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HIGHLAND VEGETATION IN SOUTH-EASTERN NIGERIA AND ITS AFFINITIES*

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Introduction

High ground in south-eastern Nigeria (Fig. 1) forms a small extension into Nigeria of the Bamenda Highlands. The area is one of Nigeria's four main highlands but the vegetation it supports differs markedly from that on the others. Published information on the vegetation is limited, the main study being that of Tuley (1966) on the grasslands.

A number of visits to the area and reference to most of the plant collections made there have indicated the presence of an extremely rich and distinctive flora. It is thus of interest to summarize the environmental conditions with which this vegetation is associated and to consider its composition and affinities.

Environmental factors

Within the area here considered, conditions for plant growth contrast both with those at lower elevations nearby and those of the main portion of the Bamenda Highlands. Interactions between factors are largely responsible for the unusual conditions which prevail. While, for convenience, notes on the environment appear below under four sub-headings, attention is drawn to important interactions.

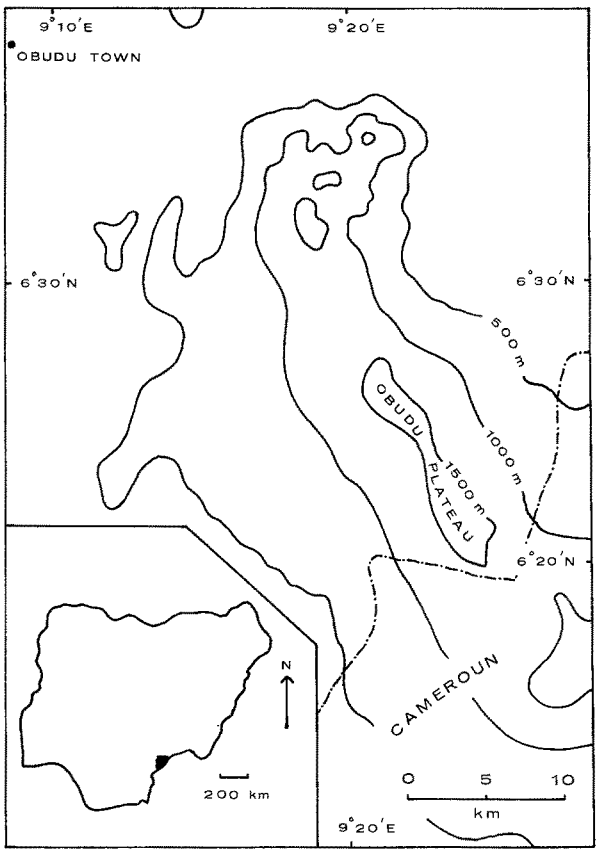

Fig. 1. Sketch map indicating location of high ground in south-eastern Nigeria. All boundaries and contours are approximate.

* Nomenclature for plants follows Alston (1959) and Hutchinson & Dalziel (1954–1972).

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Elevation and topography

No accurate contour maps of the area have been published and it is only possible to comment generally on the topography of the high ground. High, steep escarpments separate this from the lowlands (800–1000 m below) on the south, west and north. The northern portion of the high ground consists of rugged terrain; steep mountains rising to 1800–1900 m being separated by deep valleys. Closer to the Cameroun border lies an undulating area of land at an elevation of 1500–1800 m. This area (theObudu Plateau) is drained by a system of watercourses in steep-sided, narrow gullies, the floors of which mostly lie 50–100 m below the levels of the adjacent interfluves. The major watercourse draining this plateau flows in a much deeper (ca 300 m) valley into which minor watercourses often enter as cataracts.

Geology and soils

As in the surrounding lowlands, the parent materials of the soils belong to the Basement Complex and there are no volcanic rocks such as cover large areas in the nearby parts of the Cameroun Republic.

