

CHAPTER 6 – PROCESS & RESPONSE

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CHAPTER 6 -- PROCESS & RESPONSE

6.1 NATURAL SYSTEMS

Three ecosystem-types make up the natural systems of the study area; these are forest/thicket, savanna, and grassland. The various ecosystems and communities constituting each type will be dealt with in Chapter 8.

Forest and thicket are grouped together as both have similar structure and physiognomy and are only clearly separable on floristic criteria (Tinley 1975). Low scrub-thicket is confined to second growth on old cultivation sites, the coast dunes, and montane and coast fynbos communities. Savanna is a duplex ecosystem-type composed of a woody plant stratum of one or more layers, associated with a herbaceous-grass stratum forming the groundlayer. The tree canopy is closed to open, scattered or clumped in spacing. Apart from dwarf shrubs, grasslands are devoid of woody plants except where they are being invaded by elements of the other two ecosystem-types. In these circumstances the definition of a grassland remains inviolate until the woody invasion emerges above the grass stratum altering the physiognomy and structure to a savannoid form. The various criteria defining physiognomy, structure and community relations are dealt with elsewhere (Tinley 1975).

In the Gorongosa system of 8 200 km², savannas occupy 6 225 km² (76%), forest/thicket 1 150 km² (14%) and grasslands 825 km² (10%), a ratio of 8:2:1. Of these the largest single block of forest (300 km²) is on Gorongosa Mountain, and the Urema Plains is the largest grassland area (400 km²). Referring solely to the main wildlife concentration area of the Rift Valley, which is 3 650 km² in extent within the study area, savannas comprise 2 540 km² (70%), floodplain grassland 760 km² (21%) and forest/thicket 350 km² (10%) – a ratio of 7:2:1. The very small areas occupied by these ecosystem-types such as the strips of riverine forest, termitaria thickets and dambo grasslands are not included in the above calculations despite their disproportionate importance. Hence the above figures are approximate and merely serve to illustrate the kind of proportional relationships of ecosystems and their components under present circumstances which can be contrasted with the past and future situation interpreted in the following section.

The major pattern of the ecosystem-types is depicted in Fig 6.1, showing a central disconnected series of floodplain grasslands on the Rift floor, and forest/thicket concentrated mostly in the north and along the east with an isolated block on Gorongosa Mountain in the west. The largest savanna area comprises the Midlands and adjoining central western part of the Rift Valley floor, but this is not a solid block as it

DIMENSIONS OF NATURAL SYSTEMS

GORONGOSA ECOSYSTEM = 8 200 km²
RIFT VALLEY SECTOR = 3 650 km²

FOREST THICKET

MOUNTAIN	300
MIDLANDS	150
RIFT VALLEY	350
CHERINGOMA	350
Total	1150

SAVANNA

	260
	1.867
	2.540
	1.555
Total	6.222

GRASSLAND

	40
	5
	760
	20
Total	825

RATIO OF ECOSYSTEM - TYPES

- (a) IN ENTIRE ECOSYSTEM = 2:8:1
(b) IN RIFT VALLEY ONLY = 1:7:2

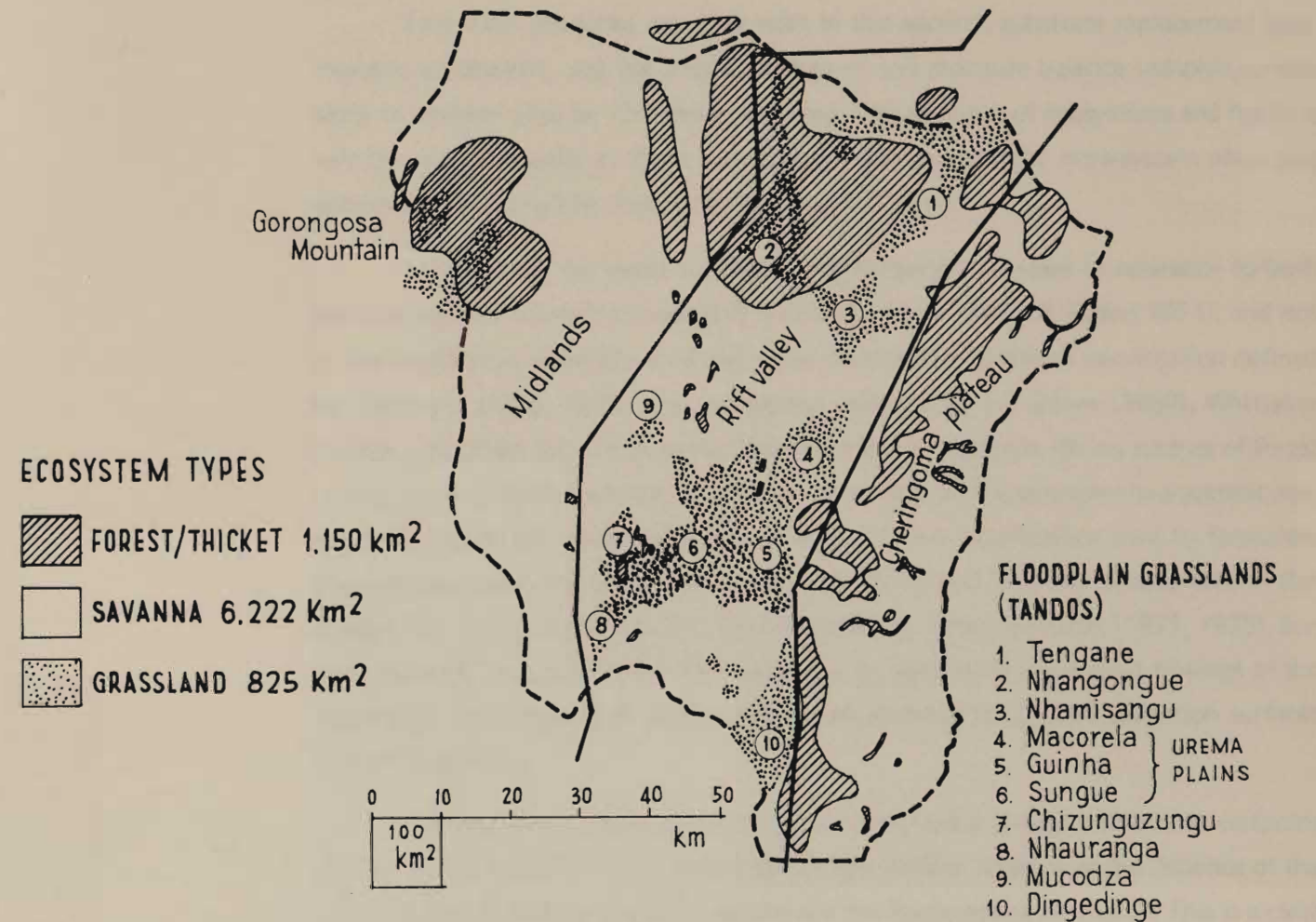


FIG. 6.1

MAJOR ECOSYSTEM PATTERNS

is traversed by a network of narrow, often discontinuous strips, of riverine forest and thicket which are the lines of contact between the larger forest/thicket blocks. On the Rift Valley floor the large island thickets on termite hills play the same role, acting as stepping stones between major forest/thicket areas.

All three ecosystem-types are associated with both denudational and aggradational land surfaces in the study area. Forest and thicket occur on erosional landforms such as scarps, incised river courses, ravines and dongas; and on depositional landforms of talus, levees, and duplex sands of splay bars and fan distributaries, and around the base of inselbergs. All these sites are characterised by having high water-retaining, yet well aerated, substrates. The savannas occur on sharply dissected hill country with skeletal soils, typified by the Midlands, as well as on low convex surfaces of depositional landforms such as the Rift Valley and coast where they are separated by microrelief from excessively flooded or waterlogged substrates occupied by grasslands. Generally the savannas are on better to excessively drained sites with seasonal contrasts in soil moisture content. By contrast, most of the grasslands in the Gorongosa–Cheringoma area owe their existence to seasonally excessive flooding or waterlogging, whether on residual impermeable soils in mountain or hill sites, on gleyed alluvia (floodplain grasslands), or on the lower parts of catenas and duplex sands (dambo grasslands) of depositional landforms. In some areas, as on the Cheringoma Plateau, new grasslands are formed on erosional landforms along the seepage slopes formed on the convex crest of retreating scarps. Both woody ecosystem-types actively invade the grasslands where excessive waterlogging or flooding is reduced.

Although ecosystems are most easily distinguished by their plant cover, on the basis that vegetation is an integrated expression of the ecosystem, certain faunal components closely tied to particular habitats are useful ecosystem and biome indicators. In this region it is far easier to use birds as faunal indicators, as the grazing components of the wild ungulate spectrum are common to both the savannas and the grasslands. However, it is possible to characterise the ecosystem-types into: a disjunct reedbuck system (the lechwe is the ideal indicator for floodplain grassland but they do not occur off the continental interior), a northern and eastern nyala/suni system, and an isolated blue duiker montane system, interspersing the larger sable, hartebeest, impala system.

6.2 GEOMORPHIC AND ECOLOGIC DYNAMICS

INTRODUCTION

The Gorongosa–Cheringoma transect provides a unique spectrum of geocological processes. In this diversity there exist extremely friable substrates subject to relatively rapid differential rates and kinds of change under the climatic regime of Recent and contemporary time. These substrates and the ecosystems they support are extremely vulnerable to natural erosional processes, and clearly demonstrate the multidirectional nature of successional changes within one area. These changes are made conspicuous by the contrasting vegetation physiognomies, quite apart from their compositional differences.

Two main processes are dealt with in this section, substrate replacement (geomorphic succession), and the in-situ changes of soil moisture balance (edaphic succession) of residual sites by changes in drainage. The response of ecosystems and habitats will be related as units to these substrate changes and specific intra-system plant and animal succession will be dealt with in Chapters 8 and 9.

In this work the terms *succession* and *dynamics* are used in reference to both geomorphic and ecologic processes in the kinetic sense (Drury & Nisbet 1971), and not in the traditional, generally accepted, rigid developmental-climax connotation defined by Clements (1916, 1928) and augmented and refined by Odum (1969), Whittaker (1970) and others for plants alone. Field evidence in southern Africa, such as of forest – the “oldest, most complex system” – occurring on the youngest geomorphic surfaces of dongas and dunes, makes nonsense of many assumptions used to formulate plant succession in the traditional context. A timely and valuable reassessment of this subject in a geocological context has been made by Drury & Nisbet (1971, 1973), but unfortunately they jeopardise their argument by dismissing some valid findings of the traditional plant ecological school, and proven evidence of uplifted planation surfaces in geomorphology.

The use of the term kinetic signifies continuous change without an endpoint (Drury & Nisbet 1971). The Oxford Dictionary defines kinetics as the “science of the relations between the motions of bodies and the forces acting on them”. This is a clear description of geocological relations, and those between the biotic associations and their components within an ecosystem. Succession in an ecosystem context can be defined simply as the sequential process of changing from one state to another through

internal and/or external influences. Such changes involve the ecosystem in its entirety, as will be demonstrated in this section, one or more of its constituent trophic or strata levels, or only a segment of one level.

The terms progressive and retrogressive are used in plant ecology to specifically signify whether lower life forms are being replaced by higher life forms in succession, or vice versa. However, in mammalian ecology the exact opposite significance pertains as the highest diversity and biomass of wildlife occur in the lower plant life form habitats (eg. floodplain grasslands), thus succession to a higher closed plant community (eg. forest) would be retrogressive from a mammalian ecological viewpoint. In geomorphology, the surface replacing another is qualified merely by young, mature, or old depending on its stage of development within the cycle. The term retrogression is defined as a return to a less advanced state, a degeneration in the attainment towards the traditional ideal of the climax community. As many discrete ecosystems within the same region show no sign of being replaced by others, they are all climax at that moment in time, but in the overall pattern of geomorphological cycles they are at the same time climax and successional. All changes are, in fact, progressive in the sense that upward, downward, lateral or cyclic (multidirectional) successional changes are occurring within a greater geomorphic cycle of landscape evolution, which in turn involves all life processes on regional and continental dimensions through geologic time.

The geomorphic cycle of erosion begins with the incision of a planation surface and passes through three stages of development – youth (initial dissection), maturity (when relief is greatest), and finally the relief is worn down to the planation surface of old age. The last stage completes one cycle of erosion, and simultaneously, provides the surface on which a new cycle is initiated (vide King 1963: 54, 202–204, Holmes 1965: 472). The controversies surrounding cycles of erosion are as legion as those which surrounded continental drift, and discussion of these aspects can be found in Pitty (1971: 48–78), Small (1972: 157–286) and Thomas (1974). The African experience across the subcontinent shows an epicyclic series, as shown by Dixey's and King's works now being substantiated by recent plate tectonic and continental margin studies such as those referred to under Section 5.3 and Thomas (1974). The use of nickpoint cycles in southern Africa is used by Partridge (1973) for correlating and dating landscape changes.

As geoecological processes are responsible for altering the soil moisture balance of substrates, a more lucid picture of interrelations is obtained by using the relevant sections (eg. Section 5.8) with the present one.

It should be emphasized that the examples of soil moisture balance from across the subcontinent, coupled with the evidence from Gorongosa, are presented not only to put the subject in greater perspective but also to counter any notion that these features are peculiar to Gorongosa, thus minimizing the far reaching implications that these interactions have outside the study area, in the field of conservation management, and in interpretations within other disciplines.

The studies from the Gorongosa–Cheringoma area substantiate and augment the outstanding works of Michelmore (1939), Smith (1949), and Cole (1963) in elucidation of the fundamental relationships of vegetation systems and substrates in Africa. It is surprising how seldom these works are referred to in ecology, particularly as they are based on verifiable field evidence across the continent.

The lack of appreciation that geomorphic surfaces and the systems they support are in a perpetual state of flux is summed by Monica Cole (1963: 290): "The views of the various writers on the African vegetation, taken either separately or in combination, fail to explain satisfactorily either the present distribution of forest and savanna or that of the many vegetation associations included within them. . . . They have failed to appreciate that geomorphological processes, themselves governed partly by the prevailing climate, are continuously modifying the relief and drainage, the soils and the micro-climate, thereby creating conditions more favourable for some plants and less favourable for others and bringing about the extension of some vegetation and the recession of others of which only relicts may remain".

Monica Cole (1960, 1963) has elucidated the relationships between vegetation and geomorphic erosion cycles. Generally grasslands or savannas occupy the planation surfaces, and forest or thicket occurs on younger incised surfaces of scarp slopes or along drainage. In the Gorongosa – Cheringoma Coast area these relationships are clearly depicted by the spatial distribution of the major natural systems. Montane grassland, Rift Valley grassland, dambo grassland, and savannas are generally related to flat or gently undulating planation surfaces. Forest and/or thicket occurs on deeply weathered slopes, stream incisions or sand deposits such as splay bars, distributory fans, scarp fans, and coast dunes. The control of vegetation on these sites is a function of moisture balance as exerted by the presence or absence of impervious horizons and the control of soil drainage by erosion or depositional processes in geomorphic succession.

In sum, periods of dissection and deposition (cut and fill) will favour forest/thicket extension due to better moisture retention and aeration, and stabler periods of planation (levelling) will promote grassland and/or savannas on soils with a poor moisture balance, often with perched impervious horizons, which are waterlogged in the

growing season and extremely dry in the winter. As these factors are the fundamental control of the disposition of natural systems they influence all life patterns and successional relationships and thus the evolution of landscapes and their living components. This theme will be expanded in subsequent sections and summarised in the final chapter.

As some Gorongosa examples show the full cycle of geocological succession in one area, they have enabled a more complete record to be obtained, which on the one hand contradicts in part some of Cole's (1963) thesis regarding system relationships with the age of surfaces, and on the other hopes to synthesize holistically the significance of these changes in an evolutionary context. Such a context comprises geomorphic, edaphic and plant interactions, and the part played by animal prime movers in the evolution of ecosystems (Ch. 8.5, 9.7 and Part III).

GORONGOSA MOUNTAIN

The striking feature of geocological relations on the mountain is the predominance of rain forest on the steeper dissected surfaces, and of grasslands on flat to strongly convex surfaces. The grasslands on the upper catchments of the Nhandare and Vundudzi Rivers appear to be extending, and the forest retreating, mainly in response to annual fires. But airphoto evidence shows that these areas are becoming lower in relief due to the action of local base-levels of resistant rock where the 1 400 and 1 500 m contours cross the valleys. This implies that change in soil moisture balance is possibly at the root of the efficiency of fire in extending the grassland cover. This cannot be verified until soil profiles have been made on the mountain summit area.

The most important event in the evolution of the Gorongosa ecosystem was the river capture of part of the upper catchment of the Nhandare by the Vundudzi. As shown by the Mucodza stream which rises on the lower part of the mountain, this zone has a lower and more seasonal rainfall, resulting in a weak perennial flow which only reaches the Mucodza marsh on the western margin of the Rift Valley at the height of the dry season. Until the Vundudzi cut back and captured the upper high rainfall catchment it too would have only reached the edge of the Rift. At this earlier time the Pungue River would have been responsible for flooding a larger shallower Urema Lake area than at present, aided by the seasonal floods of the Nhandue River.

As the Pungue River built up alluvial fans at its junction with the Rift, these blocked off and initiated new courses to the SE, cutting off the perennial supply to the Urema basin. The enlargement of the effective catchment of the Vundudzi by head-

ward erosion and river capture enables it now to traverse the Rift floor and maintain a shallow lake at the height of the dry season. This has been a fundamental factor enabling large concentrations of wildlife to develop in this sector of the Rift Valley, as elsewhere they are forced to migrate long distances due to the complete drying out of surface waters.

In the geological time scale this sole supply of perennial water to the Urema Basin, and the Nhandare flow, is doomed to ever decreasing volume due to gradual beheading of their sources by encroachment from headward erosion of the radial drainage on the western slopes of the mountain. Thus, as a natural event these two major rivers which rise on the mountain are having their effective catchment area reduced in size. Such a normally slow process can in this case be rapid as the uppermost source areas are flat, thus any microrise can form a critical height for a new divide. In this way capture of source areas by faster eroding inface, or scarp, streams diverts waters away from the major rivers which traverse the summit. Thus the concentrated flows of the Nhandare and Vundudzi are gradually being taken off into myriads of radial streams, which in separated form are ineffective as perennial water sources for the country surrounding the mountain. Shifting cultivation on the slopes of the mountain greatly accelerates these normal erosional processes, and in many places has already been responsible for altering perennial streams to seasonal flow with heavy sediment load. The contrasting muddy and clear waters in different sections of the same stream or in adjacent streams testifies to the state of their catchments.

Riverine forest/thicket occurs as a radial and annular pattern outwards from the mountain along streambanks. New riverine forest invades the incised fingers of amphitheatre drainage on precipitous mountain slopes and those developing around its base. Erosion of the larger ravines on the eastern scarp has formed cone fans and laterally confluent debris slopes covered in forest. These fans are all now incised, the trenched courses lined with narrow strips of taller riverine trees.

MIDLANDS

The sharply dissected Midlands support a sea of closed *Brachystegia* savanna. The hill and valley side substrates provide skeletal sandy and stony lithosols with narrow moister lines along the network of streams which cut their slopes. Here, strips of riverine trees connect larger patches of forest on slip-off slope deposits, and infill above resistant rocks, in the stream courses. The original Midland landscape and its subsequent alteration by diastrophic and geomorphic processes can be deciphered from the few small relics of forest-savanna-dambo mosaic on the remains of flat interfluvial crests.

