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The Inyanga Area

An Essay in Regional Biogeography

by

R. W. TOMLINSON

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THE INYANGA AREA AN ESSAY IN REGIONAL BIOGEOGRAPHY

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R. W. TOMLINSON

Lecturer in Geography

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R. W. TOMLINSON,

Salisbury, September, 1973.

INTRODUCTION

A. The Scope and Aims of Biogeography.

There have been so many attempts to define Geography that one hesitates before offering an opinion. It is, however, essential from the start of a research project to have both a clear conception of the discipline and of an approach to it otherwise the research lacks both direction and meaning. The prime aim of the Geographer should be to describe the character of the earth's surface; to provide a description of places which is at once precise and well structured but which also contains sufficient illumination to present the character of the area. Clearly such an ideal is far too large for one person to achieve; no one person can encompass and maintain the detail of all aspects of the earth's surface as a whole. Therefore, by force of circumstances, Geographers become specialists.

There are a great many specialisms within Geography. Not only do we distinguish between physical geographers and human geographers but we also have numerous divisions within each of these types; today we find specialisms even within individual branches. Given such diversity it is not surprising that there should be geographers anxious to concentrate on the description of the biological components of the landscape; such persons are biogeographers. Though all are agreed as to the main concern of biogeography, the approaches to and concepts of this specialism vary. Shimwell (1972) stresses that there are as many views on how to describe vegetation as there are men willing to attempt it. The same may be said of biogeography as a whole. In order to place biogeography in its position within geography and the natural sciences a brief review of the major contributions to the subject is appropriate.

Amongst the pioneers of biogeography was Marion Newbiggin whose *Plant and Animal Geography* first appeared in 1936. She offers no concise definition of biogeography but her view of the subject may be interpreted as being the study of relationships between plants and animals and their physical environment. Her primary aim is to identify "the influence of natural conditions on the distribution and outstanding features of the great terrestrial plant communities and the animals associated with them" and throughout her work she concentrates on adaptations to the physical environment, especially to climate. It is

significant that Miss Newbiggin called her book "*Plant and Animal Geography*" for the emphasis is on individual plants or groups of plants. This is in marked contrast to the present emphasis on *vegetation*.

Another widely used standard text is that by Dr. S. R. Eyre entitled *Vegetation and Soils: A World Picture* (1963). The change in emphasis is noteworthy; "Plant" has been replaced by "Vegetation" in the title. During the thirty years between these textbooks very few developments took place in biogeography and we owe much of the renewed interest in the subject to Eyre's book. However, the book maintains a fairly traditional approach: this is not harmful in itself, but no matter how much the author may have wished otherwise it has helped to continue the concept of the association between climate and major natural vegetation types. The book does not present a clear approach to biogeography, and it is indicative of its time in its concentration on the relationships between vegetation and soil. Eyre stresses that we should presume no deterministic attitude —

"The nature of the soil is not *determined* by vegetation any more than it is *determined* by climate: the only point being made is that the nature of the vegetation always has *some bearing* on the nature of the soil and *vice versa*. Vegetation development and soil development are intimately connected."

That such stress on vegetation and soils was characteristic of the early sixties is further exemplified by the discussion on biogeography organised by the British Geographical Association in 1964. In a Presidential Address, Edwards (1964), though by no means neglecting other features of the environment, stressed that "biogeography is concerned with the soil/vegetation complex as its central objective." Eyre at the same conference went to considerable lengths to point out that biogeographers should be concerned with the whole vegetation/soils complex. Such emphatic statements were a rebellion against the long period in which "climatic determinism" had held sway. Following Clements (1928) vegetation patterns had been regarded as a reflection of climatic conditions. Just as geography as a whole began to realise once again that it should be concerned with the whole variety of interacting forces that produce distinctive landscapes, so too biogeographers became aware of the numerous forces acting on vegetation. Eyre's paper (1964) was one of the first in which the term "ecological" appeared though it soon became commonplace. As so often occurs, however, geographers became enmeshed in methodology rather than in their prime task of describing the earth. Whereas Wilkinson (1963) produced a short, but highly informative paper in which human and physical

aspects of the environment were shown to be inextricably linked, subsequent papers, both on geography as a whole and biogeography in particular, showed a concentration on method. Today the basic texts on biogeography, are based on an ecological, i.e. holistic approach but their theme is often obscured in a wealth of methodological detail. Watts (1971) has produced a lengthy text which enunciates the "*Principles of Biogeography*". The breadth of illustrative material is breathtaking but a shorter treatment of principles and more *holistic* examples linking these principles would have achieved more. In Watt's opinion the aim of biogeography remains an explanatory account of the distribution of vegetations:

"biogeography which, in seeking to interpret the differential patterns of distribution amongst organisms and their changing relationships with each other and their environment both in time and place, must draw upon evidence from a wide range of sources".

The book achieves a notable aim; that of illustrating the necessity for a wide approach if landscapes, biological or otherwise, are to be described and understood.

Tivy (*Biogeography, A Study of Plants in the Ecosphere*, 1971) also stresses the distributional aspects of biogeography:

"The approach to and aim of the subject is geographical in so far as it is primarily concerned with the *distribution* (together with the causes and implications thereof!) of organisms and biological processes".

Of all the new texts on biogeography that stress distributional aspects that of Seddon (*Introduction to Biogeography*, 1971) is the most emphatic. Here there is little attempt at an ecological approach, indeed the book has a distinctly old-fashioned flavour with strong echoes of Newbiggin:

"In the final analysis, however, it is the concern with the spatial organisation of living things that distinguishes biogeography, and therefore only when information is expressed in relation to territorial occurrence does it become demonstrably geographical".

Such an approach is too narrow. It is much better to describe the character of an area in the field; to begin with the landscape in view and to end with the landscape in mind's eye; to begin with description and end with explanatory description.

Eyre (1971) has said "because of [terminological and methodological] problems purely descriptive writings about vegetation can never again be entirely satisfying". One suspects this is said with regret, and one wonders if it is the case. I prefer to think not; much depends on

the quality of description whether this be numerical or literary. Shmwell's (1972) admirable survey of methods of vegetation description shows that this is no easy task but can be both intellectually satisfying and can provide clear, detailed information about the character of an area. His book stresses floristic description of areas but structural and physiognomic descriptions are equally valid, probably more so for the geographer. Dansereau's text (1957) whilst open to many of the criticisms discussed above, nevertheless states the value of description. Indeed Dansereau has always been at the forefront of attempts to describe vegetation structurally.

B. The Study Area.

The consensus of contemporary opinion, however, would regard biogeography as being concerned with the distribution of biological organisms and this study should have an ecological bias. I prefer to give distribution second place and regard my primary objective as the explanatory *description* of the vegetative part of the landscape. This does not mean that a map of distributions is not required from the outset. It is a valuable part of the description but such a map can only come from careful field and laboratory descriptions. Consequently, the first aim of this study of the Inyanga area is to provide an essay in description and only secondly to provide an explanation of the distributions of the various vegetation units.

Some comment should be made on the choice of study area. Basically this concerns the variety of vegetation types in the area; within Rhodesia many different vegetation types are found but each extends over a very wide area. Only in the mountains of the eastern border region are several different types found within a restricted area. In addition, if one wishes to study the history of vegetational development one requires suitable sites and such sites are only found in a few areas, notably in the Inyanga Mountains. These mountains occupy an extensive tract to the north of Umtali and the study area lies in the central part of these mountains between latitudes 18°00'S and 18°36'S. A considerable proportion of this study area lies within the Inyanga National Park which was originally a private holding of Cecil Rhodes. Today the Park, which covers an area of 25 000 ha, is administered by the Rhodesian Department of National Parks and Wildlife Management and is a popular tourist centre with both Rhodesians and with visitors from outside the country.

THE VEGETATION OF THE INYANGA AREA

A. Techniques of Mapping and Description.

I. *The Use of Air Photographs.* The primary mapping of the vegetation of the Inyanga Area was done from analysis of air photographs viewed stereoscopically. Subsequent field descriptions of the structure and physiognomy were made and finally the vegetation units were described floristically.

The use of air photographs in vegetation studies dates from about 1920 but since then considerable developments have been made and modern techniques are refined and accurate. The vertical air photographs of the Inyanga Area were taken from a height of about 360 m in 1969 and have an average scale of 1:25 000. As a result of the extremely varied relief of the area marked distortions of scale occur so that great care had to be taken to obtain the necessary scale adjustments. There are several characteristics of the photographs which permit the identification of areas of like vegetation and allow the classification and mapping of units of vegetation. The principal characteristics of such value are described below:

Tone is the various shades of grey on the black and white photographs. These are a result of the different degrees of light reflection by the several vegetations, and indeed by different species. For example, in some woodlands *Cussonia* spp. occur and their characteristic light colour is easily distinguishable on photographs of 1:10 000 or less. As a general rule the taller and thicker the undergrowth in "grassland" areas, the darker the tone. Leaf size and texture also affect tone; large, smooth, shiny leaves often give greater reflection, and a waxy leaf surface may increase the reflection of light by as much as 15 per cent.

Texture is the degree of roughness or smoothness evident on the vegetation stand under examination. It is the product of several factors including shape of tree crowns, leaf texture and branching habit. At a scale of 1:25 000 textures are mainly a result of variations in tree height, of the occurrence of low shrubs in grassland, and other similar variables. Pure grasslands and forest plantations have a relatively smooth texture.

- Pattern** is a result of environmental factors such as slope and biotic activity. It can be valuable since it is often possible to distinguish patterns produced by clearance and subsequent growth.
- Shadow** can be an aid in vegetation mapping since it may help in the estimation of tree heights but it is also a disadvantage since shadow produced by spurs and ridges darken and obscure other areas of vegetation.
- Shape** relates to the outline of the object recorded on the photograph. This can change with position; a tree near the edge of one photograph may appear to have an entirely different shape in the centre of the adjoining, overlapping photograph. Tree crowns vary in shape considerably. The crowns of rain forest or tropical forest trees are often large, round and regular whereas those of savannah may be flat-topped and are often irregular. Conifers have small, conical crowns though in old age they may become almost round.
- Crown Closure** may be defined as the proportion of a stand which is covered by the crowns of trees. Its exact measurement is difficult but may be attempted in three ways. A crown density scale may be used in which samples of known density are compared with the area under study. The matching is difficult and the results inaccurate. Another method is to use a transparent dot-grid device. In this technique the number of dots falling on trees is expressed as a proportion of the total number of dots. For example if 20 out of 25 dots fall on trees then there is a crown closure of 80 per cent. Care should be taken to avoid use of the edges of the photograph where scale distortions are considerable. The method adopted in this study was that devised by Sisam (1947) in which the photograph is divided into very narrow sections or very small squares. Squares of 1 mm were used and the number of squares wholly covered by tree crowns was then expressed as a percentage of all squares over a stand. Absolute percentages were not used but the relative difference between various stands was of interest.





















Using these characteristics, units of vegetation were defined and delimited.

A *vegetation unit* is any demonstrably different area of vegetation and can therefore be a type, sub-type or variant. It is a general expression for any area of vegetation under discussion. The first division

of the vegetation is into broad *types* of which there are five: Grassland, Forest, Woodland, Bush/Shrubland and Plantation. These are each divided into *sub-types* on the basis of finer divisions of tone, texture, etc. than were used to distinguish the broad types. Within any one sub-type variations are bound to occur; for example, though the overall photographic impression is similar within an area, trees may be slightly smaller in one part of the sub-type: these units of variation are therefore

TABLE I.

Six categories of criteria to be applied to a structural description of vegetation. (after Dansereau, 1951)

1 LIFE FORM		4 FUNCTION	
T	 Trees	d	 deciduous
F	 Shrubs	s	 semideciduous
H	 Herbs	e	 evergreen
M	 Bryoids	j	 evergreen-succulent or evergreen leafless
E	 Epiphytes	5 LEAF SHAPE AND SIZE	
L	 Lianas	n	 needle or spine
2 SIZE		g	 graminoid
t	tall (T: min. 25m.) (F: 2-8m.) (H: min. 2m.)	a	 medium or small
m	medium (T: 10-25m.) (F, H: 0.5-2m.) (M: min. 10cm)	h	 broad
l	low (T: 8-10m.) (F, H: max. 50cm) (M: max. 10cm)	v	 compound
3 COVERAGE		q	 thalloid
b	barren or very sparse	6 LEAF TEXTURE	
i	discontinuous	f	 filmy
p	in tufts or groups	z	 membranous
c	continuous	x	 sclerophyll
		k	 succulent; or fungoid

Rwt

known as *variants*. Such terminology has been evolved so as to avoid any genetic implications. Consideration of the ecological status of a vegetation unit follows after it has been classified on the grounds of structure and physiognomy.

II. *Field Investigations*. From the analysis of the air photographs a provisional vegetation map was drawn after which it was essential to check the units in the field. This involved examination of all accessible boundaries and their modification where necessary. Only a few such changes had to be made. Following this a structural and physiognomic description of each of the major units of vegetation was made. It was not easy to decide on a method of approach. Over a long period of time several authors have suggested ways in which structure and physiognomy of vegetation may be described but generally their aim has been to provide a classification of vegetation. The latest attempt to meet with international approval is that of Fosberg (1967) who has divided vegetation into three groups: Closed vegetation, Open vegetation and Sparse vegetation. These are then divided into thirty-one categories. This classification has been adapted for the Rhodesian situation by Boulton and Woodall (1972) and this amended scheme was tried in the Inyanga Area. It was found, however, that the descriptions for each category of vegetation were not sufficiently full and that little more was gained than had already been recognised from the air photographs. Rather than use descriptions from a classification I therefore looked for a flexible system of description *per se*. The method outlined by Dansereau (1951) was the one eventually chosen. Of his method Dansereau says that he would "emphasise the fact that no causal factors need be considered, such as particular edaphic or climatic conditions . . . My principal objective is to devise a method of *recording* and *plotting* vegetation". Vegetation description may be based on structure, function, composition and dynamics, each of which he defines as follows:

- | | |
|-----------|--|
| Structure | "is the organization in space of the individuals composing a vegetation type or association. |
| Function | "essentially centres about morphology, behaviour and duration of organs, or periodicity". The most emphasis is usually placed on the vegetative parts of the plant so that the function may be described as, for example, ever-green or deciduous. |

Composition "is best shown by a complete list of all species present" but he goes on to state that this may not always be advantageous since in long lists the most significant species will be hidden. This may be overcome by noting the abundance of individual species or by only listing the dominant, abundant or characteristic species in each layer. Dansereau notes that this latter alternative has been used with great merit by the French in their vegetation maps.

Dynamics "refers to the seral position of an association". This refers to an association's status in terms of the climax community, i.e., is it sub-climax, post-climax, pioneer, etc. Whereas the other criteria are merely terms of description from what is visible to the observer, this criterion requires *interpretation* of the vegetation. As such it does not seem suitable if one is attempting to avoid "causal factors".

Of the above criteria only structure and function require little specialised knowledge; composition supposes a knowledge of the flora of an area. In order that description and mapping can be done in unfamiliar areas and by non-botanists Dansereau produced a system of description based on structure which includes function as one of its six characteristics (see Table I for details). In addition to these characteristics suggested by Dansereau six more were added — branching habit, girth at breast height, shape of crown, size of crown, spacing of individuals and growth form. The actual measures taken are included on the field sheets, an example of which is given as Appendix 1.

Although such structural descriptions are of great value and, indeed, help to fulfil the geographer's prime aim of describing the landscape, they may not aid his understanding of landscape evolution. In order to arrive at an explanatory description of the vegetation it is necessary to have data on the floristic composition. To this end, each of the major vegetation units were not only examined structurally but also floristically. In general this was done by transect studies, placing a 1 m quadrat at a pre-selected interval. The percentage cover of each species occurring in a quadrat was noted. Such a procedure was not, of course, possible in woodland or forest areas. In these as many species were collected as possible within the selected area and estimates of their percentage cover were made. Woodland and forest therefore were examined more subjectively than grasslands. In the case of grasslands, which cover such a wide area, it was necessary to ensure that a representative sample was obtained. For this purpose the grassland areas were divided

into numbered squares and several were selected randomly. All the data for each vegetation unit were then examined and the most important species appear in the floristic descriptions below.

B. The Vegetation Pattern.

I. *Grassland*. The most easily identified vegetation units on the air photographs are the grasslands. These produce a light tone which varies from white to light grey. The texture is even and smooth. Two sub-types have been recognised: those in which no trees occur (A) and those in which trees are found (B).

Grasslands-without-trees (A) are found in several situations and as a result there are a number of variants. The greatest extent of sub-type A is in the western and northern parts of the study area (vegetation unit 1 in Fig. 1): these areas comprise the gently dissected plateau area lying between 1 800 and 2 000 m. Though the tone is generally light this is disturbed by numerous, very small patches of light grey tone. Such small areas represent local concentrations of *Helichrysum* and *Pteridium* species. Small areas of this grassland also occur in the eastern section of the map where they are found on the flat, or gently rounded spurs and summits.

The summit grasslands (2)¹ occur on the Inyangani plateau; the numerous rocky outcrops being outlined by dark-toned, small to medium bushes. From field investigations these are known to belong to the *Ericaceae*. Also within the summit grasslands are areas of slightly darker tone and coarser texture. Such areas reflect the increase in tussocky sedges which occur in hollows.

