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Biotic Factors in Mima Mound Development: Evidence From the Floodplains of the Okavango Delta, Botswana

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ABSTRACT

The occurrence of earth mounds in areas with a high water table, and in association with a hard basement layer such as bedrock, hardpan or claypan, has been described in many regions of the world. Their origin is contentious, and attributed to a range of processes including zoogenic activity, geomorphological processes, periglacial phenomena or seismic events. The present review highlights the role of termite activity and vegetation processes in the formation of mounded topography in the Okavango Delta, Botswana. Termites create local relief above the upper limit of flooding, which enables the establishment of woody plants on the floodplain. Transpiration by woody plants induces the subsurface precipitation of silcrete (amorphous silica) and calcrete (calcium carbonate) locally on the floodplain, causing a volume increase in the soil, which is associated with the creation of topographic relief. Spatial variation in transpirational water loss is the primary cause of mound growth in the Okavango Delta, and we believe that this phenomenon is widespread in areas with a high water table. We further recognise that the creation of a mound that enables the establishment of woody plants is an important initiator, but that the initial mound could be of any origin, such as tectonic activity, zoogenic activity other than termites or geomorphological processes. We hypothesise that the contribution of different processes may be important in different environmental settings, such as climate and the contribution of dissolved sediments from an external source. Furthermore, we suggest that in areas where the water balance is dominated by rainfall, mounds will be smaller and more evenly spaced than in systems with an external source of dissolved chemicals.

Key Words: Mima mounds, Okavango delta, Subsurface accretion, Termite activity, Transpiration

INTRODUCTION

The occurrence of regularly spaced earth mounds of appreciable size has been described in many landscapes in North and South America and Africa. They generally occur in areas with a shallow, hard basement layer such as bedrock, hardpan, claypan, or gravel (Cox and Gakahu 1983, Cox 1984. Gakahu and Cox 1984). Frequently the mounds are associated with a discontinuous semi-concreted layer of calcium carbonate (Lovegrove and Siegfried 1989, Watson 1974, Midgley and Musil 1990, Moore and Picker 1991) or laterite hardpan (Cox and Gakahu 1983, Gakahu and Cox 1984). Furthermore, they generally appear to occur where a high, sometimes perched water table impedes drainage, creating waterlogged soil conditions for prolonged periods (Scheffer 1947). In cases where they are not associated with a high water table, they may not be modern features, but appear to have originated within such an environment at some time in the past (Moore and Picker 1991).

Their origin remains the subject of much debate despite their conspicuous nature and the widespread attention they have received. Theories are wide ranging. Several invoke a zoogenic origin, including vertebrate as well as invertebrate mound building organisms. In western North America they have been attributed to pocket gophers (Cox 1984), whereas in East Africa and in the western Cape Province of South Africa, fossorial rodents have been considered responsible (Cox and Gakahu 1983, 1984, 1985, Gakahu and Cox 1984, Lovegrove and Siegfried 1986, 1989 and Cox et al. 1987). Termites have also been considered responsible in Kenya (Darlington 1985, Martin 1988) and in the western Cape Province of South Africa (Cox et al. 1987, Moore and Picker 1991). In some cases a combination of termites and mole rats is considered responsible (Lovegrove and Siegfried 1986, 1989), although a wide variety of burrowing animals have been implicated (Milton and Dean 1990).

Alternative theories involve geomorphological processes. Either they are aggradational features that involve reworking of existing sediments in an area inundated by periodic storm surges (Aten and Bollich 1981), or alternatively, Collins (1975) suggested that mounds form as aeolian deposits around large plants or clumps of plants. Alternatively, they are residual high points left after removal of material from intermound areas by erosion (Cain 1974). Perigracial phenomena have also been proposed (Embelton and King 1975, Malde 1964, Vitek 1978) in which mounds are produced by processes that produce frost boils and sorted stone nets in arctic and alpine regions today. Furthermore, seismic events (Berg 1990) have been proposed as a cause of mima mounds. The interference patterns produced by propagating and reflecting wave peaks in situations in which unconsolidated fine sediments overlie a relatively rigid planar substratum, are considered to result in mounds being created which have the appearance of mima mounds.

A feature of mounds wherever they occur is the presence of a distinctive soil composition (Hesse 1955, Darlington 1985, Cox et al. 1987, Midgley and Musil 1990) and vegetation cover (Burtt 1942. Cox and Gakahu 1983, Gakahu and Cox 1984. Darlington 1985, Knight et al. 1989, Midgley and Musil 1990). Frequently, vegetation on mounds comprises woody plants, whereas that in intermound areas comprises grasses and/or heathland.

