling was found by examining the vegetation of a stand of open woodland two miles east of Dadanawa. The vegetation of this stand was both floristically and physiognomically heterogeneous. An area of 5000 square metres (1/2 hectare) was surveyed and divided into 25 square metre quadrats. The tree and shrub cover in each quadrat was then estimated. The mean and standard deviation of these estimates was computed and by accumulation of neighbouring quadrats this process was repeated for areas of 50, 100,

¹These four categories are approximately equivalent to the Brazilian terminology:- a) campo limpo, b) campo sujo, c) campo cerrado, d) cerrado.

FIGURE 2

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CLASSES OF WOODED SAVANNA VEGETATION

Top) Shrub savanna; Meritizero R.dge, North Rupununi. (Photo by T.L.Hills) Canopy cover approximately 2%. This is a fairly dense example of this type of savanna. The shrubs in the foreground are Curatella americana.

Centre) Open woodland savanna; site c.2 miles northeast of Dadanawa. Canopy cover 18%. The stand is almost dense enough to be classed as savanna woodland. Tree to left of vehicle is <u>Bowdichia virgiliodes</u>, tree to right is Byrsonima coccolobifolia.

Bottom) Woodland savanna; Tawatawun Pond, South Rupununi. Canopy cover 80%. All the trees in this photograph are Curatella americana.



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200, 400, 600, 800, 1200, 1400 and 1600 square metres. By plotting the increase in quadrat size against standard deviation the optimal quadrat size can be found. This is represented by the point of inflexion on the graph (Figure 3) which occurs at approximately 400 square metres; a quadrat with 20 metre sides.

The probability of estimating the population mean cover in a stand with a 400 square metre quadrat with a 95% confidence interval was as great as with a 1000 square metre quadrat. In the Dadanawa example the population mean was estimated at 10.74 (sample mean) \pm 2.21% with the 400 square metre quadrat. The 1000 square metre quadrat gave an estimate of 10.70 \pm 2.39%. Whenever it was suspected that the stand to be sampled was more heterogeneous than the original quadrat a 1000 square metre plot was used.

Location of Sample Sites

Prior to fieldwork in the Rupununi a framework for the sampling of stands had been drawn up. This envisaged the provisional assignment of each stand discernible on aerial photographs of the South Rupununi¹ to one of the four strata listed above and the subsequent random sampling of the population of each stratum. An equal and maximum number of stands was to be sampled in each unit. The principal difficulty encountered in trying to operate this scheme in the field was the impassability of much of the terrain throughout the field season, (August - November 1969).

During the wet season and for several weeks afterwards many of the creeks cannot be crossed and the trails are untrafficable to four-wheel drive vehicles. Consequently, a modified sampling scheme was used and the stands close to the main jeep trails, particularly the Dadanawa-Lethem road, were randomly sampled (Figure 4.). Later excursions were made east from Dadanawa to the Wapishana villages of Shea, Mawaruwaunawa, Awaruwaunawa; southeast to Sawariwau, Raad and Charwhy; and west to the area between Kusad Mountain and the Takutu River. The southwestern part of the savannas, around Aishalton, was omitted from the survey because it is in the main an area of herbaceous savanna and palm swamp.

¹Flown by R.A.F., October 1953, 1:30,000.



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Quadrats of 400 square metres were positioned in each selected stand by walking 150 metres (500 feet) in a random direction into the stand from the edge. The 20 x 20 metre quadrat was then laid out in a north-south direction taking the initial point as the southwest corner. When the area to be sampled had been demarcated all the woody plants over one metre in height were recorded. The following items were noted for each individual:

- a) Species
- b) Height
- c) Crown Area

The first two items were recorded in alphameric form, the third was mapped by dropping verticals from the outermost parts of the canopy onto the ground, finding the x-y coordinates of this point in the quadrat, and trasferring this to graph paper at a suitable scale. In this way the crown area of individuals could be directly computed. Three to eight peripheral points were sufficient to outline the crown of any individual. Initially it had been hoped to use the canopy shadow for this purpose but the patchy nature of the foliage and the fact that most work was done well before midday limited the usefulness of this method.

Soil Sampling

Soil samples for chemical and particle-size analysis were taken. These were representative of the rooting medium of the trees and shrubs (see Chapter Four). This procedure was standardised by taking one sample from 25 cm. (10 inches) and another from 50 cm. (20 inches) at separate points within the quadrat. The pit from which the 50 cm. sample was taken was then extended by auger until the water-table was reached or until bedrock was found. The water-table was judged to have been reached when the bore had standing water in the bottom. In cases where the water-table could not be reached by augering or an overall view of horizonation in the soil profile was sought a soil pit was dug to a depth of two metres and an auger sample taken for the third metre.

The rate of infiltration into the soil profile was measured with plastic tubes, 10 cm. (4 inches) in diameter and 25 cm. (10 inches) in length which were inserted into the soil to a depth of 20 cm. (8 inches). The end of the tube protruding from the soil surface was then filled with water to a depth of 4 cm. (1.6 inches) and the time taken for the water to drain into the profile was measured. Three replicates of this process were made at different points in the quadrat. The time taken for the water to drain into the soil varied from a few minutes for the sands and sandy loams to several hours for some clay-rich soils. Problems associated with Field Methods

Apart from some initial difficulties of taxonomic assignation no problems were associated with the collection of the vegetation data. The principal difficulty encountered when measuring the depth of the water-table was that on occasions, in shallow soils, the bedrock would be reached before the water-table. In this case the depth to bedrock was measured and substituted for the water-table measurement. In soils encrusted by fire, insolation or raindrop impact it was found to be impossible to drive in the infiltration tube without breaking the surface crust. Therefore the rates of infiltration recorded for these profiles are generally too high. In all infiltration studies using this type of method some disturbance of the soil surface and texture is inevitable so this source of error has consequently been ignored. The mean of all the infiltration measurements was taken as being representative of the quadrat as a whole.

Laboratory Analysis

The soil samples were analysed in the routine laboratory of the Quebec Soils Laboratory, Ste. Anne de la Pocatière and the Geochemistry Laboratory, McGill University. The samples were initially sieved in the Soils Laboratory, McGill University and the fraction finer than 2 mm. retained for analysis.

The method employed by the Quebec Soils Department for the determination of exchangeable cations was extraction with neutral $NH_4C_2H_3O_2$ (1 <u>N</u> solution). A flame spectrophotometer was used to determine the concentration of Ca⁺⁺, Mg⁺⁺, Na⁺, and K⁺ in the ammonium acetate extract. Exchange acidity was then calculated by subtracting the sum of these four cations from the amount of ammonium adsorbed.

Nitrogen was determined using the Kjeldahl method modified to include nitrates, and phosphates by the Dickman-Bray method. This latter method is very sensitive to small quantities of phosphorus.

Exchangeable aluminium was determined using the method of Reeve and Sumner (1970) in the Geochemistry Laboratory, McGill University. This method is a modification of that of Skeen and Sumner (1965, 1967a, 1967b), who propose a technique of successive extractions (25 in all), to estimate exchangeable Al^{+++} . Reeve. and Sumner employ only a single extraction with 0.2 NNH₄Cl (1:10 soil/solution ratio) for 2 minutes in a reciprocating shaker, to determine the exchangeable Al^{+++} index (EAI) of a soil. This method has the advantage of being much less laborious than that of Skeen and Sumner, and gives comparable results. A 2 gram soil sample was used in the analysis. Determination of Al^{+++} in the extract was made using a Perkin-Elmer Atomic Absorption Spectrophotometer.

CHAPTER THREE

PHYSICAL BACKGROUND TO THE SOUTH RUPUNUNI SAVANNAS

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Geology

The Rio Branco-Rupununi Savannas cover part of the central portion of the Guiana Shield, which forms the nucleus of the north-eastern part of the South American continent.

The South Savannas are developed entirely on the Pre-Cambrian rocks of the Rupununi Assemblage, consisting of two major lithological units, the high-grade gneisses of the Kanuku Group, which are intruded by the South Savanna Granite, a batholith outcropping over approximately 5000 square miles of country. To the west and north the savannas of the Territorio do Rio Branco in Brazil and of the Northern Rupununi are developed on the sediments of the graben known in Guyana as the North Savannas Basin, and the alluvial deposits of the Rio Branco and its tributaries.

The existence of this rift structure has been demonstrated by McConnell (1959), Wicherts (1965), and McConnell, Masson Smith and Berrangé (1969). The southern boundary of the rift is marked by the impressive fault line scarp of the Kanuku Mountains, which is in places over 2000 feet high. To the north smaller scarps can be traced along the Pakaraima Mountain front, varying in height from 600 to 1000 feet. Geomagnetic evidence indicates that there are further faults within the graben, which is infilled with over 6000 feet of sediments and volcanics. This zone of tectonic instability, which is unique in the Pre-Cambrian of South America (Kalliokowski, 1969; personal communication) probably facilitated intrusion of the Toka Dolerites and extrusion of the Apoteri Volcanic Formation, (Berrangé, 1969). Palynological analysis of cores from the graben sediments, the Takutu Formation, has indicated a Lower Cretaceous to Jurassic age for these shallow-water littoral deposits (van der Hammen and Burger, 1967).

The age of the rift structure is inferred by McConnell, Masson Smith and Berrangé (op. cit.) as early Pre-Cambrian, although faulting of the Takutu Formation and the 'youthful' topography of the Kanuku horst

Figure 5 GEOLOGY OF THE SOUTH RUPUNUNI

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Source: J.P. Berrangé Unpublished map.
suggest that post-Jurassic movement has also occurred. The graben has not been mapped in Brazil, but probably extends as far west as the Sa. Tucano, an outlier of Roraima sandstone. Barbosa and Andrade Ramos (1961) map most of the area of the Rio Branco savannas as being underlain by post-Pliocene fluvio-lacustrine deposits. A westward extension of Kanuku basement rocks occurs from the junction of the Takutu and Sawariwau Rivers to Boa Vista and numerous small outliers of Roraima volcanics and sedimentaries are found.

In the South Savannas, Singh (1966), divides the Kanuku basement complex into two groups; - veined biotite gneisses and granulites. The gneisses are composed chiefly of quartz, sodic-plagioclase, orthoclase, biotite and opaque oxides. Accessory minerals are garnets, sillimanite, hornblende and hypersthene. The Kanuku Mountains and the northwestern triangle of the South Savannas are underlain by this group (Figure 5). Many of the large residual hills of this area parallel the regional foliation of the gneisses, with elongated spurs and revetments exhibiting a northeast-southwest trend, (e.g. Shiriri Mountain and Kusad Mountain).

Although changes in metamorphic grade in the gneisses have been recognised, these are not known in sufficient detail for mapping. Close to the granite-gneiss boundary the gneisses are contact metamorphosed and intruded by apophases and small granitic stocks.