Grasslands-with-trees (I.B.) may also be divided into three variants, distinguished by the distribution of trees. In none of the variants, however, are trees of major importance. The first variant (3) has scattered, individual, low trees or bushes and has a park-like appearance. The second variant (4) is again of scattered trees but the spacing is slightly closer than in vegetation unit 3. Finally there is a grassland in which trees occur in widely spaced clumps (5).

Though a considerable part of the grasslands was examined in the field, detailed studies had to be confined in number and these were selected randomly as indicated above. Two examples of grassland-without-trees were examined. The first occurred at a height of 2 150 m on steep, though smooth slopes of dolerite. Here the grassland was of tussocky grasses. Though the tussocks were closely spaced they were of

¹ Figures in brackets refer to the vegetation units of Figure 1 and of Table 2.

TABLE 2
Classification of the Vegetation of Inyanga (units of Fig. 1 in brackets)

<i>Types</i>	<i>Sub-Types</i>	<i>Variants</i>
I Grasslands	A. without trees	(i) of the plateau (1) (ii) of the summit (2)
	B. With trees	(i) with scattered individual trees (3) (ii) slightly denser scatter of trees (4) (iii) scattered clumps of trees (5)
II Forests	A. Optimum forest of the east (6)	
	B. With a more open canopy (7)	(i) denser net of all tall trees and low- tree forest (8)
	C. Forest regrowth	(i) Mosaic of optimum forest and low-trees forest (9) (ii) Larger proportion of the area under low-tree forest (10) (iii) Individual tall trees scattered in dense low-forest (11)
	D. Dense forest of headwater valleys in the west (12)	
	E. Dense forest of bush and low tress at higher altitude than optimum forest (13)	
III Woodlands	A. Low, clumped woodland of flat-topped trees (14)	
IV Brush/Shrub Land	A. Grass and shrubs equally abundant but shrubs dominant (15)	
	B. Even texture and tone of high bush/shrub density (16)	
V Plantations	A. Mature (17)	
	B. Young (18)	

quite a large size, between 15 and 30 cm diameter at the crown (Fig. 2a). The height of the grass was about 50 cm in its flowering condition. Herbs are scattered within the grass, generally between 25 and 50 cms in height. Often, however, the herbs are smaller, having either a rosette or a creeping form. Within the grassland almost pure stands of fern occur. These are approximately 1,0 m in height and the cover is high at that level. The ground layer is very poor, however, so that much bare ground occurs.

The second area, at a similar height and again on soils derived from the underlying dolerite, has shorter grasses with the tussocks also being considerably smaller; the average diameter of the crown is only 8 to 10 cm. Unlike the previous area very little litter occurs so that the total cover is not so high. Intermixed with grasses and herbs are small shrubs, some with small, needle leaves whereas others have small to medium grey leaves with a thick covering of hairs. Both these shrubs have a height between 25 and 50 cms and the crown diameter, where this exists, is of the same order. Very often, however, these shrubs are so spindly that there is no crown.

In the much larger area of grassland-with-trees five sites were examined. The first of these was on soil derived from granite. On the upper part of the slope the grasses were short and the tussock diameter small, between 8 and 10 cm. The cover was not high and very little litter lay on the surface. Other herbs did occur, often being large leaved and rosette in form. Such plants had a thick indumentum and bore their flowers at a height of about 50 cms. Others, however, had small, lanceolate leaves and an erect growth form. At the base of the slope the tussocks became very large, between 50 and 100 cm in diameter, and the "grasses" up to a metre in height. The cover value was very high, indeed 100 per cent over most of the valley floor; grasses and sedges formed over 90 per cent of the cover and the remainder was composed of herbs about 50 cm in height, of erect form and with alternate, lanceolate leaves approximately 650 sq mm in size. Where the valley floor and the slopes meet is a line, some 2,0 to 3,0 m broad, of bushes between 1,0 and 1,5 m in height. The cover value is high and the ground surface beneath is bare of other vegetation. The bushes have small to medium-sized leaves and are a silver-grey colour. The crown diameter of an individual bush is between 1,0 and 1,5 m. Also at this situation is a discontinuous line of ferns, again about 1,0 m in height and almost devoid of other plants.

The second area that was examined again occurred on a hillside

and on soils derived from granite. This grassland, in which the tussocks were small, about 10 cm across, had occasional scattered shrubs about 1,0 m in height and with a crown diameter of 50 cm. These shrubs had broad leaves but others with evergreen, needle leaves did occur. Other herbs were found but the overall cover was not high, being in the order of 70 per cent. The ground surface was not bare since a high litter cover was maintained.

A further site examined was in the Matenderere Valley in the south of the study area. The soils here were also developed on granite, although close-by dolerite formed the basis of the hillsides. The slope, although fairly steep was smooth. In the past this grassland had suffered from burning, probably a year or so earlier, so that there was very little litter around. The tussocks of grass were large, up to 50 cm across and the average height was 1,0 m.

A sequence through a grassland leading to a fairly damp area provided a considerable variation of habitats and a number of examples of the different kinds of small areas of vegetation to be found within one sub-type or variant. The area had not been burned as was evidenced by a very high litter content. At the top of the slope the tussocks were small, about 15 cm across and the grass was approximately 50 cm in height. As sampling moved downslope the tussocks became larger, to between 25 and 30 cm, and the grasses became taller, to 1,0 m. In the wetter areas the tussocks stood a considerable distance above the ground level; in the order of 15 to 20 cm above. In the dampest parts sedges composed the tussocks and these were over 60 cm across. Between the tussocks bryophytes occurred so that the overall cover value was high. On the drier, upper parts of the slope shrubs occurred, 50 cms in height and with a crown diameter of 25-50 cm. These shrubs had medium to small, silver-grey leaves which had a covering of fine hairs. Such shrubs disappeared as the wetter parts of the slope were reached.

The final area of grassland-with-trees that was studied proved to have been a recently burned area so that the vegetation was very young. Tussocks of grass were not well established whereas other flowering herbs were frequent. There remained, however, a considerable area of open ground. The average diameter of the tussocks was only 8 to 10 cm and the grasses only 25 cm in height. The other herbs varied in appearance; some having medium to large leaves and covering up to 10 per cent of the quadrat with one plant whereas others had a small, rosette form.

In all of these areas the scattered trees or bushes fell into either two kinds of indigenous plants or two alien species. The alien species

were escapes from plantations and were coniferous and wattle. The indigenous bushes were a broad-leaved, deciduous and a needle-leaved evergreen. In both cases of indigenous bushes heights varied from 2,0 to 4,0 m and the crown diameters were of roughly the same order. Nowhere do trees of either group occur in any appreciable number¹ though the needle-leaved bushes may occur in widely-scattered groups around rock outcrops.

The two areas of summit grasslands had different structures both from each other and from the remaining areas of grassland. In the first area, which was a shallow depression running parallel with the eastern face of Inyangani at a height of 2 460 m, the cover was fairly high (c. 70 per cent) and large tussocks 15 to 40 cms across predominated (Fig. 5b). These grasses were tall (1,0 m) and in some areas provided a close cover but in others were separated by 20 to 30 cm. In these areas a small, 10 cm high, herb was found. This was broad-leaved and semi-rosette in form. The second area was much drier and had a low percentage cover (c. 45 per cent). Grasses were sparse and none of the plants was very tall, averaging about 10 to 15 cm. The grasses did not form tussocks, but very small tufts and many plants occurred as single spikes.

In Table 1 Appendix 2 the species occurring in the areas studied are listed with an average percentage cover. Very few differences between the two sub-divisions of grassland are found, and none of significance. Throughout the grasslands *Rhyncheletrum setifolium* is the most commonly occurring grass. *Themeda triandra* is also found throughout but nowhere does it have a high percentage cover with the exception of area 2 of the grassland-with-trees. *Digitaria maitlandii* also occurs throughout but is more plentiful in the two areas of grassland-without-trees. This is the result of the greater altitude of these two areas with the consequent differences in weather conditions they experience. Other local differences occur; for example, area 1 has a high cover of *Ficinia filiformis* and the most abundant grasses in area 3 are *Rendlia altera* and *Tristachya hispida*.

The species list from the summit grasslands (Table 2, Appendix 2) not only shows that they are different from other grasslands but also that the areas of damp grassland within them vary considerably from the remainder. Area 1 of the summit grasslands has *Festuca caprina* as the dominant grass with *Cephalaria pungens* covering quite a large pro-

¹ Since the fieldwork was done the Department of National Parks and Wildlife has removed the majority of the alien tree species scattered through this grassland — to the detriment of the area's attractions.

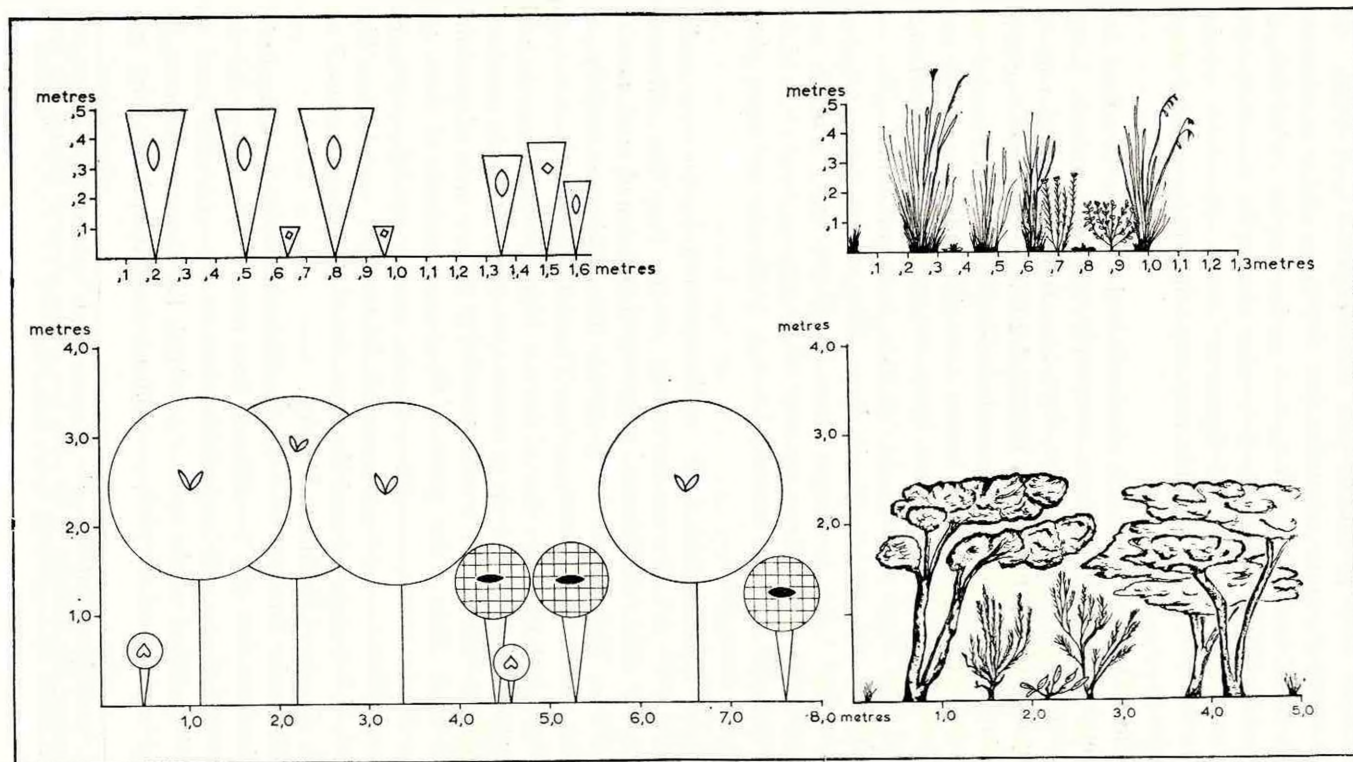


Fig. II a. Grassland without trees. b. Woodland.

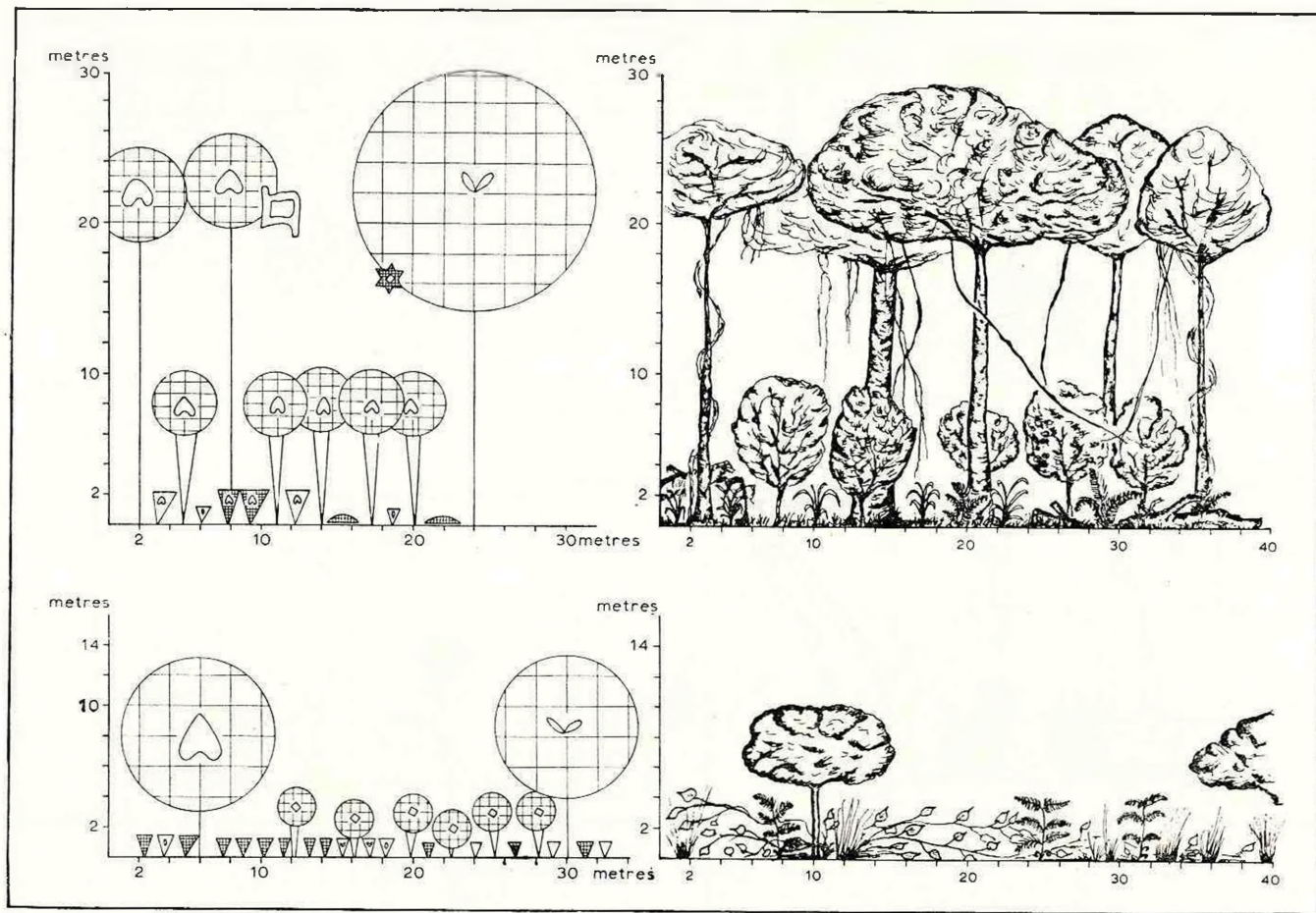
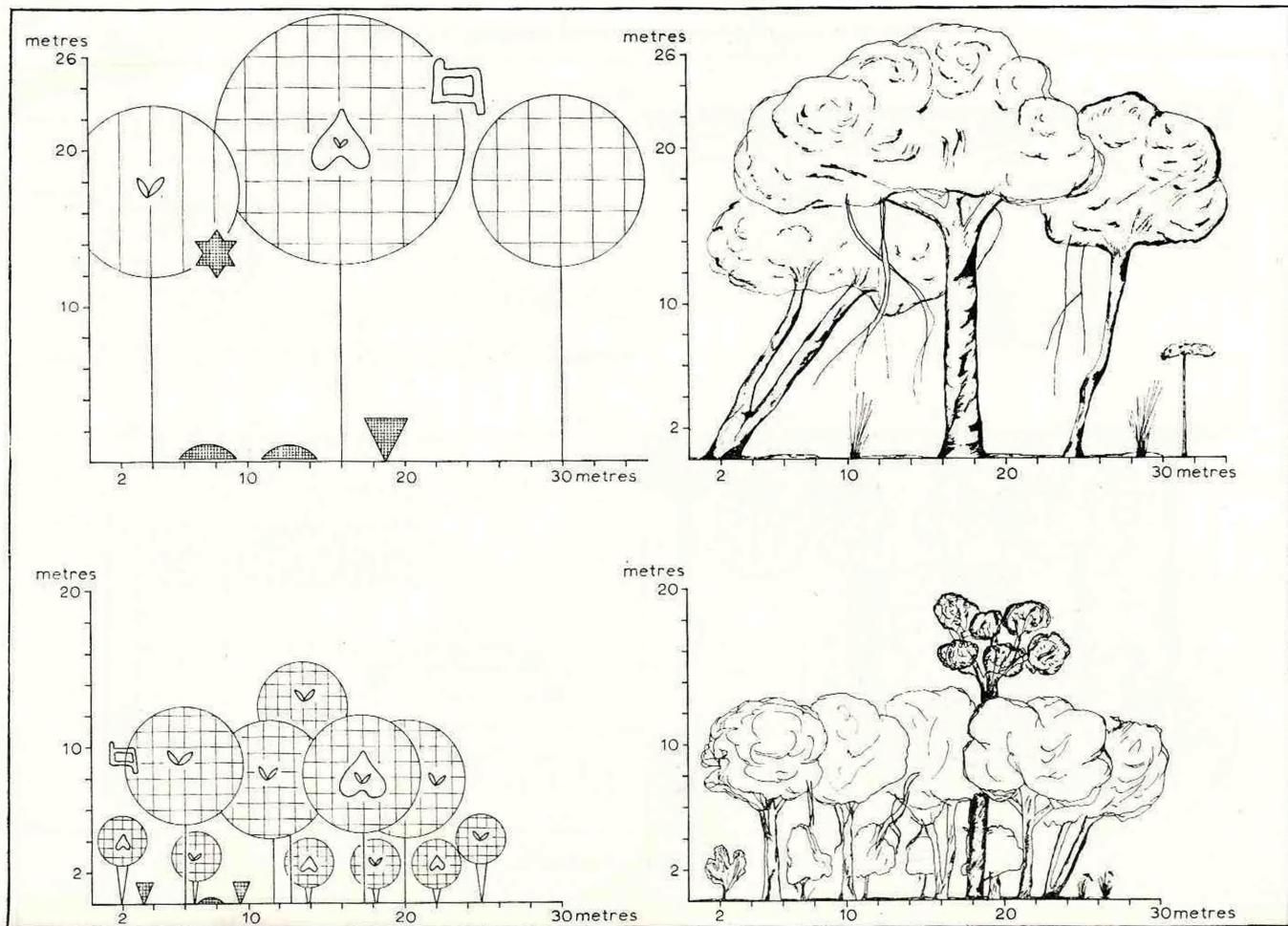


Fig. III a. Optimum forest. b. Secondary Forest Veg. Unit.