Studies in the Okavango Delta in northern Botswana over many years have identified various aspects of the role of biota in modifying the floodplain morphology of this ecosystem. These studies have identified accretionary features that result from the interactions of termite mounds (McCarthy et al. 1998) and vegetation processes (McCarthy et al. 1991, Ellery et al. 1993, McCarthy et al. 1993, McCarthy and Ellery 1994. 1995). The importance of these processes jointly has never been addressed formally. In particular, the combination of mound building organisms and the subsurface precipitation of silcrete (amorphous silica) and calcrete (calcium carbonate) induced by vegetation processes in the formation of a mounded topography has not been highlighted in the literature. We believe that our work sheds new light on the origin of mima mounds, a much discussed topic in both the ecological and geomorphological literature, and we present a synthesis of many of the ideas discussed to date on this subject. This article therefore reviews much of the work done to date on the role of biota in modifying floodplain morphology in the Okavango Delta, Botswana, and highlights the importance of these processes for mima mound origin.

THE STUDY AREA

The Okavango Delta is a large alluvial fan of some 20000 km^2, situated in a graben structure (Figure 1) which is an extension of the East African Rift Valley system. The Okavango River, which has its catchment in the moist highlands of central and eastern Angola, discharges into this graben structure, giving rise to the Okavango Delta. The fan has a shallow gradient of approximately 1:3000, and locally the topography is gently undulating, with relief in the region of 1-1.5 m.

The Okavango Delta itself is situated in the Kalahari Basin, which has a semi-arid climate. Rainfall occurs in summer, with mean annual rainfall in the region of 520 mm. Water entering the ecosystem is derived primarily from the catchment in central and eastern Angola, which is situated in the tropical zone with high summer rainfall. Peak discharge is measured in the upper Panhandle in March and April, shortly after the peak rainfall in the catchment. Total inflow via the Okavango River is 11×10^9 m^3 per annum. Downstream of the town of Seronga, water from the catchment discharges onto the fan surface itself, giving rise to the permanent swamps. An additional 5×10^9 m^3 per annum is added as rainfall, which falls in summer. The lower reaches of the Delta are flooded seasonally during the dry winter season, as indicated by peak discharges on the Thamalakane river at Maun in the month of August. Only 2% of the water entering the system each year (inflow plus rainfall) leaves as surface flow, while it appears that less than 2% leaves the system as subsurface flow (Wilson and Dincer 1976, Gieske 1996). The remainder (>96%) is lost to the atmosphere as evapotranspiration.

The catchment is situated almost entirely on aeolian Kalahari sediments, and fluvial sediment entering the Okavango Delta consists of fine sand, being transported primarily as bed-load. Of the total clastic sediment load, 170000 tonnes is bed-load. The remaining 30000 tonnes consists mainly of kaolinite, which is derived from weathering of granite which occupies a small portion of the catchment (McCarthy 1992).

Due to the virtual absence of rock weathering in the catchment, the concentration of dissolved substances in water entering the ecosystem is very low, averaging 30 ppm. However, due to the large volume of water entering the system, the total dissolved solid load is in the region of 450000 tonnes. Of the dissolved solids entering the system, a small quantity leaves as surface flow (approximately 6%) and it appears that a further 10 to 12% leaves as subsurface flow (McCarthy and Metcalfe 1990). The bulk of dissolved sediments (>80%) are therefore accumulating within the ecosystem, which must be considered an important site of chemical deposition.

The studies described in this paper were carried out in the region where permanent swamp grades into seasonal swamp, both north and south of the central Chiefs Island, as well as in the seasonal swamps on the distal reaches of the Delta.