Little precise soil information is available. Tuley (1966) describes the soil under grassland on the Obudu Plateau. Hawkins & Brunt (1965) present figures for a profile also developed under highland grassland on the Bamenda Highlands and associated with roughly similar rainfall (2250–3000 mm per year) and also from Basement Complex rocks. Hawkins & Brunt present, in addition, a useful general account of the soils of the Bamenda area. They note two principal soil types derived from Basement Complex materials, terming them 'coarse-grained' and 'fine-grained' granitic. Both are highly leached with clay fractions that are essentially inactive, high cation exchange capacities reflecting high contents of organic matter. Tuley also comments on the intense leaching. The organic matter contents tend to be low (around 4–5% at the surface) but those reported by Tuley are, however, surprisingly so, considering the high surface-soil cation exchange capacity. Equally low organic matter contents are reported by Hawkins & Brunt only from much lower elevations, where they are associated with considerably lower cation exchange capacities. More details of the soils of the area are needed to explain these inconsistencies but in both studies attention is drawn to the low base saturation percentages and the soils are clearly referable to the Ferrallitic Soils mapping unit of D'Hoore (1964).

The combination of low organic matter contents and heavily leached soil derived from Basement Complex rocks is unusual. Under forest cover higher organic matter contents can be expected. Lowland vegetation other than forest occurs on Basement Complex rocks mostly in regions of lower rainfall and thus on Ferruginous Tropical Soils.

There are no relevant data for highland soils developed under forest but much higher surface organic matter and cation exchange capacity values are likely in these and they may prove to resemble closely lowland soils under forest in areas subject to very heavy rainfall.

Climate

The discussion of climate is based principally on data presented by Papadakis (1966), Tuley (1966) and Hawkins & Brunt (1965).

Only a single meteorological station, at the Obudu Cattle Ranch on the Obudu Plateau – at 1585 m – lies within the study area. The broken terrain is likely to cause some climatic variations on a local scale, such as regular temperature inversion associated with cloud persistence in places. As the study area is small, however, the data available are believed to provide a fairly accurate impression of conditions prevailing there.

The mean annual rainfall on the Plateau is about 4300 mm and the rainy season lasts for about 275 days (as defined by Walter, 1967). The variations in precipitation and in mean temperature from month to month are shown in Fig. 2. During the rainy season, which begins in late

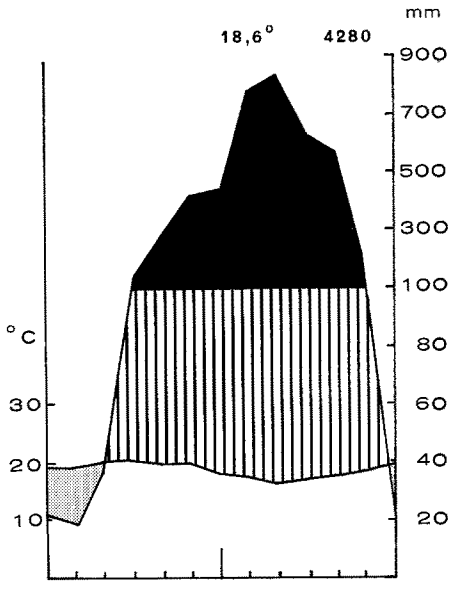

Fig. 2. Climatic diagram for Obudu Cattle Ranch (based on figures presented by Tuley, 1966).

February, rain falls very frequently – on almost every day from May until October. Not only the number of days when rain is recorded but the mean annual rainfall far exceeds that recorded at any other station in the vicinity. Within 100 km of the Obudu Cattle Ranch there is great variation in rainfall régime from place to place. On the low ground towards the north the mean annual rainfall is below 1500 mm. Less extreme decreases occur in other directions but even in the forested lowlands up to 100 km to the south values for mean annual rainfall do not exceed 3500 mm. At the highland meteorological stations in the adjacent area of the Cameroun Republic, mean annual rainfall values exceeding 3800 mm have not been reported and over most of the area the values are only 2500–3000 mm

In the lowlands to the north and north-west the rainy season commences later and is shorter. It is 30 days shorter at the only other meteorological station (Obudu town) within 50 km and is further reduced towards the north. A longer rainy season prevails, however, in the forested lowlands to the south, the difference mostly resulting from a somewhat earlier start. Compared with most of the Bamenda Highlands (though not with Bamenda town itself, which has a rainy season lasting 284 days) the Obudu Plateau enjoys a longer rainy season.