Acid granulites occur as masses of various sizes, the largest being the Darukoban-Kudiditau massif between Dadanawa and Sand Creek Village (Figure 5). Another extensive outcrop is in the area between Baiewau Creek and Raad Mountain. When fresh these rocks are greyblue but they weather to a dark brown colour. Like the gneisses they are foliated but do not possess the banded characteristics of these rocks. They are similar to the gneisses in mineralogical composition. Basic granulites (pyribolites) are also found, intruding the gneisses as masses ranging in size from boudins to areas of one or two square miles. The ridge north-west of Mountain Point airstrip, and Tup-Tup-Tyal hill west of Wichabai are formed of this material, which gives rise to red oxisols, locally noted for their fertility. They represent metamorphosed basic dykes and stocks. No reliable age-dating of Kanuku Complex rocks has yet been made (Snelling and McConnell, 1969) but from field relations with the South Savanna Granite the gneiss-granulite assemblage is known to be older (Barron, 1962; Singh, 1966; Berrangé, 1969).

Although Singh (op. cit.) recognised three distinct facies of the South Savanna Granite; Tabtau, Katiwau and Cherairontau Granites, they are generally of medium to coarse grained texture and grey in colour. The granite-gneiss margin trends southsouthwest - northnortheast, crossing the Rupununi River in the vicinity of the mouth of Arakwai Creek (Figure 5). The topography developed upon this lithological unit consists of small, rounded swells forming a plateau surface of subdued relief between 400 and 600 feet above sea level.

Age-determinations for the granite by the K-Ar method indicate an age of 1190 - 1930 million years with a mean of 1470 million years. Rb-Sr dating gives an age of 1880 \pm 100 million years.

Of lesser importance in the South Savannas are the mylonites and dolerites which both form ridges and hills which show a strong southwestnortheast trend. The mylonites may be granular or glassy depending on the intensity of the shearing which they have undergone. Zones of mylonitic shearing are particularly common immediately to the east of Dadanawa, the linear hill of Tawatawun being developed on this material. Climate

One of the recurrent problems facing the ecologist working in an area such as the Rupununi is the scarcity of available data. This problem is most acute in a study of the climate of this part of South America, and in consequence the maps and data that are presented here should be regarded as indicative of a general situation, rather than a finalised statement.

This section will deal with two problems; firstly the importance of the regional atmospheric climate as a possible genetic or maintaining factor in the evolution of the Rupununi savannas, and secondly the climate of the savannas themselves.

Two maps are presented to summarise the most pertinent features of the rainfall regimes of the region. The most reliable part of the map is the central section including Guyana, Surinam and Amapa, Brazil. The least reliable part, where data is almost wholly absent, is the area between the

Figure 6

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southern boundary of the Guianas and the Amazon River. This data is taken from the World Weather Records (1941 - 1969) and the annual reports of the Ministry of Agriculture of British Guiana (1914 - 1962).

Despite these drawbacks, the maps show some interesting regional relations and contrasts.

From the map of mean annual rainfall (Figure 6) it can be seen that the Rio Branco - Rupununi area occupies a position on the eastern edge of a belt of drier country with less than 200 cm. (80 inches) precipitation. This belt runs from the semi-arid centre of Venezuela to the Xingu Basin. A branch extends eastwards from the Northern Rupununi across Guyana into Central Surinam. This zone is also well-defined in the map showing seasonality of rainfall (Figure 7). It is noteworthy that it can be further divided into two parts; a northern half with a longer and more intensive dry season and an extensive southern half covering most of the eastern Amazon Basin. The critical threshold between dry and wet months is taken from Aubréville (1961) who stated that a monthly rainfall of 10 cm. (4 inches) is a minimal requirement for non-xerophytic plants. This figure is therefore taken as a dividing line between wet and dry months in the Southern Rupununi. A correlation between the extent of the Rio Branco-Rupununi Savannas and these two climatic variables is clear, although the correlation is by no means perfect. Not only is this area the driest in northeast South America, with the exception of central Venezuela, but it also has the greatest number of dry months.

Table 3.1 illustrates how well correlated are the savannas of Guyana and Venezuela with another simple climatic variable, the probability of a water deficit in any given year. Frost (1966) gives the following evapotranspiration estimates for St. Ignatius, Northern Rupununi:

Pan	Thornthwaite	<u>Garnier</u> 153 cms	
157 cms	179 cms		
(61 inches)	(70 inches)	(60 inches)	

A water deficit may be expected therefore in any year in which rainfall is less than evapo-transpiration. The probability of receiving less than 150 cms (c. 60 inches) was calculated for stations with 20-year

Figure 7

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records in different environments in northern South America, using the formula given by Gregory (1965):

$$d = x - \overline{x}$$

 σ

where x is the critical value (150 cms), \overline{x} is the mean annual precipation and σ is the standard deviation.

It can be seen from Table 3.1 that the areas occupied by forest ecosystems have a low probability of water deficit, which may be expected to occur with a recurrence interval of from 20 to 100 years, whereas the savanna areas may expect a water deficit at least one year in three.

It would seem therefore that the interior savannas of Guyana and Venezuela are strongly linked to certain present-day climatic variables, particularly the areal and temporal distribution of rainfall. The relative dryness of the Rupununi Savannas is principally due to the absence of the 'second' wet season which should occur in December-January in this part of the world. In some years there is a slight increase in rainfall in this period, known as the 'Christmas' or 'cashew' rains. Koch-Grunberg, quoted in Myers (1936), states that these have a periodicity of ten years and are therefore very unreliable. When these rains fail, the dry season extends from September to May. Three explanations have been advanced to account for the rain-shadow effect induced by the highland mass to the north-west, the Pakaraimas and Kanukus (e.g.Waddell 1963).

Aubréville (1961) considers that this 'haut Brancosien' climate is produced by a foehn phenomenon. Frost (1966) suggests that it may be due to the complex dynamics of the inter-tropical front associated with directional divergence over the mountain massif of North West Guyana.

Within the Southern Rupununi there are rain gauges at the following villages; Aishalton, Awarawanau, Dadanawa, Sand Creek and Shea. Of these only Dadanawa has long-term records, the rest are fairly recently established and data is often incomplete. Internal comparison

TABLE 3.1

			Probability of receiving
		Standard	<150 cms (60 inches) of
Station	Mean (mm)	Deviation	rainfall
COASTAL GUIANAS			
Georgetown	2469	538	6.6%
Paramaribo	2097	280	1.7%
Cayenne	3646	694	0.1%
Ebini	2314	360	1.4%
AMAZON BASIN			
Manaus	2106	275	1.4%
Santarem	2097	280	1.7%
Uapues	2963	401	0.0%
VENEZUELAN LLANOS			
Cuidad Bolivar	976	174	99.9%,
Tumeremo	1235	200	92.0%
Maturin	1319	213	79.5%
Santa Elena	1796	328	23.0%
RIO BRANCO-RUPUNUNI			
Annai	1630	318	32.0%
Dadanawa	1468	196	56.8%
Boa Vista	1523	220	46.0%
St. Ignatius	1621	336	35.0%



HISTOGRAMS OF RAINFALL FOR 1968

within the South Savannas is therefore difficult and in consequence data from some stations in the North Savannas are included for comparative purposes (Figure 8). Figure 8 brings out two features of rainfall patterns in the Rupununi; firstly, that as a general rule the annual total decreases with increasing distance from the forest edge; and secondly, that this difference in total is due to an increase in wet season rainfall, rather than being evenly distributed.

If we take the boundary between wet and dry months as 10 cms. (4 inches) then the wet season in 1968 began at all stations in April and ended at 'central' savanna stations (Dadanawa, Manari) in August and at peripheral stations (Moco-Moco, St. Ignatius, Aishalton) in September.

The strong seasonality of the climate produces a marked hydrological imbalance. In the wet season all of the low-lying areas are inundated and the rivers flood dramatically. The River Takutu at St. Ignatius may show an annual range of 40 feet (Eden, 1964) whilst the Rupununi at the Dadanawa-Wichabai crossing in 1969 varied from a mean wet season depth of 10 - 11 feet to peaks of more than 20 feet in flash floods. In the early dry season the Rupununi has a depth of 2 - 3 feet and in some years it may dry up altogether.

Unlike the cerrado areas of South and Central Brazil where the water table is very deep and the depth to ground-water in the dry season (17 metres) is less than in the wet season (18 metres), (Rachid, 1947, data from Emas, S. Paulo) the annual variation in depth of the water-table in the Rupununi is in phase with the rainfall regime. Eden (1964) showed that the water-table in the North Rupununi was generally 3 - 4 metres below the wet season peak at the end of the following dry season. The author, with fewer samples and a shorter sampling period than Eden, considers that in the South Rupununi there is a smaller change in the level of the water-table with the advent of the dry season.

Two examples, an ultisol (CSI) and an oxisol (CC5), from the South Rupununi are contrasted in Table 3.2 with an imperfectly drained ground water laterite (07) and a moderately well drained latosol (05) from the north. The two South Savanna soils are developed respectively on an alluvial terrace (CSI) and a ridgetop (CC5).

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Data in cms.				
early Sept.	early Oct.	early Nov.		
95	215	240		
225	a 290	350		
48	85	105		
235	280	310		
	<u>Data in cms</u> . early Sept. 95 225 48 235	Data in cms. early Sept. early Oct. 95 215 225 290 48 85 235 280		

It is commonly asserted that the intense wet season rainfall results in rapid surface runoff which is responsible for the inundation of the lower-lying areas, the flooding of the rivers, and gully or sheet erosion of the land surface:

"Some 60 to 80 percent of this total falls in the wet season, generally in downpours of considerable intensity which consequently induce erosion and extensive flooding of the savannas".

Waddell, 1963; p. 41.

".....during the wet season....a large volume of rainwater runs off the land surface and accumulates in areas of low relief, causing extensive flooding."

Eden, 1964; p. 35.

No <u>prima facie</u> evidence of this process has however been reported. It would seem much more likely that in the savannas, where infiltration rates are generally high, that the mechanism responsible for inundation of the sedge-meadows and palm-marshes is a rapid rise in water-table which produces 100 percent runoff when it reaches the ground surface. This process is only operative in areas of initially shallow groundwater, on the side-slopes and ridgetops the high permeability of the soils and the relatively deep ground-water results in lateral ground water movement being the most important process of water transport. <u>Geomorphology</u>

It is not surprising, considering the physical similarity of many of the landscapes of East and West Africa, semi-arid Australia and smaller areas in South America, such as the South Rupununi, that geographers who were concerned with regional synthesis should stress the unity of savanna landscapes. This visual similarity was not limited to the physiognomy of the vegetation but also applied to the land surface itself. The most conspicuous element of this resemblance was the contrast between the subdued plateau surface characteristic of most of the area and the prominent inselbergs which arise from it. The suite of landforms that rise from the surface of the South Savannas plateau vary considerably in height and area. The inselbergs are the largest of these features and are developed on both the gneisses of the Kanuku Complex and the South Savanna Granite. Shiriri and Kusad Mountains are both over 3000 feet high and are developed on gneissic rocks (Figure 5). Shea Rock and Wirwitau are examples of inselbergs on granitic parent material.

The smallest rock forms are ruwares, tors and kopjes. Ruwares are flattish or gently domed rock surfaces which may have a thin soil cover and occur on the tops of ridges, particularly on the South Savanna Granite. Tors and kopjes are small rock eminences with loose boulder accumulations at their base, developed from both gneissic and granitic rocks. Both forms are fairly common in the South Savannas.