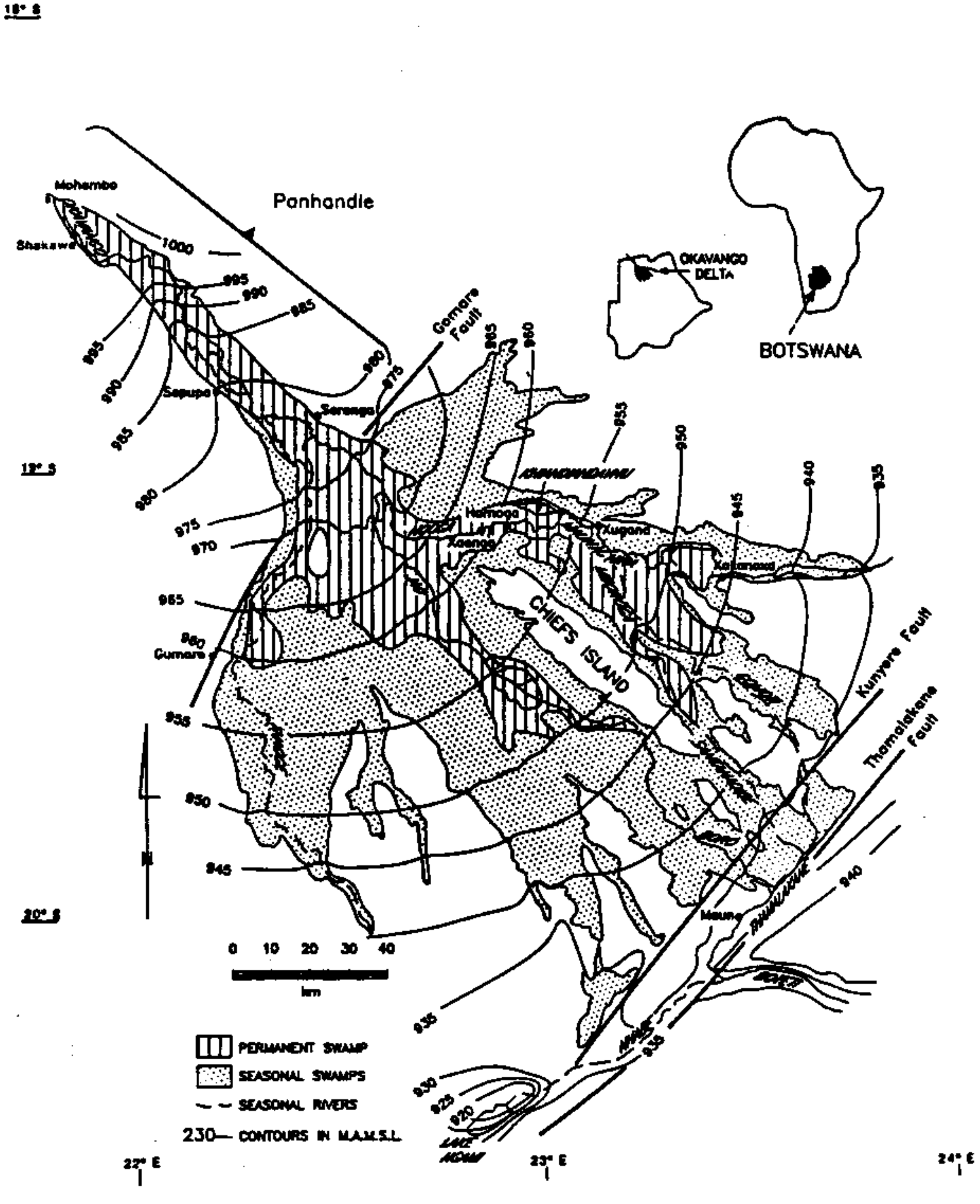

Figure 1: Map of the Okavango Delta.

Figure 2: Vertical aerial view of the terrain typical of that where the studies were carried out. Dark areas correspond to flooded areas. medium areas to floodplains and light coloured areas to islands, with woodlands and trees being dark and restricted to islands.

TOPOGRAPHY AND VEGETATION DISTRIBUTION

An aerial view of the terrain typical of that in which the studies were carried out is provided in Figure 2. The area is seasonally flooded, and dominated by an extensive floodplain grassland. Locally, small circular areas of higher relief support trees. These are not flooded and are thus referred to as islands, varying in size from a few metres in diameter to >100 metres.

One of the areas studied in detail (McCarthy et al. 1998) consists of a gently sloping alluvial plain with a slight southerly slope of about 1:1000 on which numerous mounds occur (Figure 3). Mounds range in size from a few metres to greater than 100 m in diameter, and vary in elevation from less than 1 m to about 2 m above the surrounding floodplain.