EXPLANATORY NOTES FOR FIG 6.2

(1) Probable original situation (Plio-Pleistocene Surface?, now relic), as shown in interfluvium in 5A, with extensive dambo grasslands and small thicket islands of forest and savanna components on termite hills. Invasion of convex intervening ground (initial interfluvium surfaces) between termite hills is beginning.

(2) Expansion, coalescence and maturation of forest/thicket and savanna on faintly convex surfaces, with dambos confined to faintly concave surfaces (initial valley surfaces). Convex surfaces are sands and concave surfaces are either duplex sands or clays.

(3) Donga incision of dambo floor by ascending nickpoint, resulting in increased runoff and decrease of waterlogging. Termite hill initials forming on dambo drainage and first invasion taking place by forest and/or savanna components. riverine trees invade along the fresh donga cut. If dambo soils are base-rich they are invaded by arid savanna components (eg. acacia and mopane).

(3A) If dambo soils are duplex sands they are invaded by dry forest.

(4) Headward migration of nickpoint and lateral dendritic incision of dambo. Remaining dambo soils now only seasonally waterlogged. Maturation of forest and/or savanna on dambo. Increased velocity of sheetwash off the dambo margins and erosion of interfluvium sands.

(5) Complete removal of dambo soils and the systems they supported, replaced by sandy lithosols derived from the underlying crystalline geology and the formation of shallow V-shaped valleys. Valley widening by wearing back of streamheads eating into the interfluvium, removing the sands and thus reducing the area under forest to narrow irregular strips on the interfluvium crests. Extension of miombo or mixed savanna onto most surfaces, and riverine trees up all stream cuts.

(5A) In its development to stages 6 and 7 valley cutting may exhume a resistant rock barrier which acts as a temporary base level and causes aggradational sequences to occur upstream of the barrier. These features include braided river beds, slip-off slope deposits, confluence deposits, and valley side fan and splay deposits all of which are typically invaded by the forest/thicket ecosystem-type. Incision of the structural barrier leads to stage 7. Dambos surviving on the remaining broad interfluvium and the stage described above are best shown in the area immediately west of Gorongosa Mountain.

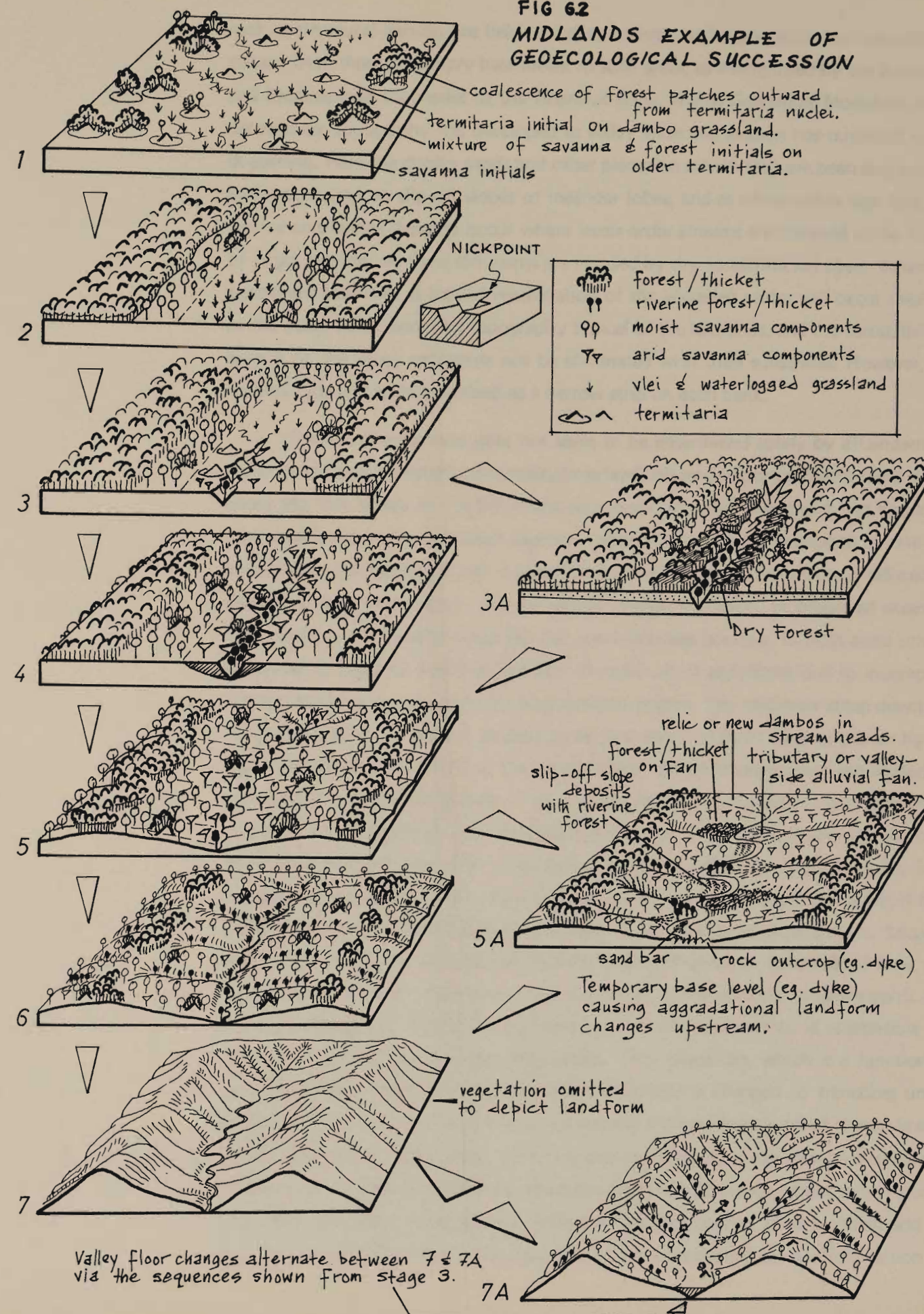
(6) On the interfluvium the remaining sands and their forest cover are reduced to isolated remnants, and savanna extends. Renewed valley cutting leads to stage 7.

(7) The present stage of landscape evolution over most of the Midlands: valley and spur topography. Deep V-shaped valleys with narrow interfluvium and fine dendritic tributary patterns. Sandy lithosols predominate and are covered in an unbroken closed miombo savanna. Narrow strips of riverine forest along streambanks, dambos mostly extinct.

(7A) In valley heads deep valley cutting can alternate with phases of aggradation forming new dambo systems, often with steeply inclined floors. The dambo infill may be eroded via the developmental processes from stage 3.

SUMMARY: The least number of ecosystems and communities occur in the primary stage (1) and in the present mature stage (7). The greatest diversity occur in intermediate stages 3, 3A, 4 and especially in 5A when a new series of landforms are developed by aggradation.

FIG 6.2
MIDLANDS EXAMPLE OF
GEOECOLOGICAL SUCCESSION



Immediately west of Gorongosa Mountain, on the broad interfluvium between the Nhandue and Vundudzi (Midland) Rivers, are areas of low undulating terrain with dambo grassland on the concave or flat surfaces, and forest patches surrounded by savanna on the faint convex surfaces. This mosaic system represents the remains of the Midland planation surface and is replicated today, in form if not in kind, by the extensive dambo-forest mosaic of the Cheringoma Plateau at present undergoing rapid surface replacement. These substrates (not necessarily the ecosystem they support today) are relic end-Tertiary planation surfaces. Change in base level, and downwarping with renewed faulting in the Plio-Pleistocene, set in train another cycle of headward incision whose nickpoints have now reached the relic dambos on the broader interfluvium crests. Some of these dambos have been protected by outcrops of resistant rock. Elsewhere this dambo-forest mosaic has been stripped off by erosion to expose skeletal sandy and stony lithosols formed on the underlying Precambrian metamorphic rocks as the rivers entrenched their courses. Some of the deepest remaining soils are on the crests of the sharply dissected interfluviums.

The salient features of this geoecological sequence shows forest/thicket and/or savanna (depending on the soils) initially on the oldest surface (the interfluvium crest) and grassland on the dambo, the youngest surface. Savanna occupies the deeper sands on the crest and the margin between the dambo and the forest (Stage 1 in Fig 6.2). Nickpoint incision changes the entire water balance of the dambo and the hygrophilous grassland is invaded by thorn savanna, if they are base saturated clays, or by dry forest if the dambo soils are duplex sands. At the same time riverine forest/thicket invades the donga incision. The donga represents the first phase of surface replacement, by which the dambo soils will be stripped off and lateral valley widening will consume the sands on the interfluvium crest, thus reducing the area of forest/thicket (Stages 2 to 4). Up to stage 4, therefore, the forest ecosystem-type occurred on the oldest local geomorphic surface, and was reduced by valley side erosion to remnants and finally extinguished by erosion processes. At the same time this type now invaded the youngest local surfaces (donga and drained dambo soils), leaving the savanna ecosystem type on the oldest local surface. In the subsequent stages, and perturbations within the cycle (Stages 5 to 8), savanna is the oldest system on the oldest local geomorphic surfaces, although these hill substrates are undergoing sheetwash, and forest is the newest, invading on the youngest eroding surfaces of streambanks and valley deposits which have the best water relations. Where dense dendritic drainage develops on hill and valley sides, riverine forest/thicket can occupy as much area as the intervening savanna cover.

Except for the old planation remnants, the stage of old age is not attained anywhere in the Midlands, although locally in some tributary basins exposure of resistant

rock, a structural barrier, has held up valley incision and aggradation has occurred upstream from these temporary base-levels. In such areas, as exemplified by the Burumazi and Mudicapinda tributaries of the Nhandue River, NW of Gorongosa Mountain, a low polyconvex topography has developed as valley widening erosion has outpaced valley deepening. Here the duplex sands, and other planation substrates, have been stripped off and redeposited on slip-off slopes of meander lobes, and as lateral valley side fans. Extensive confluence deposits occur where lesser order streams are dammed up by floods of larger streams; all these sediments are invaded by dry forest/thicket cover. When the temporary base-level is incised, rejuvenation of the aggraded sector will occur resulting in the steep valley and spur topography typical of the Midlands, and the forest/thicket system on the valley sediments will be eliminated with their substrates. However, the riverine type will replace it, albeit as a narrow strip on each bank.

Dambo development does not seem to be determined solely by attainment of grade or the occurrence of a temporary base level. Many dambos on the Midland slopes above the Rift Valley in the SW of the park occur in valley heads with flat floors sloping downward to ten or fifteen degrees. These appear to have developed by one or a combination of factors. Either concentrated flow has been disrupted or reduced by beheading from more active tributaries and headward erosion, or phases of excessive mass wasting and sheetflow aggrade the upper drainage sources. In both cases unconcentrated or lessened flow has resulted in build up of sediments due to incomplete transportation and its fixation by hygrophilous grasses. The relatively steep down valley gradient of these dambos appears to be as a result of sheet wash as shown by the high pedestalled grass tufts on the dambo floor. Where these dambos are incised by ascending nickpoints, the original V or U valley shape is exhumed. Thus phases of degradation and aggradation in Valley heads could also be related to pluvial and interpluvial influences quite apart from the presence or absence of temporary base levels. Such dambos may be able to lower, and thus narrow, their floors by sheetwash alone if they are sufficiently protected by their grasscover from nickpoint development. Leopold *et al* (1964) point out that since an increase of precipitation, or canalizing of flow, will trench valley alluvium if sediment load is reduced, either climatic or geomorphic factors can change the relation of sediment load to discharge which is responsible for changes in depositional and scouring phases. Thus planation, which is a function of sediment-loaded waterflow and base-level restriction, is changed to trenching under the same discharge when sediment is reduced and the base-level lowered (Leopold *et al* 1964). Removal of plant cover on hill slopes by cultivators can alter this trend in a relatively short time as shown by examples from the Midlands, where many incised rivers and low order streams have choked or braided courses filled by sheet and rill erosion of the valley heads. This example of a man-activated cause of deposition on

hillslopes shows that steep dambo floors can be formed at the heads of streams by an excess of available detritus moved during one or two rainstorms of high intensity. The new sediments are fixed by hygrophilous grasses and further sheetwash sediment is trapped by the cover. Under natural conditions of dambo formation at the heads of streams, a similar situation would seem to be required where groundcover was relatively sparse on an excess of mass-wasted material moved by an intense rainstorm occurrence of short duration. In other sites clearing of cover for cultivation initiates nick-points and causes deep donga erosion and heavy sedimentation downriver smothering crops and habitation. Careless land use activities, including overstocking, accelerate natural processes and can initiate new cycles of erosion.

The process of headward erosion and backwearing of slopes giving rise to isolated mesa, butte and koppie remnants on the one hand, and exhumation of hard massive rock cores, such as Bornhardt or domed inselbergs, by truncation of a deeply weathered regolith (Thomas 1974), on the other, produces outcrop relics and new outcrop surfaces respectively. The difference in origin and evolution of these two inselberg types has far reaching implications in the dynamics of biogeographic relations. The remnants from backwearing processes present disjunct relics of systems which were once far more extensive and continuous expanses associated with one of the landscape facets, such as escarpment or riverine forest, and grasslands or savanna of the oldest planation surface on the summits. In other situations, forest is on the oldest, highest surface and is replaced by savannoid systems on the backwearing slopes and pediments as shown in Fig 6.2. This represents a sequence of fragmentation, and eventually extinction with elimination of the topographic remnants. The second outcrop type becomes larger in surface area with each erosion cycle exhuming further resistant rock which could lead to fragmentation of other systems, and coalescence and predominance of the outcrop surfaces. However the Bornhardt inselberg type also undergoes weathering and erosion as traced by Thomas (1974).

The effectivity of prominences in trapping rainfall to their precincts is evinced by the occurrence of forest/thicket on easterly and southerly aspects, facing moisture-bearing winds, and the contrasting insolation and weathering regimes of these moister aspects with the drier northerly and westerly aspects. Small outcrops support forest/thicket, due primarily to deep percolation and better retention of rain water along joints and fissures compared to the surrounding plains. Any advantage afforded this cover from fire or the concentration of weathered minerals in the vicinity of outcrops is of secondary importance.

The deep NW–SE valleys of the main rivers crossing the Midlands, and their tributaries transverse to this, provide a dense criss-cross pattern of moister poleward

and eastward facing slopes and drier equatorward and west facing slopes. This kind of slope differentiation contrasts with that of the adjacent Rift plains and the broad flatter interfluvial areas on the Midlands where there is no aspect differentiation except of the microscale.

From the above account it may be thought that the replacement of a "simple" plainsland landscape by a deeply incised "complex" mature hill and valley landscape, as exemplified by the Midlands, implies equal or parallel diversification of ecosystems because of the exposure of new land facets and aspect differentiation. The Midlands example, however, shows that ecosystem diversity is not necessarily synonymous with, or a function of, topographic diversification when all substrates are derived from a single lithology. The Midlands are covered predominantly by one ecosystem, a closed canopied miombo savanna, whose monotony is relieved only by forest/thicket strips along streambanks and around the bases of occasional rock outcrops. In the Gorongosa – Cheringoma transect, the Midlands support the poorest diversity of ecosystems and the richest occur on the Rift Valley floor and the coast – both plainsland surfaces.

RIFT VALLEY

The Rift Valley plains have been formed predominantly by sequences of alluvial fan deposits from rivers debouching from the high ground on both sides of the trough. The sorting and differential emplacement of coarse and fine sediments, in and between fans respectively, has given rise to the two major features of the Rift floor: (a) sandy distributary channel fillings now supporting forest/thicket, and (b) slack basins or flats of fine clays which form the extensive open floodplain grasslands (Fig 6.4). The slacks are composed of the finer flood sediments, deposited in slack water or shallow lacustrine conditions formed by ponded flood waters. The deposits between fan distributaries, formed by braided drainage with bars and splays, are either of mixed sediments, sandy clays, silt loams and fine sands supporting savannas, or of fine clay in interdistributary slacks.

The terminology used here is basically that given in the introductory textbooks on geomorphology by Lobeck (1939: Ch 7) and Thornbury (1954: Ch 7). More comprehensive treatments of fluvial processes are given by Leopold *et al* (1964) and Chorley (1969). In dealing with fluvial deposition, confusion can result from the variety of synonyms used for floodplain features. The Urema Basin sector of the Rift trough does not conform to the classic or typical floodplain, which is formed by the lateral swinging of a river passing through an area of low relief, exemplified by the adjacent lower Pungue River and the Zambeze Delta. As noted in Section 5.6 and

above, these floodplains have instead been formed by a process of centripetal drainage from the sides of the trough, the present floodplain surfaces comprising the irregularly shaped, shallow basins formed between the outer edges of alluvial fans. Terms such as backswamp, swale, slough, slade or slack could be used for these "fanfront" deposits. The term slack is preferred as it most accurately describes a situation of ponded floodwaters. Apart from this basic difference in origin all features typical of floodplains occur on the Rift floor.

It is likely that with the original formation of the Rift Valley, the Zambeze River, or at least its floodwaters, contributed in large measure to the build up of the alluvium underlying the present Rift Valley plains. One confluent floodplain system probably existed from the lower Chire River to the Buzi, and possibly the Save Rivers. This subsequent drainage was then pinched off at intervals by the growth of alluvial fan deposits derived from both sides of the trough, especially from the larger rivers which originate inland. Of these the seasonal Nhamapaza River built up sufficient alluvium across the Rift floor to form a low divide 59 m above sea level, thus effectively separating direct confluence of Zambeze and Pungue waters.

The Nhamapaza, Nhandue, and Pungue Rivers, of which only the last is perennial, have formed the most extensive fan areas reaching across almost to the base of the Cheringoma Plateau, as is clearly shown in Fig 6.3, and becoming confluent in parts with those formed by the inface drainage of the cuesta. That the building of fans is a function of flood periods and sediment availability in the catchment, is well exemplified by the seasonal Nhamapaza River which has formed by far the largest alluvial fan area, only the southern part of which is shown in Fig 6.3. Unlike the Pungue and Nhandue a large part of the Nhamapaza River's catchment area is on extremely friable Continental Cretaceous argillaceous sandstones.