Present theorisation on the formation of inselbergs centres on the work of King (1953, 1962) in South Africa and Thomas (1962, 1966) in Nigeria. King considers that weathering can form only minor morphological features such as tors; inselbergs are formed by stream incision along joint walls. Thomas insists that inselberg formation must be viewed in a much more dynamic framework. He finds that there is considerable evidence to indicate that the inselberg landscape of West Africa is the result of small uplifts and warpings accompanied by progressive weathering, the efficacy of which depends upon the mineralogy of the rock and the intensity of fracture systems within it. Removal of the regolith by fluvial erosion concomitant with uplift will expose those areas where the weathering-front has progressed least to form sub-rounded inselbergs.

As with most theories that are developed in one area, their transfer to another is not always successful. The inselbergs of the South Rupununi are developed in a zone of tectonic instability, so meeting one of Thomas's criteria, but the weathering zone in this area at the present day appears to be too shallow to conform to his other requirements. The primary difficulty in establishing a cause for these landforms is that they could be fossil features, unrelated to the present environmental controls. The geomorphological history of this area is known in outline from reconnaissance geological surveys and the work of Barbosa and Ramos (1961), McConnell (1966), and Sinha (1968).

Much of this work is based on limited evidence and is conjectural in nature. Of the five erosion bevels identified in Guyana by McConnell (1966), probably the most widespread is his 'Rupununi Surface'. He describes this as a pediplain at 100 - 150 metres above sea level on which the savannas are developed. It has a gradient of some 3 - 4 feet per mile towards Marudi Mountain in the south-east. Erosion surfaces in the North West District of Guyana (180 - 210 metres), the Llanos of Venezuela (100 - 150 metres), and Coubert's (1957) Quatrième Peneplaine in French Guiana are correlated with this surface by McConnell (op. cit.), who dates it as end Tertiary. He also attempts to link it with the Velhas cycle of Brazil and the late Cenozoic cycle of Afric which are regarded as contemporaneous in King's (1962) intercontinental correlation.

Sinha (1968) elaborates on this schema, recognizing five erosion bevels in the Rupununi District, at the following heights:

Kanuku Surface (3000 feet)

1500 - 1700 foot surface

1000 foot surface of convex inselbergs

North Savanna surface (500 feet)

Buried Takutu shale surface (300 - 325 feet)

Marakanata surface (340 feet)

Ireng - Takutu surface (280 - 300 feet)

Only the first four of these erosion bevels are to be found in the South Savannas. The geomorphological history of the North Savannas in the Cenozoic has been adequately described by Sinha (ibid.) and others. Only the most tenuous links have been established however between events in the north and the development of the inselberg landscape of the south. This is primarily because the processes operating in these areas were so different. In the north the principal processes were the infilling of the rift structure, laterisation of the deposits, and capture of the Takutu-Ireng by the Rio Branco. In the south the main developments were the erosion or etching of the inselberg surface and the deposition of thin fluvio-lacustrine and slopewash sediments.

Palaeogeography

The palaeogeography of the Guiana Shield during the Pleistocene is little known. Most of the evidence for changing vegetation boundaries is inferential and drawn from fields as far apart as sedimentology and avian evolution. Also most of the hypotheses are developed for the Amazon Basin or the Guianas as a whole and do not refer to the Rio Branco-Rupununi Savannas in particular. Therefore their validity for this area must be regarded as conjectural, and their conclusions as tentative.

However, whilst accepting these limitations, two conclusions can be forwarded which are substantiated by research in independent disciplines and areas. The first of these conclusions is that savanna vegetation has existed in northern South America throughout most of the Pleistocene and during this time there have been periods when it was considerably more extensive than at the present day.

Haffer (1969) supports the latter conclusion from an analysis of faunal evolution in the Amazon Basin, particularly of forest birds. He states that with the uplift of the Andes in the Upper Pliocene -Lower Pleistocene the very restricted Tertiary forest vegetation expanded rapidly across the Andean foreland. Climatic fluctuations in the Pleistocene associated with mid-latitude glaciation may have later restricted forest environments to small refugia, one of which he considers to be the Guiana Highlands. It is interesting to note in this connection that the botanist Guppy (1958) stated that the forest flora of the Acarai Mountains on the Guyana-Brazil border was richer than areas to north and south. He considered that this was due to the presence of the 'White Sand Sea' which surrounded the massif. Marine conditions never extended as far south as this however (Krook, 1969) and, assuming that this floral distinction is due to the vegetational history of the area rather than present-day ecological differences, then it would seem that the Acarai may at one time have been a forest refuge surrounded by savanna.

During the dry periods an 'open, non-forest vegetation' (Haffer, 1969) expanded across the Amazon Basin allowing the migration of faunal and floral elements from Central Brazil to reach northern South America (Haffer, ibid; van Donselaar, 1968). The endemic nonhylean flora and fauna of the Amazon campos is evidence of this process, rattlesnakes for instance have a disjunct distribution, being limited entirely to areas of savanna vegetation (Ducke and Black, 1953; Hueck, 1966).

Sombroek (1966) points out that a much more uniformitarian view has traditionally been accepted for the Amazon Basin; with a virtually constant climate since the Early Mesozoic apart from mild coolings during the Pleistocene. This view of an essentially static situation is challenged by Sombroek, who points out the contrast in sediment type currently being carried by the Amazon system (clays and fine silt), with the kaolinitic, often stony Pleistocene terraces which indicate a local sediment supply and more markedly seasonal climate. Krook (1969), bears out this conclusion by drawing attention to the presence in the Pleistocene of a fringing reef off the coast of Guyana and Surinam, a situation impossible at the present time due to the amount of fine sediment released by the Guianese and Amazon river systems. He concludes that coarser sediments must have been transported during the Pleistocene.

In both the Northern and Southern Savannas extensive deposits of fluvial sands and gravels are found. Cobbles and boulders of Roraima sandstone are widespread on laterite surfaces in the Norther Rupununi which to Sinha (1967) "indicate(s) that the rivers ...once carried much coarser loads than at present". The interpretation of these statements as evidence for a strongly seasonal climate associated with a more open vegetation than exists at present in most of northern South America, would be hazardous if it were not for the existence of more direct evidence of this situation.

The most direct evidence available, though still not necessarily unequivocal in its interpretation, is the palynological data assembled by van der Hammen and his associates. In twenty years of research in northern South America, ranging from the high Andes of Colombia to the coastal plain of Surinam, a great deal of data has been collected on the post-Cretaceous phytogeography of this area.

In the Guianas, Wijmstra (1969) shows that an alternating savannamangrove sequence, correlated with marine fluctuations, is the dominant feature of coastal vegetation formations throughout the Plio-Pleistocene. Pollen of <u>Byrsonima</u>, <u>Curatella</u>, <u>Didymopanax</u> and <u>Vismia</u> genera are the most prominent in this assemblage. Very similar sequences have been discussed by van der Hammen (1961, 1963) for the coastal Quaternary sediments of Guyana. Cores taken from Lake Morieru, Rupununi (Wijmstra and van der Hammen, 1966); Laguna de Agua Sucia, Colombia (ibid.); and Sabana de Bogota (van der Hammen and Gonzalez, 1960), all of them in present-day savanna areas, cover more restricted time-scales but exhibit savanna pollen assemblages throughout the post-glacial.

Because 'natural niches' of savanna species (e.g. <u>Byrsonima</u>, <u>Curatella</u>) are known to have been present in the Guianas throughout the Plio-Pleistocene (Wijmstra, 1969) it does not seem improbable that the interior savannas of Guyana and Surinam may have existed for all or part of this time, expanding during the inter-glacials and becoming more restricted during glacial periods.

CHAPTER FOUR

VEGETATION OF THE SOUTH RUPUNUNI SAVANNAS

The dichotomy between savanna and forest is the most striking feature of the vegetation of the Rupununi. The southern savannas are encompassed to north, east and south by the forests of the Amazon hylea, which is here termed disturbed Semi-Deciduous by Myers (1936). Fanshawe (1952) in his survey of the vegetation of British Guiana, called the forest formations of the Kanukus-Montane Forest, and the lowland forests of the south and east, Dry Evergreen Forest. Other forest types in the area are the Galeria Forest and Bush Islands.

The Bush Islands are of variable size and are composed of tall forest trees, the most common families being Leguminosae and Myrtaceae (Myers, 1936). Abandoned dwelling sites may form a nucleus for some of the smaller of these Bush Islands, trees of economic importance then being common (e.g. mango, cashew).

Galeria Forest is found along the courses of many of the major creeks. The prominence of palms (especially <u>Mauritia</u> spp.) distinguishes this vegetation type from the upland forests.

Other non-savanna elements in the vegetation complex are associated with sources of perennial water-supply; aquatic vegetation, palm swamps and marshes. The last vegetation type is composed of aquatics, suffrutex shrubs and sedges (Goodland, 1964). The most difficult type of vegetation to place in this classification is the sedge-meadow, which is intermediate between herbaceous savanna and true marsh and was therefore omitted from the vegetation sampling programme.

The savanna vegetation of the Rupununi comprises a floristically rich ground layer of grasses, sedges and forbs and a varied tree and shrub layer made up of small trees, tree-like shrubs, sub-shrubs, woody herbs, occasional climbing plants and rare epiphytes and succulents. This distinction cannot be regarded as rigid for some species may be herblike on regularly burned savanna but develop into shrubs where fire is excluded. An example of this was demonstrated by Schauer in Martius (1840) for Lippia lupulina in Southern Brazil. The dominant and ubiquitous grass in these savannas is <u>Trachypogon plumosus</u>. Species of <u>Paspalum</u>, <u>Andropogon angustatus</u>, <u>Aristida setifolia</u>, <u>Axonopus chrysites</u> and <u>Mesosetum loliiforme</u> are of secondary importance (Goodland, 1964). Myers (op. cit.) described this vegetation as a short bunch-grass savanna but in many habitats the tussock habit is not encountered and frequently the grasses may reach one metre in height.

In terms of presence, sedges (Cyperaceae) are the second most important family in the Rupununi, the commonest genera are <u>Fimbristylis</u>, <u>Bulbostylis</u>, <u>Rhynchospora</u> and <u>Dichromena</u>. The first two are usually found in the moister meadows whilst the latter, along with species of <u>Scleria</u>, are more abundant on drier sites (Goodland, op.cit.). Forbs such as <u>Polygala</u> and species of <u>Cassia</u> are common elements in the sward.

The number of species of trees and shrubs is low and their density on the ground is highly variable. The following table (Table 4.1) shows their relative importance in the North and South Savannas. The data for the North is taken from Goodland (op. cit.) and for the South from work by the author. Note however that these estimates of presence are not strictly comparable as they are derived by different methods, Goodland's data was collected using the quarter method of Curtis and Cottam, (1962) where the estimates for the South Rupununi are from an analysis of quadrats. The latter method probably tends to underestimate the presence of a species in an area. It is noteworthy however that the South Savanna seem to possess much less variety than the north, with a smaller total of tree species and fewer very common species.

The majority of the tree and shrub species have a wide distribution. Floristic affinities are highest with the Rio Branco savanna, the Llanos of Venezuela, and the cerrado of central Brazil. There are fewer tree species common to the Rupununi and the other Guianese savannas; Ebini, Sipaliwini and coastal Surinam (Harrison, 1958; van Donselaar, 1969).