Monthly means of daily temperature maxima on the Plateau range from 18–25 °C but the corresponding minima are much more constant, ranging from 14–16 °C. In the drier lowlands, temperatures are generally higher, maxima by about 10 °C and minima by from 3–9 °C according to the month. There is also much more seasonal variation in both maxima and minima. In the wetter lowlands also temperatures are higher – by 8–10 °C in the case of maxima but by only 6–7 °C where minima are concerned. The maxima are rather more constant than at higher altitudes but the minima are a little more variable. The monthly means of daily maxima reported from the Plateau are lower than on the highlands to the east but the range differs little. Monthly means of daily minima differ much less whether value or range is considered. Only in places which experience regular temperature inversions are appreciably lower minima recorded.

Compared with the lowlands there are fewer hours of bright sunshine from April to October. During the remainder of the year, and including the dry season, there is more sunshine than in the lowlands. Yearly totals, however, reveal that while the Obudu Plateau is subject to many fewer hours of bright sunshine than the drier lowlands to the north and north-west, it receives more bright sunshine than the forested lowlands to the south. Nor is there any other highland station receiving as little sunshine during the April to October period. In the remaining part of the year certain areas of the Bamenda Hjghlands receive less than the Obudu Plateau.

The very low sunshine totals for the Plateau clearly reflect the frequency of rain and the association of a heavy cloud cover with the escarpments, particularly those first encountered by the moisture-bearing winds. This cloud cover is reflected also in the constancy of temperatures and their generally low values.

Human activities

At the present time the population density within the area is highest on and close to the Cattle Ranch (20–30 persons per sq. km.) but elsewhere it is considerably lower. Nevertheless, there has been, over a long period, considerable modification of the vegetation as a result of human activities, and despite the heavy rainfall and the long rainy season there are extensive grasslands, containing many species adapted to survive annual fires.

The date and purpose of the forest clearance which led to the development of the grasslands are not clear but it is believed that a local population dwelling in the valleys eventually made use of the grasslands for hunting, presumably using fire. More recently (until about 1947) the Fulani made annual visits to the area to graze cattle, moving away when the rains became heavy.

Vegetation

There are two main vegetation types, the grassland and the forest. The boundary between them is usually marked by a transition zone where shade-sensitive and fire-sensitive species are best represented. It is convenient to regard the vegetation of this transition zone as a third type.

Grassland (Fig. 3)

The grassland is the most extensive vegetation type, covering interfluves, upper parts of valley sides and in places even valley bottoms. Tuley (1966) gives a generalised species list for the grassland and reports five grassland associations, including the intentionally established sward of *Pennisetum clandestinum* and *Trifolium baccarinii* and the *Ctenium ledermannii* stands found at old dwelling sites.

Andropogon auriculatus, *Setaria anceps* and *Hyparrhenia diplandra* characterize the major association. The sward of this reaches a height of 120 cm and associated with the three principal species are *Hyparrhenia rufa*, *H. brac-*

Fig. 3. *Sporobolus* grassland (photograph by J. A. Medler).

teata and *Andropogon gayanus* var. *squamulatus*. Between tufts of these larger species *Panicum hochstetteri* and *Loudetia simplex* are abundant, and the cover is continuous. Various small herbs, including *Eragrostis camerunensis* and *E. tenuifolia* grow beneath the larger species. Intensive grazing of this association results in the development of a poorer sward, with *Sporobolus africanus* the principal constituent, about 60 cm in height. The remaining association occurs where drainage is impeded. *Rhytachne rottboellioides* usually predominates, forming a sward some 30 cm tall within which the smaller components are mainly those of the major association. Locally, however, a lower sward occurs consisting particularly of sedges (e.g. *Fuirena stricta* var. *chlorocarpa*, *Pycreus lanceolatus*, *P. smithianus* and *Rhynchospora rugosa*).

Hall (1971) has referred to the absence of extensive rock exposures on the Obudu Plateau. Few species typical of rocky situations occur but *Nephrolepis undulata*, *Dryopteris athamantica* and *Bulbophyllum* spp. have been recorded. Rock surfaces which remain wet for long periods carry ephemerals such as *Drosera madagascariensis* and *Trichopteryx elegantula*.