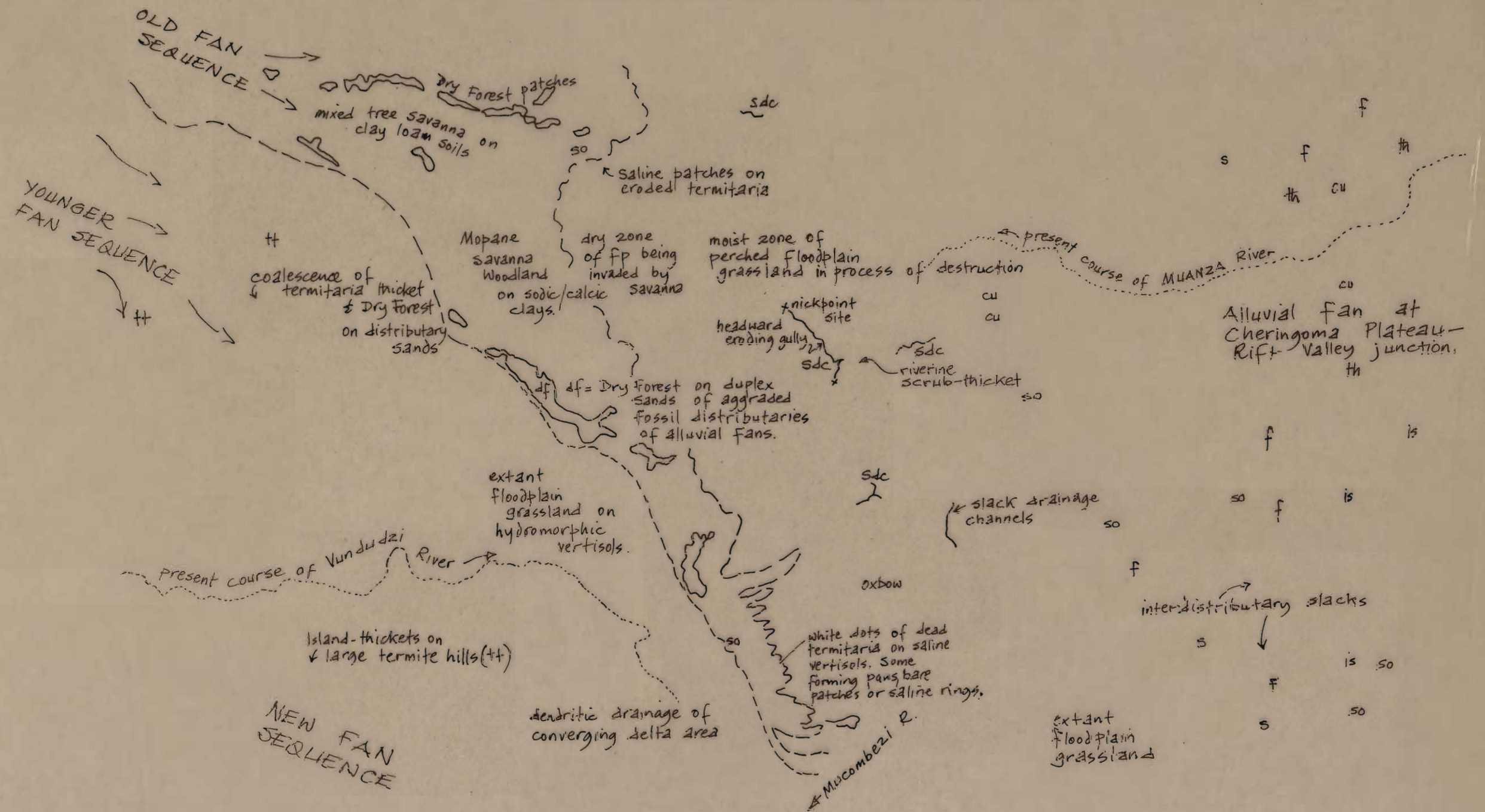
Alluvial fans grow by the repeated lateral shifting of distributary streams as their courses become filled with coarser sandy sediments, to above the level of the surrounding fan. This and their blockage by alluvial deposits, such as splays and bars from colliding flows causes streams to spill over and follow lower courses in the fan surface. All the sediments are waterlaid, and excessive seasonal flooding would have maintained floodplain grassland and marshes over the entire Rift floor. By this means, channel fill deposits are aggraded to above excessive flooding, and the lower interdistributary slacks formed by overbank deposits during floods become the new distributary courses. Distributary courses aggraded to above the general level of their fans are thus the first surface available above flooding for invasion by hill building termites and woody plants. In time, the main river is closed off on all sides by its own alluvial deposits and at this stage floods break through along the lowest part of the fan, trenching into the

fan deposits. Once trenching occurs, the braided or anastomosing fan drainage become fossil; left high and dry above the reach of river flooding although some of the old unfilled abandoned courses may flow briefly during exceptional floods. The anastomosing channel of braided drainage are separated by channel bar deposits which grow upward, and like the levees, can become some of the first surfaces available for woody plant invasion. All these processes are clearly portrayed on the Rift floor.

All the fans in the study area have been trenched, and modern sediments are deposited at the junction of the canalized river courses with the major interfan Urema slack, where new fan and slack material is being superimposed over the old in front of the earlier fans. New deposits are also occurring within the slack basin at the head of the Urema Lake, gradually filling in the shallows adjoining the converging delta of the Vundudzi – Mucombezi Rivers. The Urema slack basin has also undergone deep drainage incision to over 10 m below the adjacent floodplain surfaces, and active headward donga erosion is in the process of destroying all other slacks or floodplain surfaces.

The extremely small modern fan sediments being formed indicate that the rivers which built the original fan and slack floodplain system either had much larger discharges and sediment loads, or similar discharges as present but with higher sediment load. Leopold and his co-workers (1964, Ch 11) discuss the relation between rainfall, vegetative cover and sediment yield and suggest that in moist areas an increase in precipitation would result in a more complete vegetative cover thus cutting down the sediment yield, resulting in incision. This implies that lower rainfall with sparser plant cover would lead to greater sediment loads and thus aggradation, but they remark that donga *cutting* seems to be generally related to aridity (p. 453). Their data does not allow for a definitive answer as equal and opposite effects occur under different conditions of cover and substrate friability in different areas with the same rainfall regime.

The typical floodplain features of levees, splays, meander scrolls, cut-off meanders and backswamps developed by a meandering river system is shown by the Vundudzi, Mucombezi, Urema and Pungue Rivers. In traversing a flat area moving water is forced into a deranged course by the irregularities of microrelief, and by deposition on the inside of curves and erosion of the outside, indefinite drainage is transformed into meanders (Lobeck 1939: 227). As the river incises its course, undercutting of the outer curve increases as the slip-off slope deposits grow on the inside of curves, and these processes lead to narrowing of the neck between loops until the river cuts across the neck shortening the river course and steepening the local gradient. Growth of the point bar deposits enlarges the meander at the same time as the neck is being eroded. In this way meanders are continually changing their positions, migrating downstream, and leaving behind cut-off meanders and meander scrolls as evidence of their previous positions (Lobeck 1939, Thornbury 1954).



- tt termitaria thickets
- f forest
- th thicket
- is inter-distributary slacks
- sdc slack drainage channels
- cu cultivation
- df Dry Forest
- s savanna
- so sodic areas

PLATE 7 TYPICAL JUXTAPOSED PATTERN OF FAN-SLACK ALLUVIOCATENA SEQUENCES
ON THE UREMA RIFT VALLEY FLOOR

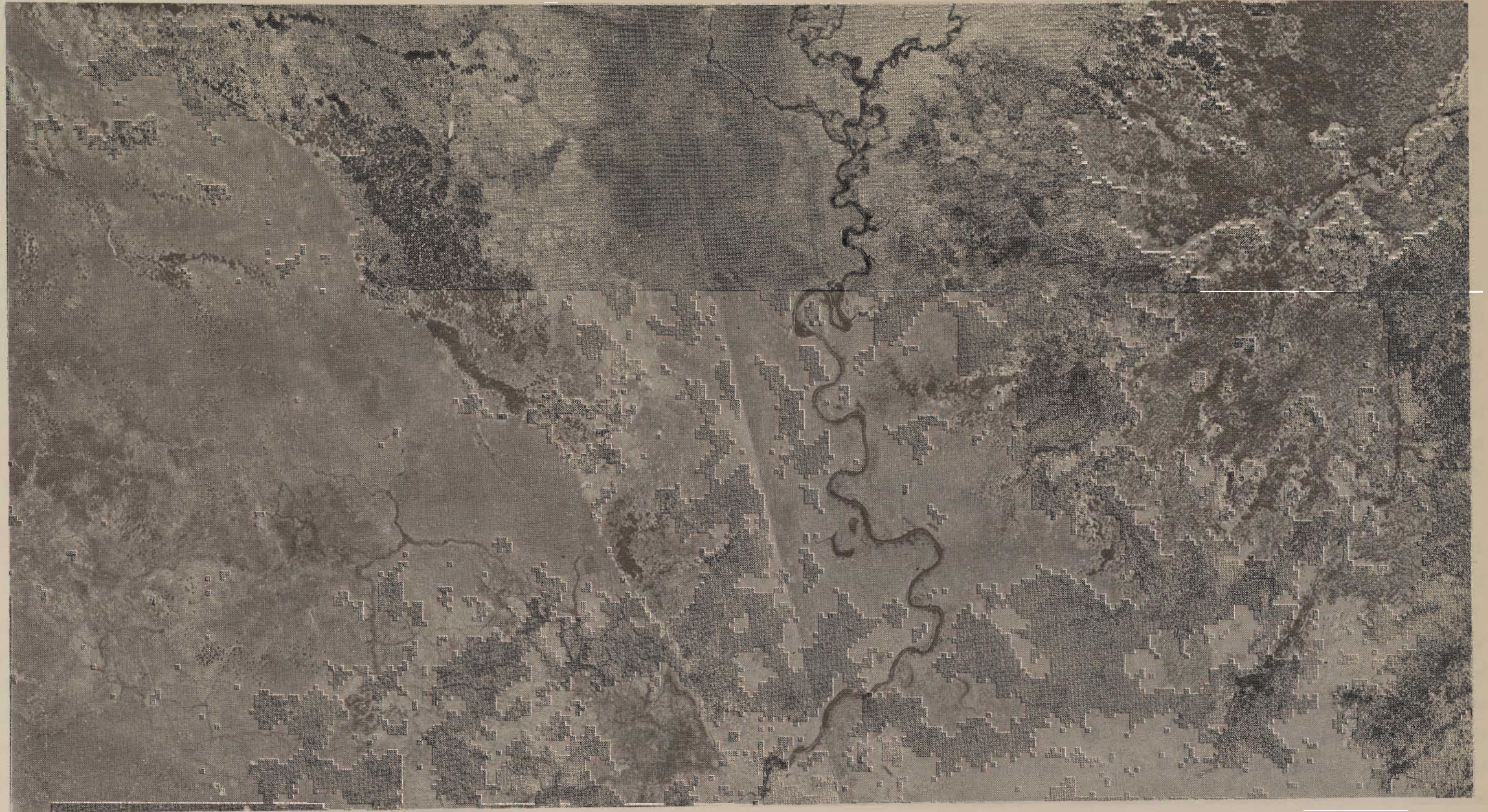
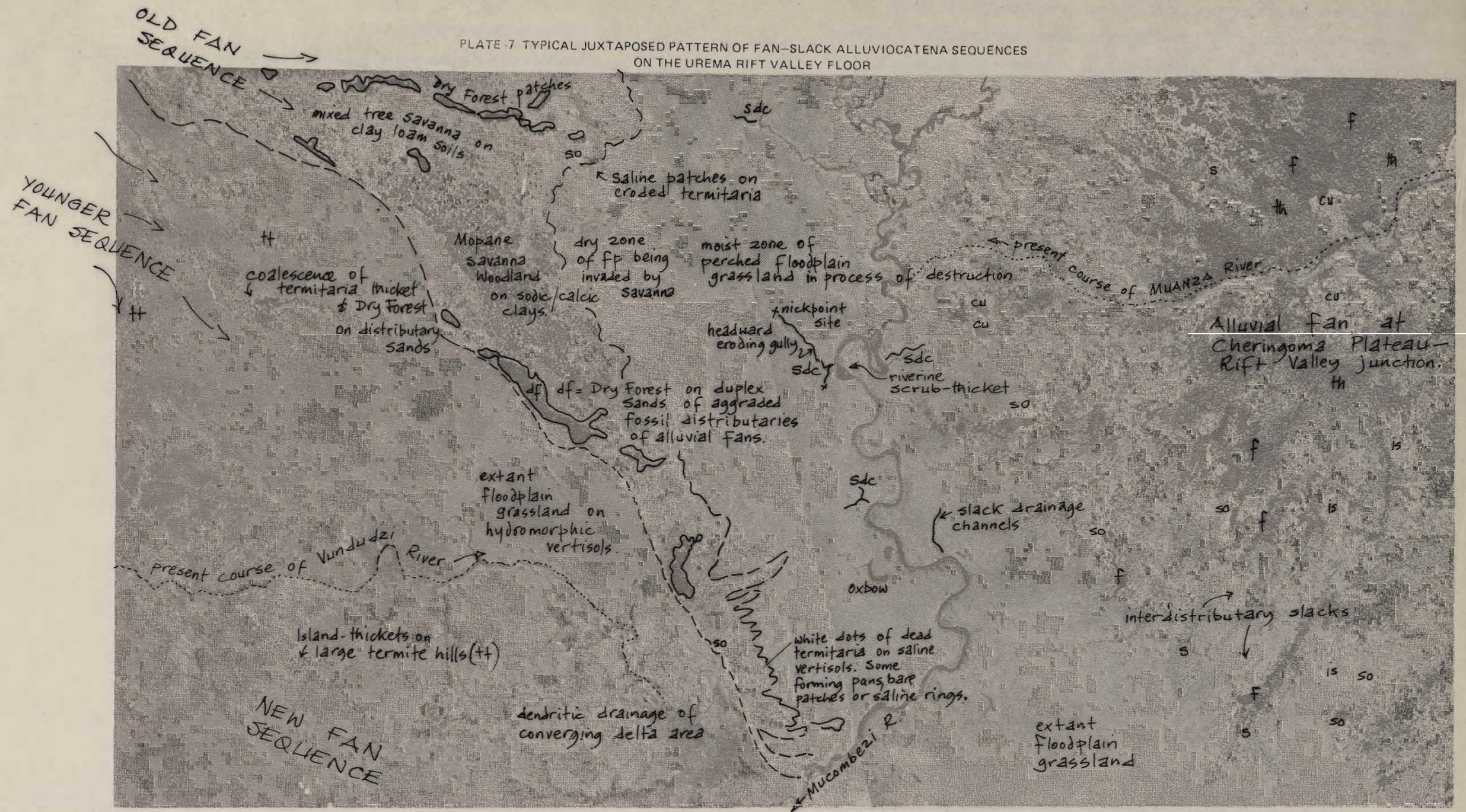


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The deposits formed on the slip-off slope, referred to as meander scrolls or point bars, are typically an arcuate series of alternating ridges and shallow troughs clearly defined by wooded cover on the rises, alternating with grass in the depressions. Levees are formed along the immediate river banks by overbank deposits during floods and where these are breached, splay deposits are formed by coarser channel fill sediments. The finer material is deposited away from the river in backswamps when the levees are overtopped.

Breached levees are self-sealing by the plug of splay material, if the backswamps are flooded at the time. Where backswamps are drained by incised flood breaches lower down in the course, the splays are cut through and new river channels are formed across the backswamps when they are the lowest part of the floodplain profile. This entire sequence is shown in the Dingedinge tract at the confluence of the Urema and Pungue Rivers (Fig 10.3). In this example, the Urema has incised its course lower than the braided Pungue River bed upstream from their junction, and the inner levees on both rivers have been breached and deeply incised. Through these breaks the Pungue River has formed a new course which cuts across the confluence marshes, and is in the process of rapidly eroding and drying them out. Primary stabilizers of splay deposits are reeds, followed by woody plants.

The distribution of vegetation on the floodplains reflects conspicuously every nuance of deposition and erosion. In particular, it reflects those processes which alter the degree of flooding or waterlogging either by the differential sorting and deposition of sediments, providing a microrelief of lower and higher surfaces, or by closing off or draining surfaces, ie. by blockage or erosion of alluvial plugs. Thus, the grassland ecosystem and associated grassy marsh areas occur on the following flat, faintly sloping, or faintly concave surfaces: fanfront or interfan slacks, interdistributary slacks, backswamps, abandoned channel fillings, point bar swales or sloughs, and splays. All these are subject to the rule of effective flooding or waterlogging for the maintenance of hygrophilous grasslands. Where this is lost the grasslands are invaded by the two woody ecosystem types. All the faintly convex surfaces such as levees, fan and splay channel bars, point bar ridges, flood plain terraces, and incised surfaces are invaded by one or both of the woody ecosystems. As on emergent fan surfaces, hill building termites invade all microconvex surfaces, whether depositional, or exposed by increase of drainage. The hills are typically the first surfaces to be colonized by woody plants, even on abandoned aggraded river courses, and these island thickets are in many areas the nuclei for woody plant invasion of the intervening ground when flooding or waterlogging is reduced to a tolerable state. The intervening surfaces are also invaded from the apex of fans and the higher colluvial filled margins of the Rift.