The most common arboreal species is <u>Curatella americana</u>, a monospecific genus with a range extending from Central America

TABLE 4.1

PERCENTAGE I	PRESENCE OF	TREE	SPECIES	IN THE	RUPUNUNI

		SAVAN	NAS		
Northern Rupununi		·····	Southern Rup	inuni	
(Goodland, 1964)		All Sites	Woodland	Open Woodland	Shrub
Curatella americana l	00	67	89	100	78
Byrsonima crassifo- lia	83	39	44	73	30
Plumeria inodora	75	19	11	45	10
Byrsonima coccolobi- folia	70	28	33	53	20
Bowdichia virgiliodes	70	22	30	40	10
Erythroxylum spp.	50	9	11	20	-
Roupala complicata	30	11	-	30	-
Antonia ovata	22	7	11	13	-
Genipa americana	17	-	-	-	-
Couepia spp.	11	2	11	20	-
Tabebuia dura	11	-	-	-	-
Anacardium occiden-					
tale	6	-	-	-	-
Cereus spp.	3	-	-	-	-
Hirtella spp.	3	2	-	13	-
Myrtaceae	-	4	-	13	-
Bursera spp.	-	, ²	-	6	-
Apocynaceae	-	2	-	6	-

(Johanneson, 1963) to Minas Gerais and Sao Paulo in Brazil (Rizzini, 1960). It is a medium-sized tree with a wide ecological tolerance and according to W.A.E. van Donselaar (1966) it can tolerate a water surplus. The commonest tree genus is Byrsonima. Species of this genus are difficult to distinguish in the field and a morphological classification was adopted to facilitate identification. B. crassifolia, B. coccolobifolia and to a lesser extent B. verbascifolia should therefore be regarded as lumped species, comprising sub-species and varieties of this genus. Byrsonima crassifolia is most commonly a shrub or small tree which Goodland (op. cit.) considers to reach its optimum in "mesic or dry-mesic" sites. It can be distinguished from B. coccolobifolia by its more elongate leaves. The latter species is usually a medium-sized tree. B. verbascifolia has a suffrutex habit and large pubescent leaves and was never found to grow more than one metre high in the South Savannas. Other important tree species are Plumeria inodora, which grows up to ten metres in height; Bowdichia virgilioides and Roupala complicata. Antonia ovata, Hirtella spp., and shrubs of the Erythroxylum genus are also fairly common.

Table 4.1 also illustrates how the presence of trees and tree species varies in different types of savanna. Although the four commonest species are listed in the same order in all the South Rupununi data, (<u>C. americana, B. crassifolia, B. coccolobifolia, Bowdichia virgiliodes</u>), there are interesting contrasts between savanna types. Savanna woodland appears to be less heterogeneous floristically than open woodland and shrub savanna bears more resemblance to savanna woodland in its composition than to open woodland.

Germination of Savanna Species

There is little doubt that most savanna trees can reproduce vegetatively and that this form of reproduction is overwhelmingly predominant over seed germination. Ferri (1961a) states: "after many years of studies in cerrados we were struck by the fact that we never found seedlings of permanent plants that we could say with certainty had come from seeds". Nevertheless the majority of studies that deal with seedling development in South American savannas are based on laboratory experiments using seeds. It is therefore difficult to apply

TABLE 4.2

SHOOT AND ROOT MORPHOLOGY FOR VARIOUS SAVANNA SPECIES

Species	Shoot Height (m.)	Crown Area (sq. m.)	Shoot Weight (Kg.)	Root Area* (sq. m.)	Root Weight* (Kg.)
C. americana	1.55	0.75	6.00	19.00	NR
C. americana	2.50	2.51	1 1. 30	63.00	NR
C. americana	3.00	2.94	6.20	5.85	2.00
B. coccolobi- folia	1.80	0.67	2.88	7.30	1.53
B. crassifolia	2.10	3.26	15.30	16.00	4.70
Bowdichia virgiloides	5.80	7.02	68.50	72.26	45.30
Roupala comp licata	- 1.75	0.62	1.17	1.70	1.24

*Values approximate

NR - Not recorded

TABLE 4.3

SI	ZE AND SHAF	E VARIABLES FO	OR SAVANNA	
	TREES	AND SHRUBS		
Species	Weight (Kg.)	Cone Volume (cu. m.)	Height (m.)	Radius (m.)
	47.7	8.38	2.06	1.97
	27.0	11.33	2.65	2.02
B. crassi-	15.3	2.52	2.10	1.07
folia	11.8	2.45	1.80	1 - 14
	1.8	0.65	1.75	0.34
	122.2	25.62	4.10	2.44
	14.8	3.55	4.10	0.87
B. coccolo-	7.5	1.54	3.82	0.62
bifolia	2.9	0.62	1.80	0.58
Diumeria	189.5	28.06	6.90	1.97
inodora	28.6	4.84	3.68	1.12
	163.4	29.00	3.91	2.66
	48.5	11.01	5.52	1.38
C. ameri-	14.2	3.26	3.93	0.89
cana	5.9	2.98	3.00	0.98
	21. 2	4.10	2.25	1. 32
Roupala complicata	1.1	0.38	1.75	0.46
Bowdichia virgilioides	68.8	13.49	5.80	1.49



the results of these researches to field conditons. The foremost specialists in germination studies are two Brazilians; Rizzini and Labouriau. The result of their work of most interest to the savanna ecologist is the division of cerrado seedlings into two types based on their root development.

The first group, represented by species of <u>Hancornia</u>, and <u>Kielmeyera</u> and is distinguished by the development of a thickened central subterranean organ which may be either woody and fibrous or soft and watery. This organ is termed a lignotuber or xylopodium (Rizzini and Herringer, 1961). An example of such a thickening can be seen in an individual of <u>Bowdichia</u> virgilioides from the South Rupununi (Figure 10).

Both these forms are regarded as xeromorphic adaptations, for storing nutrients and water; enabling the plant to survive through the first critical dry seasons. Goodland (ibid.) suggests that the lignotuber may be a 'pyrophytic adaptation' increasing the plant's chance of survival if the aerial parts are destroyed by fire.

The second group develops very long primary roots in the initial, and most critical, years of development, thus minimizing the time that the plants have to depend on surficial water supplies.

Root Morphology

Rooting systems of various species were excavated in the Rupununi by the author to investigate differences between species and to assess the importance of the soil type as a determinant of root depth and area. The results of these researches are presented in Figures 9 - 13. These diagrams and the data in Table 4.2 are the first available data for rooting systems of trees in the Rupununi apart from Eden's (1964) excavation of the roots of a 35 cm. tall 'tree' of Plumeria inodora and some river-bank observations by the same author. All the evidence gathered in the South Savannas opposes the conclusion of Eden (ibid.) that "the roots of savanna tree species....extend deeply into the soil". All the trees excavated, growing in both latosols and free-draining sands had developed extensive superficial root systems with only minor vertical growth. This conclusion accords well with the results obtained by Foldats (1968) in the Llanos of Venezuela and the observations of W.A.E. van Donselaar on the rooting systems of trees in the coastal savannas of of Surinam. (van Donselaar-Ten Bokkel Huinink, 1966). She found that almost all species had long lateral roots, few in number, and tap-roots were



ELEVATION VIEW OF ROOT SYSTEMS OF THREE INDIVIDUALS OF CURATELLA AMERICANA.

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Horizontal and vertical are the same.





Figure 12

ROOT SYSTEMS OF BYRSONIMA SPECIES

Top) Byrsonima crassifolia

The aerial parts of this plant and most of the laterals have been removed for clarity. The thin tortuous primary roots are characteristic of this species. The shrub was 2.1 metres high and the roots covered an area 5x that of the canopy. The shrub grew in a sandy entisol one mile east of Dadanawa. The horizontal and vertical extension of the roots is shown in Figures 10 and 11.

Bottom) Byrsonima coccolobifolia

The shrub grew to a height of 1.8 metres. Note the few , long lateral roots. The site is the same as the above.



Leaf 59 missing

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limited to situations where the water-table was at greater depth. The situation in the Rupununi may be contrasted with the researches carried out by Rawitscher (1948) and Rawitscher and Rachid (1946) in the cerrado of Sao Paulo. The found that most trees and shrubs were deeply rooted, some tapping the water-table at 18 metres below the surface. Specht and Rayson (1958) produced similar results in their examination of the savanna-like heath vegetation of South Australia. It would seem therefore that there is good reason to believe that the roots of savanna shrubs and trees may be divisible into two ecologically distinct types, dependent on the depth of the water-table.

A tentative model of root development for savanna trees in the South Rupununi can be forwarded, based partly on germination studies on cerrado trees but mainly on the data derived from the excavation of the roots of mature trees. The depth to the water-table under 'wooded' savanna in the Rupununi varies seasonally and from site to site but generally falls in the range of one to four metres.

It is hypothesised that development begins with the growth of a tap-root down to the vadose zone immediately above the water-table. The second stage is the development of small lateral roots from the uppermost part of the tap-root. The selective growth of some of these laterals continues until, for a mature tree, they may cover an area ten to twenty times that covered by the canopy. In the final stages of development infilling of the area immediately under the canopy by secondary laterals may occur. Shoot Systems

The structure of the root and shoot systems of trees and shrubs is a function of both genotype and ecological influence. The parameters which are generally used to define the shape and size of the aerial parts of the plant are one- or two-dimensional indices:- height, basal area, diameter at breast height, canopy area. For species in the Rupununi savannas none of these is a particularly good expression of the complex three-dimensional structure of the shoot system. Basal area and DBH are difficult to measure when dealing with shrubs possessing multiple shoots.

In most trees there is an allometric relationship between the height of a tree and the area of its canopy. The trees and shrubs of the Rupununi do Figure 13

ROOT SYSTEM OF BOWDICHIA VIRGILIODES

Top) Close-up of primary roots of an individual of B. virgiliodes

Bottom) Lateral root system of same tree.

The tree was 5.8 metres in height and the roots covered an area 10x that of the crown. The tree was growing in the same as the <u>Byrsonima</u> specimens on page 58.

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not show this relationship and these two variables show only a low correlation (Table 4. 4 and Figures 14 and 15). Many previous savanna ecologists have referred to this phenomenon in qualitative terms, stating that the trees have a 'gnarled' or 'stunted' appearance (Warming, 1892; Boulliène, 1930; Tamayo, 1961). All three authors consider that this is due to the destruction of the terminal bud which does not maintain the same growth direction. There is as yet no explanation for this change of direction and evidence from the savannas of East Africa (Lebrun, 1947), indicates that there is no directional change following fire injury.

Whatever the reason for these gnarled forms the structure of the plant is inadequately described by these variables. Patently a volumetric index would be the most effective parameter to use. An inverted cone was chosen as the best index. The volume of this is calculated by:-

$$V = 1/3 \Pi r^2 H$$

where H = Tree height $\Pi r^2 = Canopy$ area

Because it combines canopy area and height data no information is lost. Very few trees conform to a conical shape, and therefore the index is obviously an artificial one, but it was found to correlate better than either tree height or canopy area with what is the most precise measure of the size of the plant - the mass of the aerial parts (Table 4.4).

The raw data on which Table 4.4 is based was drawn from a sample of two open woodland areas; the first three miles north of Sawariwau village, the second, one mile northeast of Dadanawa.