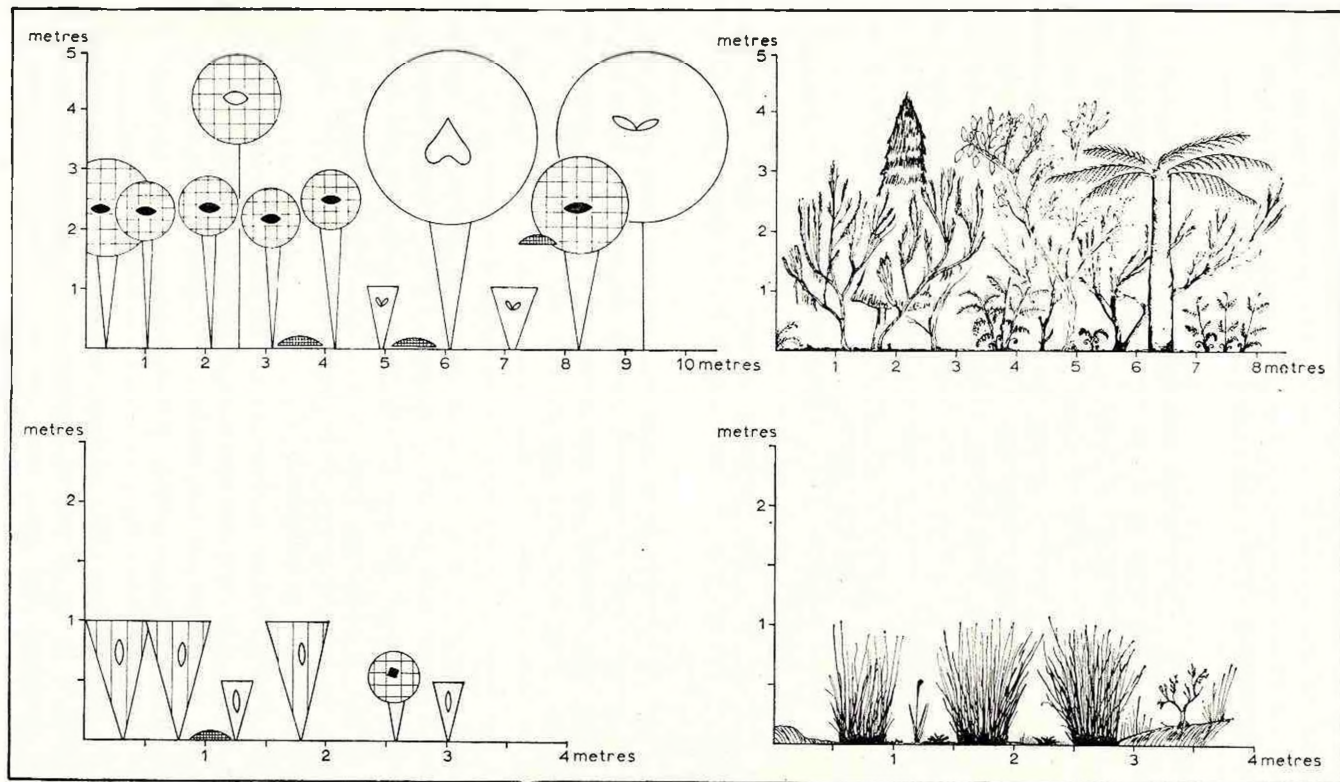


Fig. V a. *Ericaceous bush of N. Valleys.* b. *Summit Grassland.*

portion of the space between tussocks. In the second area of summit grassland no one species is dominant. The grasses occurring almost equally are *Elionurus argenteus*, *Festuca caprina*, *Panicum ecklonii* and *Themeda triandra*, whilst a wide variety of herbs is found.

II. *Forests*. Photo-analysis revealed five sub-types of forest, the majority of which occur on the eastern side of the Inyanga mountains. The optimum development of forest is IIA — vegetation unit 6. This has a dark-grey tone in general though on closer inspection a variety of tones may be distinguished among the individual trees. Such variety indicates a wide species composition. The emergents are characteristically lighter in tone. The rough texture, which is best described as cauliflower-like, is evidence of a variety of tree heights. The canopy is a closed one with the individual crowns of trees overlapping one another. With the use of high-power binoculars on the stereoscope it is possible to note the rounded shape of the tree crowns.

The second sub-type (IIB), vegetation unit 7, has a more open canopy and although some tall trees occur the main canopy layer is lower than in IIA. The vegetation remains quite dense, however. A variation of this sub-type (8) has a slightly higher density and tall trees occur in clumps.

Within this eastern forest area are vegetation units which appear to be in various stages of regrowth towards the optimum forest but the units have been classified on appearance and not on any genetic considerations. They have been grouped into one sub-type (IIC) within which are three variants. The first consists of those areas in which the forest has fewer tall trees than the optimum development (9). The dominant vegetation is a very dense growth of bushes and low trees forming a mosaic with patches of optimum forest. More widespread is the variant in which the low growth covers a wide area and in which only clumps of optimum forest occur (10). Finally there are areas in which the low-tree growth-form predominates and the tall trees are scattered throughout as individuals (11).

The fourth sub-type of forest (IID) occurs mainly in steep head-water valleys. The trees are not quite so tall as in the optimum forest areas and the crowns are also smaller. The trees are, however, closely spaced and the canopy is closed. Although no emergents are visible the texture is uneven, indicating a variety of tree heights (12).

The final sub-type (IIE) of dense, relatively low growing vegetation is believed to be an altitudinal response of the optimum forest. It is mainly shrubland and small trees intermixed though the shrubs are

taller than in the shrubland described below. The crowns are also larger (13).

Not all of these sub-types and variants could be examined in the field since there were great problems of access in this very rugged terrain. An area of the optimum forest (IIA) was examined (Fig. 3a). This lay at a height of approximately 900 m in the valley of the Nyamungura River, and about 60 m above the level of the river. The three-fold structure of the forest was clearly seen. In the tree layer the canopy was at a height of more than 25 m and occasional emergents occurred. The individual crowns were large, 7-15 m, and the girth at breast height 1,5 m. Branching took place about two-thirds of the way up the stem, which was erect and without buttresses. These trees were spaced between 6 and 15 m apart. The shrub layer, which was between 8 and 10 m, had a high cover value of approximately 60 per cent and was composed of broad-leaved, evergreen shrubs. Branching began at about half the total height and the stems were about 30 cm in diameter. The crowns were about 4 m in width. The herb layer was extremely dense, and gave a cover of almost 100 per cent. It consisted of a mixture of tall, broad but lanceolate leaved plants with a low-growing grass and some ferns. The height range of the herb layer was therefore between 25 cm and 2,0 m. This example of the forest had a great number of epiphytes; almost everything was covered in moss and lichens. Lianas were also quite plentiful. The high cover value of the lower strata is explained by the presence of large gaps in the canopy caused by the fall of trees; several such trees lay covered in undergrowth.

A second area examined was one in which the trees had been removed and the vegetation was secondary. It corresponds most closely to the low growth form of vegetation unit 11 (IIC(iii)) (Fig. 3b). The trees which occurred were scattered and relatively small, of only about 10 m in height. The crowns were rounded and approximately 10 m in diameter. The leaves were medium to broad and the trees evergreen. The cover value of this layer was low, only 10 per cent. The shrub layer was fairly extensive but it was the herb layer which dominated. Ferns were quite plentiful throughout but it was a broad-leaved creeper which was most abundant. The litter layer was very thick, about 12 cm, and was further evidence of a lack of human interference for some considerable time.

A further area of disturbed vegetation (IIC) was examined further to the north than the last example and at a height of 1 760 m in a tributary of the Gairezi River. The trees were very closely spaced, no

more than 1 to 2 m apart, and the stems were quite thin, 15-30 cm in diameter. The trees were for the most part even in age and the cover about 40 per cent. The height of the canopy was about 8 to 10 m. Occasional larger, emergent trees were found which reached heights of about 20 m and had a girth at breast height of 75 to 100 cm. The shrub layer had a considerable number of saplings of the larger trees but needle-leaved evergreen shrubs were fairly common. The saplings, with their large, broad leaves, were no more than 1,0 to 1,5 m in height but the needle-leaved shrubs often reached 10 m. The herb layer was not thick but nevertheless a variety did exist; ferns were quite common together with tussocks of grasses and a creeping plant which had fine, scale-like leaves arranged close to the stems. This area corresponds with vegetation unit 9. An area which is representative of the clumps of larger trees in vegetation unit 10 was also examined in the field. This was also located in a tributary valley of the Gairezi river and at a similar height to the last sample area. The trees in this area were much taller, about 25 m in height and the cover was also higher, approximately 60 per cent. The crown diameter was 9 m on average and the girth at breast height 1,0 m. The ground layer is sparse and few bushes are found save for a number of saplings of the main forest trees. Lianas are more abundant in this area and mosses and lichens abound. A number of emergents occur which have a girth of about 2,0 m (Fig. 4a).

The areas of forest which occur at the heads of steep-sided, tributary valleys in the western grassland area were also examined (12). Two such areas were studied in which the canopy was between 12 and 22 m in height and the cover about 60 per cent. Two species were co-dominant, one with compound leaves in which the leaflets were small; the other had broad, compound leaves. Girth at breast height also varied in the two species; the broad-leafed had a girth of 90 cm to 1,30 m and the small-leafed 60 to 80 cm. Crown size in the two species was between 6 and 9 m and the spacing was 1,5 to 4,7 m. The trunks were without buttresses. A shrub layer, between 2,5 and 4,7 m in height was also evident though it was discontinuous and only gave a cover value of 10 per cent. The crown diameter of such shrubs was very small, 50 cm to 1,0 m. No herb layer was detected but a few scattered plants did occur; these were mainly wood-rushes. Mosses and lichens were common throughout. (Fig. 4b).

The species list is by no means complete (Table 3, Appendix 2), but an attempt was made to sample all the more abundant species and the dominant species in each location. It will be observed that very few

species are found in several locations. Only *Aphloia theiformis*, *Schefflera barteri* and *Dissotis princeps* occur in more than one of the areas. It is significant that with the exception of *Dissotis* none of the species found in the optimum forest areas are found in the other two areas. This is again a probable reflection of altitude and climatic conditions. The other eastern area and the forests in the valleys of the west do have some common species, for example, *Aphloia* and *Schefflera*.

III. *Woodland*. True Woodland is rare in the area of the Inyanga mountains studied. Only one sub-type has been recognised (14) which occurs in the northwest and produces a light tone in general on the air photographs, though with a darker, speckled effect. The texture is uneven. Trees are low, even dwarf and grow in a markedly clumped fashion. It is these clumps which provide the speckled effect; the very light-toned areas between clumps are ones of bare soil. Soil erosion is rife and gullies are strongly developed.

Three areas of woodland were studied in the field, within each of which several sampling points were taken as was the usual practice adopted for other vegetation units. Quadrats could not of course be used for the tree growth but they were used to record the undergrowth. The structure of the woodlands was simple (Fig. 2b), there being a dwarf-tree layer; a shrub layer which was very discontinuous and often extended into the tree layer; and finally a herb layer which was again discontinuous. Though to the northwest of the woodland area the trees became larger, mainly a result of sheltered valley locations, the majority of trees in the woodland were very small. The average tree height was between 2,0 and 4,0 m. The trees were flat-topped, but irregular in outline and they often leaned over away from the prevailing wind direction. The tree crowns were between 2,0 and 3,0 m in diameter. In all the stands under study the trees were arranged in clumps, these being separated from each other by areas of almost bare ground approximately 9 m across. Within each clump the tree spacing was irregular, but between 50 cm and 4,5 m.

Two main shrub types occurred. One, a needle-leaved evergreen which was between 50 cm and 2,0 m tall, was discontinuous in its occurrence. It had a crown diameter of 50 cm to 1,5 m but the crowns were very irregular in outline. In some stands this shrub reached greater heights and became intermixed with the tree layer. The other shrub was broad-leaved and deciduous with a very irregular crown. The most distinguishing feature of this shrub is its flowers which are very broad in diameter, about 7,5 cm, and though there is an outer ring of "petals" the main part of the flower is a mass of furry spikes.

The examples of this shrub were very poor indeed; they were generally very young and tended to be quite gnarled and twisted. Their average height was approximately 50 cm.

The herb layer, 10 to 50 cm in height, was very sparse. It consisted of graminoid-leaved herbs, and ferns together with small to medium leaved plants in which the silver-grey leaves had a thick covering of fine hairs. These plants were rosette in form. Similar plants also occurred as very small shrubs. All have "everlasting" yellow flowers.

The species list for the areas of woodland examined reveal a very poor flora which is in keeping with the very barren nature of the ground surface beneath and between the trees. (Table 4, Appendix 2). With the exception of alien conifers, which have been excluded from the discussion though they appear in the profile diagram, the trees were *Brachystegia* (the species is not given since work on the hybrid nature of these trees is still in progress). The shrub layer was a mixture of ericaceous species and *Protea inyangani* which was very small and widely scattered, together with *Helichrysum odoratissimum*. The herb layer was not greatly dissimilar from the surrounding grasslands except that it was extremely poor and sparse.

IV. *Bush/Shrubland*. Two sub-types have been established based on the relative density of shrubs. In vegetation unit 15 the tone is relatively light but has a freckled effect as a result of bushes which have a darker tone, growing within grassland. Shrubs and grassland are equally abundant but this unit was designated as shrubland since shrubs are the dominant life-form. In vegetation unit 16 the tone is predominantly grey as a result of the higher density of bushes and shrubs. The texture is relatively even and the bushes are closely spaced so that the effect is not unlike a fine stippled shading.

The structure of each is similar, the difference lying in the spacing of the bushes. The majority are needle-leaved evergreens about 2,0 to 3,0 m in height, but medium to broad-leaved shrubs also occur. These again are about 2,0 to 3,0 m in height but the crowns are more regular and about 2,0 m across. The total cover at about 2,0 m is very high so that herbs are rare but where the cover thins slightly there are ferns at about 0,5 to 1,0 m. Along water courses in these areas tree-ferns stand out above the general level of the canopy and are between 3,0 and 4,0 m in height (Fig. 5b). Occasional conifer trees also stand above the general level. Lichens are abundant on all bushes.

The most abundant species are *Walafrida swynnertonii* and *Philippia* spp. but *Hypericum aethiopicum* is also plentiful. *H. revolutum* and

Crysanthemoides manicifera also occur. Species of *Protea* are occasional and *Pteridium aquilinum* is found wherever the shrub layer thins slightly. *Widdringtonia cupressoides* (*whytei*) is the only conifer present.

V. *Plantations*. Plantations are easily identified. Both tone and texture are even but two sub-types have been recognised depending on the height and age of the trees. The younger trees of the plantations produce a lighter tone. The majority of the plantations are coniferous with *Pinus patula* the main species grown.

THE ORIGIN OF THE VEGETATION PATTERN

A. The Environmental Factors.

The origin of the vegetation pattern involves consideration of the physical environment and also of the biotic factors which affect the vegetation. In the physical environment climate, topography and soil are the dominant factors.

I. *Climate.* Of the climatic variables temperature and rainfall are of prime concern. The summit grasslands bear an obvious relationship with climate; rainfall is greater and temperatures lower than in the plateau areas of the west and the dissected country of the east. Montane grassland with ericaceous species around rock outcrops, where drainage is better, is the manifestation. The easterly distribution of the forest also seems to be related to climate. The rainfall to the east of Inyangani is much higher than it is to the west; compare for example the records for Inyanga with those for Luleche in Figure 6. Not only is the total rainfall greater but the rainy season is longer. During the rainy season of 1971/2 the only month in which no rain was recorded at Luleche was August, 1971. At Inyanga no rainfall was recorded for the months of July, August and September, 1971.