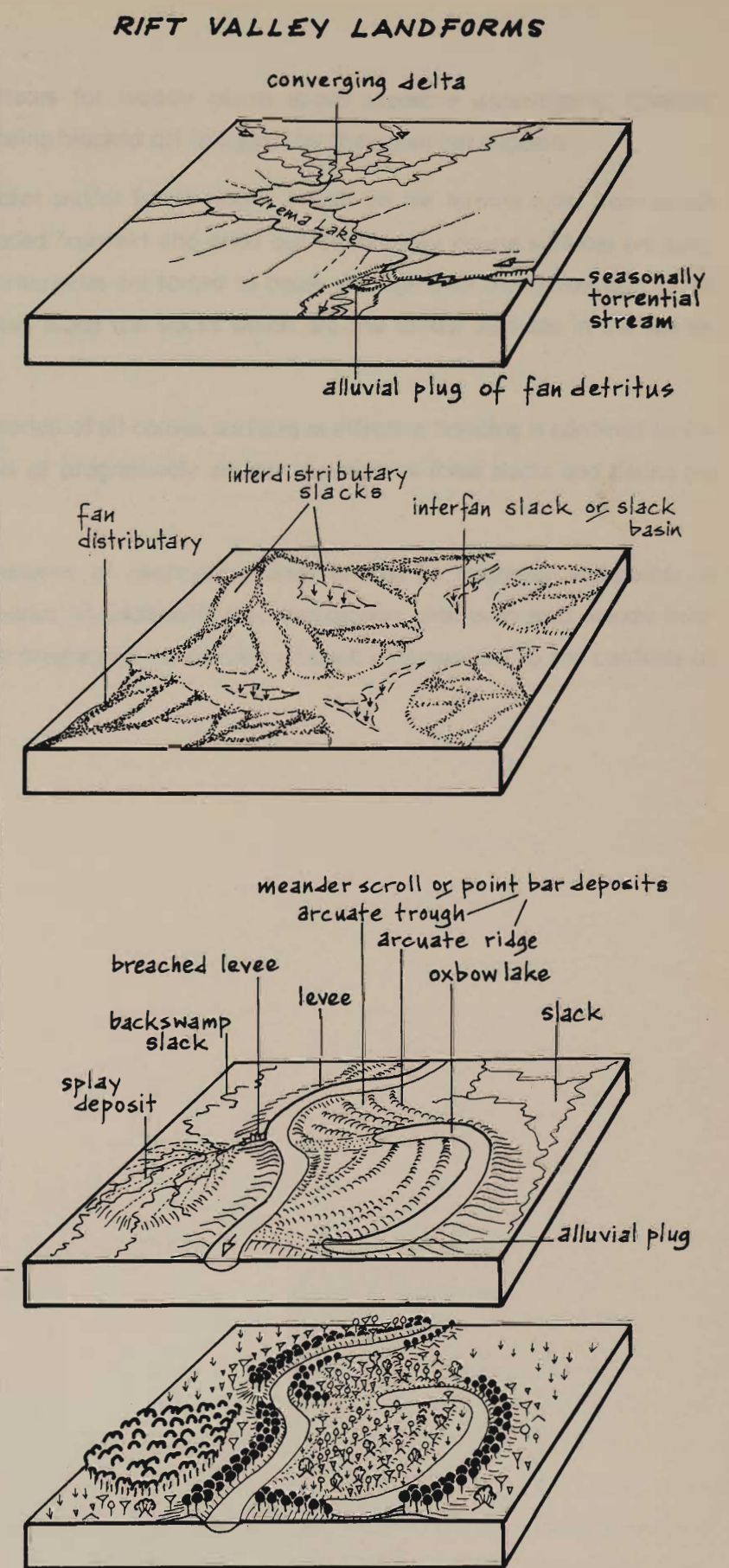
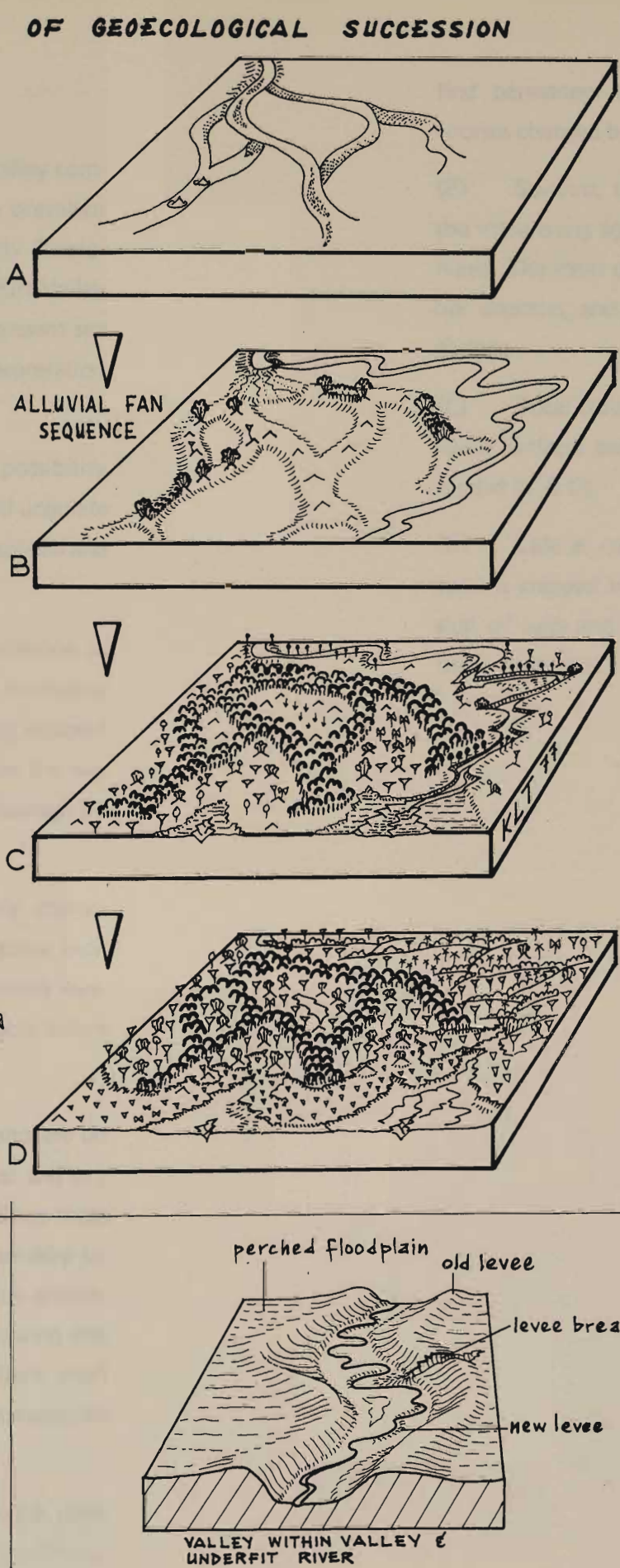
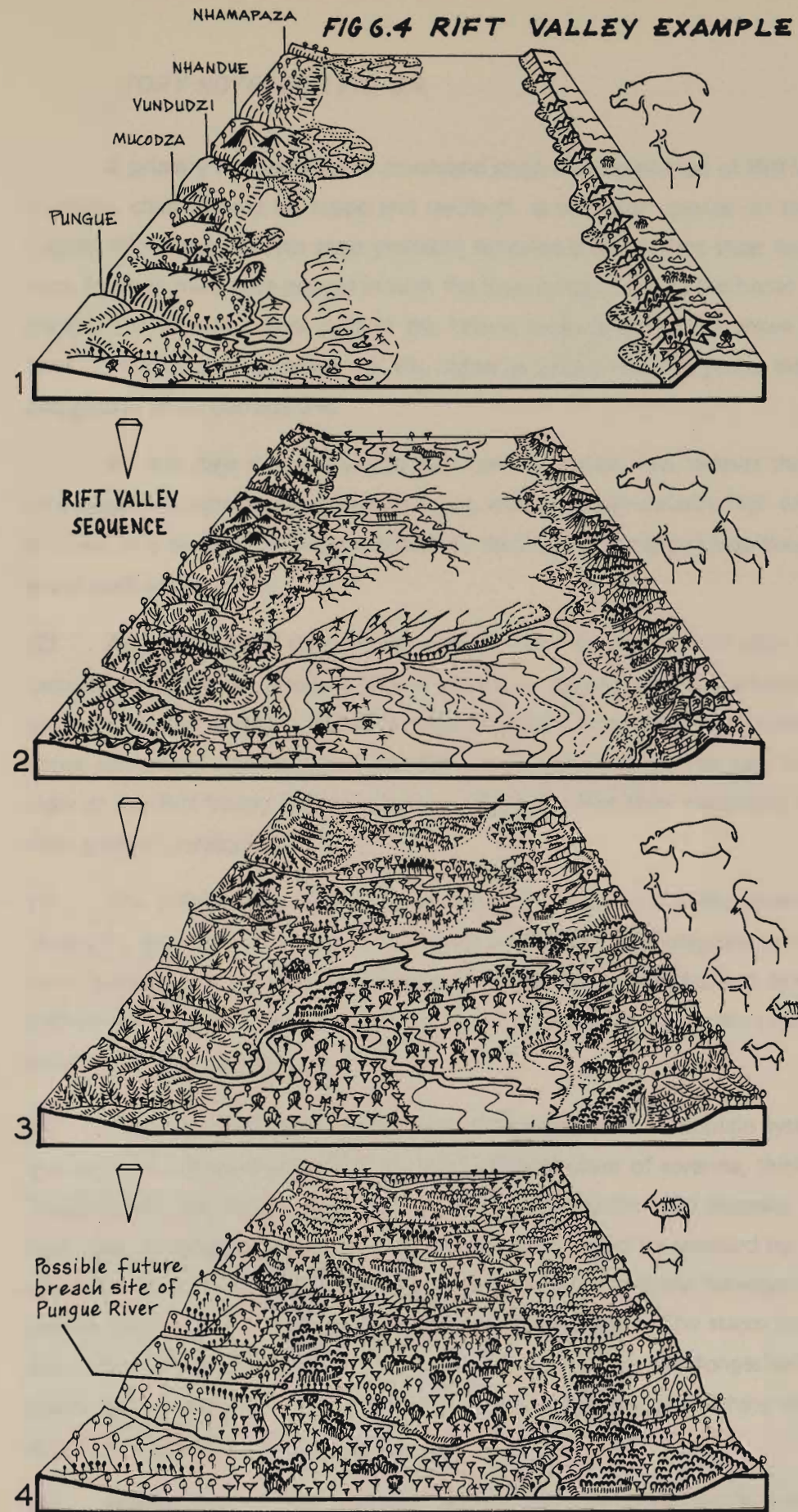
Substrate differentiation by sedimentary processes alone has resulted in a complex of alluvio-catenas, mosaics, overlap and interdigitation, made clear by the distinctive vegetation they support. Superimposed on this is the overriding primary control of flooding, the influence of which is directed by microrelief and changes in drainage. As pointed out in the sections on soil (5.7) and soil moisture balance (5.8), excessive flooding or waterlogging results in a single hygrophilous grassland made up of a large variety of plant associations, themselves related to soil properties, which in turn are affected by microrelief and duration of flooding. Progressive reduction in excessive soil moisture is the release to habitat diversification, and it is this factor alone which permits invasion of woody plants, the composition and successional tendencies of which express the climo-edaphic properties and changes in these relationships.

Microrelief is developed by disparate vertical and lateral accretion of sediments and by animal activity. Deposits laid by exceptional floods, or through gradual upward growth, are put out of reach of prolonged flooding allowing the invasion of woody plants. Once established, many species can withstand floodwaters of several weeks duration. Levees are an example of surfaces that grow upward away from flooding and become exposed to erosion and woody invasion. Simultaneously, these irregularities are accentuated by coactive changes in local drainage due to the fluvial processes themselves and their erosion by changing base levels.

In flat maldrained terrain, small surface irregularities can have far reaching effects on drainage, and thus on succession and primary productivity. Water movement is, to begin with, hindered by gravity resistance and the edaphic properties of the surface. A faintly concave surface of any dimension forms a marsh covered with hygrophilous grasses which provide green pasture deep into the winter dry season. A gap or furrow, as little as 10 cm depth, (such as a hippo path for example) in the sill rimming such a surface effectively 'pulls the plug out' and transforms these marsh surfaces into dry land systems which are then invaded by savanna. Many of these potentially long lasting marsh and pan areas are easily restored by the simple expedient of replugging the outlet with large clods of soil held together by the turf grass *Cynodon dactylon*.

The fundamental function of microrelief as the determinant of plant zonation in poorly drained areas of low relief is strikingly demonstrated in marshes and estuaries where centimeter differences in level will determine whether a surface dries quickly or forms a drainage channel (eg. Chapman 1961, 1964; Thom 1967; Thom *et al* 1975).

Like hill building termites, hippo are potent geomorphic agents of floodplain change due to their path making habit. Traditionally used paths radiate out from lake and river waters to grazing, and link otherwise discontinuous depressions. During the rains and floodperiod when soils are soft, constant use of paths makes them into deep



EXPLANATORY NOTES FOR FIG 6.4

(1) A primary freshwater/brak marshland stage in the evolution of Rift Valley communities, characterised by hippo and reedbuck as indicator species of the prevalent habitat (Holocene ?). This stage probably followed a shallow sea stage (early Pleistocene ?) which must have poured in with the foundering of the 40 km broad Rift Valley trench. The present lowest part of the Urema basin is only 12 m above present sea level. The alluvial fans shown are the oldest as judged from air photo interpretation and ground study correlations.

At this stage diversity would have been extremely low, despite the possibility of a mosaic of waterlogged grassland types, and an extraordinarily high wild ungulate biomass of a few species as exemplified by the present Zambeze Delta floodplains and marshlands at Marromeu.

(2) An intermediate stage to the present, with the addition of sable antelope to indicate an extensive dambo-woodland mosaic on the aggraded fan surfaces. Increasing plant and animal diversity related to the progressive array of substrates being exposed above permanent waterlogging. Note differential growth of alluvial fans from the two sides of the Rift Valley and the pinching off of the Rift floor marshland drainage by their gradual coalescence.

(3) The present stage with maximal substrate, habitat, and biotic diversity, characterised by the addition of impala, bushbuck, and forest mini-ungulate as habitat indicator species. The drainage and erosion of floodplains and slacks, and extensive invasion by woody plants throughout most of these surfaces indicates the probable future stage of the Rift floor systems.

(4) Probable future stage within several decades, when floodplain systems are on the verge of extinction by occlusion of a prevalent cover of savanna, thicket and dry forest mosaic, the latter remaining confined to the duplex sand deposits. Once these have been truncated, dry forest will become extinct and be replaced by scrubby savanna or thicket. This stage indicates a return to a relatively homogenous physiognomy and structure, this time of woody plant dominance. The stages following this will probably remain scrub-dominated as valley side erosion of dongas eat back small scarps and pediments in the alluvia, and slack areas are ever diminishing (see examples A to D of the successional evolution of an alluvial fan).

(A) Anastomosis of distributary courses and of fines deposited as overbank slack deposits. The distributary courses aggraded by coarser sand deposits. First colonization on the aggraded courses by *Macrotermes* hill building termites, providing the

first permanent surfaces for woody plants above excessive waterlogging. Channel courses changed by being blocked off (plugged) by their own bar deposits.

(B) Savanna, thicket and/or forest woody initials on the termite hills, from which the intervening aggraded (convex) and dried out distributary course surfaces are colonized. The main distributaries are forced to break through their own levees due to the bar deposits, and flow along the slacks which are the lowest surfaces in the fan sequence.

(C) Total colonization of all convex surfaces as effective flooding is confined to the lower surfaces and is of progressively shorter duration as these slacks and basins are eroded (C & D).

(D) Lateral coalescence of microvalley sides formed by migrating nickpoints to form a stepped sequence of pediments and microscarps with even-aged woody invasion of each and the progressive contraction of slack communities to the confines of the stream beds.

channels with a levee of mud pushed up on either side. Whilst aiding the dispersal of floodwaters these paths are also the beginning of the end for marshes and pans as rain and floodwater are immediately lost with the ebb. The junctions of deep footpaths made in soft alluvium with hard ground forms nickpoints and initiates headward gully erosion. On a microscale the classic (Leopold 1964: 448–453) cut and fill chain of migrating nickpoints are developed in the canalized footpaths. A deep bare section is developed below the undercut and slumping nick, and lower down deposition of this material forms a small fan within the channel which is then fixed by grass. The crest of the levee, formed by the animal's movement when the alluvium is soft, and the sides of the channels are bare eroding surfaces and thus extremely xeric. The radial drainage incision of the floodplains surrounding the Urema Lake is shown clearly on air photographs, and a series of gullies are a feature of most paths. These paths not only canalize rainfall but also rapidly drain off this source of moisture. On a yet smaller scale, faint undulations on the same floodplain soil determine whether the same species of grass remains green or dries out fast, and large tufted grasses in drainage lines pedicelled by sheet erosion provide sites for woody plant invasion. These features re-emphasize the importance of soil moisture balance at all levels from the micro- to the macroscale.

A characteristic indicator of new or modified surfaces made available to invasion in the past, and more recently by geomorphic or like action such as cultivation, overstocking, or fire are the presence of even-aged or quasi-even-aged stands of woody plants. New surfaces are invaded according to circumstances of the seasonal or episodic availability and dispersal of plant propagules. On any surface subject to flood and ebb movements of water, propagules are concentrated along contour and microrelief by stillstand, swash and wind action. Patches of even-aged scrub in a dambo or vleis indicate either that the plug has been pulled out of the system, often discernable only after fires has temporarily removed the grasscover to expose the small headward incision responsible, or new sediment has been deposited to above the level of excessive inundation.

In arid savannas, episodic woody invasion of seasonal dambos and vleis may occur during a series of consecutively dry years and be killed off by subsequent exceptionally wet periods. Here soil moisture balance is altered solely by the swing of climate, elsewhere simulated by the cut and fill of geomorphic processes. On almost any landform, sequences of different even-aged stands indicate successive erosion, deposition, or altered soil moisture balance. This phenomenon is particularly well illustrated in the study area by the zonation of acacia and palm in even-aged invasions, related to lowering and stillstand of flood regimes in the Urema slack basin. The oldest and tallest stands occur on the highest periphery of the slack basin, with younger groups at successively lower levels toward the present lake area. Similar evidence on many erosional

and depositional features of other landforms and physiographic situations testify to the relative ages of surfaces and the sequence or direction of succession. This feature is exhibited by components of all biomes and ecosystems on the subcontinent, particular by fynbos, subdesert dwarf-shrub, acacia, mopane, palm, miombo, mangrove, thicket and forest initials.

The periphery of discontinuous concave surfaces form the temporary base level to each individual depression, and where these are linked by drainage lines the outlet of each depression is its temporary base level. The many Rift Valley (and coast plain) surfaces, all at slightly different levels are thus controlled by a multiplicity of temporary base levels. The duration of temporary base levels and changes in local moisture input are two salient factors in floodplain ecosystems.

On the macroscale, evolution of systems on the Rift floor has been directed by the interplay of the major rivers entering the Rift from the hinterland. The large alluvial fans of the Nhamapaza, Nhandue, and Pungue, traced from aerial photographs, show clearly in Fig 6.3 . The Urema Lake was probably of much greater extent in the past, fed directly by the Pungue River's now abandoned distributaries. Pungue waters entered the Urema slack basin at different times from the west and along the southern margins. The evidence of the more recent abandoned distributaries shows that Pungue water flowed into the lake at its present exit, at the site of the present alluvial plug formed by the Muaredzi Stream from the Cheringoma Plateau. This means that the interfan slack basin was filled and then overflowed either in the west, forming a circle, or back past its exit into the lake and down the present Urema River.

The area of the present alluvial plug appears to have been the site of a temporary base level during most, if not all of the Urema slack basin's development. The direction of abandoned distributaries and narrowed lower end of the Urema Lake show that sediments deposited by the Pungue River also contributed to forming the convexity of the critical height. Only when the Urema slack basin was filled did overflow push past the distributary mouth into the Urema River. This parallels the situation today in the Banhine basin in Gazaland, which is also partially endoreic, outflow down the Changane River only being affected after the basin is filled by the upper Changane and other seasonal drainage. The much larger meandering valley of the Urema River must have been formed at the time when both the Pungue and Nhamapaza Rivers entered the Urema slack basin. Today the underfit tightly meandering Urema River has incised into the old meandering valley. As channel fill and plug deposits sealed off the distributaries the Pungue River became completely separated from the Urema Basin and now during exceptional floods only, does it enter part of its old course along the western edge of the Rift, (formed along the north trending fracture line responsible

for the Muche Valley) and dams up the Urema waters at the confluence. In the north the Nhamapaza River once flowed into the Urema, but it too blocked itself off by its own deposits and now drains north to the Zambeze River along the Rift floor.

The Urema slack basin therefore developed under regimes of much greater discharge and flooding and was beheaded by fluvial processes of deposition and gullyng. This has left the Nhandue River as the largest, though seasonal, river entering the basin, the Mucodza and Vundudzi derived directly from Gorongosa Mountain, and the series of small seasonal streams from the Chringoma Plateau as the sole contributors to the present basin. Of these only the small Vundudzi River is perennial because it rises on the upper catchment of Gorongosa Mountain. This massive cut of water input and sediment load has resulted in the establishment of a cycle of incision affecting the dynamics of the remaining floodplains particularly through the processes noted above. The remaining floodplains of the Urema slack basin are all deeply incised and are now out of reach of the lake's present flood zone (Fig 5.11). These surfaces are now perched above the gullied drainage and are thus under an inexorable tendency to change as they are actually relic systems poised in time and space by the resistance of flatness. On every side these surfaces are being invaded by woody plants of the other two ecosystem types and they can only continue to be called floodplain grasslands because the saplings have not yet grown above the grass canopy. In a relatively short time, possibly within twenty years, only part of the lower flood zone of the Urema Lake will remain pure grassland.

Figure 6.3 shows the past, present, and probable future of Rift Valley ecosystem-types as shown by present evidence traced through this section. The extinction of floodplain grasslands and their conversion to savanna grasslands, and finally to a thicket-savanna mosaic is a natural consequence of drainage evolution on the plains, i.e. the lechwe ecosystem is replaced by the impala ecosystem, which in turn will be increasingly invaded by the nyala ecosystem. The Urema floodplains are the nucleus of the Gorongosa Ecosystem and their survival is dependent on two fundamental factors: the water from the mountain, and maintenance of the temporary base level at the outlet of the lake formed by the Muaredzi alluvial plug. The efficacy of the sill formed by the alluvial plug of Muaredzi Stream deposits at its right angle junction with the Urema, in damming up the Urema slack basin, depends on adequate annual sediment replacement to fill the cut made through it by the water running out of the lake and accentuated by hippo movement.