In the poorly-drained and heavily-grazed parts it is very unusual to find woody plants and these are infrequent in the grassland generally. Trees in the grassland are usually of wide-ranging savanna species (e.g. *Entada abyssinica* and *Lophira lanceolata*) and seldom attain heights of even 5 m. Smaller woody plants 2–3 m tall (especially *Harungana madagascariensis* and *Psorospermum aurantiacum*) are commoner. Climbing species (e.g. *Ipomoea involucrata*) are rare and usually herbaceous. There are many forbs present, often coarse and subwoody but rather small in size except around the watercourse gullies where the grassland grades into transition zone vegetation. Tuley remarks on the local abundance of *Pteridium aquilinum*.

The grassland flora is known to contain over 200 species. The main families represented are *Poaceae* (25%), *Asteraceae* (14%), *Fabaceae* (13%), *Cyperaceae* (12%) and *Lamiaceae* (9%).* About 80% of the grassland species are herbaceous.

Forest (Fig. 4)

Forest lines many of the steep-sided valleys separating areas of grassland It is also present on the escarpments and in rare instances on saddles or level ground.

The tallest trees rarely exceed 25 m in height and in the valleys these are those trees rooted close to the streams. The canopy remains level with the break in slope which corresponds to the forest/grassland boundary, trees towards the forest edge being shorter than those nearer the

* Usual family names: *Gramineae*, *Compositae*, *Papilonaceae* and *Labiatae* are changed according to the adopted nomenclature rules.

Fig. 4. Internal view of disturbed and relatively open forest on a level area (photograph by J. M. Lock).

streams. On the more level ground the forest canopy is generally at 20–25 m.

Among the largest trees *Carapa procera*, *Eriocoelum macrocarpum*, *Symphonia globulifera* and *Syzygium staudtii* are widespread and frequent. *Bridelia speciosa*, *Cephaelis mannii*, *Sapium ellipticum* and *Tabernaemontana ventricosa* often reach 10–15 m and there are many smaller trees and shrubs such as *Afrardisia buesgenii*, *Cephaelis peduncularis*, *Dasylepis racemosa*, *Dracaena viridiflora*, *Ochna membranacea*, *Pauridiantha paucinervis*, *Pavetta owariensis* and *Schumanniophyton magnificum*. Common climbers include *Flabellaria paniculata*, *Leptoderris congolensis* and *Mussaenda erythrophylla* and there is a varied terrestrial and epiphytic herb flora.

There is at present insufficient information to permit subdivision of the forest into associations but it is clear that considerable floristic variation exists. Some differences between the forests of the upper parts of the very wet southern escaprment and forest close to the Cattle Ranch have been noted and there are certainly variations in the field layer related to site conditions. In freely-drained situations the field-layer may be almost completely replaced by pure stands of small woody species, such as *Psychotria* spp. Towards the valley bottoms, however, tall coarse herbs (e.g. *Adhatoda robusta*) are present in abundance while various species (e.g. *Lomariopsis decrescens*) seem confined to stream banks and the rocky beds of gullies.

The forest flora is diverse (almost 300 species have been recorded), the best represented families being the Rubiaceae and the Acanthaceae – which account for about 10% and 5% respectively – where the terrestrial flora is concerned. There are many epiphytic orchids. The Rubiaceae are particularly prominent among the woody species and the Acanthaceae among the herbs. Well over 10% of the recorded forest species are vascular cryptogams. Together shrubs and trees account for about 36% and terrestrial herbs for around 33% of the species. Climbing and scandent species account for around 18% and the remainder are epiphytic herbs.

Transition zone (Fig. 5)

The closely grazed interfluve grasslands become coarser as the slopes steepen near the watercourses. Shrubby herbs become more prominent in both number and variety and scattered shrubs and trees are usually present. The most frequent of these are *Harungana madagascariensis* (3–4 m tall) and *Psorospermum aurantiacum* (2–3 m tall) which sometimes form stands with a closed canopy. Closer to the forest margin, where the clopes are steepest, *Pteridium aquilinum* and *Aframomum daniellii* are extremely abundant. Climbing species (e.g. *Raphidiocystis phyllocalyx*, *Rubus pinnatus* var. *afrotropicus*, *Sabicea tchapensis* and *Smilax kraussianus*) are particularly conspicuous at the forest edge, being present in abundance on the exposed side of the marginal trees and forming a screen behind which the forest interior is fairly open and heavily shaded. Most of the forest trees are rare or absent and there are trees typical of this vegetation type (e.g. *Macaranga occidentalis* and *Polyscias fulva*). Large coarse herbs are prominent at the forest edge, but whereas Melastomataceae, *Aframomum daniellii* and *Pteridium aquilinum* are abundant, the Acanthaceae are rare or absent. Within the forest the situation is reversed.