The distribution of the rainfall over the study area closely follows the trend of the main relief features. The highest rainfall occurs on the Inyangani summit plateau and the isohyets run parallel with this plateau; a distinct rain shadow is created by the Inyangani hill mass so that the lowest rainfall occurs in the northwest of the area which is that occupied by the *Brachystegia* woodland. The grasslands therefore occur in the intermediate areas although within them a pattern is distinguishable which is associated with rainfall. For example, it was noted earlier that in the south of the grasslands, where rainfall is higher than in the north, *Rendlia altera* and *Tristachya hispida* are the most abundant species.

II *Topography.* Grasslands, with the exception of summit grasslands, tend to be located mainly on areas of intermediate altitude. In the west of the Inyanga area they occur generally between 1 650 m and 2 300 m. (In the east at 1 850 m and below, the vegetation is some kind of forest.) The *Brachystegia* woodland of the northwest is found at a height of 2 060 m but at this altitude the trees are very stunted

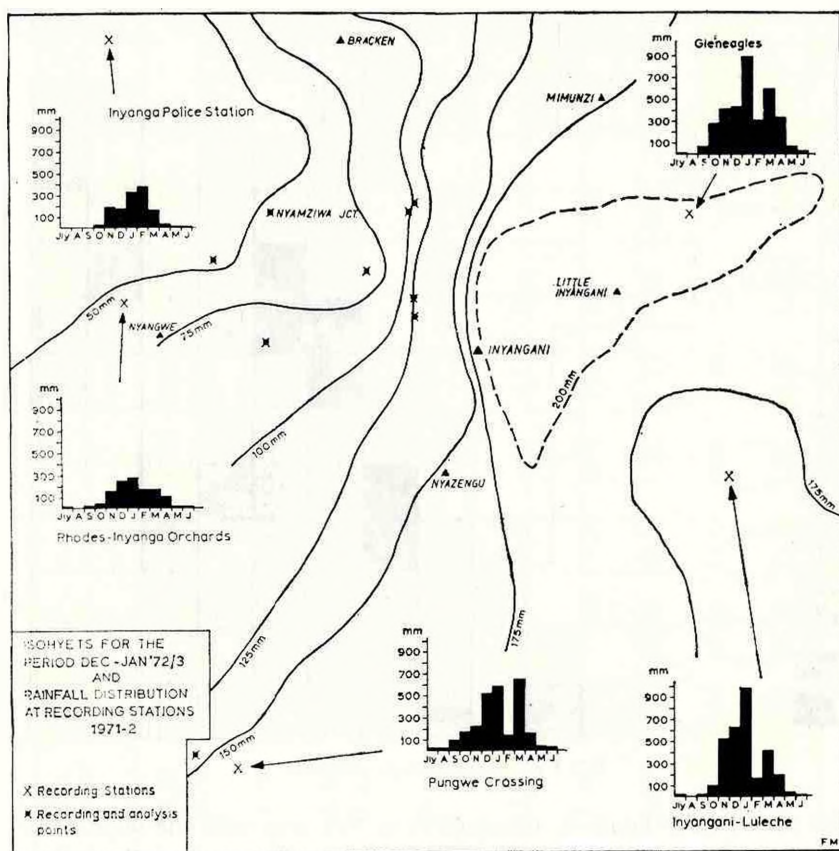


Fig. VI.

(see p. 29) and they only reach more normal proportions at heights below 1 850 m.

In the distribution of the vegetation units slope is as important as altitude. A slope map of the Inyanga area was compiled following the method of Wentworth (1930). Squares of side 2,54 cms were drawn on a 1:50 000 map of the area and within each of these squares four transects were drawn; one north-south, another east-west and two diagonals. Along each of these transects the number of contour crossings was counted. The total number of such crossings per square was calculated and this figure was divided by the total length of the transects to give the number of contour crossings per mile. This figure was then used in the formula outlined by Wentworth to give the average angle of slope. These average slope values were then used to produce the slope

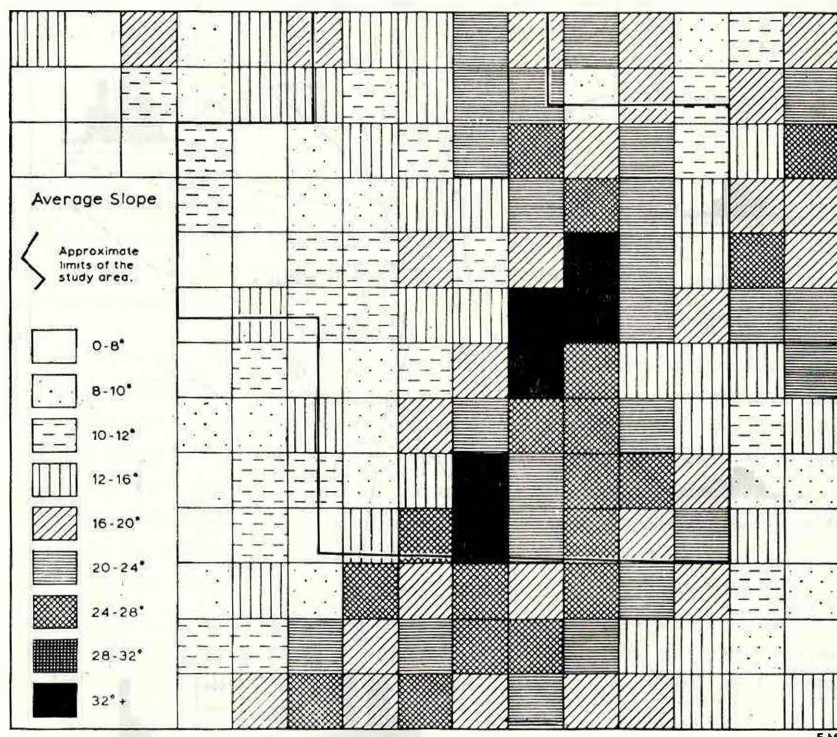


Fig. VII. Average slope diagram.

map presented as figure 7. Comparison of this map with the vegetation map demonstrates that grasslands are confined to areas of gentle slopes, generally between 7° and 10° whilst forested areas generally lie on steeper slopes between 16° and 22° . In the southeast of the study area forest is also found on more gently sloping areas. The steepest slopes are bare rock but the steepest vegetated slopes carry some kind of scrub or bushland, generally ericaceous. The *Brachystegia* woodland is found in an area of slightly steeper slopes than the grassland, between 12° and 14° .

III Soils. The soils of the Inyanga area as a whole belong to the Orthoferrallitic Group, part of the Kaolinitic Order of Rhodesian soils (Thompson, 1965). Orthoferrallitic soils are developed as a result of climatic factors. Since temperatures are lower, both in their mean and maxima than in the majority of the country, evaporation is more limited and the subsoil remains moist throughout the year. Under such condi-

<i>Parent rock</i>	<i>Site</i>	<i>Coarse Sand %</i>	<i>Fine Sand %</i>	<i>Silt %</i>	<i>Clay %</i>	<i>Organic Matter %</i>	<i>pH</i>	<i>Ca</i>	<i>Mg p.p.m.</i>	<i>Na</i>	<i>K</i>
Dolerite	Grassland	26,44	20,45	30,78	23,66	10,28	4,90	8,73	3,33	3,54	6,44
Granite	Grassland	37,27	16,58	17,31	13,09	8,10	4,53	4,32	1,55	2,70	4,66
Dolerite	Summit										
	Grassland	2,12	5,74	16,11	36,50	40,00	5,73	13,50	5,20	4,95	13,00
Granite	Western forest patches	28,08	16,41	15,44	23,18	19,79	4,35	10,00	2,74	3,48	9,70
Granite	Forest — secondary (Veg. Unit 10)	35,54	15,62	11,12	22,71	24,62	4,18	18,75	3,26	6,40	3,75
Granite	Optimum Forest Secondary Vegetation (Veg. Unit 11)	25,08	13,11	12,13	23,19	18,00	4,65	18,50 3,90	5,00 1,40	2,15 2,00	13,00 5,30
Granite	Woodland	42,52	15,73	20,07	6,51?	6,05	4,73	6,61	3,12	3,06	6,19
	Woodland — green areas between	39,40	17,32	23,23	13,62	4,86	4,78	7,46	2,99	3,06	6,43
Average Dolerite		14,28	13,09	23,44	30,08	25,14	5,32	11,11	4,26	4,24	9,72
Average Granite		34,64	15,79	16,54	17,05	13,57	4,03	9,93	2,86	3,26	8,43
Overall Average		30,16	14,59	19,17	20,72	15,18	4,73	10,19	3,17	3,48	8,71

TABLE 3.
Some aspects of the mechanical and chemical composition of Inyanga
Soils

tions all reserves of weatherable minerals are destroyed and, in addition, the highly permeable nature of the soil allows it to become thoroughly leached. Sesquioxides of iron and aluminium remain.

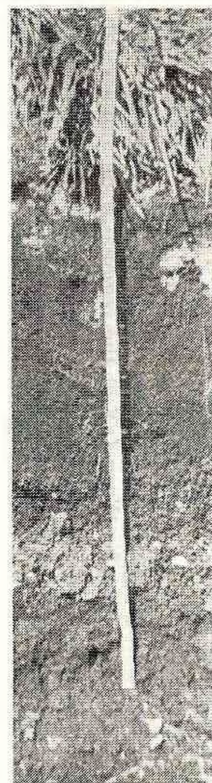
Soil samples taken from the major vegetation units studied were analysed; greatest attention was paid to the rooting zone but profiles from the soils developed on the two main parent materials were also studied (Plate I). The mechanical analysis of the soil followed the pipette method (Piper 1950) and the organic fraction was determined by the method of Walkerley and Black as described in Jackson (1958). The pH was estimated with a potassium chloride electrode in a 2:1 suspension of water and soil. The nutrients were leached from the soil with ammonium chloride and concentrations (in p.p.m.) measured by absorption spectrophotometry. The colour notation is that of the Munsell system. The results are presented in Table 3.

Though climate is of great importance in the formation of the Inyanga soils parent materials do have a considerable effect. Dolerite and granite which form the parent rocks produce very different soils. Those developed on dolerite were generally below average in sand content but above average in silt and clay. The organic matter and the pH of those soils overlying dolerite were also higher than those soils on granite which tended to be higher in the sand fractions and to be low in both the finer fractions of the soil and in organic matter.

In addition to the importance of climate and parent material the type of vegetation also has a marked influence on the soils. The forest areas, both the extensive areas in the east and the small patches in the valleys in the west, had much higher levels of nutrients as did the summit soils. This is a reflection of the higher levels of organic matter and greater clay content. It is noteworthy that these forest areas are on granite and the results may be an indication of a closed cycling of nutrients within the forest areas. This point will be examined later.

The summit grasslands have two contrasting soil types. In the depressions, in which sedges and large tussock grasses occur, soils are highly organic and have a high clay content. The remaining area, in which the vegetation is sparse, have a very high coarse-sand fraction and are low in organic matter. These differences are partly a result of changes in moisture supply as a result of changes in slope. The soil types in the large area occupied by grasslands are also affected by slope so that catenas are developed. Soils vary from reddish-brown at the top of the slope to black at the bottom and whilst the organic matter increases downslope the sand content is reduced.

Plate 1. Soil Profiles (a) Humic profile of a moist valley site (b) a profile on granite (c) a profile on dolerite



(a)

humic horizon

stone line

weathered
granite



(b)

stone line

prismatic
structure

weathered
granite



(c)

shallow soil
layer

shadow — not
an horizon

weathered
dolerite

The biotic factor in soil formation may also be illustrated. If a comparison is made between the soils found in areas of optimum forest and those underlying areas of forest regrowth then it is discovered that the former have four times the level of calcium, nearly four times as much magnesium and nearly double the amount of potassium. According to both Nye (1961) and Kenworthy (1970) potassium is a very mobile element in the cycling of nutrients, whereas calcium and magnesium are less so. This may account for the narrower difference between the two sites in potassium; nevertheless, the differences are considerable and show clearly how in a given environment clearance of vegetation affects the nutrient balance. Even after a considerable period of regrowth, and an estimate of at least ten years would seem in order for the sample area, nutrient levels are well below those of 'virgin' forest.

The soils on which *Brachystegia* woodland occurs were examined and it was found that they tend, as a whole, to be slightly more sandy than other areas of granitic soils. Their nutrient status is, however, slightly higher than the granite soils under grassland. Within the *Brachystegia* area soil samples were taken from under the trees and also in the bare regions between the clumps. No difference was detected in either mechanical composition or in nutrient levels in these two areas but there was a pronounced structural difference. In the areas between clumps the soil surface was extremely hard and plate-like; beneath this soils were moist even in the dry season. No such structure occurs within the tree clumps. It would appear to be a result of compaction by rain and rapid desiccation, but whatever its origin this plate-like surface provides a barrier to plant growth.

IV. Summary

The environmental factors as they affect vegetation may be examined under two headings (a) at the regional scale and (b) at the local level. In the former, the moister, cooler climate of the Inyanga area, a result of greater altitude and of position with respect to the direction of the rain-bearing winds, has produced a vegetation distinctly different from the majority of Rhodesia. Within the Inyanga area the plant cover is in general more luxuriant than, for example, on the Middle or High Veld. In addition, many of the species belong to the more temperate vegetations; for example ericaceous species are extremely abundant; bracken covers a large proportion of the area and the *Helichrysum* species are very plentiful. Soils in the Inyanga region

are more weathered but contain more organic matter than the soils of much of the lower parts of Rhodesia.

At the local level factors of geology have, directly and indirectly, had a considerable effect on the vegetation. The dolerite sheet which has given rise to the Inyangani mass has not only produced a particular summit vegetation but by affecting the distribution of rainfall has aided the development of many kinds of vegetation. The dolerite has also given rise to steep slopes on which distinct vegetation types and sub-types occur. Within the granite area the vegetation is by no means uniform and factors such as slope are of great importance; thus in the steep-sided valleys of the smaller tributary streams which abound in the western part of the area are patches of dense forest.

B. Biotic Factors and Time

Biotic factors are concerned with the role of man in modifying and changing the vegetation pattern. Clearance by slash and burn is now widely accepted as the cause of savannah grasslands so that if one wishes to consider the origin of the Inyanga grasslands this should be taken into account. Three lines of evidence are available: existing and recent, archaeological relics and palynological evidence. In searching for present-day evidence of forest clearance the logical area in which to look would seem to be the east. It has already been noted that patches of secondary forest exist and gradations from forest to grassland have been recognised. Field data also support the evidence of air photographs. During an extended field survey in December 1972 large, regular areas in which the forest had been burned were observed on the eastern slopes of the Inyangani mountains and several of these were being cleared.

Historic evidence visible at the present time includes the distribution of ruins and terraces both of which are believed to date to about A.D. 1500 (Summers 1958). The existence of these terraces indicates that a developed agricultural society was established at that time. A map of the distribution of these relics reveals a predominantly western and northern trend. They are almost completely confined to the grassland areas (Fig. 8). Such evidence is not conclusive as to whether or not the grassland owes its origin to clearance. Settlement may have taken place in the west because of easier clearance of the vegetation because there was no forest in that area at the time of settlement.

In the absence of reliable historical evidence some other method of tracing past events is required. In Europe and America the vegetational history of many regions is now well established. This has been achieved following the development of pollen analysis. Though developed in

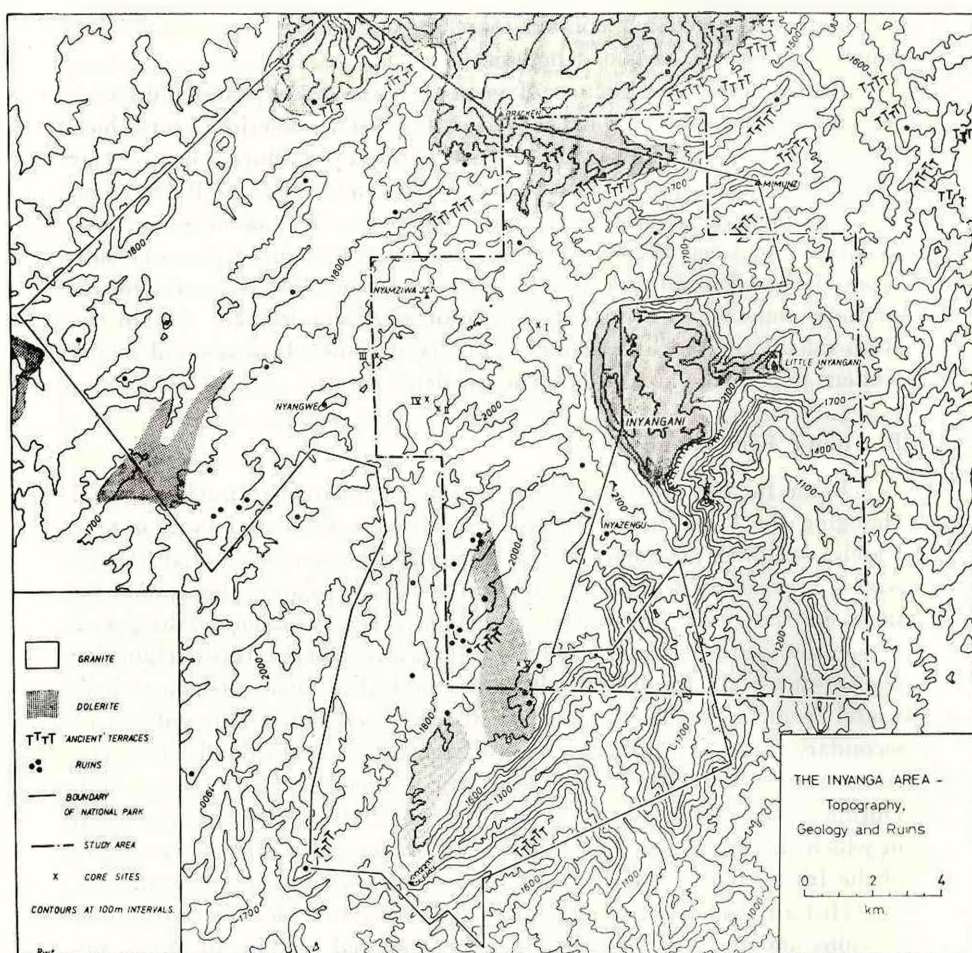


Fig. VIII.