The lowest part of the Muaredzi River is an incised course cut through a channel-fan that is formed upstream where the cuesta slopes meet the Rift floor. Headward incision of the lowest part of the course has not yet cut through the well defined river

course 2,5 km upstream from the plug. Inspection of this site shows the formation of a new fan, mostly of sand, which has choked up the incised stream course. Thus most of the sediment is lost to the alluvial plug because it is being deposited further upstream. There is evidence that seasonal road maintenance activities across the Muaredzi course just above the new fan is, in part if not wholly, responsible for these depositional changes. The high river banks just above the fan site, are cut down and used as infill to build up a causeway across the sandy riverbed. This river crossing has been repeatedly repaired over a period of some 20 years. With the first rains, build-up of sediments behind the causeway results in breaching of the whole blockage and this excessive load of detritus is dropped at the break in slope some 200 m below the road crossing.

These examples of geocological relations in a fluvio-lacustrine system emphasize the importance of microrelief changes in controlling geomorphic processes, the ecologic response, and co-relations in the evolution of floodplain landscapes. The poorly drained a substrate, the more important the smallest differences in microrelief, but these lose their significance once the area becomes well drained. Under the former regime the preceding degree of saturation from rain or previous flooding has an important influence on the extent of subsequent inundations.

On the Rift Valley floor, plant succession, and thus change in habitats and their animal components, is primarily determined by edaphic and landform changes wrought by geomorphic processes of accretion and erosion. This induces a continual response to ecosystem and habitat change in dynamic equilibrium with the geomorphic influences, and plant succession within each system occurs during the varying stages of relative quiescence. Substrate diversity and the superimposed control of changing flood levels are thus the determinants of ecosystems and ecotone diversity on the Rift Valley floor. A topographically homogeneous plainland thus supports a homogeneous ecosystem-type at the two ends of its cyclical succession.

Initially, there is a grassland ecosystem-type in which excessive flooding is the overriding control, well exemplified in the transect of the Cheringoma Coast plain. This is followed by a stage of small scale dissection and incision of temporary base levels reducing the duration of flooding and waterlogging. This allows for the full expression of the soil properties of each substrate in their influence on the kind and variety of plant cover they support. The Rift floor sector of the ecosystem is at this intermediate stage when ecosystem diversity is greatest. The final stage of floodplain dissection when runoff is greatest will be a relatively homogeneous cover comprising a mosaic of the other two woody ecosystem-types with a predominance of forest/thicket (Figs 6.3 and 6.4), paralleling the situation on the Midlands. Further erosion and sedimentation of valley

floors will again increase diversity, followed by a decrease when the valley sides are eliminated and well drained low relief again predominates.

CHERINGOMA PLATEAU

The present day form and cover of the cuesta has been derived from an original broad waterlogged grass plain forming an apron, or piedmont, in front of the interior *oldland* and subsequently separated from this by the Rift Valley down faulting. Isolated as a remnant block, the crest of the newly exposed scarp slopes would have formed the new drainage divide along the top of the plateau. Differential erosion of the cuesta scarp and dip slope resulted in the eastward shift of the divide, beheading further all the seaward drainage. The same process continues today and is most active in the central and southern parts.

After separation by trough faulting, the entire dip slope area will have remained predominantly a waterlogged dambo grassland with termite hills as the first invaders of all convex surfaces. The termite hills would have been primary sites of woody plant invasion, unless suitable vleis with flowing water had already provided substrates for swamp forest patches. The Riftward inface would have been invaded by both forest and savanna ecosystem-types. Eventually all convex surfaces including the major divide and interdambo surfaces were invaded by miombo and forest. The termite hills were major nuclei for invasion of intervening terrain as the soils became better drained. While this process continues today, a more striking process of landsurfaces and ecosystems replacement is taking place on the cuesta where the duplex sands are being rapidly stripped off by natural headward erosion.

Due to the exposure of alternating bands of hard and soft sedimentary rock the Riftward inface of the cuesta has been eroded into a series of steps; the hard quartzitic limestones forming a major scarp crest. Above this, another scarp crest is formed by the convex slope of eroding duplex sands and latosols. In the northern and central sectors of the cuesta inface where hard rock exposures predominate, a fretwork of deep canyon-like ravines have cut back from the Rift into the inface leaving hanging tributary valleys and waterfalls along their sides. The edges of the ravines, their nickpoints, are held up by the white to pinkish-white calcareous sandstone of the Cheringoma Formation. The sandstone weathers into overhangs and steep talus cones are formed below the cliffs. Where the original dambo surface remains on the uppermost sands, tall closed miombo savannas mosaic with dambo grasslands, most of which are now relic in the heads of the inface drainage. Near the ravines these sands and their cover have been stripped off leaving skeletal soils over the sandstone sheets where low scrub now predominates. On the margins of the ravines a band of pure grassland is formed by seasonal

lateral ooze of rain water. Where this hard sandstone has been removed by erosion on the crest of the slopes above the Rift, glauconitic sandstones of the Cretaceous have been exposed on which an impervious marl soil developed, supporting pure grassland. These now occur as remnants on the rounded landforms of inter-ravine spurs.

By contrast, the weakly cemented calcic-argillaceous sandstone of the Mazamba Formation is exposed and deeply weathered in the central upper catchment of the dip slope and on the inface of the southern end of the cuesta. In these areas where the overlying sands and dambos are being stripped off they are replaced by a badlands topography. It is here where the most pronounced spatial replacement of surfaces and systems is taking place in the transect.

The uppermost sands are a mosaic of deep latosols and duplex sands (with an impervious clay at 1 to 2 m depth) which mantle the deeply weathered sandy clay material on which badlands develop when they are exposed. On these sands are broadly meandered dambos covered in grass and dotted with thicket islands on termite hills. On the broad convex interfluvies are tall closed miombo savanna, and in many areas this has been invaded and replaced by evergreen forest. On air photographs the change in leaf texture from miombo to forest is clearly defined. Thus the savanna ecosystem-type forms a band or zone parallel to the adjacent dambo grassland. Most of the dambos are in the process of stream incision some of which have reached headward to the present divide. These streams which are underfit and tightly meandered are initiating a process of valley within valley development. This, and the beheading of dambo drainage by inface scarp retreat and tributary capture by strong headward eroding streams has resulted in the drying out and complete obliteration of many dambos by savanna and forest invasion.

Eating into this sand-dambo system, outlined above, is the active headward erosion of deeply incised drainage on the underlying sandy clays. The steeply undulating badlands topography so formed has local relief of a 100 m separating the interfluvial crests and the incised stream bottoms. Retreat of the overlying ecosystem occurs along valley sides and around valley heads where a dense dendritic drainage is replacing the broad dambo drainage above. Headward retreat of the friable convex scarp is thus increasing the badlands topography and reducing and eliminating all the upper systems. A drastic immediate result of this is the extinction of perennial vleis and dambos. Where the headwaters of the Musappaso and Musambezi streams abut for example, interfluvial spurs supporting the upper systems have become isolated and are now on their way to being eliminated. In Gazaland, similar processes pertain where surface sands supporting miombo and dry forest are being replaced by exposure of underlying calcareous clays, which is extending the mopane or arid savanna biome at the expense of

PLATE 8 KINETIC MULTIDIRECTIONAL GEOCOLOGICAL SUCCESSION RESULTING FROM DIFFERENTIAL EROSION OF A CUESTA LANDFORM – THE CHERINGOMA EXAMPLE.

Active headward erosion of Riftward scarp slope river (the Mussapasso) beheading further the older seaward Plio-Pleistocene (?) dipslope dambo drainage. Resulting in seaward shift or divide, extinguishing of forest and miombo woodland along the crest and its replacement by waterlogged convex (waxing) slope grassland.

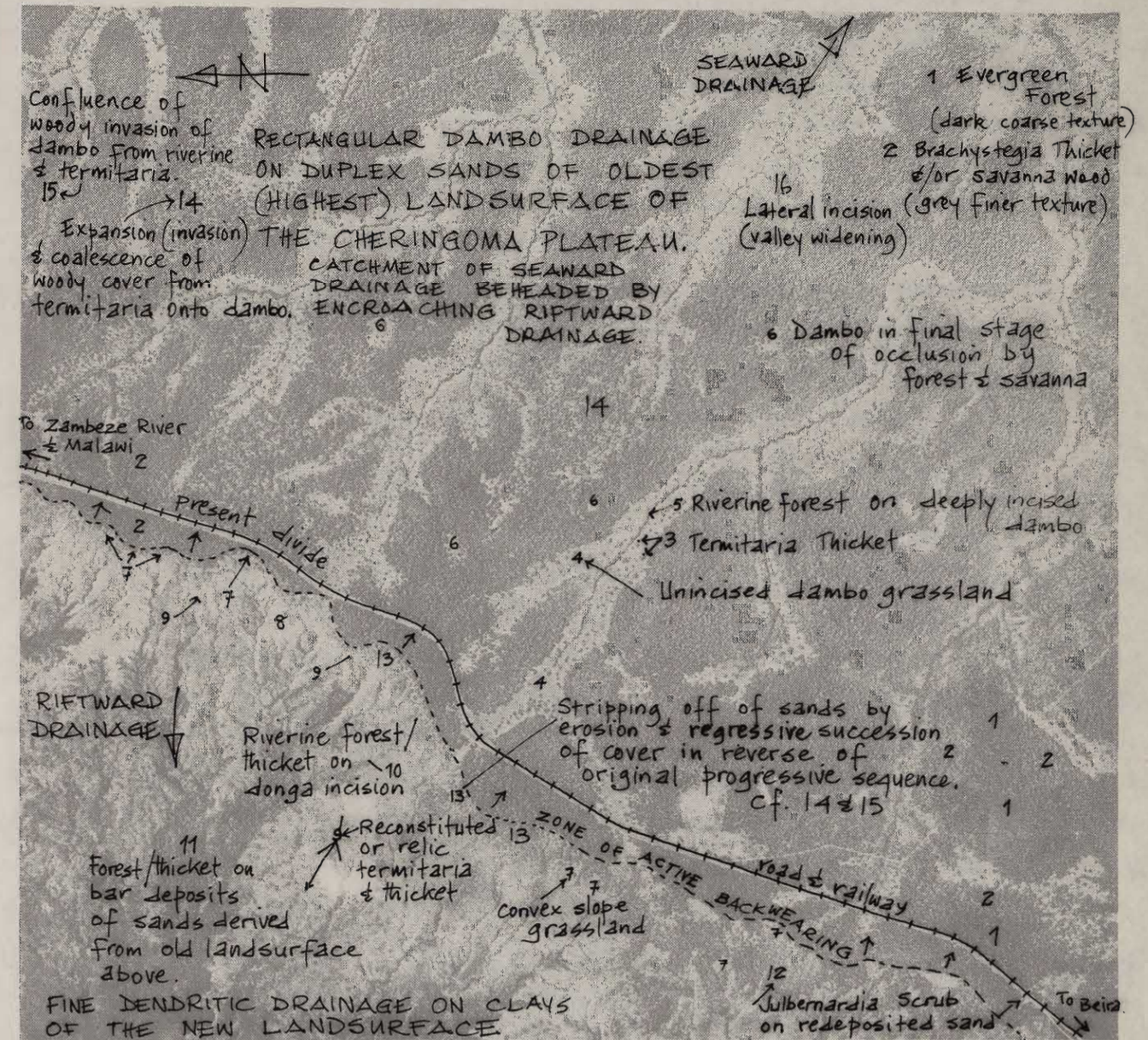
Concurrently, progressive succession is occurring above and below the zone of active backwearing – riverine forest development in donga drainage, forest invasion of miombo on duplex sands, coalescence of termitaria thickets and occlusion of dambos and oval pans on the dipslope.



PLATE 8 KINETIC MULTIDIRECTIONAL GEOECOLOGICAL SUCCESSION RESULTING FROM DIFFERENTIAL EROSION OF A CUESTA LANDFORM - THE CHERINGOMA EXAMPLE.

Active headward erosion of Riftward scarp slope river (the Mussapasso) beheading further the older seaward Plio-Pleistocene (?) dip slope dambo drainage. Resulting in seaward shift or divide, extinguishing of forest and miombo woodland along the crest and its replacement by waterlogged convex (waxing) slope grassland.

Concurrently, progressive succession is occurring above and below the zone of active backwearing - riverine forest development in donga drainage, forest invasion of miombo on duplex sands, coalescence of termitaria thickets and occlusion of dambos and oval pans on the dipslope.



the moist savanna and forest biomes. On the Cheringoma, the sandy clays exposed from beneath the overlying sands are highly leached acid substrates hence there is not a clearcut process of ecosystem extinction as the vegetation invading these badlands is essentially similar, though depauperate in species content to that it is replacing, thus the striking difference is in physiognomy and the recombinations of species associations. Lower down on the Cheringoma towards the Rift, a comparable situation to Gazaland occurs where base rich clays support many more arid savanna elements.

The convex slope of the retreating scarp formed on the sand-clay contact forms a new waterlogged surface and here new dambo-type grasslands form. The eroded material is deposited lower down the slope where it is fixed by scrubby miombo or dambo margin trees which are typical of partially waterlogged soils. The mid and upper courses of the seaward drainage, particularly the Sanga, Zuni, Chinizua and Sambazo Rivers have cut deep valleys in which aggraded flat valley floors have been formed by the meandering braided courses with the development of typical floodplain landforms such as meander scrolls, levees splays, cut-off meanders, and backswamps. These valleys have been choked by the sand load derived from the catchment and the immediate valley sides where there is active retreat of the duplex sands. Except for the slackwater deposits, all the others noted above are composed of sandy material derived from the stripped duplex sands, and all these are colonized by forest and/or closed miombo savannas. The slackwater areas support sour grass and vleis systems similar to the dambos, all of which are acid substrates.

The forest ecosystem invades up all donga and stream cuts, and where the dendritic tributary heads have incised in close spacing, riverine forest predominates, with narrow strips of scrub covering the intervening narrow ridges. The badlands topography erodes by massive cone-shaped slumping at the heads of the dendritic tributaries on divides and spurs. The donga slumping results in the formation of cirque-like valley heads, and the slumped material is deposited immediately below to form a temporary base level; in this way valley-head vleis and dambos grassland pockets are formed. Other dambos parallel to the convex-slope grasslands are formed, occasionally on lower slopes where bands of more compact or durable strata outcrop and cause accretion upward of the blockage.

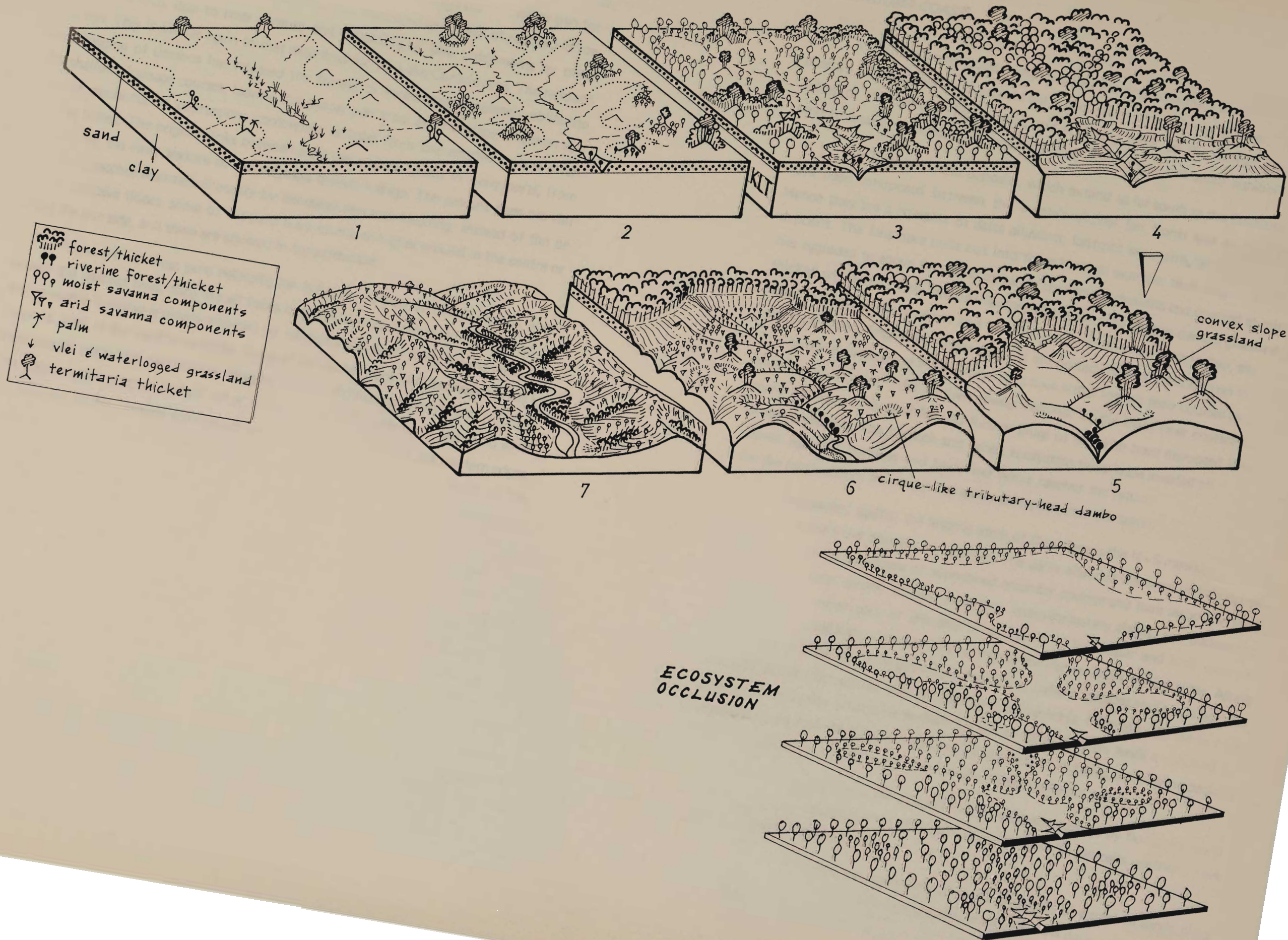
Investigation of many contact areas between the two surfaces shows that in some parts there is now a period of dynamic equilibrium (quiescence), where the convex slopes are stabilized by grass, and sheet erosion is the main erosive activity. In other areas active donga erosion, slumping, and stripping off of the upper sands is in progress. These low and high intensity geomorphic cycles appear to be related to years of lower than mean rainfall (low intensity erosion), and the years of exceptional rainfall, when profiles are saturated to great depth and slumping occurs.

It is significant that termite hills, which are one of the first sites colonized by woody plants in waterlogged grasslands, become the last sites of forest remnants when the sands are stripped off interfluves, and the intervening terrain which once supported a closed savanna and forest is replaced by scrub. Stripping of the sand accentuates the hills to nearly 6 m in height, but eventually these are eroded away as well.