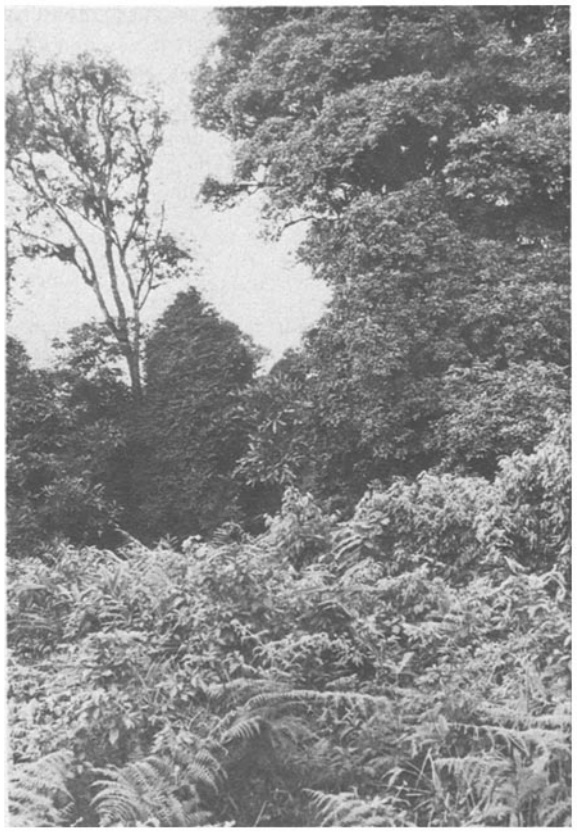

Fig. 5. Well-developed transition zone vegetation. Note *Aframomum* and *Pteridium* (photograph by J. A. Medler).

The species characteristic of the transition zone will occur away from the forest/grassland boundary provided there is adequate illumination and protection from fire. Also, as might be expected, the transition zone vegetation is in most respects intermediate in floristics between the other

types and many transition zone species occur in these. The main family represented (the Rubiaceae) accounts for about 13% of the recorded species (nearly 200). It is in this vegetation that climbers are most conspicuous and climbers, shrubs and trees together account for some 60% of the species present.

Affinities of the vegetation

Over 600 species are known from the area. In addition to recognizing the three major vegetation types, most species can be assigned to categories of 'highland' and 'lowland' plants. 'Highland' species are those which are confined to or are concentrated in areas attaining an elevation of over 1220 m (4000 ft) in Nigeria. 'Lowland' species are those of wide occurrence in the Nigerian lowlands. A number of species cannot be assigned with certainty to either of the preceding categories and are therefore classed as a 'remainder'. The representation of each category within each vegetation type and in the vegetation as a whole is shown in Table 1. The large proportion (almost half) of highland species in the vegetation is clear. It is principally this which accounts for the contrast between the flora here and elsewhere in Nigeria (including the three other highland masses).

Table 1. Representation in each vegetation type of "highland" and "lowland species"

Category	Vegetation types			Vegetation as a whole
	Forest	Transition zone	Grassland	
Highland	25	18	20	49
Lowland	10	8	10	26
Remainder	13	6	7	25
Total	48	32	37	100

Entries are percentages of the total flora (estimated at 605 species). Many species occur in more than one vegetation type and account has been taken of this in calculating the values for the vegetation as a whole.