The ratio of the mass of shoots to roots was plotted for five individuals. Rogers (1935) states that this ratio is lowest in poor soils where a greater weight of roots is necessary to support a given mass of shoots. This ratio is probably species-dependent also, but a rule-of-thumb estimate can be derived from the following mixed population (Figure 16).



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Inter-relations between physiognomic parameters for species in the South Rupununi





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	CORRE	LATIONS BET	WEEN SIZ	E AND SHAPE VARIABLES
	WT.	CONE VOL	нт.	RAD.
WEIGHT	-	. 977	. 692	. 869
CONE VOLUME	**	-	. 679	. 916
HEIGHT	*	*	-	. 439
RADIUS	**	**	NS	-

**	Significant at 1% probability level
*	Significant at 5% probability level
NS	Not Significant

N = 18

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-64-
Figure 16

RELATIONSHIP BETWEEN SHOOT AND ROOT WEIGHT FOR A MIXED-POPULATION OF SAVANNA SPECIES.



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The equation of this line is:

$$\log_{10} y = -0.204 + 0.224 (\sqrt{x})$$

Further research on a larger sample is needed to confirm this relationship. The 'Adaptation' of Savanna Tree Species

The teleological concepts of xerophytism and pyrophytism have been widely applied to savanna vegetation. 'Adaptations' may be of two sorts; either to ensure survival of the plant or to promote reproduction if the above-ground portions of the plant are destroyed. Bark and root morphology, periodicity, foliar anatomy and protection of primordia are the commonest 'adaptations' to either fire or drought.

Bark morphology

One of the functions of bark is to protect the cambium from damage. Vines (1968) showed that the increase in cambial temperatures during a fire was related to the diffusion of heat through the bark, which was controlled by bark thickness, and was independent of the structure or moisture content of the cork and phloem layers. Gill and Ashton (1968) however questioned this conclusion, and recorded greater thermal diffusion rates in thick fibrous-barked trees than in specimens with thin decorticating bark. Bark thickness increases with tree girth, and consequently mature trees should be more fire-resistant than younger individuals. Rupununi savanna tree species are generally thick-barked. Curatella americana has bark 2 - 3 cms. thick, and although Bowdichia virgiliodes has thinner bark and it is locally considered to be the most fire-resistant of the savanna trees. (J. Brown, 1969; personal communication).

The <u>Byrsonima</u> genus, though it possesses thick, suberose bark is in general use throughout the Rupununi as firewood, and probably comprises the least resistant of the common species.

Periodicity

There is some dispute as to whether savanna woody vegetation is evergreen or deciduous. Warming (1892) noted that the leaves of cerrado trees are shed annually, and Dansereau (1951) considers savanna trees to be semideciduous but Beard (1953) stated that the trees are evergreen and the leaves are shed only after a fire. With this latter view the author tends to agree. van Donselaar-Ten Bokkel Huinink (1966) recorded that in the coastal savannas of Surinam only three species out of a flora of 174 species were completely deciduous. Two of these species, both members of the Leguminosae occur in the Rupununi (<u>Galactia jussieuana and Cassia hispidula</u>; Goodland, 1964).

Most Rupununi trees and shrubs flower and fruit in the early to middle dry season (November to January) and it would seem therefore that the phenological behaviour of the plant is out of phase with the seasonal climate.

CHAPTER FIVE

SOILS OF THE SOUTH RUPUNUNI SAVANNAS

Previous investigations of the soils of the Southern Rupununi have ranged from the broad-scale reconnaissance mapping of Suggett (1964) for the F.A.O. to the much more detailed mapping; accompanied by profile descriptions and laboratory analyses, conducted by Loxton, Rutherford and Spector (1958) for the Imperial College of Tropical Agriculture, Trinidad, Land Use Series. The series names used in this chapter are taken from the latter publication. Description and Pedogenesis

Texturally, the soils of the area fall mainly in the sandy to sandy loam classes, with limited areas of fragmental and fine-textured soils. Most of the soils are highly quartzose and of slightly acid to acid reaction. They are extremely low in base status, and most of the exchange sites are occupied by the aluminium ion because of the low level of calcium and magnesium. If we accept McConnell's (1966) contention that the surface on which these soils have developed is mid-Tertiary in age, then they have been subject of weathering for perhaps as long as 20 million years. Consequently they have attained an end stage in pedogenesis where leaching has removed practically all the reactive feldspar and ferromagnesian minerals in the soil profile leaving a virtually inert solum, of little agricultural value. The lack of relief on this surface has halted the erosional processes which would have led to stripping and rejuvenation of the profile.

The sandy nature of the soils of the Rupununi may be the result of the intense and lengthy weathering to which they have been subject or it may be the product of a colluvial parent material, or both. We are as yet not able to state which of these processes has been predominant. Loxton $\underline{\text{et al}}$ (ibid) use the catenary position of the soil as a first approximation in their classification scheme. Catenary sequences are not as well developed in the Rupununi as in some other savanna areas, for instance those of East and West Africa (Nye, 1954 and 1955; Morison, Hoyle and Hope-Simpson, 1948). The only strong correlation between lit hology and

and soil type is found between the Wichabai Series and outcrops of basic granulite.

Soil Fertility

Except where otherwise stated all data in this section are derived from the sample survey. The organic matter content of Rupununi soils is generally low. Apart from the swamp soils and the Wichabai Series all the soils have low organic matter percentages throughout the profile generally below 1.5% in the topsoil and 0.5% in the subsoil. The periodic destruction of surface litter and grasses in dry season fires is probably the principal cause of this deficiency.

All profiles apart from one swamp soil recorded low and uniform levels of nitrogen (0.02-0.07%) throughout the solum. Muck soils associated with swamp vegetation may contain up to 0.5% N in the topsoil.

Rupununi topsoils contain only 5 - 20 ppm of P_2O_5 and subsoils vary between 0 and 10 ppm. The reasons for this very low phosphate level are threefold. Firstly, as Wild (1961) has shown, leaching of apatite, the chief mineral source of P, is particularly intense on sandy soils formed from granite and gneiss. The second mechanism to account for the low content of available P is that much of the organic P is rapidly adsorbed by ferric and aluminium oxides and stored in the soil in the sparingly soluble orthophosphate form. Cunningham (1963), working on forest clearance sites in Ghana, showed that this was particularly rapid in exposed situations where soil temperatures and evaporation were high, analogous to conditions in the Rupununi. This same reaction also occurs with the return of oxidising conditions to inundated soils. In these soils reductant-soluble P may be volatilized under the anaerobic conditions which occur during the wet season (Tsubota, 1959).

The availability of exchangeable bases in Rupununi soils is very low, as would be expected from their leached nature, and there are marked deficiencies in all cations. In the sample the C.E.C. varies from 0.5 - 5.5 meq./100 g. and base saturation is 5 - 50%. The pH of the soils correlates highly with C.E.C. and more especially Ca and Mg content. Hardy (1958), in a review of the "senile soils" of the Neotropics, lists fifteen features of the soil which he considers to be indices of senility. He divides there into ten chemical and five mineralogical tests. Of the chemical tests the soils of the South Rupununi are classed as senile on seven counts. No data for the other two tests are available, (low sulphate content and low $Si_2:Al_2_0$ ratio) although it is probable that these savanna soils, like the cerrado soils of Brazil, are very deficient in sulphur (McClung and de Freitas, 1959). The only test that the soils of the study area fail is that of acidity. Hardy considers that a pH of 4.5 discriminates between senile and non-senile soils; pH determinations from the Southern Rupununi indicate a range of 4.8 to 6.1.

The most conclusive tests are those on the exchangeable bases. Rupununi soils have very low levels of potassium, and because of its greater geochemical stability magnesium is more important in the exchange complex than calcium. From the sample data the Ca + Mg : K ratio varies in Rupununi soils from 3 to 46, but two-thirds of the samples fall below Hardy's senility index of 12.

Soil Classification

The principal criteria which are employed in tropical soil science for taxonomic purposes are the ratios of Si02:Al203 and Al203:Fe203 in the clay fraction. (Maignien, 1966; Buringh, 1968). The system that is employed most widely in South America, developed by Bennema and others in Brazil, also uses these ratios. This type of data is at present not available for the soils of the Rupununi. The only information that we have is a general statement by Brinkman (1967) that kaolinite is the predominant clay mineral in the 'interior' of Guyana. Thus the most suitable classification scheme to use in the Rupununi would seem to be one based on morphology rather than mineralogy of the soil. Such a scheme was developed in Australia by Stephens (1962), however the U.S.D.A. 7th Approximation (1960) uses both morphological and chemical criteria as discriminating factors and because it is now becoming applied and accepted internationally this latter system was preferred to the Australian one. However, wherever possible correlations between the U.S. and Australian soil names will be given.

Several difficulties arise in the interpretation of the U. S. soil orders, especially in the Oxisol order, which is not yet well-defined. The features which Haantjens (1967) considers most useful for distinguishing Oxisols are as follows:

a) Strong weathering

- b) Reddish and bright brown colours
- c) Low C.E.C.
- d) Lack of strong or sudden texture contrast

These supplement the U.S. D.A. (1960) requirements of less than 1% weatherable minerals in the profile and predominance of 1:1 (kaolinitic) clays. These latter requirements are probably met in the Rupununi, but at present there is no data to support this assertion. Colouration and the presence of a texture-contrast horizon are the principal distinguishing features between Oxisols and Ultisols in the Rupununi.

Ultisols

In terms of area these are the most important soils in the southern Rupununi. They cover extensive continuous areas between the Kanukus and Sawariwau Creek, between Sawariwau and Raad and between Dadanawa and Shea. They are distinguished by the presence of an argillic horizon of low base status (less than 35% base saturation). Above this horizon there is commonly an albic horizon of sandy texture.

Plintaquults and Plintochrults

These are Ultisols which are saturated during the wet season and have distinct mottling below the A horizon. They are distinguished by the depth of the plinthite layer, which is deeper in the Plintochrults, exceeding 1.25 m. (four feet) in depth. These soils were formerly called Low-Humic Gleys or Ground-Water Laterites. The Kuma, Ambrose, Makushi and Sawariwau Series fall into these classes.

Profile Description

Makushi Series: Site 2 1/2 miles W. of Sawarab Creek on Lethem road. Low-lying area close to gallery forest. Woodland Savanna, <u>Curatella</u> americana predominant.

10YR3/1	Very dark-gray sandy loam, structureless.
	pH 5.2
10YR4/4	Dark yellowish-brown sandy-loam, structureless.
	Slight yellow-orange mottling. pH 5.4
2.5¥6/2	Light brownish-gray clay loam, distinct red
	mottling. pH 5.8
	Pisolitic plinthite, sandy matrix.
	10YR3/1 10YR4/4 2.5Y6/2

This profile is typical of most of the soils of this order, except that the indurated horizon is generally not developed. It is a latent feature in these soils, developing when the water-table is lowered and the mottlings harden into nodules and then into discontinuous plinthite. These soils are very low in nutrient reserves.

The depth to the argillic layer is variable from one series to another but generally falls within the range 15 cms. (6 inches) to 70 cms. (26 inches) The depth to this layer and the topographic position of the profile are consequently very important controls on the length of the period for which the soils are saturated and the depth to which they are inundated.