In the southern sector of the cuesta, similar surface replacement has occurred on the upper duplex sands without the deep incision described above. In the upper catchment of the Savane River coast drainage there has been merely a stripping off of the Bp sand surface, and exposure of its clay subsoil by sheet and rill erosion. This area has not been studied in the field, but it seems that a much shallower sand cover over the clay has allowed its easy removal. The mature evergreen forests on the convex interfluves are contracting as sands are being eroded away from all sides and no savanna margins remain, the forest on duplex sand remnants meets dambo grassland abruptly on the exposed subsoil clays. The forest breaks down via the same route that it originally invaded and colonized the dambo grasslands, becoming remnant on termite hills and convex surfaces and eventually disappearing from these sites as well. However, as the termite hills are composed of extremely friable subsoil, they are easily waterlogged and eroded when the sands are removed. Thus the most actively eroding zones are around the forest patches on the convex surfaces, where forest is replaced by waterlogged grassland. Further down the slope, redeposition of the sands permits colonization by miombo savanna. Thus on the one hand, the process of surface replacement is immediate and sharp between forest and the grassland that replaces it, as in the badlands example above, or it is a more gradual breaking up of the forest into a pattern of islands on and around termite hills as the sands are thinned off. New forest ecosystems are formed in the incised streams and their bar deposits. Although the badlands example of surface and ecosystem replacement is more dramatic, it is merely the incised variant of the more surficial replacement sequence just described.

In the northern sector of the cuesta's coastward dip slope, large areas of dambo drainage with oval shaped pans occur on the original overlying sands, and these are being obliterated by savanna and forest invasion (extension) in response to only lowered soil moisture content of the dambos. No surface replacement, other than narrow incised drainage invading some of the dambos, is evident. The oval and circular pans are all derived from the deeper vleis (rietkuile) areas of shallow dambo drainage lines. Oval and round pans related to straight course sectors, and kidney-shaped pans to meander curves and confluences, but all eventually are eroded into an oval shape. The complete story of their origin and eventual extinction is shown in the Cheringoma example. Their origin is similar to that described for the pans in the Lake Chrissie area of the Eastern Transvaal by Wellington (1955: 477). Many originate too from inter-

FIG 6.5
 CHERINGOMA PLATEAU EXAMPLE OF GEOECOLOGICAL SUCCESSION



distributary backswamps or slacks as shown where the dipslope fans abut against the delta floodplains. The pans are formed only on areas of duplex sands which is in agreement with Wellington's (1955: 475) observation that "... the surface is in most places sandy, with a limey substratum an ideal combination of ground conditions for pan formation". The pans on the Cheringoma have all developed as a result of reduced inflow into the dambos due to river capture and beheading of their catchments by other drainage. This is similar again to that described for the Lake Chrissie area. The reduced waterlogging of dambos has released the forests to invade and completely obliterate the shallow drainage courses, leaving the deeper pan areas as a necklace, and then as a line of disconnected depressions completely isolated from one another by the intervening forest. The original links between pans can still be traced in many parts, from the air, by the finer texture of the miombo thicket foliage. The present pans are vlei grassland patches maintained purely by excessive seasonal flooding. Instead of flat or faintly concave floors, some of the pans have islands of higher ground in the centre or along the one side, and these are covered in forest/thicket.

Nowhere are these pans enlarging by deflation, as they do in arid regions, and, except the deepest ones, they are all liable to eventual extinction by forest invasion as the excessive flooding is slowly reduced by evapotranspiration from the margins, and colluvial infill of the weathered edges. Some of the deeper pans have permanent vleis in their lowest parts and others have margins sharply defined by erosion and flooding. The only possible erosive periods are at times of heavy thunderstorm rains, and when the pans are totally flooded some small wind-wave action may cut the western edges. Much of the pan drainage area is in a similar topographic context to those on the Kalahari 'Schwelle' which forms a broad convex critical height in plainsland drainage, and in turn become broad watershed areas when river capture and beheading occurs. The Cheringoma, and similar pans in two other areas of Mocambique, show clearly that lack of evidence of old channels is not proof that they were not part of an old drainage system. The author's limited experience of both the Kalahari Pans and those in the western Orange Free State indicates that they are all relics of fossil deranged, or plainsland drainage systems, now deepened and enlarged mainly by deflation, as well as salinization and solution which together are secondary factors. Wellington (1955: 474-482) and Boocock & Van Straten (1962) show that the Free State and Kalahari pans are all related to fossil drainage systems. Modern workers have either totally ignored any past drainage relations (de Bruijn 1971/1) or have thrown out this origin in favour of deflation (Lancaster 1974). The evidence and interpretations given by the older works, and the proof from Mocambique, shows that the origin of pan systems is related to drainage courses whose inflow was cut by the processes of river capture and beheading; the shallow parts becoming choked with sediment and finally obliterated by dry land vegetation.

CHERINGOMA COAST

The Cheringoma Coast comprises four major landforms: (1) alluvial fans of the cuesta's dipslope rivers, (2) arcuate delta floodplains of the Zambeze River, (3) estuary deltas of the cuesta's river mouths and enclosing these on the seaward margin, (4) straight barrier beaches with recurved spits, dune ridges and small parabolic dunes.

The Zambeze Delta deposits, which extend as far south as the Chiniziua River, have been interposed between the cuesta's alluvial fan fronts and an offshore bar. Hence they are a complex of delta alluvium, fanfront sediments, and backbar swamp deposits. The fans have built out into these backbar swamps, their original distributaries aggraded to above floodlevel by sandy, channel fill deposits and covered in miombo thicket and forest. The interdistributary slacks are waterlogged dambo grasslands covered in large numbers of old and new termite hills. As in the Rift Valley, the ends of the distributary fingers and splay deposits are dotted by island thickets on termitaria. The terminal drainage of the cuesta's rivers have either incised their courses as tortuous meandering streams, tidal in their lowest reaches, or the main river courses have become aggraded with sand fill and further plugs of alluvium have disrupted links with present estuaries. The savanna and forest ecosystem-types have invaded all these abandoned aggraded surfaces and here river water reaches the estuaries only during rains, for the remainder of the season the water disappears into the sands.

Juxtaposed against the leading edges of these fans is the N-S meander drainage of the Zambeze's old distributary courses. The delta alluvium has been laid almost exclusively from the sequences of abandoned meander courses and their associated landforms of meander scrolls, cut-off meanders, interdistributary slacks, and backswamp deposits. The major part of the area is a mosaic of freshwater and brak swamps, marshes, and grasslands, with papyrus swamps in the deeper abandoned courses. Along only a few of these old distributaries, is invasion of convex surfaces (such as levees and meander scrolls) by woody ecosystems into the grasslands. Here too, the dense invasion or colonization of convex surfaces by hill building termites lends a speckled appearance to all these landforms. The river bar deposits of all types, and marine backbar marshes open to tidal influence, are covered by dense mangrove woods.

The estuary deltas of the cuesta's rivers have been formed by fluvio-marine deposition, and the distributary mouths cut off by channel-fill deposits upstream have been kept open by tidal scouring.

A large part of the estuarine sediments are sequences of terrestrial sands, clays and silts laid down in the summer rains season when high tides dam up floodwaters. In summer, coincidence of high tides and river flooding with on-shore winds is usual on

EXPLANATORY NOTES FOR FIG 6.5

(1) Probable pre-Rift appearance of entire Cheringoma coast plain, with march grasslands predominant over laterally coalesced anastomosis of alluvial fans of the rivers from the interior (Plio-Pleistocene). Woody plants, if any, confined to termite hills and highest bar deposits.

(2) Beheadment of drainage by downthrow of Rift trough at right angles to the inland drainage (parallel to the coast). Invasion of all convex surfaces by woody plants (savanna, thicket and forest initials).

Lowering of primary base level (sea level) contemporaneously with rifting, isolated the Cheringoma coast as an islanded block. Initiation of nickpoints and rapid headward erosion of dambos and slacks of old drainage on friable calcareous sandy clays (weathered Mazamba Formation).

(3) Progressive nickpoint erosion, drainage of waterlogged plains and invasion of woody communities over all faintly convex surfaces by a process of coalescence from the termite hill islands, and along the nickpoint incisions (riverine forest/thicket components with blacked in canopy).

(4) Stage of complete dambo occlusion and forest maturation, with simultaneous destruction of forest and closed miombo savanna by headward erosion of scarps formed from the donga erosion. Resulting in a convex (waxing) slope where the forest-miombo mosaic is being replaced by waterlogged seepage-line grassland (where impervious clay of duplex sands are exposed at the surface) — a sequence of retrogressive succession (in physiognomic and structural terms only). The original woody initial sites on termitaria islanded a second time now be erosive processes. These original communities are shown as cross-hatched areas within the forest canopy.

(5) Further stage in retrogressive succession resulting from scarp retreat and rounding off of exhumed leached clays.

(6) Colonization of exhumed clays particularly where the upper surface sands have been redeposited as talus or waning slope deposits (ie. reformation of a duplex substrate with markedly different soil moisture balance to the surrounding inorganic clays). Formation of new cirque-like dambos at heads of detritic stream network developed on the friable clays. Scarp retreat resulting in further extinction of the mosaic of forest and closed miombo systems.

Valley broadening, and aggradation of sandy alluvium deposited in meander belt sequences with new slacks and fan deposits of valley side tributaries, all the

convex surfaces colonized by a variety of woody communities including forest, and grassland on concave surfaces and any others that are excessively waterlogged.

(7) Total extinction of the mosaic of forest and miombo woodland and its replacement by scrubby mixed acacia and miombo savanna species. Formation of forest by recombination of upper (now extinct) forest components with riverine components in gullies, on levee and splay deposits of aggraded valley floor, and in stream head sites where the oval cirque-like dambos have been breached and drained.

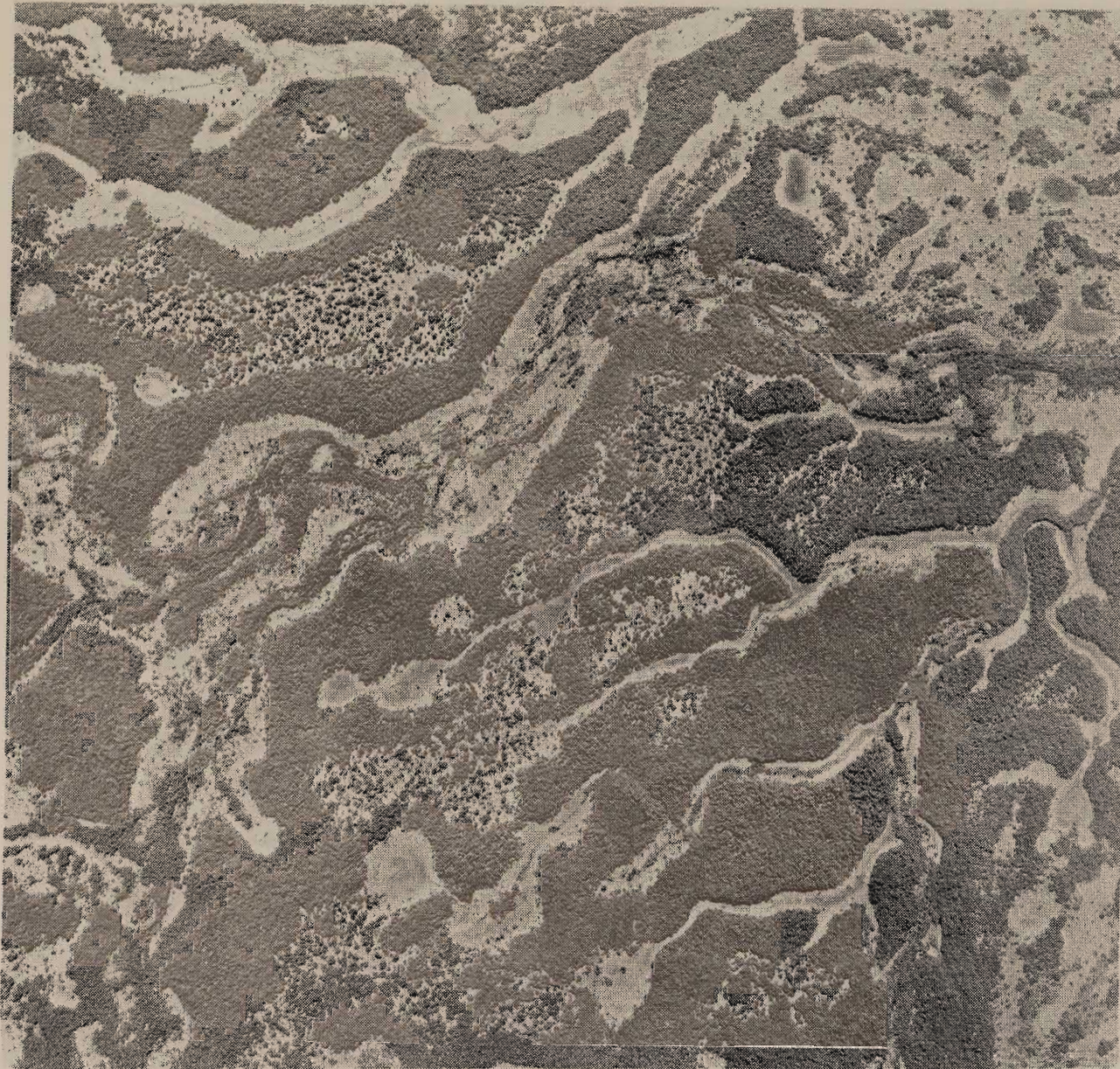
The Cheringoma example is a fine illustration of the phenomena of kinetic multidirectional geocological succession.

ECOSYSTEM OCCLUSION

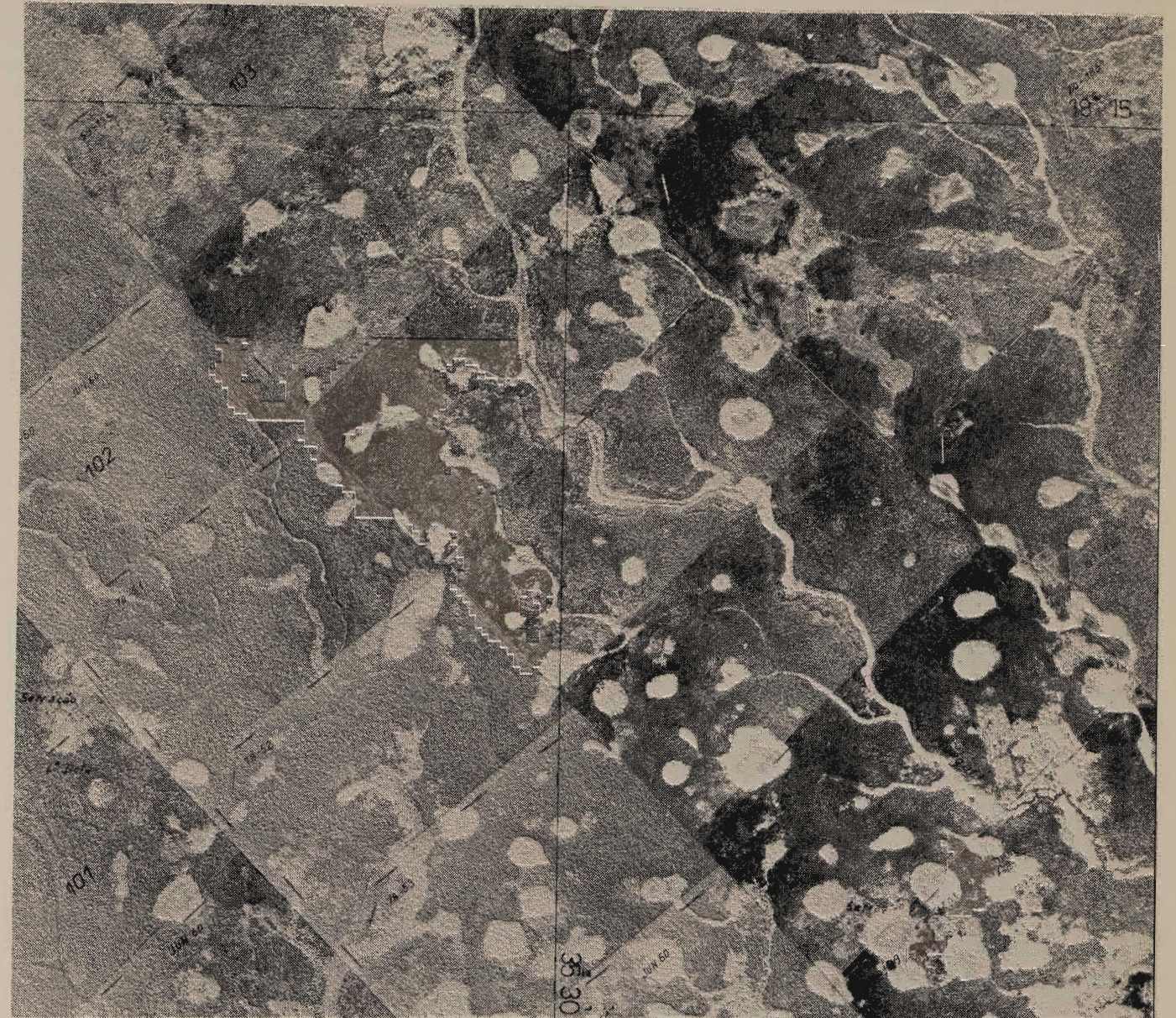
The *in situ* sequential replacement of dambo and floodplain grasslands (by invasion of woody components from the margins), as these surfaces dry out progressively from the canalizing effect imposed when the sill responsible for their existence is breached by a nickpoint of any dimension.

As these grasslands can be reinstated by the simple expedient of re-blocking the original sill site, the diagram can be read in two directions showing the progressive die-off of woody components as the high watertable condition is restored.

PLATE 9 OVAL PAN LANDSCAPE OF THE CHERINGOMA COAST



(A) Habitat patterns on alluvial fan anastomosis. From the top, (1) unincised dambo drainage line grassland, (2) broad bar deposit (convex surface) with forested margins (cf. islands in Okovango Delta) and central maldrained area with termitaria thicket islands in the process of coalescence, (4) incised dambo with gallery and swamp forest (pale canopied sinuous line of swamp forest in dambo on extreme right centre of photo), (5) various stages in the occlusion of oval pans, (6) darker canopied areas are evergreen forest surrounded by paler canopy of seral miombo thicket.



(B) Oval pans in various stages of occlusion by forest, due to drying out of high watertable duplex sands from beheadment of the seaward (dipslope) dambo drainage. Depicting clearly the origin of oval pans from the deeper parts of dambos, and pinched off by forest invading on convexities in the plainsland of the dipslope.

the Central Coast due to the predominance of the SE Trades during the day at ground level and storm winds from the south, or east in the case of hurricanes (Tinley 1971). The other deposits are from tidal currents and wave action, by wind erosion and redeposition of sediments by flood and tidal scour involving undercutting and slumping and light deflation of bare salt flats.