In Table 2 the percentage, for each vegetation type, of species known also from several other areas are shown. The table emphasizes that the affinities vary between the three types and that those of the flora as a whole give an accurate impression of none of them. The overall affinities suggest that there are many species occurring also on the Bamenda Highlands in Cameroun, Cameroun Mountain, Fernando Po and in East Africa. Closer examination provides, however, indications that these relationships result from the high proportions of forest species as they are those of the areas considered with which the forest and transition zone floras display the strongest affinities. For every vegetation type strong affinities are, nevertheless, evident with the Bamenda Highland vegetation and that of East Africa and in no case are either of the two strongest affinities with another Nigerian area. This further emphasizes the peculiarity in Nigerian terms of the area's vegetation. The similarity with the Bamenda Highlands is to be expected on the basis of the contiguity of that area. The similarity with East African vegetation is a characteristic feature of Nigerian highland floras (Keay, 1959; Hepper, 1965) and is equally pronounced in the Mount Cameroun vegetation (Hall, 1973a). The forest and transition zone affinities with the vegetation of Mount Cameroun and Fernando Po are not surprising. Neither of these localities is far removed from the area under consideration and forest is extensive in both. Lower affinities – markedly lower for the forest vegetation – are indicated with the Jos and Mambilla Plateaux and the Vogel Peak Massif floras because, although none of these is much further away than Fernando Po, forest is much more restricted in extent. Where the grassland is concerned the reverse applies, there being strong affinities with the vegetation of both the Jos and Mambilla Plateaux but much lower affinities with that of Fernando Po and Mount Cameroun.

The affinities of the vegetation with that of more distant areas are of interest since they are much higher

Table 2. Approximate percentages of the flora of the highlands of south-eastern Nigeria represented in the flora of other areas

Localities	Total flora	Forest flora	Transition zone flora	Grassland flora
Europe	1	<1	1	1
South Africa	8	6	6	15
Sudan/Ethiopia	28	14	25	46
East Africa	47	33	44	69
Fernando Po	40	51	45	27
Mount Cameroun	46	53	55	35
Bamenda Highlands	57	43	63	75
Jos Plateau	26	10	30	47
Mambilla Plateau	34	22	37	54
Vogel Peak Massif	17	12	21	26
Widespread lowland vegetation (Nigerian)	26	20	24	28
Endemic	1	1	2	<1

Sources of information: Hutchinson & Dalziel (1954 - 72), Alston (1959), Hawkings & Brunt (1965), Hepper (1965, 1966), Tuley & Jackson (1971), Hall (1973b), Sanford (1971) and unpublished data.

for the grassland. The low proportion of forest species reflecting affinities with other areas listed suggests that many of the species show distribution patterns quite distinct from those that prevail among the grassland plants. Few are components of the forest vegetation occurring in the more distant areas listed in Table 2. Such differences in distribution suggest that the forest and grassland floras have originated separately from one another.

The grassland flora contains many widely distributed species which are evidently tolerant of the variations in growing conditions associated with a range of elevations. It contains also species which both within and beyond Nigeria are concentrated on areas of high elevation. The absence today from the African lowlands of the latter species has been discussed by several earlier workers and especially by Moreau (1963, 1966). Moreau has estimated that long-term temperature fluctuations in the past have greatly influenced the distributions of many of the species now restricted to high ground and thus much more frequent in East than in West Africa. Because these species appear to thrive at temperatures which today prevail at higher elevations (mean annual temperature around 19–22 °C) they were more widely distributed in West Africa during a cool period prior to about 18000 B.P. and with the subsequent increases in temperature disappeared from almost everywhere below 1200 m elevation.