The size and number of mottles increases with depth in the profile and their colour changes from yellow to red. The soil underlying the Aripo Savanna, Trinidad is a Plintaquult which is very similar to those developed in the Rupununi. A comprehensive study of this soil was made by Ahmad and Jones, (1969). They show that following drainage of the soil the mottles harden irreversibly to nodules of noncrystalline iron oxides.

In the dry season ferric iron is probably being precipitated continuously in the argillic layer, but during the period of stauration the soils become neutral in reaction (pH 6.5 - 7.0), the more soluble ferrous iron is mobilised (Islah and Elahi, 1954) and the level of exchangeable Al^{+++} drops sharply (Cate and Sukhai, 1964). With the return of aerobic conditions the ferrous iron is oxidised and exchangeable Al^{+++} and H^{+} accumulate in the soil solution.

The significance of this soil type for plant growth centres on the presence of the argillic horizon and its generally low-lying topographic position. These features impede soil drainage and may lead to oxygen deficiency. <u>Curatella</u> americana, which can root in the surface decimetre of the soil, is the tree species which is apparently most adapted to this habitat. In the dry season the plant must be able to withstand high levels of Al⁺⁺⁺ and in the wet season, at low redox potentials, severe ferrous iron toxicity may be produced (Black, 1968; Betremieux, 1951; 1955). Both these conditions can produce chlorosis and death in sensitive plants. In some waterlogged soils sulphides can act as plant inhibitors but low sulphate levels and free Fe⁺⁺ (forming ferrous sulphides) nullify the effect of this in Rupununi soils.

Oxisols

In the original 7th Approximation classification (1960) the differentiation of the great groups Udox and Ustox in the Oxisol order was on the basis of base saturation. This was supposed to reflect differential genesis, the Ustox developing in seasonal climates where leaching was non-continuous, and the Udox under humid forest conditions. Haantjens (1967) subdivides them on acidity, the Ustox having reactions above pH 6.0 and the Udox below this figure. On this basis the Oxisols of the Southern Rupununi are placed in the Udox group although genetically they conform to the hypothetical development of the Ustox. Haantjens also notes that the Udox are generally deep soils (greater than 110 cms., 44 inches), a feature that the Oxisols of the Rupununi share.

Umbrudox

These are deep, uniformly red or reddish-brown clay loams. The surface horizon does not have a darker colour than underlying horizons but the high C:N ratio (25) distinguishes it as an umbric epipedon. Despite being developed from base-rich parent material the soils have a pH of 5.2 - 5.3 in the sub-soil. They would be classed as Krasnozems in the Australian system.

They are the most fertile soils in the Southern Rupununi but are very limited in extent, confined to outcroppings of basic granulite such as Tup-Tup-Tyal mountain 2 miles west of Wichabai. Loxton, <u>et al</u> (op. cit.) record the following profile on the north side of this hill.

Profile Description

<u>cms</u>.

- 0-25 10R3/3 Dusky red clay; hard humic layer; strong coarse granular structure; few hard Fe concretions. pH 5.2
- 25-67 10R3/3 Dusky red clay; weak angular blocky structure; few hard round small Fe concretions. Roots common. pH 5.2
- 67-134 7.5R2/4 Very dusky red clay; soft, weak coarse angular blocky structure; few roots. pH 5.3
- 134 7.5R4/4 Weak red cemented ironstone gravel; semi-indurated to indurated ironstone concretions cemented by indurated clay. pH 5.3

Because of their high clay content and the steep (10°) pediment slopes on which they are developed slumping is common. Despite the comparatively high C. E. C. of these soils the reserve of weatherable minerals in the profile is low.

Ochrudox

The Ochrudox great group is well-developed in the Rupununi and most of the upper slopes of ridges and pediments develop this soil type. In the Australian system they would be classed as concretionary red or yellow earths. They may belong to either the argillic or orthic subgroups, that is, they are either uniformly textured throughout or possess a coarsertextured surface horizon. This latter feature is not sufficiently distinct or abrupt to warrant their inclusion in the Ochrults. In some cases, particularly on ridge crests, the surficial horizon has been stripped. Evidence of this process is the very thin and discontinuous lag gravel of concretions and quartz pebbles on the soil surface, which points to the removal of fines.

An example of an argillic ochrudox found on a ridge-top 4 miles northeast of Sawariwau Village is given below:

Profile Description

cms.

Surface accumulation of quartz and gneiss pebbles, Fe and Mn nodules.

- 0-20 7.5YR6/8 Reddish-yellow clay loam, many nodules. pH 6.0
- 20-125 7.5YR6/8 Reddish-yellow clay; blocky structure; fewer nodules pH 5.8
- 125-220 2.5YR5/8 Red clay loam, nodules, pH 5.8
- 220 Gneissic rock.

The soil described by Loxton <u>et al</u> (ibid.) as the Mountain Point Series is placed in this subgroup. The Ochrudox attain their fullest development on the gneissic ridges and pediments around Shiriri Mountain, the southern flanks of the Kanukus and east of Dadanawa.

Entisols

The Entisols are those soils which do not display natural genetic horizonation. In the Rupununi these include the skeletal soils of the mountains, the young alluvial soils along rivers and creeks and the quartzose sands of the Emprensa and Jacaré Series of Loxton <u>et al</u> (ibid.) which are placed in the Psamments suborder.

The alluvial and fragmental soils are forest soils and consequently are omitted from this discussion.

Orthic Quarzopsamments

These are coarse-textured soils, sands and sandy loams that contain more than 95% resistant minerals (quartz, rutile, zircon etc.). They outcrop extensively along the eastern bank of the Takutu River south from Inaja to Baiewau creeks. They are also developed on granitic parent material east of the Rupununi River. There is a slight colour differentiation probably due to small amounts of organic matter in the A horizon which imparts a grey-brown colour to the sand, beneath this they are typically brownish-yellow.

Below two metres (80 inches) faint orange mottles may appear in the profile. The following profile is representative of the Emprensa Series. <u>Profile Description</u>

Site: Flat terrace near Katiwau Creek, 5 miles NNE of Kusad Mountain

Open woodland vegetation, <u>Curatella</u> and <u>Bowdichia</u> predominant. cms.

0 - 15	10YR6/2	Light brownish grey sandy loam; structureless, pH 5.2
15 -50	10YR6/2	Light brownish grey sand; loose, structureless, pH 5.0
50-200	10YR6/8	Brownish-yellow sand; loose, structureless, pH 5.0
200+	10YR7/8	Yellow sand; faint orange mottling, pH 5.4

These are deep, very well-drained soils with rapid infiltration rates through the loose sandy solum. Because of this characteristic they probably posses the driest physical climate of all soils of the South Rupununi.

CHAPTER SIX

DATA ANALYSIS

The problem we are dealing with is the determination of which. if any of a large set of variables is responsible for the variation in the 'standing crop' of savanna trees and shrubs. The independent variable can be expressed in two ways; in a general fashion, by dividing savanna vegetation into a discrete number of classes based on the amount of tree and shrub growth per stand (the scheme used in this study is presented at the beginning of Chapter Two) or in a more specific manner by considering a continuous distribution, such as the volume or weight of tree growth per unit area. Both methods are employed below.

For most of the variables for which data was accumulated an assumption of normality would seem to be erroneous. The Modified Cramér Statistic test for normality (Table 6.1) clearly indicates that all but two variables are not normally distributed in the sample, and whilst transformations have a tendency to introduce symmetry in some variables, in others strongly-skewed or polymodal distributions are characteristic. Furthermore, the population frequency distribution for many of these variables is not known. These factors would seem to exclude statistical testing and inferences based on the normal distribution curve. and consequently only non-parametric tests which are independent of distribution are used.

Analysis of Variance

To test whether the variables measured over each of the savanna classes; from herbaceous to woodland savanna, come from the same population, the Kruskal-Wallis One Way Analysis of Variance technique (Siegel, 1956), was employed. This method ranks data for a single variable series and then sums the ranks for each group (Rj).

The H statistic for each variable is calculated by the following equation:

H =
$$\frac{12}{N(N+1)}$$
 (Rj)² - 3 (N-1) /1 - ΣT
 $\frac{12}{N^3 - N}$

MODIFIED CRAMER STATISTIC : NORMALITY OF VARIABLE

Variable	Cramér S	Statistic
Crown Area	0.6028	**
Shoot Volume Estimate	0.8228	**
Shoot Weight Estimate	0.7310	**
Shoot Height	0.0762	
Water Table	0.0988	
Slope Angle	0.6908	**
Infiltration	1. 1997	**
pH	0.1564	*
% Carbon	0.6703	**
% Nitrogen	0.6872	**
P ₂ 0 ₅	0.2237	**
H exch.	0.5054	**
Potassium	0.6534	**
Sodium	0.3992	**
Calcium	0.2707	**
Magnesium	0.3180	**
Ex. Al Index	0.2540	**

DISTRIBUTIONS

** Significantly Different from normal at 1% level.

* Significantly Different from normal at 2.5% level.

TABLE 6.2

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KRUSKAL - WALLIS ANALYSIS OF VARIANCE

Variable	<u>H</u> Value	Significance Level
Water Table	11.61	1%
Slope Angle	4.95	NS
Infiltration	153	NS
pH	4.13	NS
% Carbon	0.93	NS
% Nitrogen	4.84	NS
P205	6.53	NS
Exch. Hydrogen	14.89	1%
Potassium	33.97	1%
Sodium	-48.13	NS
Calcium	- 5.61	NS
Magnesium	-16.89	NS
Aluminium	7.32	NS

Sample Size

	Savanna	Savanna Type					
Herbaceous	Shrub	OW	Woodland				
11	9	15	10	45			

where

N is total sample size

- nj is sample size per class
- Rj is sum of ranks per class
- $\frac{1 \sum T}{N^3 N}$ is a tie correction

The results of this test are presented in Table 6.2 and it can be seen that the null hypothesis of no significant difference in the individual variables over the four savanna classes is rejected, at a 0.01 probability level, for only three variables - the depth to the water-table, and the concentration of exchangeable potassium and hydrogen. Note that the Exchangeable Aluminium Index is only just accepted at a 0.05 probability level however.

Spearman's Rank Correlation

The degree of association between each variable was assessed using Spearman's correlation coefficient (Rs). The matrix of these coefficients is presented in Table 6.3. Variable 1, Shoot Volume Estimate, is derived by the cone method presented in Chapter Four. It is taken as the independent variable in this study, as an estimate of the tree biomass at a site.

The significant correlations in the matrix can be grouped into three clusters (Figure 17):

- a) Correlations between Exchangeable Bases and Shoot Volume Estimate
- b) Correlations between pH, Ca Mg, Exchangeable Aluminium and Exchangeable Hydrogen
- c) A tight cluster of high intercorrelations between the Exchangeable Bases

Factor Analysis

To assess further the associations between variables a principal components analysis was performed on this correlation matrix, using the California BMDO3M program. It is generally recognised that principal components analysis is the most useful factor analytical technique for generating hypotheses from a set of data (Armstrong, 1967).