On the inner landward margins of mangroves, are small to extensive areas of hypersaline bare mud flats. The largest such area occurs in the northern sector of the Zambeze Delta near Quelimane. Within the transect all bare salt flats are of small extent. Thom *et al* (1975) describe how these bare flats are derived from an earlier stage covered in mangrove woods, by the process of accretion to above high tide level, and subsequent dessiccation and development of hypersaline conditions killing off the mangroves due to lack of flooding. Examples of dead and dying mangroves on the margins of the flats in the transect uphold their interpretation. These workers suggest that contraction of mangroves to the margins of channels and creeks with maximal extent of salt flats represents a stage of quasi-equilibrium although they record the presence of shallow gullies (pp. 224–226). The examples from the northern Zambeze Delta show that as soon as the bare flats become incised by springtide scour and rain into creeks and rills, these surface cuts, extended by typical headward erosion of nickpoints, are invaded by mangroves (typically pure stands of *Avicennia marina*). In other sites these higher flats, many of which are point bar and interchannel deposits, are colonized by dry land communities, or a combination of both, as they become leached of their excessive salt content.

Enclosing these sediments along the immediate shore, is a narrow low dune barrier composed of parallel dune ridges and fronted by a wave eroded shore with small remnant sections of hummock dunes formed by pioneer strand plants. The dune barrier is cut at intervals by tidal inlets linking the estuaries with the sea and which are constantly changing position. In other sectors, as between the Zuni and Chinizua estuaries, the barrier bar has been transported landward and deposited over mangroves and other estuarine and backbar habitats. The process of landward migration of barrier bars is described by Holmes (1965: 828–829). The peats and muds of these habitats and dead mangroves are now exposed within the mid to high tide zone. Closer to the main Zambeze Delta distributaries, the parallel barrier dune ridges curve landward towards an estuary bay forming a system of arcuate ridges covered in thicket and alternating with freshwater or brak troughs. Some of the older recurved beach ridges appear to be related to old breaches in the dune barrier. From the older ridges, small parabolic dunes were formed and these are now covered by dune thicket. A new series of small, active, parabolic dunes have been initiated where the barrier bar has been undercut and

slumped by wave action. The younger dune ridges are colonized by strand plants and scrub initials, and the older ridges closer to the backbar marshes are covered in thicket.

Hill building termites colonize all convex surfaces, except the barrier dunes, to the very edge and into the mangrove swamps where dry islands occur. These sites, as on the flood plains and fans, are one of the first sites of dry land woody plant invasion.

The overlap and interdigitation of land and sea is most intimate and extensive where shallow seas meet low coast plains as on the Cheringoma Coast. Here fluvial and marine processes alternately deposit and erode the same, or incoming sediments, with each tide and with greater or lesser influence seasonally. Superimposed on this are periodic hurricane or frontal storms at sea, and floodrains or droughts inland which interrupt the longer lasting cycles of lower intensity.

These major perturbations disrupt cycles of prograding or retrograding surfaces, and initiate or redirect the surfaces into other landform sequences clearly depicted by the resulting vegetation patterns. Thom and his co-workers (1965: 229–230) conclude from the study of mangrove in northern Australia that geomorphologically induced substrate change, rather than zonation resulting from plant succession *per se*, is responsible for a dynamic equilibrium between plant cover and habitat change.

A more subtle change which can have far reaching effects, especially on unconsolidated coastland of low relief held in place by plants, is a minor alteration in mean sea level resulting either from world-wide eustatic effects or from more local isostatic changes related to increasing sediment load of the Zambeze Delta on the continental shelf. Important too, are the small but important influences on geomorphic and habitat succession caused by changes in local temporary base levels and changes in distributary discharge, due to catchment changes or plugging and rerouting of river waters in the alluvial fans nearby. Unlike the Rift Valley floodplains, the coast plains are subject to the additional influences of tidal rhythms, wind, waves, alternative flooding by sea and freshwater, and tidal and longshore currents. Like floodplains, seashores most dramatically show the elimination of habitats or alternatively the formation of new land surfaces.

SYNOPSIS OF SALIENT FEATURES

As they are friable surfaces susceptible to relatively rapid change, the Cheringoma cuesta and the floodplain systems demonstrate, in Recent to contemporary time, what appear to be fundamental principles of geocological kinetics. These include the differential flux in intensity and duration of geomorphic processes and the reaction of

ecological responses which produce a succession of irregular rhythms of fast and slow tempo. The spasmodic mode of this rhythm results from the interplay of several main chords each made up of two irregular oscillations of different wavelength.

First, the seasonal rhythm of annual cycles within long-term climatic swings. Second, geomorphic succession within larger erosion cycles of geological time scale whose course and tempo is interrupted, and redirected, by diastrophism or base level change. Third, the differential effect of the intensity and duration of these forces on friable and durable surfaces imposes either rapid spatial replacement of ecosystems under the same climatic regime, or the predominance of in-situ edaphic and vegetation change. In-situ changes would result from leaching or hardpan formation, and from biotic succession and interactions, tempered by major swings in climate. Though durable substrates arrest landscape development in a Recent context, over geological time these surfaces also undergo inexorable replacement. The resultant complex is a mosaic of geomorphic surfaces and ecosystems of all ages at different stages of kinetic flux, from active to relative quiescence. Fourth, the role of biotic components in accelerating or damping habitat and landscape change (see Ch. 9). Change in density of vegetative cover influences discharge and sediment load (Leopold *et al* 1964: 457–458), and the far reaching influences of hippo and hill building termites in floodplain systems are just a few examples of such interactions.

Process and response must be seen therefore as an interacting feedback system where the response and activities of the biotic components are processes, in themselves, influencing and modifying geomorphic activity. The examples from friable surfaces, and of hippo eliminating their own aquatic habitat, emphasizes the phenomenon of differential sensitivity to change on ecosystem or biome components at every level. The examples of active surface replacement demonstrate how geomorphic processes alone, separate, isolate, and eliminate ecosystems or their physiognomic and structural make up, and provide new surfaces adjacent for recombination of biotic components filtered out by opportunistic availability of propagules and suitability of the new spectrum of landforms. Moreover, these processes also reunite different ecosystem components on new surfaces or extend a whole biome at the expense of another, as demonstrated by the situation in Gazaland, without any change in the climatic regime. Superimposed on this is the differential filtering out of species by dispersal efficiency and distance from source areas, competition, climatic oscillations, and influences such as fire and grazing.

On the Cheringoma cuesta, a pure grassland system replaces forest or closed savanna as headward erosion of scarps contracts the upper, older plains surface. This process, referred to rarely in the literature, is described as *retrogressive* succession

(Cowles 1911), or *reversal* of succession (Ross 1962: 272–280). Woodworth (1894) realized the ecological significance of geomorphic succession in fluvial processes to organic evolution, and this approach was developed by Adams (1901) and Cowles (1901, 1911). Cowles (1901: 78–82) suggested that there was an order of succession of plant communities related to the order of succession of landforms in a changing landscape. Later he showed that comparable stages of youth, maturity and old age in cycles of erosion were found in cycles of vegetation, with the generalization that deposition influenced progressive succession, and erosion resulted in retrogressive succession (Cowles 1911: 170–171). By progressive, Cowles meant development towards mesic conditions and by retrogressive, the opposite.

The correlations from across the transect, described in this section, showed that there is a succession of habitats and ecosystems related to the provision of new surfaces by denudation and deposition, or merely by change in temporary base level affecting soil moisture balance, and that this succession is kinetic or multidirectional. Succession on sequence of new surfaces is basically one or a combination of three kinds depending on the properties of the substrates: (a) similar species or ecosystems at different stages of development affecting physiognomy and structure only (eg. age zonation of fever trees on floodplain), (b) different species or ecosystems on contiguous surfaces with similar form (eg. savanna woodland of the arid savanna biome replacing savanna woodland of the moist savanna biome on exhumed calcic-saline subsoils), (c) different species or ecosystems with different form (eg. forest replaced by grassland on convex slopes of scarps).

As evolution of ecosystems is the subject dealt with in this thesis, the term retrogressive or reversal as applied to succession needs clarification and restatement to avoid confusion when used in reference to whole systems of any dimension. Cowles' (1911) generalization regarding deposition and progressive succession and erosion and retrogressive succession is not supported by the evidence from the Gorongosa – Cheringoma transect, which shows the most highly developed plant habitat (rain forest) on both depositional and erosional landforms and the simplest habitat, grassland, also on both landforms. Ross (1962: 272) defines reversal as the process whereby a community (of plants and animals) of a later successional stage is replaced by one of an earlier successional stage. Ross appears to use the term *age* synonymously with *stage* of succession. There is also the implication that earlier or later stages of succession are respectively less or more advanced in an evolutionary context. Such approaches are confusing and mask the real significance of flux in substrate and biotic relations in the field.

Grassland, the simplest terrestrial system in the transect, and forest, the most complex, both occur on the oldest and the youngest land surfaces due to soil moisture balance in different situations. Superimposed on this is the quite opposite relationship of the most complex and diverse wild ungulate associations with grassland and duplex savanna systems, and the poorest with forest. Simplification in physiognomy and composition of the plant habitat by regressive succession therefore, does not necessarily cause a corresponding reduction in animal diversity, and quite the reverse result holds with the ungulate components. The terms progressive and regressive should thus be applied only to the change of physiognomic complexity of the plant habitat, and not to species diversity of either the plant or animal components. Nor should the use of these terms in a successional context be confused with regressive evolution in organisms, involving loss of functional adaptations characteristic of their ancestors (Allee *et al* 1949: 672). Both forward and backward, or upgrade and downgrade, succession in physiognomic terms is part of the natural progressive cyclic change of most landscapes and their habitats, not only of estuary and seashore sites where the more ephemeral nature of substrates makes such changes conspicuous.

Many of the surface changes described may seem trivial, but the profound effects they have, especially conspicuous on friable substrates, verify their fundamental importance. The most significant changes are those in base levels of all kinds and nick-point formation which set in train sequences of landscape and ecosystem change. An outstanding feature of these processes is that, that which happens on the micro scale happens on the macro, the dynamics are essentially the same at all scales.

As pointed out at the beginning of the synopsis, the differential rates of landscape changes imposed by contrasting properties of the surfaces themselves, results in a spatial spectrum of surfaces of different ages. Some geomorphic processes are therefore of geological time scale whilst others are Recent or contemporary. Many more geomorphic events are of contemporary time than is accredited. One such feature, which can be verified by examples from across the whole subcontinent, is the drainage of vleis by nickpoint incision of their temporary base levels resulting in aquatic communities being replaced by savanna within several years, (ie. lechwe replaced by impala or duck by sandgrouse). Like the delayed response of plants to rain, the vlei and perched floodplain examples illustrate a basic characteristic of geocological kinetics, the time lag between geomorphic process, landscape adjustment, and ecologic response (*vide* Pitty 1971: 254–257). These lagged responses are also found in many other biotic interactions noted in the following chapters. In certain situations some processes are self-arresting, such as dune blow-outs which become stable when deflation reaches groundwater.

The last three sections have emphasized the overwhelming importance of soil moisture balance in the evolution of ecosystems and the interaction of their component parts. The invasion of grasslands by woody systems due to changes in soil moisture is probably the most conspicuous widespread in-situ change in landscapes during contemporary times. Such changes are affected by natural geomorphic processes and biotic activities (eg. overgrazing) which accelerate these processes or initiate new ones. Alteration of the soil moisture balance to xeric or mesic conditions simulates decrease or increase in the rainfall regimen, as explained for the change in successional tendency in regions above or below the 600 mm isohyet.

These landscape changes require no surface replacement but involve the dynamic of plant succession, resultant on a shift in moisture status of the substrate. Where two contrasting ecosystem-types are replacing each other in response to the above edaphic shift, such as forest or closed savanna invading grassland, the grassland areas undergo phases of fragmentation where convex drier surfaces are invaded first, leaving narrow strips linking the larger wetter areas of the grassland. These larger areas are then islanded off by confluence of the invading woody plants on the drier surfaces. Eventually the isolated larger areas are encroached from all sides and the grassland (or any other habitat) becomes occluded in the manner analogous to the occlusion of a weather front. Fragmentation and extinction, on the one hand, and coalescence and predominance on the other, of biomes, ecosystems or their components, evolves by parallel mechanisms. One such mechanism involves surface replacement (geomorphic succession) and the other, habitat occlusion (biotic succession in response to edaphic change or influences such as fire or overgrazing).

Detailed studies of fluvial (Leopold *et al* 1964), and coastal (Steers 1962) processes have shown that the largest percentage of sediment removed is by moderate erosive events which occur relatively frequently and not by catastrophic events. They also point out the tendency for such events to occur in groups, probably related to the persistence of climatic events.

The central importance of coincidence in geomorphic and ecological events is borne out by the flux of different landforms and biotic components, brought together during landscape development, resulting in continued recombinations of contact and mixing. Coincidence of events such as the alluvial plug, responsible for formation and maintenance of the Urema floodplains, and the river capture of the upper mountain catchment by Urema drainage, or simultaneous flooding of rivers with equinox tides and onshore winds, are examples of concurrent events which result in a contrasting diversity of substrates and biotic associations to the prevailing surrounding conditions.

In conclusion, a subject central to the appreciation of succession and climax in an ecological context rather than a purely botanical one, is the concept of a dynamic or moving equilibrium in geomorphology. Such a geomorphological equilibrium refers to open systems where a state of balance or homeostasis is reached between supply and removal of material, resulting in the maintenance of the form or character of the system. A reciprocal multidirectional effect between processes and response operates with each perturbation, resulting in, or tending to restore, a new dynamic equilibrium. In this way an episodic state of flux is maintained, each shift affecting a new balance; in short they are shifts in system kinetics (Strahler 1952, Hack 1960, Chorley 1962, Leopold *et al* 1964: 266–268, 274–275). These authors give examples from drainage basins stream dynamics, hill slopes, coastlines and superposing landscapes.

An analagous relationship is put forward by Allee *et al* (1949: 507–508) for ecological homeostasis in biotic communities:

“communities are in a condition of flux in all their strata and within each stratum the species populations are in almost continual readjustment to each other and to the varying physical portion of the environment, the result is a biotic balance achieved by complex regulation of community oscillations”. As Cowles (1901) first pointed out, vegetation changes are certain to follow landform changes, but the cover also develops faster to attain a dynamic equilibrium with the environmental controls and its own biotic interactions. The changes in ecosystems and communities, which are correlated with changes in climate and substrate, exhibit different tempos due to the lag in time resulting from the transmission of the changes through the system. Out of unison changes also derive from the independant evolution of levels or components within an ecosystem (Ross 1964: 259–261, 265).

Fundamental considerations in defining which are seral or climax communities are, the time scale involved, and the spatial dimension of the system – the smaller units of a system are expected to have quite different orders of temporal equilibrium to the larger units (Mueller-Bombois & Ellenberg 1974: 406–408). These authors suggest that a climax community is one which retains its structural and species content over several decades. This definition fits Whittaker’s (1975: 183–185) climax pattern concept, but contradicts his (p. 178–179) and Odum’s (1971: 251) traditional succession and climax statements, as do the correlations presented here in the last four sections. The field evidence from a diversity of ecosystems across the subcontinent, and the Gorongosa study area in particular, with the discussion above, reaffirms my earlier assertion that all ecosystems and many of their ecotones are at once climo-edaphic climaxes (in kinetic equilibrium), and successional in the short, medium or longterm. It is meaningless therefore to recognize climatic or edaphic formations, as both factors work in unison at all times, and are thus climo-edaphic, whether at the community or biome level.

An ecosystem with high physiognomic and biotic complexity, such as forest, does not therefore necessarily indicate ecological stability or the culmination of biotic succession, but merely attests to favourable soil moisture balance; the forest in many instances being related to young unstable surfaces which provide a suitable moisture regime allowing for its full development in contemporary time. By contrast a grassland on a senile planation surface may be far older (more stable) in time and space, yet exhibits a relatively simple structural and biotic plexus. The contrasting make-up of these ecosystems is related simply to climo-edaphic constraints (soil moisture balance), and to the duration of substrate homeostasis available for the development of communities and biotic interactions before a renewed shift in flux asserts another set of changes and combinations and thus a new dynamic equilibrium, driven by what Ross (1962: 336) aptly calls the ‘geotectonic machine’.

This analysis of geomorphic and ecological interactions in the Gorongosa ecosystem emphasizes the striking and far reaching impact of geocological succession, and in-situ changes in soil moisture balance. Such changes include uplift, valley cutting, river capture, beheadment of drainage, and reduction of effective catchment area. Any one of these alone, can account for local or regional climo-edaphic changes under a particular macro-climatic regime with persistent temporal oscillations seasonally and in the longterm, rather than the extreme changes in macroclimate interpreted from the field evidence by many disciplines to account for the flux (extinction, predominance or species mix) of flora and fauna in an area or region. The above in-situ and replacement changes result in a cyclical sequence of low and high ecological diversity and species content, relative phyto and zoomass ratios, primary productivity and the extension or contraction, mixing and recombinations of communities and biomes or their components.

6.3 GEOECOLOGY OF TERMITARIA

Hill building termites play a vital and unique role in the evolution of landscapes and their ecosystems across the subcontinent – from the Southwest Cape, the desertic regions, through the savannas to the moist forests of the east coast. Their impact on the landscape is most clearly seen from the air. The dots of their evenly spaced hills are made conspicuous either by being bare (in desertic areas especially), or covered in thicket clumps; islands in an otherwise pure grassland landscape. These patches in the SW Cape and Namib Desert have long been an enigma to both scientists and laymen and a profusion of explanations for their origin, ranging from geological phenomena to zebra rolling sites, have been suggested. Some of the current explanations are listed by Van der Merwe (1962: 28–29) and Liebenberg *et. al.* (1976: 38). Their origin as termitaria was first put forward by the author in a study of the Etosha and Kaokoveld region (Tinley 1971). Their fairly regular spacing and form are field diagnostic features wherever they occur.

Closer field investigation in the desertic regions shows large numbers of dead ('fossil') mounds of bare hypersaline soils deepened by deflation into the form of round shallow basins (Tinley 1971), and living termitaria of the same shape but with convex surfaces either within the same area or on the subdesert margin. In southwest Angola (Iona) and the Kaokoveld, 'fossil' termitaria of watchglass form occur in the Namib Desert to within 30 km of the coast on clay flats, hill pediments and in quasi-stable dune areas. Their presence attests to former moister conditions when subdesert and arid savanna conditions were closer to the coast. These termitaria were built by *Macrotermes* termites, probably *M. mossambicus* and *M. subhyalinus* which form the large hills across the subcontinent from the Namib fringe to the Gorongosa study area. In the Richtersveld a similar pock-marked landscape is formed by a mosaic of termitaria, some dead, thus flat or concave, and others living and in convex form. The termite here responsible, collected by the author, is *Microhodotermes viator*. The same species is responsible for the living, and dead, "heuweltjies" or hillocks of the Southwest Cape's Swartland and west coast flats, where an air view shows the greener status of crops and other plants due to better soil moisture and nutritional status in the mounds than in the intervening soils. Repeated cultivation of termitaria kills off colonies and this may be the reason for the prevalence of dead or 'fossil' termitaria in the Swartland, rather than change in rainfall regimes suggested above for the northern Namib examples. The pedologist Van der Merwe (1962: 28–30, 114, 306–308) discussed and gave a detailed soil profile description of a "heuweltjie", and despite the honey-combed structure recorded between 20–50 cm depth and other peculiarities, did not recognize it as a termite hill.