Scandinavia in 1916 its use in Southern Africa is of relatively recent origin and in Rhodesia in particular very little work has been done. Since the technique is so new to the country a brief account of the methods and procedures involved is essential in order that the reader may more readily appreciate the value and limitations of pollen analysis.

I. Techniques of Pollen Analysis. For the creation of seeds in flowering plants the male and female gametes must fuse. This involves transfer of pollen, which contains the male gametes, to the carpel in which the ovule is located. This transfer may occur in two ways—

(a) by insect and animal transfer, and (b) by wind dispersion. In the latter case it is fairly obvious that not all, and indeed only a very small proportion will reach the stigma. The vast majority will fall to the ground as 'pollen rain'. Under suitable conditions this pollen is preserved. The pollen produced year by year will be deposited in layers so that if a core of soil can be extracted it is possible to follow the pollen history of the area. Since the pollen will be a reflection of the plants within that area at each period in time it is possible to establish a history of the vegetation of the area. There are, however, numerous problems and difficulties and it is essential that the most important of these should be discussed.

First, not all pollen is wind-borne; some is carried by insects. In such a case any pollen falling to the ground will be very local in its distribution and as such is only of value in the description of the history of a local vegetation. Second, some plant species are more prolific producers of pollen than others and such species will be over-represented in a study of the pollen assemblage at any point in the soil core. The nature of the pollen grain itself is also important. Some grains are small and light whereas others are large and heavy; the distance they may be carried by the wind will therefore vary. These difficulties, which may be called perhaps 'floristic' difficulties, should be noted when the analysis of a pollen assemblage is made.

Pollen is only preserved 'under suitable conditions'. The area on which the pollen grain falls must be both anaerobic and moist; such an environment therefore is usually acidic. Lake-beds are an ideal location from which to take a core for analysis and of second importance are peat deposits. In south-central Africa the distribution of both lakes and peat is somewhat scanty but in Rhodesia in the range of relatively high mountains which form the eastern border areas are a few small areas of peat-like deposits. An important question is whether pollen assemblages from these small deposits yield results which are representative of the vegetation of larger areas. It is generally maintained that lake deposits are of greatest value in pollen analysis because with their intake of stream waters they provide a regional picture. However, if within a relatively restricted area several cores are taken then it is fair to assume that the pollen assemblages do give a valid picture of the vegetational history of that small region. It is on this belief that the present interpretation of the vegetation history of the Inyanga region depends.

The methods of pollen analysis should now be briefly discussed. The first stage, once suitable sites have been located, is to take samples from the deposit. A corer is required which will take soil material from

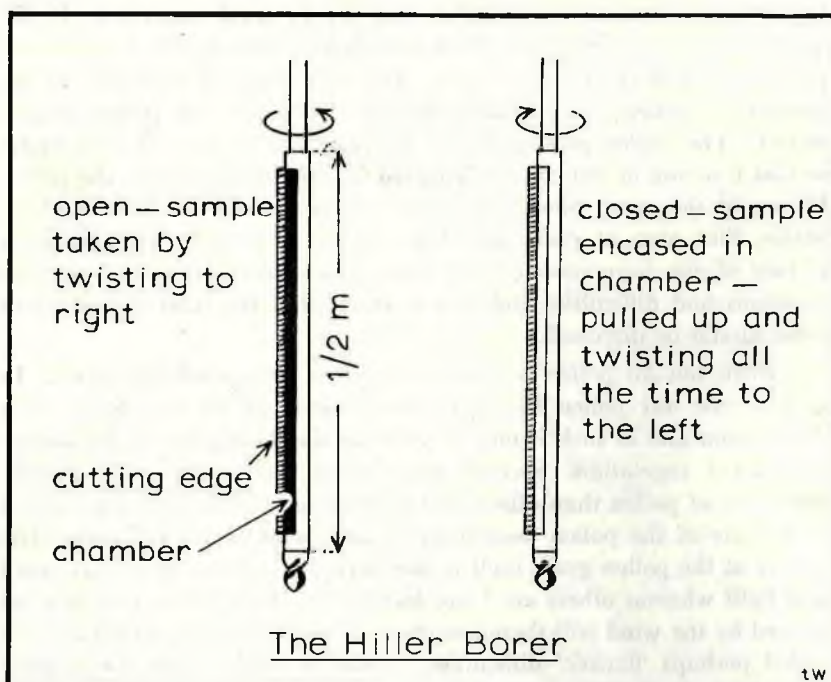


Fig. IX.

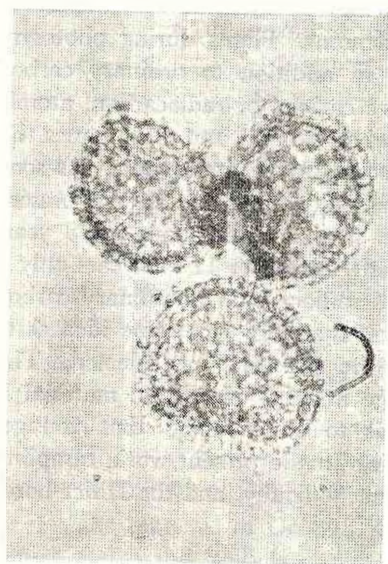
precise depths without that sample being contaminated by soil from other levels. In the present study a Hiller borer (Fig. 9) was used which will take cores from depths of up to 30 m. Each section of the core is 50 cm long and this is protected from contact with other soils by a revolving plate. For subsequent analysis each 50 cm section of the core is divided into suitable lengths—usually of 5 to 10 cm, although in very detailed work 2 cm samples may be required (Tomlinson, 1970); in the present study the core sections were divided into 8 cm lengths. Each of these lengths is carefully stored away from contact with other samples until ready for use. Such storage must not be too long or the pollen may be damaged in the dry atmosphere. From each small part of the core one gram of peat is taken and put through a standard procedure so that all organic and mineral matter, or at least as much as possible, is removed leaving behind the various pollen grains. The method of treatment of the samples varies from one worker to another, much depending on the type of material being analysed. For peat deposits the method developed by the Scandinavians is almost universally accepted. A brief outline of the method used on the Inyanga deposits is given in Appendix



Kyllinga alba



Stomatanthus africanus



Lycopodium clavatum

Magnification x 900
on Panatomic X

3. It will be noticed that it includes both acetolysis for the removal of resistant organic material and treatment with hydrofluoric acid to remove silica.

Once a slide has been produced, on which one hopes there is pollen, it remains to identify the genera and species to which the pollen grain belongs. In northern Europe, and now for some South African species, detailed descriptions of the pollen of the flora are available and provided that one is conversant with the terminology used to describe the pollen grain an identification of a particular pollen grain is possible. For more detailed and accurate work it is necessary to compare the unknown grain with reference grains of the particular species one suspects it may belong to. The procedure is not unlike that of the ballistic expert comparing shells from a gun and indeed comparative microscopes alike to those used by such experts are often used by pollen analysts. In Rhodesia both descriptions of pollen grains and a reference collection are lacking so that the first task which had to be done for the Inyanga work was the construction of a reference collection. This task is not complete though the indicative species have been assembled. Examples of some of the grains are given in plate II.

If the evolution of the vegetation of an area is to be studied some idea of the time scale is required. This may be obtained with the aid of the radio-carbon dating of the peat deposits. Plants during photosynthesis use atmospheric carbon which in addition to ordinary carbon (atomic weight 12) contains radioactive carbon, or radiocarbon, atomic weight 14 (C_{14}). Plants therefore absorb and build into their tissues this C_{14} at the same concentration as it occurs in the atmosphere. As soon as the plant dies no further radiocarbon is added and that already present in the plant will begin to disintegrate so that after about 5 568 years only half the original amount will be left, and after 11 140 years only a quarter. Determination of the ratio of radiocarbon to ordinary carbon in a given weight of plant material will therefore give some idea as to the age of the particular horizon in the core one has selected. The method has the difficulties that a large amount of organic material is required and secondly great care has to be exercised that younger deposits do not contaminate the sample. In the present work, sampling from peat-like deposits overcame the first difficulty, and the Hiller borer the second.

II. *Inyanga Core Sites.* Several sites have been investigated in the Inyanga area but not all proved suitable for analysis. High silica content prevented examination of samples from some locations and even treat-

ment with hydrofluoric acid failed to remove sufficient to allow the slides to be examined. Five locations proved to be suitable and these are now described.

Core I was obtained from a small *Sphagnum* patch located on a terrace alongside the upper reaches of the Nyamziwa river. The origins of this small depression are difficult to discern but it would appear to be some kind of infilled sink-hole. Such features are common on *Molinia caerulea* slopes in various parts of Scotland and also occur on the peat slopes of northern England. The surrounding area is one of fairly gently rolling hills, grass covered and barren of trees with the exception of 'escapes' from the plantations. Few bushes occur other than *Helichrysum odoratissimum* which forms small almost pure stands. The slopes are dominated in general by grasses and estimates of cover would be approximately 80 per cent. Dominant species on the slopes include *Ficinia filiformis*, *Themeda triandra*, and *Loudetia simplex*. The grasslands, however, contain *Vernonia natalense* and some small ericaceous plants.

The soil material is peaty for the first metre, thereafter becoming a highly organic clay to a depth of about 1,5 m. The organic matter slowly decreases so that between 1,5 and 2,0 m the core is mainly of clay. At 2,0 m the percentage of sand increases to give a sandy clay down to about 2,30 m where all trace of organic and clay materials disappear leaving only a white sand in which no pollen has been found.

Core II was extracted from a pond located in a shallow, though wide depression at the head of one of the tributaries to the Mare river. The pond has some fluctuation in level during the course of the year but this is slight and it has not been known to dry up. Again the site is located within a predominantly grassland area though much of this has been flooded recently by the creation of Lake Gulliver. On the dry, upper slopes the predominant grasses are *Rhyncholetrum setifolium* with *Themeda triandra*; the latter becomes more plentiful downslope. As the ground becomes damper the tussocks become larger and *Eragrostis volkensii* dominates; this is replaced by *Koeleria capensis* in even damper sites. In the damp places the areas between tussocks are carpeted with bryophytes, including *Sphagnum* species, which dominate in the pond. In addition to grasses the slopes have patches of *Helichrysum* spp. and of bracken, both of which may occur as fairly dense stands.

The material of Core II is peatier than that of I. For almost the first metre the 'soil' is a true peat, thereafter becoming much more fibrous. At approximately 1,75 m the soil is more clayey and at about 2,0 m begins an organic sandy-clay. At approximately 2,25 m the peat element ceases so that a sandy clay is left.

Core III was taken from a damp terrace area alongside a tributary of the Inyangombe river. The surrounding country was somewhat different from that previously described in that it lay in an area of grassland with scattered trees. Most of these trees are escapees from the pine plantations but some *Protea* sp. and ericaceous species also occur on the surrounding hills. In general, however, the slopes are dominated by *Themeda triandra*, *Rhyncheletrum setifolium*, *Digitaria maitlandii* and also by patches of bracken. In the immediate area around the core site *Koeleria capensis* and *Scirpus costatus* var. *macer* are dominant.

The materials composing Core III vary from a white sand at the base of the core, which contains little or no pollen, to a highly organic clay in the top 50 cms. Immediately above the white sand, which occurs from 2,50 to 2,25 m, lies a sandy clay. At about 1,75 m and continuing to 1,0 m the material is a smooth, black clay containing some sand. Thereafter the deposit becomes more organic; from about 1,0 m to the 50 cm level is a sandy, fibrous clay and above this a highly organic, fibrous clay leading into an organic clay at the surface.

Core IV was obtained from the same general area as core II but the actual site now lies beneath Lake Gulliver.

Core V was bored in an infilled oxbow-lake on the Matenderere river, a tributary of the Pungwe. The oxbow itself contains *Scirpus costatus* but the meander plain in which it occurs is fairly open, not having a high percentage cover. The dominant grasses are *Rendlia altera* and *Tristachya hispida* but other plants occurring in quantity are *Koeleria capensis*, *Rhyncheletrum setifolium*, *Microchloa caffra*, *Haplo-carpha scaposa* and *Peucedanum* sp. On the surrounding hills *Rendlia altera* and *Tristachya hispida* are again dominant. Although bracken occurs alongside the river, neither bracken nor ericaceous species form stands and even species of *Helichrysum* occur as scattered individuals and not in patches. In the fairly steep-sided valleys of the tributaries to the Matenderere river small patches of forest occur (see p. 28) but otherwise trees are absent. The material which composes this core is remarkably consistent throughout and is an organic clay. Some slight increase in organic material is found nearer the surface but nowhere is there any peat-like material.

III. *The Inyanga Pollen Diagrams.* The grains of the individual pollen types were summed to produce a total land pollen for each slide. Two slides were examined for each layer and the counts for each summed. The individual types are expressed as percentages of total land pollen (% T.L.P.). The percentages were then graphed in two forms (a) for each core (Figs. 10-13) and (b) for each major pollen

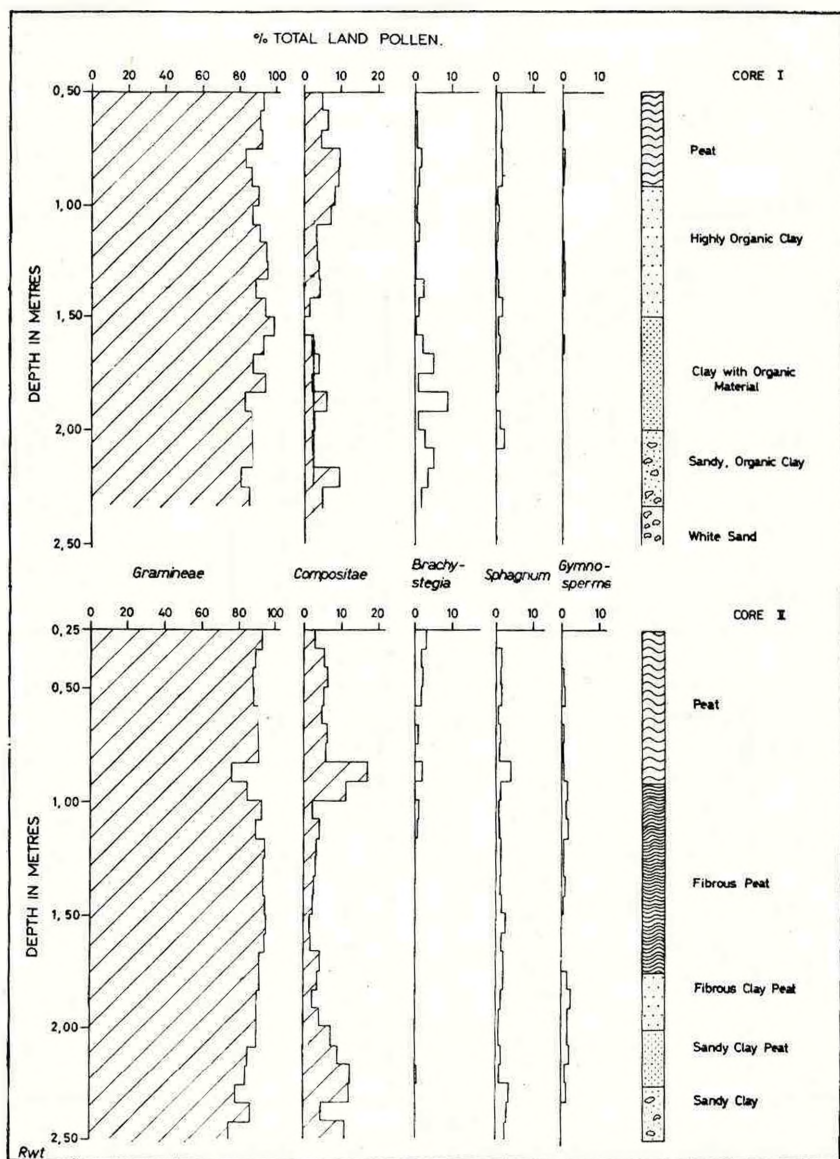


Fig. X.

type (Figs. 14-16). This enables discussion of the local situation and, secondly of the regional picture.