VARIABLES	Shoot Vol.	Water-Table	Slope Angle	Infiltration	Hd	% C	N %	P205	Exch. H ⁺	Exch. K ⁺	Exch. Na ⁺	Exch. Ca ⁺⁺	Exch. Mg ⁺⁺	EAI
Shoot Vol.	-	. 301	045	002	033	. 192	.288	.236	.450	.476	.450	.253	. 428	. 388
Water-Table Depth	*	-	. 291	. 389	046	.034	055	. 197	.031	. 047	.224	.134	. 153	.205
Slope Angle			-	010	.258	. 422	124	. 337	.026	.214	. 273	. 354	. 494	126
Infiltration Rate		**		-	.264	043	122	.015	. 231	. 187	. 191	. 329	.292	.035
pH					-	058	- 252	064	212	. 125	. 252	. 546	. 382	380
% C			**			-	.243	.570	.263	.267	.289	.233	. 353	. 182
% N							-	. 233	. 257	.043	016	139	- 269	.203
P205			*			**		-	. 421	.237	. 345	.245	. 313	. 316
Exch. H ⁺	**							**	-	. 178	. 159	.170	.084	.541
Exch. K ⁺	**									-	. 597	.418	.652	.067
Exch. Na ⁺	**							*		**	-	. 615	. 637	. 202
Exch. Ca ⁺⁺			*	*	**					**	**	-	.675	.093
Exch. Mg ⁺⁺	**		**		**	*		*		**	**	**	-	.055
EAI	**				**			*	**					-





Figure 18 HISTOGRAM OF 'SIGNIFICANT' AND 'NON-SIGNIFICANT' FACTOR LOADINGS.

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The Kaiser criterion of only accepting eigenvalues greater than 1.0 was employed and a varimax orthogonal rotation was performed on the matrix because it is considered that underlying factors are statistically independent of each other. This technique extracted four factors which explain 68% of the variance in the correlation matrix. The eigenvalues and the percentage variance accounted for by each factor are presented in Table 6.4. A decision rule minimising the overlap on each factor, using only those variables with a loading greater than 0.70 was made. This utilised eleven of the fourteen variables in the four factor solution. The three variables not loading highly with any of the four factors were: shoot volume, pH, and % nitrogen. This threshold of 0.70 proved a very useful discriminatory level between 'significant' and 'non-significant' loadings (Figure 18). The factor loadings for each variable are presented in Table 6.5.

From this table it can clearly be seen that the extracted factors are associated with the clusters obtained in the correlation analysis and the theoretical controls outlined in Chapter One.

Factor One is highly linked with the Exchangeable Bases; Factor Two is associated with EAI and Exchangeable H^+ ; Factor Three with Water Table Depth and Infiltration Rate and Factor Four loads highly with % Carbon, Phosphate availability and Slope Angle. These correspond in turn to the Nutrient Deficiency, Toxicity, and Root Inhibition controls outlined in the Introduction. The final factor is another nutrient factor linked with organic matter.

Thus the empirical appraoch employed here would seem to fit, and therefore support the conceptual approaches of Hardy (1960) and others, who stressed the interaction of edaphic controls in the Neotropical savanna ecosystem.

The ecological significance of these results will now be discussed. Tree Growth and Edaphic Control

The investigation of the complex interactions between the plant and the nature of the soil on which it grows centres on the supply and movement of water and nutrients through the soil to the root; and the EIGENVALUE VECTOR

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CUMULATIVE % OF TOTAL VARIANCE 'EXPLAINED'

- 4. 1087 29. 5
 - 2.5316 47.4
 - 1.5359 58.4
 - 1.2765 67.5

TABLE 6.5

FACTOR LOADINGS ON ENVIRONMENTAL VARIABLES; PRINCIPAL COMPONENTS SOLUTION WITH ORTHOGONAL ROTATION

Variable	Factor 1	Factor 2	Factor 3	Factor 4	
Shoot Volume	0.5774	0.5848	-0.2523	- 0.1165	
Water Table	0.2440	0.0565	-0.8299	0.5446	
Slope Angle	-0.2984	-0.3238	-0.2086	0.7027	
Infiltration	0.3850	0.0169	0.7399	- 0.0917	
pH	0.4919	-0.5828	0.2083	0.0187	
% Carbon	0.1469	0.2399	0.0187	0.8198	
% Nitrogen	-0.1562	0.5558	0.0427	0.2114	
P205	0.2078	0.3823	-0.0481	0.7086	
Exch. H*	0.2000	0.7305	0.2042	0.1788	
Potassium	<u>0.7235</u>	0.1613	0.0229	0.1005	
Sodium	<u>0.8087</u>	0.1189	-0.0990	0.1516	
Calcium	0.7928	-0.1903	0.1326	0.2142	
Magnesium	0.8384	-0.0682	0.0095	0.2992	
Exch. Al. Index	0.0984	0.7742	-0.1270	-0.0039	

underlined loadings represent 'significant' linkages.



c) Water Table Depth (m.)



VARIATION OF SOME PHYSICAL AND BIOLOGICAL PARAMETERS WITH SAVANNA TYPE (x-axis)

1 Woodland

Fig 19

- 2 Open Woodland
- 3 Shrub
- 4 Herbaceous

Mean

Mean \pm 1 St. Deviation

nature of soil acidity, cation-exchange properties, soil texture and aeration on root and shoot growth. The response of plants to any of these stimuli varies with the relative importance of the latter in the soil, and also varies between plant species.

The application of the results obtained in agronomy or physiology to field problems in ecology often requires that a 'logical jump' be made from the laboratory to the field situation. This is particularly true of areas such as the South Rupununi which possess a large and little known flora. However, by removing the effect of species-reaction and treating tree species as being subject to concommitant variation, that is , by looking at the patterns of vegetation rather than investigating the presence or absence of a species, we gain a general view of edaphic controls by removing a major source of variation.

Tree Growth and Exchangeable Bases

The Kruskal-Wallis test indicated that the concentration of exchangeable K^+ increased from herbaceous to woodland savanna. The correlation matrix (Table 6.3) verified this result and also showed that Mg^{++} and Na^+ increased significantly in the same direction. Ca^{++} however did not show the same increase, despite the high inter-correlations between it and the other bases. Two questions are raised by these results.

Firstly, what is the reason for the increase in exchangeable bases in the soil? Secondly, what is the ecological effect of this increased availability? The reserves of non-exchangeable bases in the soil may occur in either unweathered primary minerals, (feldspars, micas or amphiboles); silicate clay minerals; or organic matter. The amount in exchangeable form in the soil at any one time, or the % saturation of a particular ion, is an index of equilibrium between the loss by leaching of that base and its release from a non-exchangeable form. From this standpoint all soils in the Rupununi show severe deficiencies in bases.

It is accepted by most pedologists that the majority of exchange sites in tropical soils are located in organic matter in the topsoil, rather than in the mineral fraction. The amount of organic matter, estimated by the unreliable relationship % carbon x 1.72, does not increase significantly along the vegetation gradient but the evidence



Figure 20 Scatter Diagrams of Association between selected variables

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Figure 20 (contd.)

presented in the next section, based on the relative levels of exchangeable H^+ and the EAI,tend to confirm that most of the exchange-sites are located in the organic component. Other possible sources are the 2:1 clay minerals illite and montmorillonite, which possess K^+ and Mg^{++} as interlayer cations. It is doubtful however whether these minerals occur in Rupununi soils since they have passed the weathering stage where such minerals might be present.

The continuum from herbaceous to woodland savanna is not a gradient from deficiency to sufficiency, but one from severe to less severe dificiency. Potassium deficiency results in several plant responses similar to those described by Loveless (1961, 1962), for phosphorusdeficient sclerophyllous vegetation. Only limited protein synthesis can occur and various nitrogenous breakdown products accumulate in the cell. These may be toxic in high concentrations (Coleman and Richards, 1956). The toxic amino acid involved (putrescine) is also a produce of P-deficiency (Black, 1968). The main difference between K^+ and P-deficiency is that the crude fibre content of the cell (sclerenchyma) does not increase as a result of K^+ deficiency.

An interesting point, although requiring experimental support, is that K^{\dagger} deficiency is known to increase the respiration rate (and therefore also the transpiration rate) of plants (Mann, 1924). This can be explained by the findings of Humble (1969) who noted that an influx of K^{\dagger} into stomatal guard cells was the mechanism responsible for stomatal movement. Plants deficient in K^{\dagger} will therefore possibly show slower stomatal reactions than would otherwise be the case. This will be particularly true of old leaves where deficiencies of this ion are most pronounced (Black, 1968).

Rawitscher (1948) and Ferri (1961a, 1961b) considered that the slow motility of stomata in cerrado plants was indicative of a sufficiency of water in the soil. It may however be a reaction to K^{\dagger} deficiency which was reported for cerrado soils by de Freitas, McClung and Lott (1960).

Magnesium deficiency may also limit protein synthesis but the gravest result of this deficiency is its limiting effect on phosphorus metabolism. If the enzyme systems which mediate in the production of ATP are limited by Mg^{++} then the response of the plant of P will be minimal.

The effect of an increased supply of Na⁺ is controlled by the K⁺ status of the soil and is also highly species-dependent (Russell, 1961). In areas such as the Rupununi with severe K⁺ deficiencies an increased Na⁺ supply may benefit some of the tree species present, as Na⁺ can take the place of K⁺ in some metabolic processes. One of the main results (in species which can utilise Na⁺ in place of K⁺) is that the succulence of the plant, and therefore its ability to withstand drought, is increased.

With an increase in the base status of the soil an increase in protein synthesis, and a more balanced metabolism, will result. It is possible that the plant is more able to control stomatal movement and to increase the water content of the cell. Because of these benefits an improvement in growth, an increase in biomass and possibly a change in physiognomy will become possible.

Tree Growth and Soil Acidity

This section will deal in turn with the relationship beween pH, exchangeable hydrogen (exchange acidity), and exchangeable aluminium (EAI); and the link between these variables and tree growth.

In the Kruskal-Wallis analysis exchangeable H^{\dagger} increased significantly along the vegetation gradient. The exchangeable H^{\dagger} ion and EAI were highly correlated with each other and with Shoot Volume and in the oprincipal-components analysis Factor Two was interpreted as the influence of these two ions in the data matrix.

In the soils of the Rupununi the exchange-sites are dominated by the hydrogen (hydronium), hydroxyaluminium and aluminium ions. The exchangeable H^+ ions are those H^+ ions which are adsorbed onto soil particles following either a decrease in pH or an increase in the concentration of metallic cations. They are derived in leached soils chiefly in an exchange reaction with carbonic acid by a metallic cation. Ionization of water and contact-exchange between root exchangeable H^+ and bases of soil particles are further sources of supply.

The cation exchange sites of a soil are divisible into those which are 'pH - dependent' and those which are 'permanent'. The pH - dependent sites preferentially adsorb H^+ ions without instability resulting and

other cations (particularly Al^{+++}) being released. Pratt and Bair (1962) have shown that almost all these pH-dependent sites are located in the organic matter component. Schwertmann (quoted in Black, 1968) found that only soils high in organic matter released exchangeable hydrogen. Although the two soils highest in organic matter in the sample (2.85% and 2.40%) also have the highest H^+ ion content (5.0 meq/100 g.) the two variables are not significantly correlated (Table 6.3). In the sample the level of exchangeable H^+ (0.5-5.0 meq/100 g.) is considerably greater than the EAI (0.0-0.1 meq/100 g.).