A recently published manual on map and air photo interpretation of South African scenery shows many examples, although unrecognized as such, of termite hill landscapes, the prevalence of which emphasizes their edaphic and ecological importance (Liebenberg *et. al.* 1976: Photos 4, 9, 15, 18, 31, 38, 42, 46, 48, 51, 62, 66, 72). The ecological role of termites in other regions is detailed by Lee & Wood (1971) and for Africa in a brilliant paper by Trapnell *et. al.* (1976). Detailed studies on termites in southern Africa have been made by Dr W.G.H. Coaton and his co-workers at the Plant Protection Institute, Pretoria (eg. Coaton *et. al.* "National Survey of the Isoptera of Southern Africa" series in *Cimbebasia*).

In the Gorongosa transect six termite genera were collected: *Amitermes*, *Ancistrotermes*, *Cubitermes*, *Grallatormes*, *Macrotermes* and *Odontotermes*, of which *Macrotermes mossambicus*, *M. subhyalinus* and *Odontotermes* are hill building species. *M. mossambicus* appeared to be the most common across the study area. The *Cubitermes* construct rounded mounds of soil up to 50 cm high glued together with faecal matter and occur characteristically on the dambo grasslands of the Cheringoma cuesta. *Grallotermes africanus* construct arboreal nests, also glued with faecal matter, on tree trunks 10 m or more above the ground, and occur mainly in the miombo savannas south to about the 22° latitude in Mocambique.

The fundamental geocological role of hill building termites in the evolution of floodplain and high watertable landscapes has been detailed in the preceding sections on soil development, soil moisture balance, and geomorphic and ecologic dynamics. In these examples, illustrated by photographs, profiles and block diagrams, the emphasis has been on the multiplicity of influences brought about by formation of a hill landform of subsoil built above the surroundings. But this is only part of the story; a further array of influences is generated by the erosion of termite hills, in areas with high densities of browsing ungulates.

The development of a termite hill, as opposed to a mound, often results in the formation of an annular depression around part of the base of the hill due to either slight subsidence resulting from removal of subsoil for the formation of the hill, or to rain swash action, or to both. On the microscale these resemble the basal annular depressions formed by rainwash off inselbergs in desert. These annular depressions around termitaria hold water during the rains and are initial sites of pan development by enlargement through the wallowing action of wild ungulates. The initiation and development of pans by wallowing is recorded by many authors (eg. Young 1970, Weir 1960, Jarman 1972, Hall-Martin 1972, Flint & Bond 1968 and personal data including pans formed by gemsbok in South West Africa). The annular depression is perfectly

PLATE 10 TERMITES HILL LANDSCAPES OF THE RIFT VALLEY FLOOR



(A) Termitaria thicket islands (archipelago-like) on a convex surface of the floodplain grasslands. Note incised game paths radiating from the termitaria thicket area draining the convexity further.



(B) Mature thicket on termite hill with associated rain-filled pan and aquatic communities adjacent.



(C) Bare arcuate depression around base of termite hill (covered in thicket on right) in area lightly stocked by wild ungulates.



(D) Bare, invasive stage, of *Macrotermes* hills in drying sectors of the converging delta area at the head of the Urema Lake.

preserved in areas where wild ungulates are rare. In areas of intermediate population the annular depression is enlarged and eroded to an irregular oval shape immediately at the base of the hill.

A unique phenomenon, apparently unrecorded, is the development of pans on the actual sites occupied by termite hills, a process of landscape reversal by biotic and geomorphic interactions. In areas with a high ungulate browsing population density, as on the Rift floor in Gorongosa, the hills are replaced by oval pans. The cyclical evolution of "termitaria pans" follows the sequence outlined by Fig 6.6.

In open plainsland termite hills become centres of attraction to all forms of life as perches, observation posts, or refuges from flooding or fire. Seeds are concentrated here; deposited by the animals attracted to these sites. The ensuing thicket growth is therefore composed of almost all the species whose fruits are most favoured by birds and mammals (see Chapters 8 and 9). The cover and rich browse available is then used by all browsing ungulates, and because these sites are islands in a sea of grass or in savannas composed of other species, they are under disproportionate utilization pressure which results in destruction of the cover and the break up of the surface by trampling (plus digging and eating salt-rich soil in some areas) which promotes rapid erosion. The hills are worn down primarily by hoof action and rain, and once hollow they are enlarged, chiefly by species such as warthog and elephant. As the main hill is truncated, new hills are formed beneath the protection of remnant thicket or scrub patches on the periphery and grow upward as the pan develops on the original termite hill site. These satellite colonies may originate by fragmentation of the original colony.

The significance of this micro-landform evolution by interacting biotic and geomorphic processes is the proliferation of diverse substrates, communities and resources. On the one hand, convex surfaces above excessive flooding are enlarged or initiated by hill building activity of the termites, and these coalesce by erosion and radial deposition of material extending the areas of dry land communities at the expense of flood dependent communities. The patterns formed by multiple hill areas is closely related to the template of microrelief developed during floodplain sedimentary processes, and also to the convexities left by former colonisations made during periods of consecutive low flood years and killed by subsequent excessive flood. At the same time there is the multiplication of pans and thus a wider reticulation of water and seasonal aquatic communities (including seasonal fish such as *Nothobranchius rachovi*). The increase of number of termite hills per unit area proliferates the amount of island thicket habitats, ecotones and the concentration of preferred foodplants they support.

If wild ungulates disappear from an area, for one or other reason, pans become filled in by sediment washed from the surroundings and they go through a stage of

senescence and eventual extinction. If, however, there is a dense plant cover and no ungulates, especially if the hill is on duplex soils, the annular depressions or their enlarged forms may remain for the duration of the termite hill's life.

In sum, termite hills increase arid biome substrates in moist areas by bringing saline subsoils to the surface which act as "stepping-stones" for arid elements between separate arid biomes. In areas with non-saline subsoils the hills carry forest or moist savanna biome elements into, and through, extreme arid or upland areas. They also carry savanna biome elements through the Cape Fynbos region, and link them with the west coast desert biome (pers. obs.). In the evolution of landscapes, termite hills provide initial or relic sites for the forest/thicket ecosystem-type, and multiply seasonal aquatic communities by the combined action of rainwash and the eroding activities (trampling and wallowing) of ungulates where they occur in high density. The degree of impact expressed by termite hills in different landscapes depends on contrasting properties of the subsoils brought to the surface and/or to their contrasting soil moisture balance with the juxtaposed intervening ground.

PLATE 11 DEVELOPMENT OF PANS FROM ERODED TERMITE HILLS & NATURAL FIREBREAKS



(A) Flat-topped (mesa-stage) of termite hill erosion. Thicket now confined to hill slopes.



(B) Later dome-stage with thicket relic prior to being eroded flat. Note tree-base thicket in the background.



(C) Primary development of a pan on the original termite hill site (watch-glass-stage). Seasonal hygrophilous grasses in the centre (next to 3 m measuring rod) and bare rim. Note heavy utilization by wild ungulates.

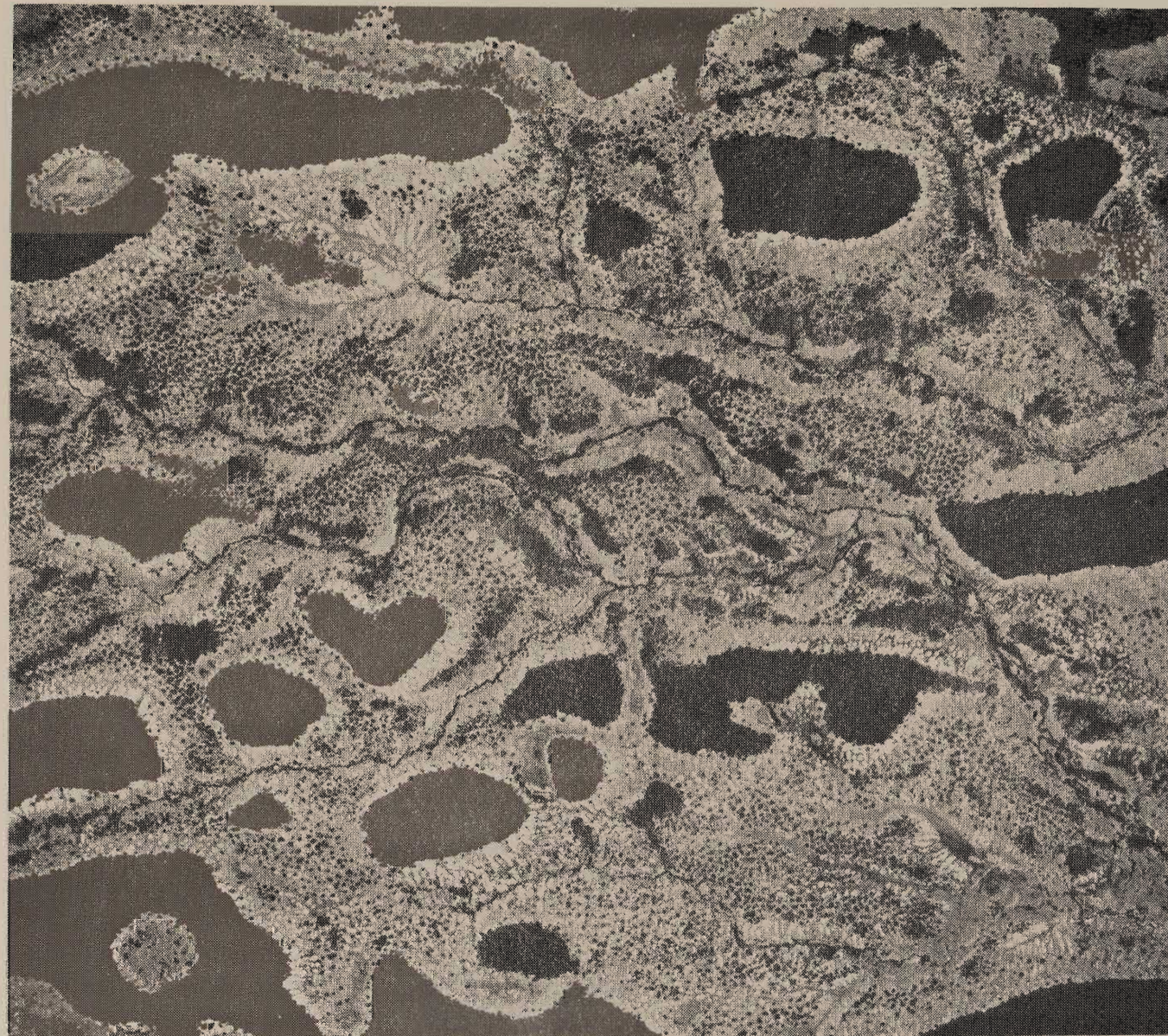


(D) Natural firebreak, of lawn grasses on change of soil of termite hill pediment, protecting the thicket cover. In other sites a similar ring is formed by the trampling of browsing ungulates feeding on the thicket.

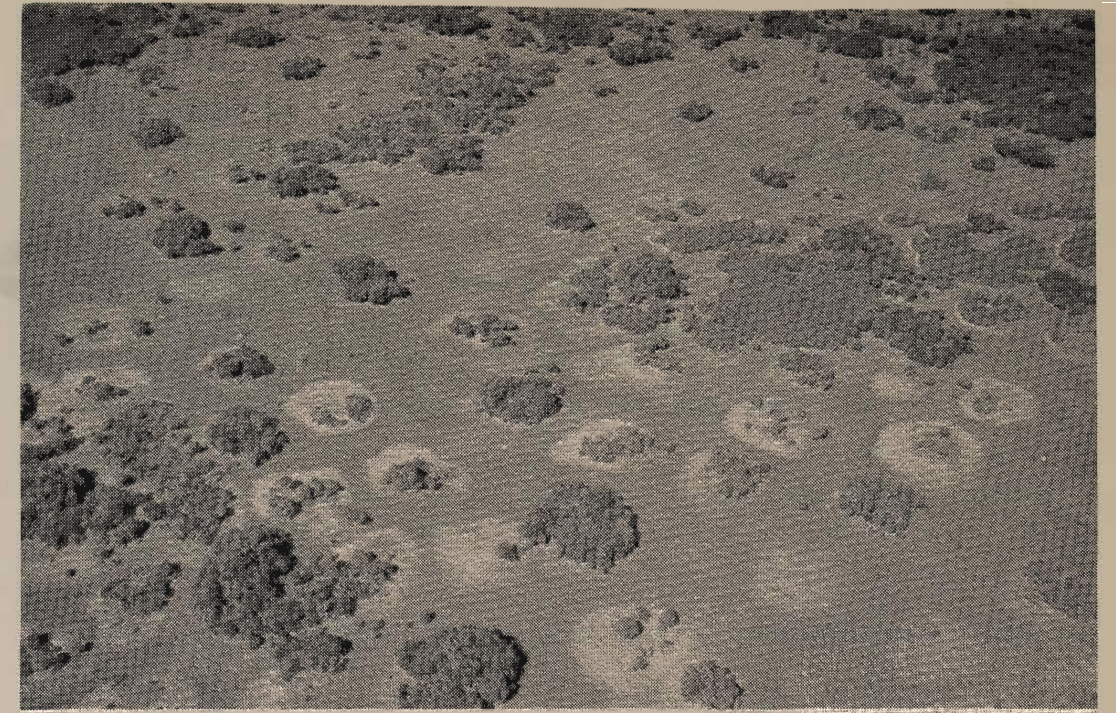
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PLATE 12 TERMITE HILL LANDSCAPE OF THE
 CHERINGOMA COAST.



(A) Natural sheet erosion of friable white duplex sands in the plains headwater catchment of the Sambazo River. Note (1) large black areas of mature evergreen forest contracting as sands are stripped off the underlying leached clays (white margins to forest and white dots of dead termitaria), (2) incised dambos with active headward and lateral erosion, (3) dark dots are termitaria thickets, coalescing in zones of redeposition of sands on the waning slopes.



(B) Oblique air view of the 50 m broad termitaria on white duplex sands. The white soil is from erosion of friable leached subsoil clay brought to the surface by the termites.



(C) Young *Parinari curatellifolia* tree on microrise of *Cubitermes* termite mound in an otherwise flat waterlogged dambo.

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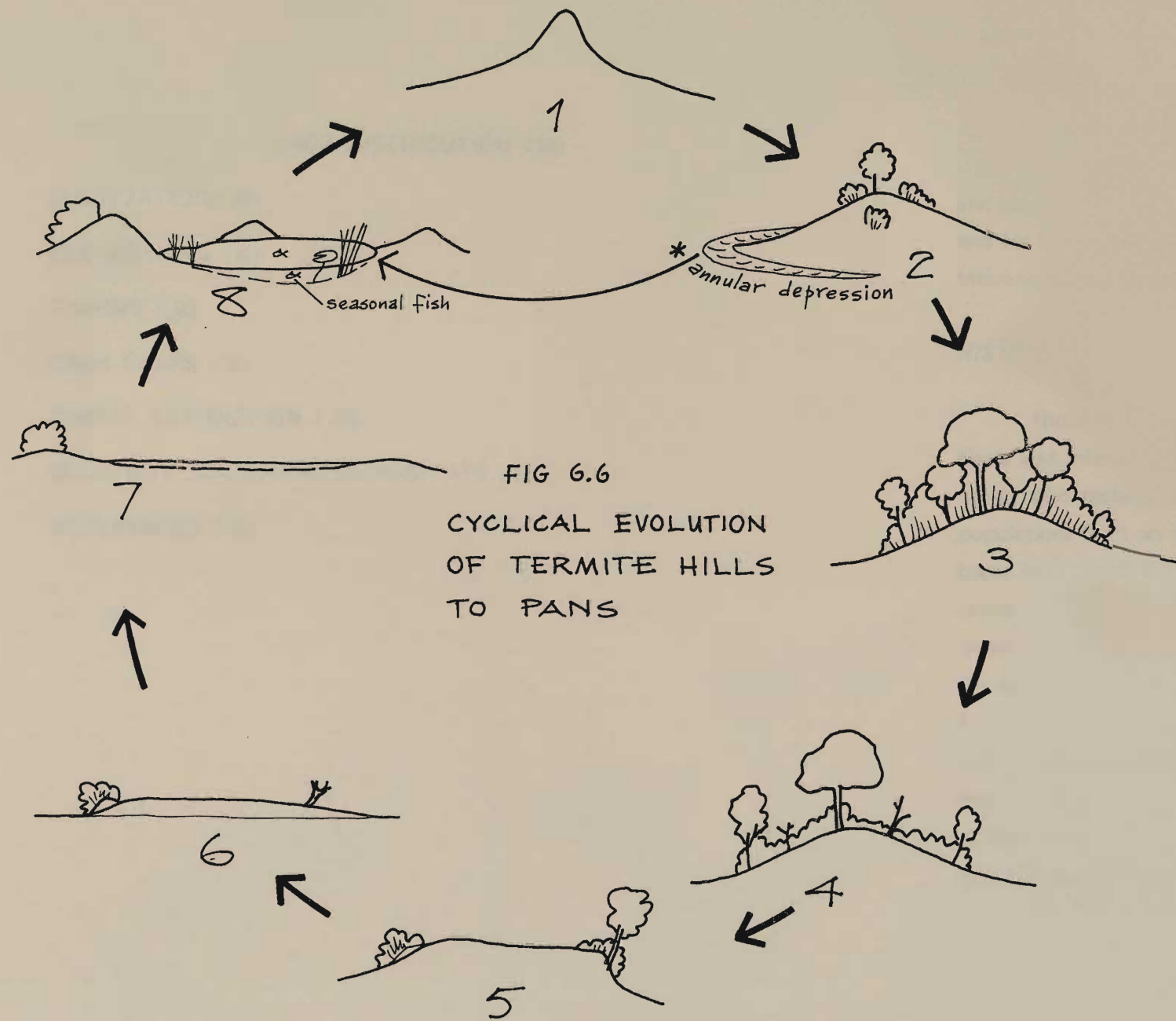


FIG 6.6
CYCLICAL EVOLUTION
OF TERMITE HILLS
TO PANS

- 1 Growth of termite hill above surrounding flat ground. Enlargement of hill by termite building activities, erosion & radial deposition of material forming a pediment apron. Conical prominence attracts seed dispersing animals (birds, primates, ungulates), which use it for perching & resting, or as a look-out, & defaecation here concentrates seed accumulation.
- 2 Annular depression formed around base of termite hill*. Growth of plants, particularly woody species, cover the hill & provides new habitats - food, cover & edge effect, reinforcing the hill's attractiveness to animals. Increased input of drupe-fruit woody species by animals & from parent plants. Typical development of single large tree (primary colonist) on apex of hill. Increasingly attractive to browsing ungulates.
- 3 Maturation of thicket on termite hill.
- 4 Over-utilization of thicket by browsing ungulates opens up the cover & breaks up the surface by trampling which promotes rapid erosion.
- 5 Lowering of the termitarium (mesa stage), the remnant thicket or scrub patches, under which termite building activities are protected & continue, become confined to the convex edge of the hill.
- 6 Penultimate stage of erosion. Hollows often formed on chamber within the termitarium.
- 7 Faintly concave (watchglass) oval depression formed with the rim breached by footpaths & rainwash. Primary deepening to level of surrounding ground by scouring (mostly by rain & a little by deflation). Growth of one or more satellite termite hills on the rim of the depression.
- 8 Final stage of pan formation, further deepening & enlargement due solely to wallowing & trampling action of wild ungulates. Entire sequence can be initiated again on one or other of the new termitaria resulting eventually in further enlargement of the depression.

* In areas of medium to low ungulate density the annular depression can be enlarged to form a pan without involving the mature thicket covered termitarium.