In Core I although small percentages of *Brachystegia* pollen occur throughout they are not in general significant. Only at a depth of 1,8 m

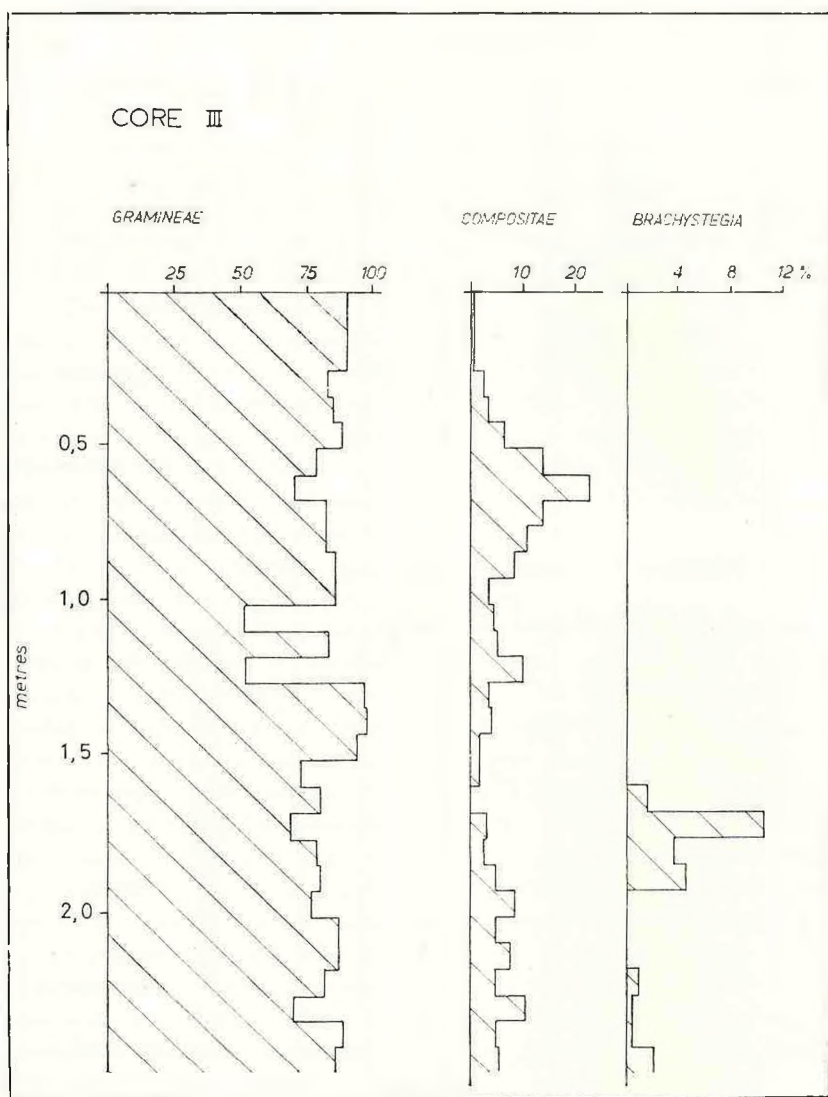


Fig. XI.

does this pollen approach the 10 per cent level. Pollen of grasses on the other hand dominate, being seldom less than 70 per cent. From the pollen data it appears that the vegetation has always been predominantly grassland with scattered trees in the earlier part of its history. A radio-carbon date for the bottom of Core I, at 2,25 m, has been given as 4670 ± 60 B.P. Within the grassland members of the Compositae are

CORE IV

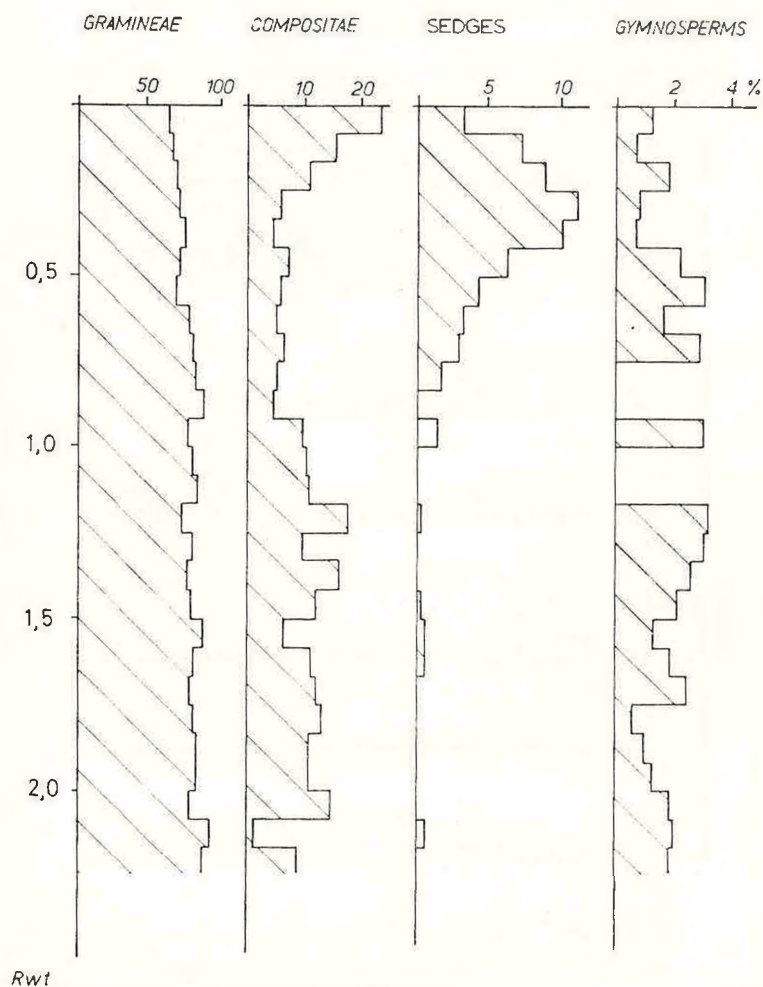


Fig. XII.

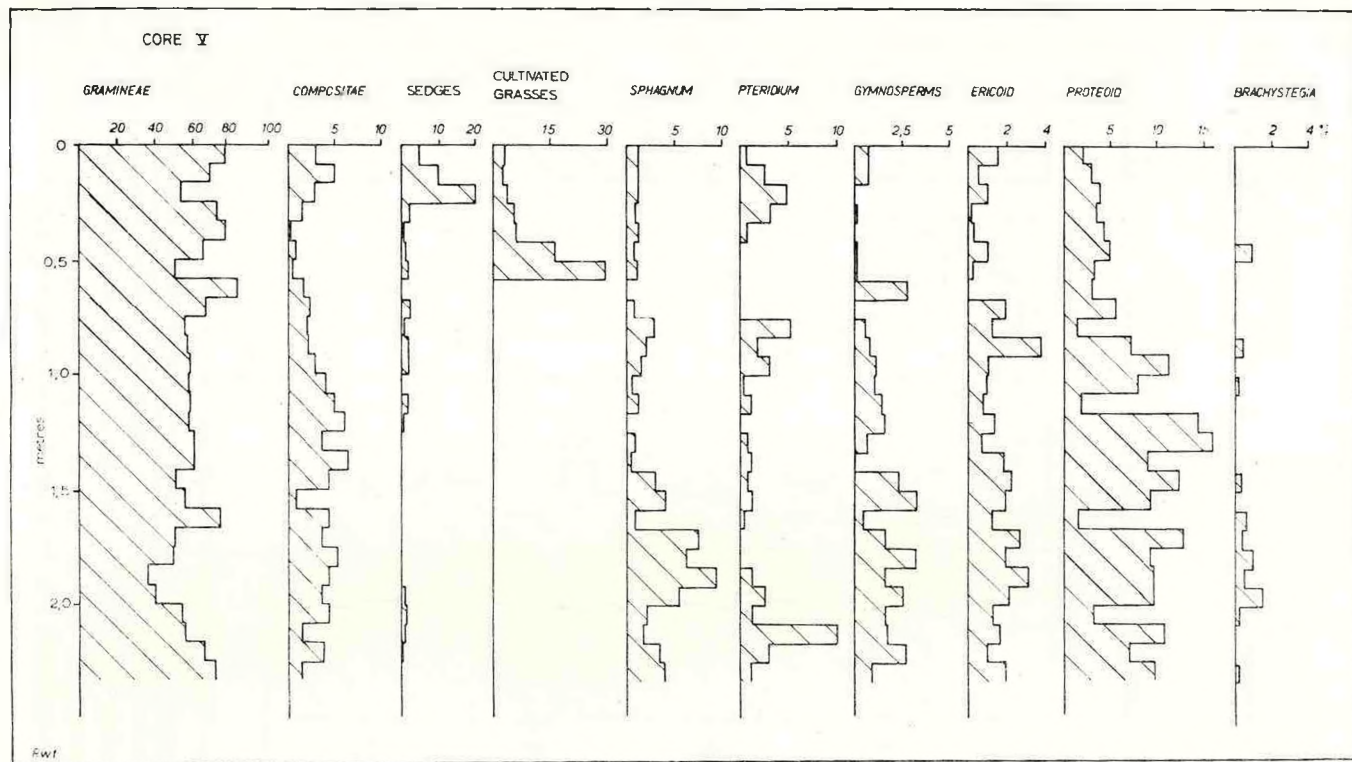
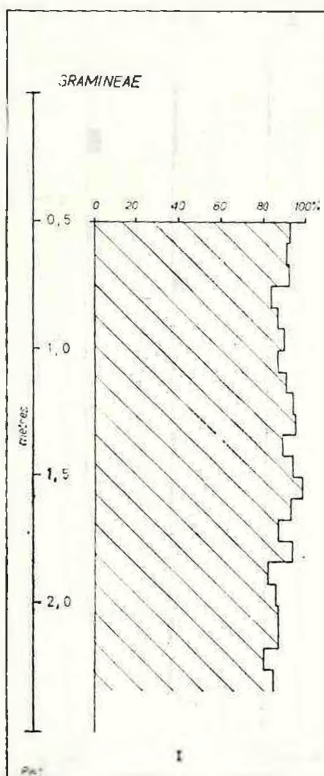


Fig. XIII. Pollen diagram for Core V.



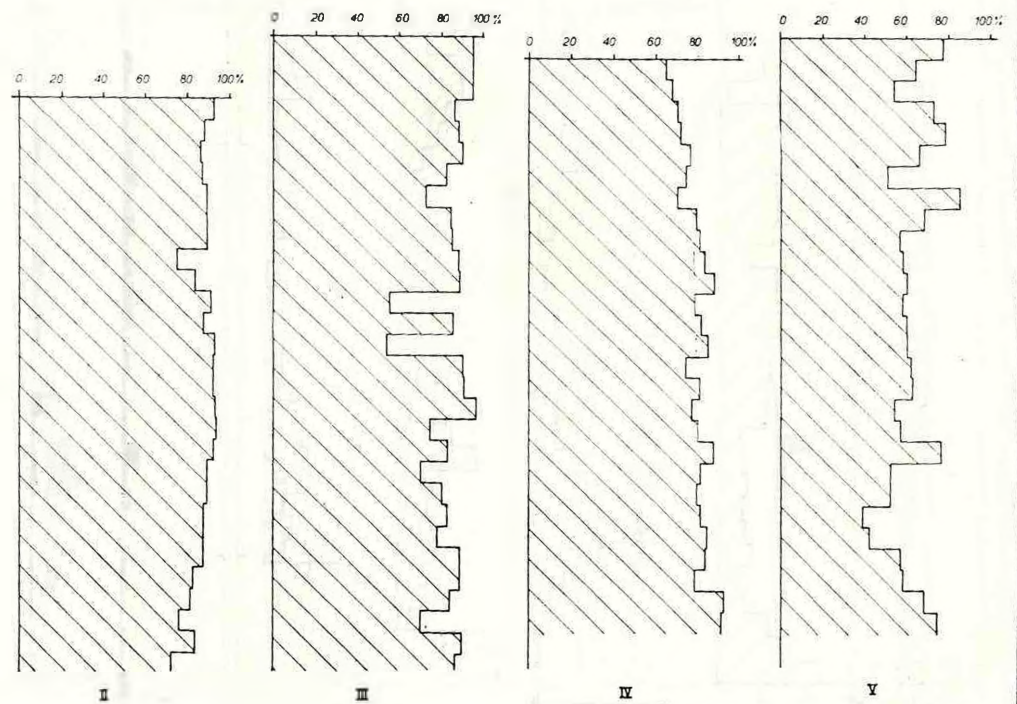


Fig. XIV

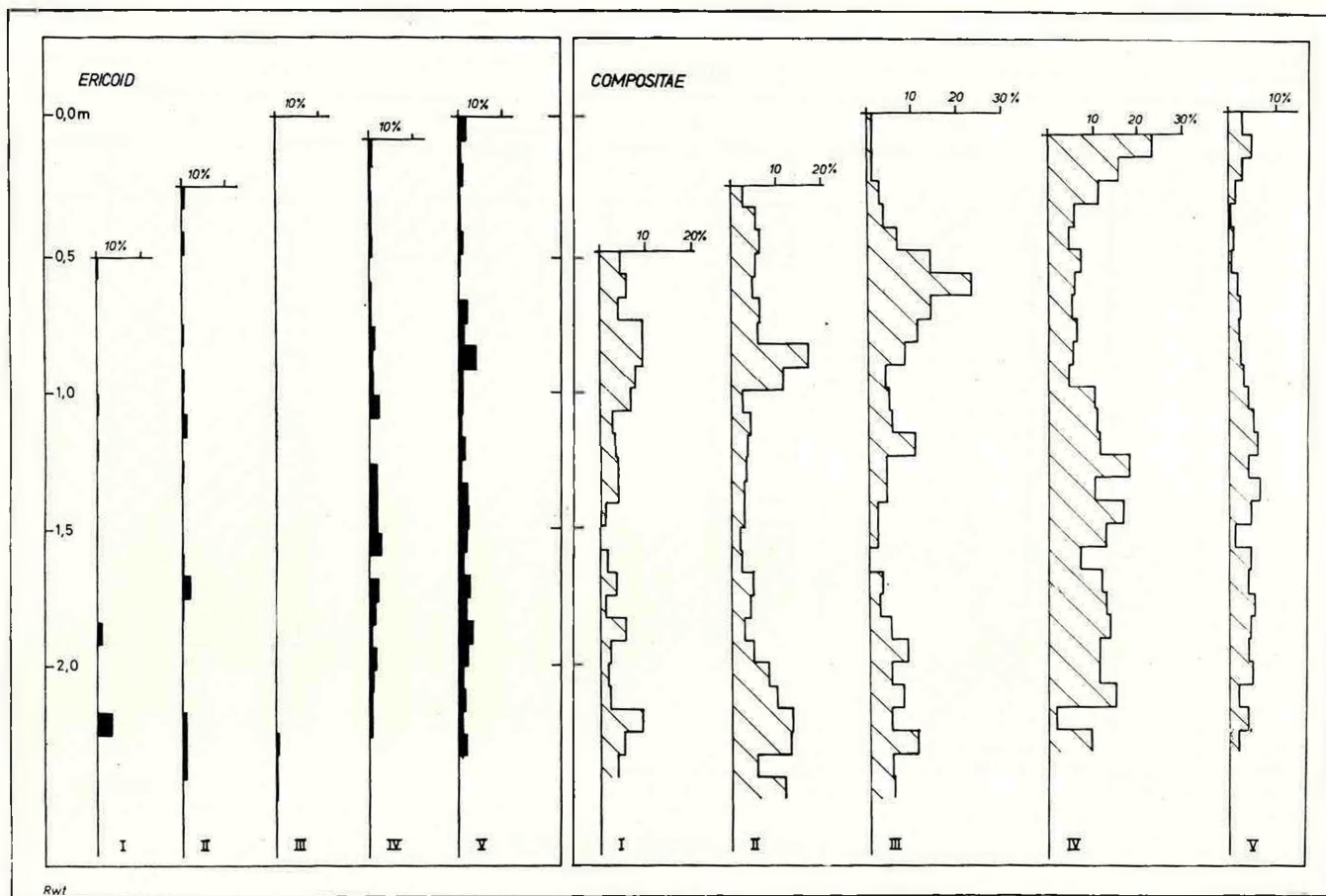


Fig. XV.