In the forest vegetation also there are tolerant, wide-ranging species found at various elevations in Nigeria but while such species account for 27% of the grassland flora they account for only 21% of that constituting the forest. Species which cannot be assigned with certainty to either the highland or lowland category are, however, better represented (27%, as opposed to 18% of the grassland flora). Whereas around 64% of the highland species in the grassland also occur in East Africa, this is true of only about 38% of the highland species of the forests. Since the contribution of endemic species to the flora is negligible it is evident that the forest flora has affinities with that of areas other than the West African lowlands and East Africa. The most likely region to contain a similar flora is the forest area to the east of Nigeria but it was not possible to compile data permitting the inclusion of this among the areas listed in Table 2. Certainly, a number of species in the forest which are absent from the lowland forest of Nigeria away from the Cameroun Highlands do occur at low elevations in the Cameroun Republic and further east. There are no indications of this type of distribution with the grassland species. Thus, whilst within Nigeria many of the forest species are essentially highland plants there is no reason to associate their presence at high elevations with the lower temperatures and it is improbable that past temperature fluctuations have greatly influenced their distribution patterns. Accordingly, it is necessary to consider why such species are not found throughout much more of the Nigerian forest zone. Again, past climatic changes provide an explanation. The area's soils and its climate are today favourable for forest development. In the past 20000 years conditions in West Africa generally have varied markedly with respect to the rainfall régime (Burke, Durotoye & Whiteman, 1971). The presence of the adjacent Cameroun Highlands throughout this period will have been responsible for locally wet conditions. This must have ensured that forest species persisted here even though almost all the Nigerian forest to the west disappeared 20000 – perhaps only 5000 – years ago during dry phases. The forest associated with the Cameroun Highlands is thus much older than that elsewhere in Nigeria but forest further east has probably persisted just as long. The forest further west is mostly poorer in species and of those present many are relatively efficiently dispersed. These, entering from other lowland areas, probably spread rapidly within what is now the Nigerian forest zone when conditions suitable for forest returned. Re-invasion by species able to persist in the wetter areas on and close to the high ground would be minimal because of relatively inefficient dispersal methods. Wind dispersal is rare among the forest plants of these highlands.

Since dry climatic phases have not been associated with sufficient reduction in precipitation for the forest on the high ground to disappear a reason must be sought for the presence of a grassland flora rich in highland species. Within Nigeria the extent of the high ground is limited; it is all very wet and it is highly improbable that there has been at any time a marked rain-shadow effect. The adjacent high ground in the Cameroun Republic is, however, much more extensive and there are portions located in a rain shadow and now receiving only 1200–1300 mm of rainfall per year. At a drier past period highland and other species which now reflect East African affinities probably first became established here. Disturbance associated with the human population of the area would probably encourage the persistence and spread of these species as has been noted elsewhere (Keay, 1959; Hall, 1971). Continued disturbance would further encourage these species to spread and with time it would be possible for them to become established on the high ground of the western margin of the Cameroun Highlands, which today is part of Nigeria. The grassland flora of the Obudu Plateau and associated high ground is

thus a biotic climax vegetation which through recent human activities has replaced extensive areas of much older forest.

Summary

The environmental conditions and vegetation associated with high elevations in south-eastern Nigeria are described. The forest flora is the richest and very diverse, many families in it being represented by small numbers of species. In the grassland flora the majority of species belong to a few well-represented families. The transition zone vegetation is poorest in species but in other respects intermediate between the forest and the grassland.

The affinities of the vegetation are discussed. Highland species are very well represented throughout. The forest vegetation shows affinities with forest further east, is of considerable age and contains fewer species restricted to higher elevations because of lower temperatures there. The grassland is younger, reflects interference and many of its highland constituents have invaded this area from high ground to the east. The grassland shows high affinities with the vegetation of distant elevated areas and this is considered to indicate the sensitivity of many of the species to the higher temperatures of the lowlands.

Zusammenfassung

Standortsverhältnisse und Vegetation auf großen Höhen im Südosten von Nigeria werden beschrieben. Die Waldflora ist am reichsten und mit vielen Familien durch jeweils wenige Arten vertreten. Die Mehrzahl der Arten von Weiden und Wiesen gehört zu einigen weit vertretenen Familien. Die Vegetation der Übergangszone ist floristisch am armsten, jedoch intermediär in anderen Hinsichten.

Die floristische Ähnlichkeitsbeziehungen werden diskutiert. Hochland-Arten sind durchaus gut vertreten. Die Waldvegetation zeigt Übereinstimmung mit weiter östlich vorhandenen Wäldern, hat ein hohes Altertum und enthält weniger Arten mit einer Beschränkung auf großeren Höhen wegen der dortigen niedrigen Temperaturen. Die Weiden und Wiesen sind junger und zeigen menschlichen Einfluß. Manche Hochland-Arten haben dieses Gebiet von östlichen Hochländern erreicht. Die Weiden zeigen eine große Ähnlichkeit mit der Vegetation von weiter entfernten Hochländern. Diese Erscheinung hängt mit der Empfindsamkeit vieler Arten für die höheren Temperaturen im Tiefland zusammen.

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