Yuan (1963) reported a similar situation in acid sandy soils in Florida, although the reverse is more general (Coleman <u>et al.</u>, 1959). The cause of this difference may be attributable to the location of the majority of the exchange-sites in the organic component (Rutherford and Hills, 1968).

The release of the Al⁺⁺⁺ ion is controlled by the concentrations of exchangeable H^{\dagger} , other cations, and not solely by pH (Riley and Arnold, 1969), although there is a strong inverse correlation between the two in the sample (Figure 20). Coleman et al. (1959) noted that the level of exchangeable Al^{+++} rose slowly from pH 6.0 to pH 5.0 and then rapidly below pH 5.0 in soils from North Carolina. Rupununi soils show a similar increment but the absolute values recorded are much lower. It is possible that the EAI method may be responsible for this low result. The extractant used (NH_4Cl) is not the most efficient for the determination of aluminium (McLean, 1965), but in the original paper (Reeve and Sumner, 1970), it gave results similar to those derived by theoretical solubility measurements (Garrels and Christ, 1966). It is probable that these sandy soils, with only small percentages of lowexchange sites for the hydrated aluminium ion. The interlayer aluminium polymers in these clays are not exchangeable (Jackson, 1963). The limitation of exchange sites to the organic fraction is suggested as the cause of the low concentration of exchangeable Al^{+++} ions in Rupununi soils.

Leaf 92 missing

The plant response to different levels of exchangeable H^+ is very difficult to assess. Concentrations in the pH range encountered in this study do not directly affect plant growth. It is only at much lower pH values (below pH 3.0) that 'acid-toxicity' symptoms are found. The main process by which exchangeable H^+ could affect the growth of trees is through competition for exchange-sites within the root cortex. The increase in tree growth correlated with increasing H^+ concentration would suggest that this competition is not important in the sample.

Goodland's (1969) aluminotoxic hypothesis of cerrado vegetation states that tree biomass and floristic variety in the Central Brasilian cerrado decreases with increasing aluminium saturation of the exchangesites. Aluminium saturation was defined by Coleman et al. (1959) as:

$$\frac{Al^{++}}{Ca^{++}+Mg^{++}+Al^{+++}} \times 100$$

In the Brazilian cerrado, (Goodland, op. cit.), exchangeable Al concentrations averaged 75 ppm (0.7 meg/100 g.), and the Al^{+++} saturation ranges from 35% to 58%. For Rupununi soils, which cover a similar pH range, absolute levels of EAI range from 0 - 9 ppm (0-0.1 meq/100 g.) and saturation levels are considerably less than 10%. Concentrations as low as 10 ppm are known to affect some very sensitive plants but it is doubtful whether any members of the Rupununi tree flora are affected by such low levels. Known aluminium accumulators in the tree flora include such common genera as Roupala, Palicourea and Miconia and the families Rubiaceae (Genipa americana, Randia formosa) and Melastomaceae (Tibouchina aspera). Tolerant nonaccumulator plants such as the families Leguminosae, Malpighiaceae (Byrsonima), Dilleniaceae (Curatella), Myrtaceae and Compositae include the majority of tree species in the South Rupununi. The process by which these plants can accumulate and detoxify this element is not known, but $Al^{\frac{1}{2}\frac{1}{2}}$ ions may be excluded by a cell membrane, excreted from the roots, or fixed in an insoluble form immediately upon entry.

The results obtained from the quantitative analysis indicate that there is a direct linear correlation between shoot volume and EAI. Goodland (1969) found that there was no significant correlation between $A1^{+++}$ concentration and basal area per hectare of cerrado trees, but noted the strong association between the degree of $A1^{+++}$ saturation and the vegetation gradient.

It is therefore suggested on the evidence assembled above that the predominantly tolerant tree flora of the study area does not react to the low concentrations of Al^{+++} found in South Rupununi soils and the Al^{+++} saturation levels recorded are not associated with variations in tree biomass. The aluminotoxic hypothesis cannot therefore be demonstrated for this sample of savanna vegetation. Tree Growth and Soil Water

The depth to ground-water is a fairly insensitive measure of water availability to the plant. Nevertheless the Kruskal-Wallis test indicates that there is a significant difference in water-table depth with savanna type (Table 6.2). The correlation analysis also indicated that there is a strong association between the vegetation gradient and watertable depth. This relationship is plotted in Figure 19, which shows that all the 'wooded' savanna classes have similar ranges of water-table depth. Although all three overlap to some extent with the depths recorded under herbaceous savanna, the latter is distinct.

The mean depth to the water-table under herbaceous savanna in the early dry season is 1.0 metres (40 inches) whereas in the other savanna classes it varies from 1.8 - 2.2 metres (72 - 86 inches). Also the variance of the herbaceous class is much less than the others, Open savanna woodland occurs on soils with the deepest water-tables and there is little difference between savanna woodland and shrub savanna.

It is an ecological principle that the plant response is conditioned by extreme, rather than average conditions. The rise of the watertable to the surface in the wet season is one of these extremes. A one metre rise of the water-table from the level recorded in the sample would bring it to the surface in 50% of the herbaceous sites, 20% of the shrub savanna sites, none of the open woodland sites, and 20% of the woodland sites. As this does not completely discriminate between classes there must be other factors at work.

Two of the woodland sites that were sampled (representing 20% of the class sample) had water-tables within 60 cms. (24 inches) of the surface. One site was located one mile north of Tawatawun Mtn., the other 2 1/2 miles north-west of Cutenarib. Both these were in low-lying topographic positions and both had high contents of organic matter in the soil. The most noteworthy feature of these sites was the complete predominance of <u>Curatella americana</u>, which grew in dense stands at both places.

It is suggested that the two sites form a special and localised sub-type of savanna woodland. There was good lateral drainage in both sites, one (at Tawatawun), draining into a pond, and the second straight into the Rupununi River. This probably accounts for the ability of the trees to survive. The soil profiles at these sites are saturated, and possibly inundated, regularly throughout the wet season. However, their situation in small drainage basins, and the proximity of a drainage outlet, produces rapid changes in the water-table depth so that saturation probably only exists for short periods. The ability of <u>Curatella americana</u> to root within 20 cms. (8 inches) of the surface (see Chapter Four), enables it to grow well in these sites. Growth is encouraged by the accumulation of organic matter and the lateral leaching of essential nutrients into these areas.

It is proposed therefore that a strong discriminating factor between 'wooded' and herbaceous savanna is the depth to the water-table. Shallow water-tables inhibit root-growth of trees by the mechanisms outlined in Chapters One and Four, chiefly by causing oxygen deficiency. There are some exceptions to this rule however; for where rapidly draining, seasonally high water-table soils are found the tolerant species Curatella americana can grow well.

Ground-water depth is also correlated with infiltration rate (Table 6.3) and the factor analysis indicates that these two variables, (expressed as Factor Three) 'explain' 10% of the total variance.

Phosphate Deficiency, Organic Matter and Tree Growth

Unlike the results reported from the Brasilian cerrado (Goodland, 1969), the availability of P_2O_5 in Rupununi soils is not correlated with tree growth. All sites must be regarded as severely deficient in phosphate but the availability and uptake of this mineral by the plant will be determined by the following factors, which may well differ from one type of savanna to another.

Phosphate is very immobile in the soil and cannot diffuse more than a few millimetres to a root surface (Nye, 1969), consequently when root competition is slight the uptake of this mineral will depend upon the coarseness of the root system as well as the initial concentration of this element.

As most of the phosphate is associated with organic matter in Rupununi soils (Table 6.3), (also Rutherford and Hills, 1968), a surficial root system will enable the plant to maximise the extraction of this element. Nye and Foster (1961) found that non-grass plants in Nigerian savannas obtained 60% of their P requirements from the surface 25 cms. (10 inches) of the soil.

Fixation of P on root cell walls by Al⁺⁺⁺ cations (Clarkson, 1969) and competition between root exchange-sites and Al⁺⁺⁺ in the soil may also affect P uptake. The effect of increased Mg⁺⁺ supply on P metabolism in the plant has been dealt with above. The interaction of any or all of these processes in Rupununi soils can produce very complex situations, which may be either limiting or auxiliary factors in P uptake. Further research on this question is needed before any assessment on the importance of these factors can be made.

CHAPTER SEVEN

CONCLUSIONS

The control of plant growth and vegetation pattern by edaphic factors has been demonstrated in several tropical situations. Florence (1964) illustrated this for the east coast forests of Australia; Richards (1952) noted the importance of soil type in the coastal forest of Guyana and Goodland (1969) verified that edaphic factors were determinants of cerrado vegetation type in Brazil.

On the porous and physically uniform substrates of the South Rupununi, with a low supply of essential nutrients, a correspondence between edaphic variables and vegetation does exist. However, the interpretation of the results presented in the last chapter is not unequivocal. Some of the interpretations are well supported by field evidence; some, such as the effect of an increased Mg^{++} supply on the phosphorus metabolism of the plant, are more tentative; and still others, such as the possible control of stomatal motility by varying levels of potassium, are frankly speculative.

A correspondence has been demonstrated between the depth to the water-table and tree growth. The water-table appears to be inhibitory to tree growth in areas where in the early dry season depths do not exceed one metre (40 inches). It is proposed that throughout the wet season these sites have mal-aerated surface horizons and are subject to regular inundation. Perhaps 80 - 90% of the South Rupununi savanna would be classed as herbaceous, and over half of this area it is considered that the vegetation is subject to ground-water control. It is only where this ceases to be a limiting factor that other controls such as the nutrient status of the soil become important. Other areas of herbaceous savanna may owe their origin to very severe nutrient deficiency.

Most of the cation-exchange sites in Rupununi soils are located in the organic component, and are therefore pH-dependent. Although the amount of organic matter does not increase significantly along the vegetation gradient, the concentration of exchangeable bases does. To exploit this source of nutrients, which is located in the surficial horizon of the solum, and also to maintain the root systems above wet season water-tables, the root network of savanna trees of a wide variety of species is superficial and consists of few, long, lateral roots, with only limited tap root development. It is noteworthy that other savanna areas subject to inundation or high seasonal water-tables (Llanos, Trinidad, Surinam), exhibit trees with similar characteristics.

An increased supply of metallic cations in areas not subject to groundwater control will lead to increased protein synthesis in the plant and therefore to improved growth. In the South Rupununi, increases in Mg^{++} , Na^{+} , and particularly K^{+} , are associated with increased tree growth. Ca⁺⁺ does not show a similar increase. Positive correlations have been shown to exist between the concentration of the exchangeable H^{+} and Al^{+++} ions in the soil and the 'standing crop' of trees and shrubs. It is suggested that these are associated with an increase in the cation-exchange capacity of the organic fraction, but apart from the competition between these ions and the bases for exchange-sites in soil organic matter, their importance as determinants of vegetation type is dubious. The evidence from the Rupununi is clear and does not support the 'aluminotoxic xeromorphism' hypothesis advanced by Goodland (1969) for cerrado vegetation in Brazil.

It is suggested that where a lack of correspondence between the vegetation type and the mineral and water status of the soil does exist, that this is due to disruption of the nutrient cycle in the topsoil, probably induced by a series of severe burns.

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