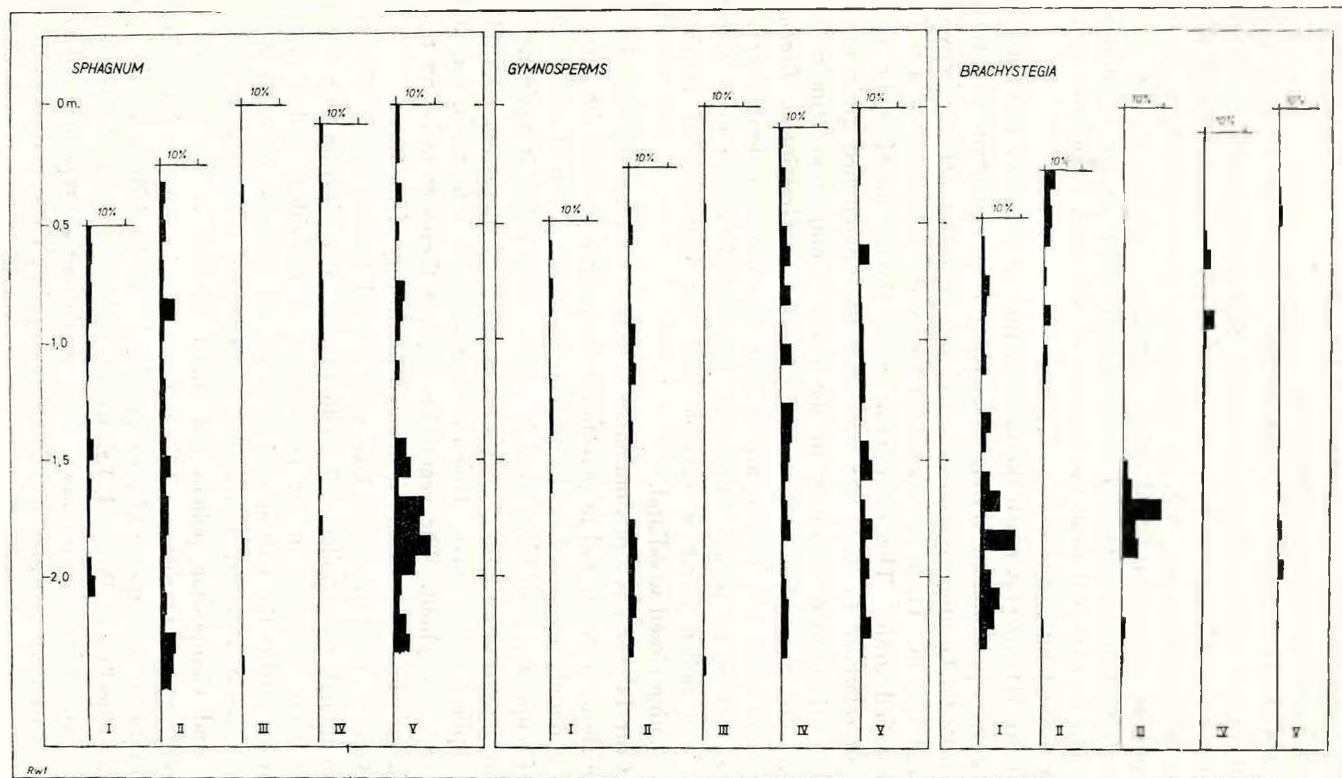


Fig. XVI.

quite significant, approaching the 10 per cent level, and this approximates to the present day type of community.

In Core II grasses are also the predominant pollen. Only in fairly recent times is there evidence for a rather scanty distribution of *Brachystegia* pollen. Other tree species are absent. Pollen of gymnosperms does occur though these are not at a significant level. Members of the Compositae are again found in the grassland community and show fluctuations which correspond inversely with those in the Gramineae. As might be expected from the location of this core, *Sphagnum* spores occur throughout.

Core III presents much the same picture as the other two cores in that grasses predominate throughout. There is no significant pattern in the curve for Gramineae with the exception of sudden declines between 1,0 and 1,25 m. These are accounted for by the occurrence of a so-far unidentified grain. The Gramineae curve should therefore be read without reference to these two falls since the unidentified grain never reaches significance elsewhere in the cores. Compositae remain important and again show increases with falls in the Gramineae. *Brachystegia* and other tree pollens are of little significance, indeed after the bottom 1,4 m no pollen remains of *Brachystegia* occur; even before then, the pollen curve is variable and not indicative of anything approaching closed woodland.

Core IV also has a predominance of grasses although the Gramineae curve shows a steady fall in percentage occurrence towards the surface. This is mainly accounted for by an increase in the pollen of both sedges and Compositae both being local in origin. Tree pollen is again nearly absent, indeed so little *Brachystegia* pollen occurred that it was impossible to compile a pollen curve. Pollen of Gymnosperms is found in very low numbers throughout. The vegetation appears therefore to be an open grassland which has continued through the history of the area.

Core V, from the oxbow lake, gives a much greater variety of pollen grains though grass pollen still predominates. The diagram as a whole shows more variation in the percentages of individual pollen grains. From the 2,10 to the 1,70 m level there are, for example, increases in the percentages of Proteoid, Ericaceous, *Brachystegia*, Gymnosperm, *Sphagnum* and Compositae pollens but sharp declines in the amount of Gramineae and *Pteridium*. This indicates an increase in bush/shrub vegetation at the expense of pure grassland. At the 1,70 m level a pronounced decline in Proteoid, Ericaceous, Gymnosperms and *Sphagnum* occurs but an increase in grasses. Such oscillations are repeated and may reflect variations in water availability or supply. These variations, how-

ever, are better discussed with reference to the complete regional picture. Perhaps of greatest importance in this diagram is the very sudden appearance of very large grains of the Gramineae; the size of these grains indicates that they may be cultivated grasses. The appearance of these grains is marked by a decrease in the percentage of ordinary grasses, of Compositae, and of *Pteridium* and this may indicate clearance of the slopes for cultivation. *Sphagnum* and sedges also show a decline just before this and may be a response to a slightly drier environment.

IV. *Interpretation of the Diagrams.* All the diagrams have demonstrated the predominance of Gramineae pollen and all indicate that much of the Inyanga area has been covered by grassland communities for a very long period. At Core I a date of 4670 ± 60 B.P. was given for a depth of 2,25 m whereas at Core II a depth of 3,0 m was assigned at date of $11\,750 \pm 110$ B.P. It thus appears that the area was grassland long before the arrival of man and that it was not man that gave the region its smooth, grassy slopes by clearance. The only core which shows evidence of clearance is that taken from the oxbow lake in the Matenderere valley (Core V). In this diagram pollen of cultivated grasses appear suddenly and coincide with the decline of other grassland species. It is unfortunate that no date for this appearance is available but an estimate may be made. At Core I a sample from a depth of 1,0 m was dated as 750 ± 55 BP; if it is assumed that the material comprising the last 50 cm or so of Core V accumulated at a similar rate this would place the proposed period of cultivation at about A.D. 1500-1700 (assuming an accumulation rate of c. 5-8 cm/year). According to Summers (1958) the Inyanga peoples who lived in the upland areas above 1500 m did so during the sixteenth century and it appears reasonable to suppose that these were the people responsible for the cultivation. In the Matenderere valley are several examples of the terraces attributed to these people. The period of cultivation would appear to have been a short one since the peak in the curve for the pollen of cultivated grasses is a short one, no more than sixty years. Again this fits the general hypothesis of the Inyanga peoples of the sixteenth century since they are assumed to have been a type of shifting agriculturists, cultivating the hillsides for a period and then moving to other slopes.

Several of the diagrams show fluctuations in the percentages of various types of pollen; particularly is this true of Gramineae and Compositae, but as in Core V such fluctuations are not confined to these two species. One explanation of these variations would be a change in the environmental conditions; for example, a move toward

wetter or drier climatic conditions. If such changes did occur then the results of these changes would be apparent on a regional scale; if therefore percentages for a pollen of an individual type are examined throughout all the profiles it would be expected that rises and falls in the percentages would occur at the same levels, always allowing for small errors in the field measurement of core lengths.

The curves for the Gramineae in several cores showed variations. In Figure 14 these curves have been drawn alongside each other at their approximate position relative to one another, with the top of Core III taken as an arbitrary datum. From this diagram it is possible to recognise three levels at which changes in percentage of Gramineae pollen occur in all profiles. The first is a period of decrease and occurs at a depth of between 2,25 and 2,30 m. Second, a period of high levels of Gramineae pollen at about 1,70 m and third a period with low percentages at about 0,60 m. These changes should be echoed by relevant changes in another pollen or pollens. In the Compositae curves (Fig. 15) there is such evidence for two of these periods, first an increase in the percentage of Compositae pollen at about 2,25 m and second a decrease at approximately 1,70 m. There is, however, no corresponding rise in Compositae pollen to compensate for the Gramineae decline at 0,6 m. This inverse relationship between Gramineae and Compositae has long been recognised; Van Zinderen Bakker (1955) has said that when Gramineae pollen predominate then the climate became more wet. Before such an explanation can be accepted it is necessary to examine curves for other pollens, for example the curve for *Sphagnum spp.*, or the ericaceous species curve. It should be expected that more *Sphagnum* will occur in wetter times thereby increasing the number of *Sphagnum* spores. Similarly in a moister, and presumably cooler, period ericoid pollen would be expected to increase as also might Proteoid. None of the curves for these pollen types gives corroborative evidence. The point may be raised as to whether sufficient time elapses in which plant distribution and spread may take place thereby producing such changes in the diagram as would be expected. If one takes the length of time between 2,25 m and 1,0 m in Core I, that is about 4 000 years, as being representative for the rate of accumulation of these consolidated deposits then one arrives at about 1 cm per 30 years. The base of Core II is dated at about 12 000 years which gives a rate of accumulation for the core of approximately 1 cm per 38-40 years. Within any one sample from *consolidated* material one is dealing with something in the order of 280 years. Such a length of time should be sufficient for plant distribution to become settled in a small area. It would therefore appear

that there is no evidence for any regional change in climate of great magnitude. There may have been slight changes, for example wetter summers or winters which would encourage grass growth at the expense of Compositae but would not cause substantial change in the vegetation pattern.

Examination of the curves for *Brachystegia* pollen (Fig. 16) reveals little other than further proof, were it needed, that no pattern in the occurrence, or non-occurrence, of the species is to be found. The values are low throughout and indicate either a fairly distant source of supply or a scattered distribution of trees through the area. Since Core I gives the highest and most consistent values, and since this core is the nearest to the present-day distribution of the *Brachystegia* woodland the first hypothesis is to be favoured. This may indicate that the distribution of *Brachystegia* woodland has in the past not been significantly different from today.

CONCLUSIONS

Geography must stand or fall by its ability to describe landscape. The geographer must "begin with the landscape in view and end with the landscape in mind's eye; begin with description and end with explanatory description". The first task of the present study was an attempt to describe the biological landscape of a selected area. In this task air photographs proved of immense value; field investigations added to the descriptions but also demonstrated the accuracy and worth of air photographs in vegetation description and mapping. The vegetation has been described mainly in terms of its structure. To the geographer such descriptions are of greatest value and it is hoped that those included in this study are complete enough to create an impression of the vegetative landscape. Floristic descriptions may be of considerable value, especially in ecological studies of detailed causes and effects of plant distribution, but not even the botanist can carry precise knowledge of all plants in his head; he knows only those plants from a restricted area or group.

The origin of the vegetation pattern of the Inyanga area has been investigated and both the physical and human factors affecting the vegetation have been discussed. The relative importance of each of these factors requires assessment with reference to the individual vegetation units. The forest of the east is clearly a response to a very warm, moist climate but its complex of sub-types and variants owes much to human factor as well as to relief and slope. Summit grasslands are again a response to the physical environment. The units of dispute are the grasslands of the plateau, the forests of headwater valleys in the west and the *Brachystegia* woodlands.

The concept of clearance of vegetation by man using fire is so well entrenched that almost any grassland area is now explained in these terms. It is almost automatic that the Inyanga grasslands have been so interpreted. The headwater forest patches are assumed to be remnants of a once more extensive forest or woodland that have survived as a result of their protected situation. Similar conclusions were reached by Phipps and Goodier (1962) for the kloof forests of the Chimanimani Mountains. No evidence has been found in the present study to support the contention that the western areas were once forested. Investigations have gone back nearly 12 000 years and tree pollen grains have been

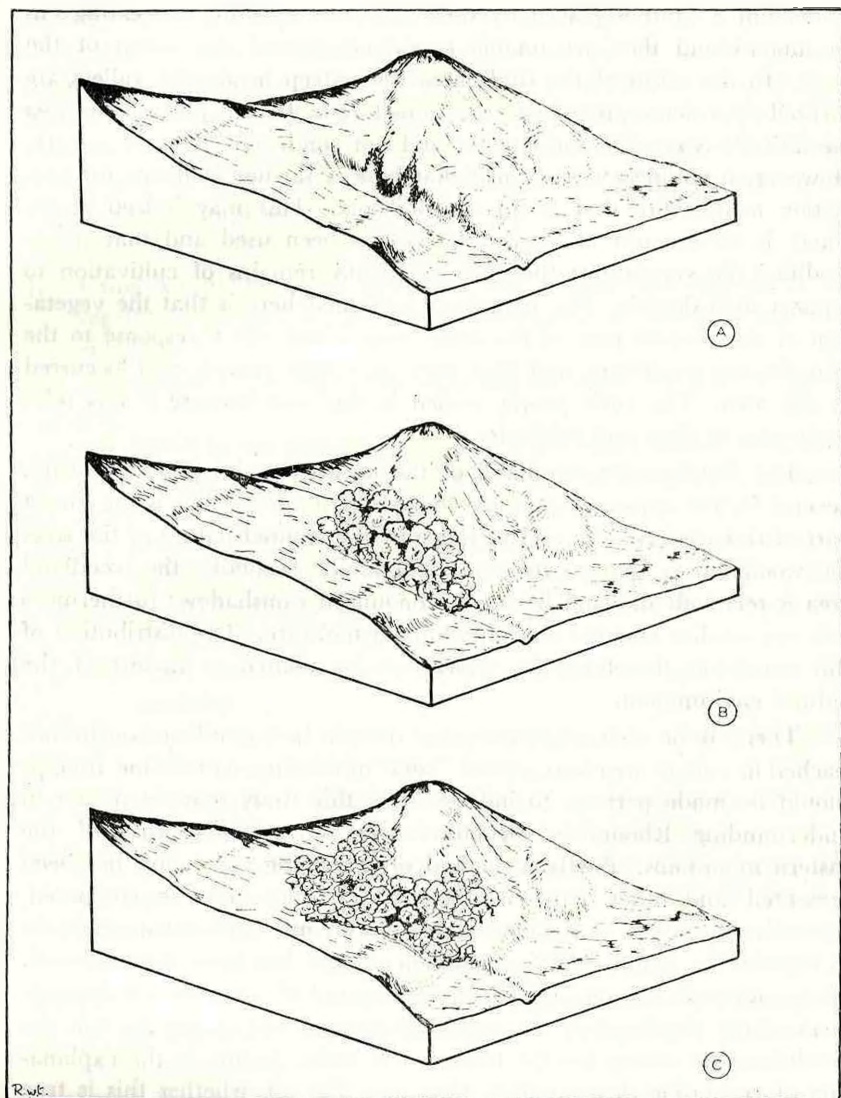


Fig. XVII. Proposed development of valley forest.

shown not to reach significant levels. It is postulated that these forest patches are a response to soil moisture conditions and a closed cycling of water and nutrients (Fig. 17). It may be argued that these areas often extend beyond the confines of the steep valleys but closer examination reveals that they extend only as far as the crown of the slopes. The forests are believed to be able to carry their moisture with them to some

extent but a limit is placed by their exposure to more desiccating environments and they are unable to extend beyond the crown of the slope. In the north of the study area these steep headwater valleys are covered by a dense growth of ericaceous forest. In this part of the area the altitude is considerably greater and not conducive to forest growth. However, it could be maintained that here is further evidence for protection against fire that swept the plateaux. This may indeed be so. There is no attempt to deny that fire has been used and that it has modified the vegetation; there are too many remains of cultivation to support such denials. The hypothesis presented here is that the vegetation of the western part of the study area is basically a response to the rain shadow conditions and that very little tree growth ever occurred in this area. The early people settled in the west because it was relatively easy to clear and cultivate.

The *Brachystegia* woodland of the northwest also poses problems. Several factors appear responsible for its distribution. This is the lowest part of this western area and to judge by the stunted nature of the trees the woodland is near to its altitudinal limit. Secondly, the woodland area is relatively dry and lies in a pronounced rainshadow; furthermore soils are sandier and less able to withhold moisture. The distribution of this woodland therefore also appears to be related to factors of the natural environment.

There is of course always great danger in extending conclusions reached in a small area into general "laws" of development. Some attempt should be made perhaps to indicate how this study may be of use in understanding Rhodesia's vegetation and in particular that of the eastern mountains. Firstly a method of describing vegetation has been presented and other parts of the country may now be compared. Secondly, the value of detailed investigations into past events in order to explain the origins of the vegetation pattern has been demonstrated. The results will, I hope, call for a reassessment of views on the development of the grasslands of the eastern mountains and it may be that the pendulum has swung too far towards the biotic factors in the explanation of vegetation development. One may also ask whether this is true of the current view on the development of savannahs.

The choice of the Inyanga Mountains Area as the centre for study has been examined in the introduction but it may be asked, why choose an area? Regional Geography is out of fashion at the present time but it remains true that only in the description of a limited area, with all its complex interactions, does the geographer approach his aim of landscape description. Biogeography is a specialism within geography and

provides an opportunity to examine the landscape from a particular viewpoint; it requires knowledge of, and ability to combine, many features of the environment of a particular area. Such relatively local studies allow the geographer to leave aside systematic enquiries (for example, world vegetation types) and approach his aim of landscape description. It is hoped that the present study will encourage more regional biogeographies.

SUMMARY

1. Using air photographs, structural and floristic descriptions of the vegetation of part of the eastern mountains of Rhodesia are provided.
2. The origins of the vegetation units are discussed and it is concluded that
 - (a) forests in the east are a response to the moist, humid conditions.
 - (b) summit grasslands are also a response to the physical environment.
 - (c) grasslands of the plateau are not the product of clearance of woodland by man. Studies of pollen have shown that even 12 000 years ago there were very few trees in these areas now occupied by grassland.
 - (d) valley forests are the result of a closed cycling of water and nutrients.
 - (e) the distribution of *Brachystegia* woodland is related to factors of altitude, relief and soils.
 - (f) It is suggested that the biotic factor in vegetation development may have been overstated and requires reassessment.
3. The paper is presented as an essay in regional biogeography and attempts to illustrate the holistic viewpoint required in the geographer's aim of landscape description.

BIBLIOGRAPHY

- BAKKER, E. M. VAN ZINDEREN (1955) A Pollen Analytical Investigation of the Florisbad Deposits (S. Africa). *Proc. Third Pan-African Congress on Pre-History*.
- BOULTON, R. and WOODALL, P. (1972) *Conservation of Terrestrial Ecological Communities* IBP/CT Guide to the Fieldwork Sheet. Rhodesia. Manuscript.
- CHALLENGER, G. (1964) The Relationship of Land Use to Ecology in the Inyanga Area of Southern Rhodesia. *The Ecology of Man in the Tropical Environment*. I.U.C.N. Publ. New Series No. 4.
- CLEMENTS, F. E. (1928) *Plant Succession and Indicators*. H. W. Wilson & Co., New York.

- DANSEREAU, P. (1951) Description and Recording of Vegetation upon a Structural Basis. *Ecology* 32.
- (1957) *Biogeography*. Ronald Press Co., New York.
- EDWARDS, K. C. (1964) The Importance of Biogeography. *Geography* Vol. 49.
- EYRE, S. R. (1963) *Vegetation and Soils. A World Picture*. Edward Arnold, London.
- (1971) *World Vegetation Types*. MacMillan, London.
- FOSBERG, F. R. (1967) A Classification of Vegetation for General Purposes. In *Guide to the Check Sheet for IBP Areas*. Ed. G. F. Peterken. IBP Handbook No. 4. Blackwell.
- JACKSON, M. L. (1958) *Soil Chemical Analysis*. Prentice-Hall. Englewood-Cliffs.
- KENWORTHY, J. B. (1970) Water and Nutrient Cycling in a Tropical Rain-forest. In the Aberdeen-Hull Symposium on Malaysian Ecology. *Misc. Series In Geography No. 11*. The University, Hull
- NEWBIGGIN, M. (1936) *Plant and Animal Geography*.
- NORLINDH, T. and WEIMARK, H. (1932-7) *Flora van Sud-Rhodesia 1-6*, being a collection of papers from Botaniska Notiser. Lund.
- NYE, P. H. (1961) Organic Matter and Nutrient Cycles under Moist Tropical Forest. *Plant and Soil* 13.
- PIPER, C. S. (1950) *Soil and Plant Analysis*. The University, Adelaide.
- PHIPPS, J. B. and GOODIER, R. (1962) A Preliminary Account of the Plant Ecology of the Chimanimani Mountains. *J. Ecol.* 50.
- SEDDON, B. (1971) *Introduction to Biogeography*. Duckworth, London.
- SHIMWELL, D. W. (1971) *The Description and Classification of Vegetation*. Sidgwick & Jackson, London.
- SISAM, J. W. (1947) *The Use of Aerial Survey in Forestry and Agriculture*. Imp. Agr. Bureau. Joint Pub. No. 9.
- SUMMERS, R. (1958) *Inyanga*. The University Press, Cambridge.
- THOMPSON, J. G. (1965) *The Soils of Rhodesia*. Rhod. Agri. J. Techn. Bull. No. 6. Govt. Printer, Salisbury.
- TIVY, J. (1971) *Biogeography. A Study of Plants in the Ecosphere*. Oliver and Boyd, Edinburgh.
- TOMLINSON, R. W. (1970) Studies on the Development and Morphology of a Peat Bog in Kirkcudbrightshire. Unpubl. Ph.D. Thesis. Univ. of Hull.
- WATTS, D. (1971) *Principles of Biogeography*. McGraw-Hill, London.
- WENTWORTH, C. K. (1930) A Simplified Method of Determining the Average Slope of Land Surfaces. *Am. J. of Sci.* Vol. 20.
- WILKINSON, H. R. (1963) *Man and the Natural Environment*. Occ. Papers in Geography No. 1. The University, Hull.

APPENDIX 1
DESCRIPTION OF VEGETATION UNITS

Site	Life forms present	Height	Function	Leaf Shape	Leaf Size	Leaf Texture	Cover	Branching Habit	Size of stem	Size of crowns	Spacing	Shape of crowns	Growth form	Others:—
	T													
	F													
	H													
	M													
	E													
	L													

Notes:

- (i) Life form : T—trees, F—shrubs; H—Herbs, M—moss or bryoid, E—epiphytes, L—lianas.
- (ii) Height : 1—above 25m, 2—10-25m, 3—8-10m, 4—2-8m, 5—0.5-2m, 6—0.1-0.5m, 7—0.1m.
- (iii) Function : d—deciduous, e—evergreen, s—semi-deciduous, j—evergreen succulent or leafless always.
- (iv) Leaf size : a—25mm² or less, b—25-225mm², c—225-2025 mm², d—2025-18225mm², e—18225-164025mm², f—164025mm²+
- (v) Leaf shape : n—needle, g—grass, a—medium or small, h—broad, v—compound, c—thalloid.
- (vi) Leaf texture : f—filmy, z—membranous, x—sclerophyll, k—succulent or fungoid.
- (vii) Cover : b—barren or very sparse, i—discontinuous, p—tufts or groups, c—continuous.
- (viii) Branching habit : a—at ground level, b—at about $\frac{1}{2}$ overall height, c—only $\frac{3}{4}$ way up.
- (ix) Size of stem : girth at breast height (4'3").
- (x) Shape of crown : a—rounded, b—flat-topped, c—pointed (e.g. conifers), d—spindle, e—irregular, f—palmoid, g—Euphorbias.
- (xi) Growth Form : E—erect, P—prostrate, R—rosette, C—caespitose, B—climbing.

APPENDIX 2

Table 1 SPECIES LIST FOR THE GRASSLAND AREAS

	Grassland with Trees					Grassland without Trees	
Sites	1	2	3	4	5	1	2
<i>Alchemilla cryptantha</i>	—	—	—	—	—	P	—
<i>Anthericum galpinii</i>	—	—	P	—	—	—	—
<i>Anthospermum rigidum</i>	—	—	—	—	P	—	—
<i>Asclepis capensis</i>	P	—	—	—	—	—	—
<i>Becium obovatum</i>	—	—	—	—	P	—	—
<i>Berkheya zeyheri</i>	—	—	—	—	—	—	1
<i>Blaeria freisii</i>	2	10	P	P	P	12	P
<i>Carex petitiiana</i>	P	—	—	—	—	2	—
<i>Carex (unspec.)</i>	—	—	—	30	—	—	—
<i>Chironia kresbii</i>	—	—	—	P	—	—	—
<i>Clutia hirsuta</i>	—	—	—	P	—	—	P
<i>Conyza welwitschii</i>	—	—	—	P	—	—	—
<i>Cyphalia sp.</i>	—	—	—	P	—	—	P
<i>Digitaria maitlandii</i>	P	10	—	P	—	40	20
<i>Dolichos kilimandscharicus</i>	5	P	—	P	6	P	—
<i>Eragrostis volkensii</i>	P	—	—	—	—	—	—
<i>Eragrostis curvula</i>	—	—	—	P	—	—	—
<i>Eragrostis sclerantha</i>	—	—	—	P	—	—	—
<i>Eriochrysis brachypogon</i>	—	—	—	P	—	—	—
<i>Elionurus argenteus</i>	—	—	—	—	3	P	—
<i>Eucomis undulata</i>	—	—	—	—	—	—	P
<i>Euphorbia depauperata</i>	—	—	—	—	—	—	P
<i>Ficinia filiformis</i>	50	—	—	—	—	—	—
<i>Gerardiina angolensis</i>	—	—	—	P	—	—	—
<i>Geranium incanum</i>	P	—	—	—	—	—	P
<i>Gnidia kraussiana</i>	P	—	2	—	P	—	—
<i>Haplocarpha scaposa</i>	—	—	—	—	—	—	P
<i>Helichrysum acervatum</i>	—	—	—	—	—	P	P
<i>H. nudifolium</i>	—	—	—	—	—	—	P
<i>H. odoratissimum</i>	P	—	—	P	—	—	—
<i>H. setosum</i>	—	—	—	—	P	—	—
<i>H. splendidum</i>	P	—	—	P	—	—	—
<i>Hemizygia teucrifolia</i>	—	—	P	—	—	—	—
<i>Hypericum revolutum</i>	—	P	—	—	—	—	—
<i>Koeleria capensis</i>	—	—	—	P	P	—	—
<i>Kyllinga alba</i>	—	—	—	—	P	—	—
<i>Loudetia simplex</i>	2	—	—	—	—	—	—
<i>Leucus milaniana</i>	—	—	—	P	P	—	—
<i>Lobelia chamaedryfolia</i>	—	—	—	P	—	—	—
<i>Labiatae sp.</i>	—	—	—	—	—	P	P
<i>Nidorella auriculata</i>	—	—	—	—	—	—	P
<i>Otiophora inyanga</i>	2	—	—	—	P	—	—
<i>Oxalis sp.</i>	P	—	P	—	P	P	—
<i>Oldenlandia sp.</i>	—	—	—	P	—	—	—
<i>Pentzia schiztostephoideis</i>	—	—	—	P	P	—	—
<i>Pentas purpurea</i>	—	—	—	—	—	—	P
<i>Pentzia schiztostephoideis</i>	P	—	—	—	—	—	—
<i>Phyllanthus retinervis</i>	—	—	—	P	—	—	—
<i>Plectranthus sp.</i>	—	—	P	—	—	—	—
<i>Protea inyangani</i>	P	—	—	—	—	—	—
<i>Pteridium aquilinum</i>	5	P	—	—	—	*	P
<i>Rendlia altera</i>	—	—	25	—	—	—	—
<i>Rhyncheletrum setifolium</i>	—	25	—	40	16	25	25
<i>Senecio scleratus</i>	—	—	—	P	P	P	P
<i>Sporobolus centrifugus</i>	—	5	—	—	10	—	—
<i>Stoebe vulgaris</i>	—	—	—	—	—	P	—
<i>Stomatanthus africanus</i>	P	P	—	—	—	—	—

(*may be 75+ in stands or may be O)

(*may be 75+ in stands or may be 0)

	Sites	Grassland with Trees					Grassland without Trees	
		1	2	3	4	5	1	2
<i>Thelypteris confluentis</i>	—	—	—	—	P	—	—	—
<i>Themeda triandra</i>	10	30	—	—	4	—	—	25
<i>Trachyandra saltii</i>	—	—	—	—	P	—	—	—
<i>Trachycalymma fimbriatum</i>	—	—	—	—	P	—	—	—
<i>Tristachya hispida</i>	—	—	30	—	—	—	—	—
<i>Tryphostemma friesii</i>	—	P	P	—	—	—	P	—
<i>Vernonia natalensis</i>	3	P	P	7	—	—	P	6
<i>Walafrida swynnertonii</i>	—	—	—	—	P	—	—	—
<i>Xyris obscura</i>	—	—	—	—	P	—	—	—

APPENDIX 2
SPECIES LIST FOR SUMMIT GRASSLANDS

Table 2

	1	2
<i>Alepedea gracilis</i>	—	7
<i>Andropogon flabellifer</i>	P	—
<i>Anthericum galpinii</i>	—	P
<i>Carex</i> (unspec.)	10	—
<i>Cephalaria pungens</i>	25	—
<i>Crassula nodulosa</i>	—	P
<i>Elionurus argenteus</i>	—	7
<i>Festuca caprina</i>	30	6
<i>Haplocarpha scaposa</i>	P	—
<i>Helichrysum latifolium</i>	P	P
<i>Hypoxis dregei</i>	—	P
<i>Hypoxis obtusa</i>	—	P
<i>Indigofera longepedicellata</i>	—	P
<i>Koeleria capensis</i>	P	—
<i>Landtia</i> sp.	10	—
<i>Ladebouria cooperi</i>	—	P
<i>Ladebouria revoluta</i>	—	P
<i>Lotus namulensis</i>	—	P
<i>Microchloa caffra</i>	—	P
<i>Oxalis</i> sp.	—	P
<i>Panicum ecklonii</i>	—	7
<i>Peucedanum</i> sp.	P	—
<i>Satyrium longicanda</i>	P	—
<i>Schoenoxiphium sparteum</i>	—	P
<i>Senecio ohlendorffiana</i>	—	P
<i>S. verdoorniae</i>	P	—
<i>Sporobolus centrifugus</i>	—	P
<i>Themeda triandra</i>	—	7
<i>Trachycalymma fimbriatum</i>	—	P
<i>Trachyandra saltii</i>	—	P
<i>Valeriana capensis</i>	—	P

APPENDIX 2

Table 3 SPECIES LIST FOR FOREST AREAS

	Optimum Forest	Dis- turbed (Veg. Unit 9)	Dis- turbed (Veg. Unit 10)	Dis- turbed (Veg. Unit 11)	Western Valley Forests
<i>Adina microcephala</i>	P				
<i>Aframomum</i> sp.	P				
<i>Agelaea heterophylla</i>	P				
<i>Annona senegalensis</i>				P	
<i>Apodytes dimidiata</i>			P		
<i>Aphloia theiformis</i>		P	P		P
<i>Asplenium rutifolium</i>	P				
<i>Aspilia pluriseta</i>				P	
<i>Canthium</i> sp.		P			
<i>Cassinopsis tinifolia</i>			P		
<i>Cremaspora trifolia</i>	P				
<i>Cyperus albostratus</i>	P				
<i>Cyperus diffusus</i>					P
<i>Cussonia</i> sp.		P			
<i>Dissotis princeps</i>		P		P	
<i>Dumasia villosa</i>	P				
<i>Dryopteris inaequalis</i>	P				
<i>Emilia coccinea</i>				P	
<i>Eragrostis acraea</i>		P			
<i>Ericaceous</i> spp.					
<i>Gerardina eylesiana</i>			P		
<i>Harungana madagascariensis</i>				P	
<i>Impatiens cecillii</i>	P				
<i>Ipomoea involucrata</i>				P	
<i>Isachne mauritiana</i>	P				
<i>Lycopodium clavatum</i>		P	P		
<i>Lygodium kerstenii</i>				P	
<i>Macaranga capensis</i>	P				
<i>Marattia fraxinea</i>	P				
<i>Myrianthus holstii</i>	P				
<i>Myrica pilulifera</i>		P			
<i>Myrsine africana</i>		P			P
<i>Mucuna poggei</i>				P	
<i>Newtonia buchananii</i>	P				
<i>Oxyanthus speciosus</i>	P				
<i>Osyridicarpus schimperanus</i>		P			
<i>Paretha johnstonii</i>		P			
<i>Peddiea africana</i>					P
<i>Phyllanthus cappilaris</i>				P	
<i>Piper capensis</i>			P		
<i>Polystichum zambesiacum</i>					P
<i>Psychotria zombanamontana</i>					P
<i>Pteridium aquilinum</i>				P	
<i>Rhus chirindensis</i>				P	
<i>Rytigynia</i> sp.			P		
<i>Schefflera barteri</i>					P
<i>Senecio tarnoides</i>		P	P		P
<i>Setaria megaphylla</i>	P			P	
<i>Tectaria gemmifera</i>	P				
<i>Tephrosia montana</i>			P		
<i>Trema orientalis</i>	P				

APPENDIX 2

Table 4 SPECIES LIST FOR WOODLAND

Species	Sites:	1	2	3
<i>Brachystegia</i> (spiciformis?)	30	30	20	
<i>Bulbostylis schoenoides</i>	—	—	—	5
<i>Carex spicato-paniculata</i>	—	—	—	P
<i>Digitaria nitens</i>	5	20	—	—
<i>Digitaria maitlandii</i>	—	—	—	15
<i>Ericaceous</i> spp.	P	5	—	P
<i>Ficinia filliformis</i>	—	P	—	—
<i>Helichrysum gazense</i>	—	P	—	—
<i>H. krausii</i>	P	—	—	—
<i>H. latifolium</i>	P	—	—	—
<i>H. odoratissimum</i>	—	—	—	5
<i>Kotschya thymodora</i>	—	—	—	5
<i>Loudetia simplex</i>	—	—	—	P
<i>Otiophora inyangana</i>	P	—	—	—
<i>Panicum natalense</i>	15	—	—	—
<i>Protea inyangani</i>	P	P	P	P
<i>Pteridium aquilinum</i>	P	P	P	15
<i>Rhyncheletrum setifolium</i>	—	10	P	P
<i>Senecio ohlendorffiana</i>	P	P	P	5
<i>Stomatanthes africanus</i>	—	P	—	—
<i>Tryphostemma friesii</i>	P	—	—	—
<i>Vernonia natalensis</i>	P	—	—	—

APPENDIX 3

PREPARATION OF MATERIAL FOR POLLEN ANALYSIS

1. Place the peat material in a boiling tube and add 10% KOH.
2. Place the boiling tube in a water bath and boil for a short time.
3. Filter through a gauge to remove the coarse material.
4. Centrifuge the filtrate. Tip off the KOH and re-suspend the pellet in distilled water. Centrifuge.
5. Boil for about 3 mins. with 30 to 40% hydrofluoric acid in a nickel crucible.
6. Pour into a Pyrex centrifuge tube and centrifuge.
7. Pour off the liquid and then add 10% HCl. Heat and centrifuge and tip off liquid.
8. Add acetic anhydride mixture and place in a water bath for about a minute.
9. Centrifuge and tip off the liquid.
10. Add glacial acetic acid. Centrifuge. Tip off liquid.
11. Add distilled water. Centrifuge and tip off liquid.
12. Add 10% KOH. Heat for a few minutes.
13. Centrifuge. Tip off liquid. Add water.
14. Centrifuge. Tip off liquid and add 6 drops of safranin glycerol jelly.