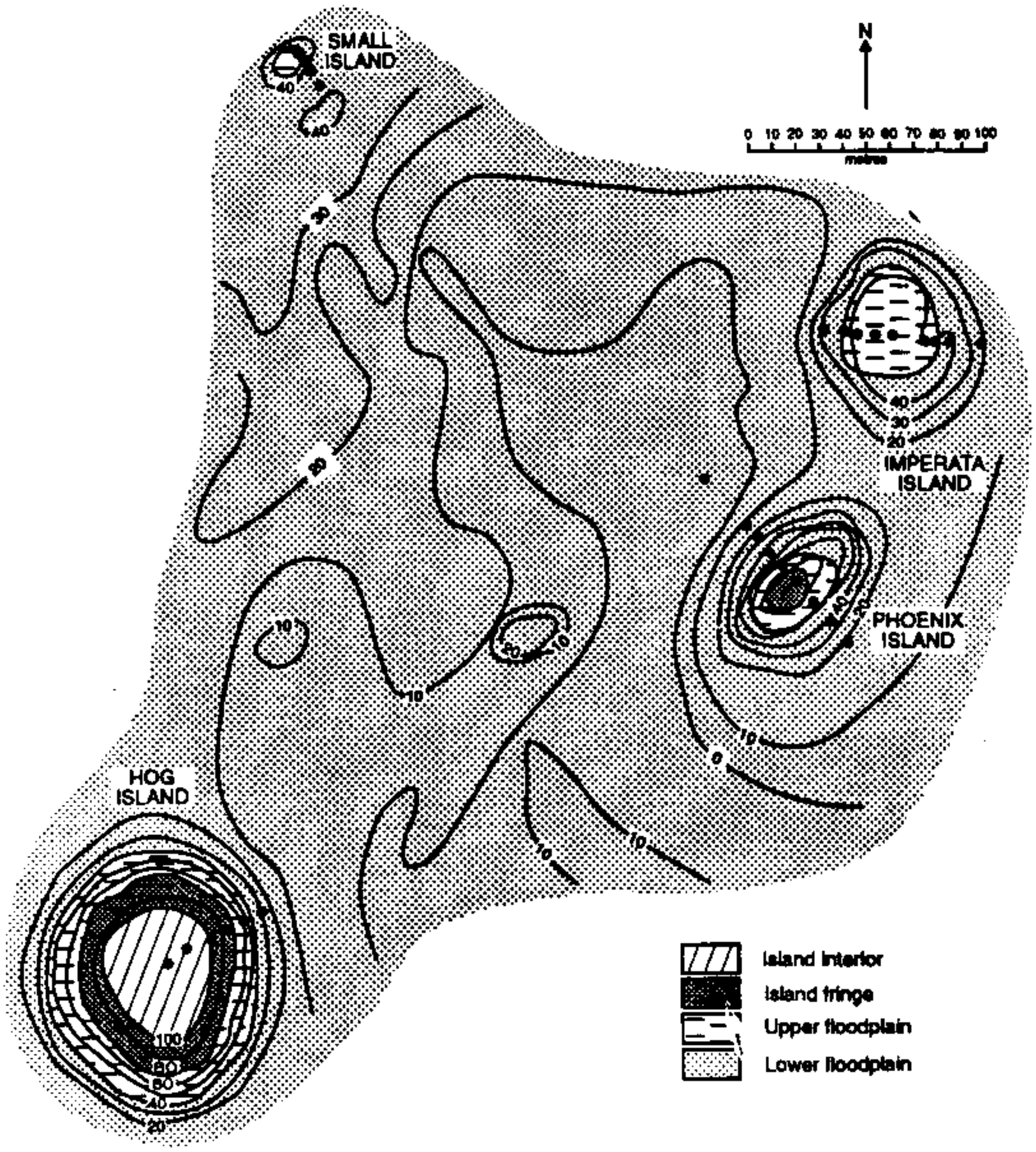

Figure 3: Topography and vegetation distribution of the four major plant communities in the study area described by McCarthy et al. (1997) showing the location of Small, Imperata, Phoenix and Hog Islands which were studied in detail.

Low lying areas are dominated by a plant community referred to as a lower floodplain grassland (McCarthy et al. 1998. Figure 3), which is flooded for prolonged periods each year. On higher lying ground an upper floodplain grassland occurs, and above the upper limit of flooding, islands support trees. Two plant communities were distinguished on these islands, one with the palm *Phoenix reclinata* Jacq. and other broad-leaved trees, referred to as an island fringe community, the other with deciduous trees and the palm *Hyphaene petersiana* Klotzsch, and referred to as an island interior community. Islands support one or both of these communities depending on their size and/or elevation above the floodplain.

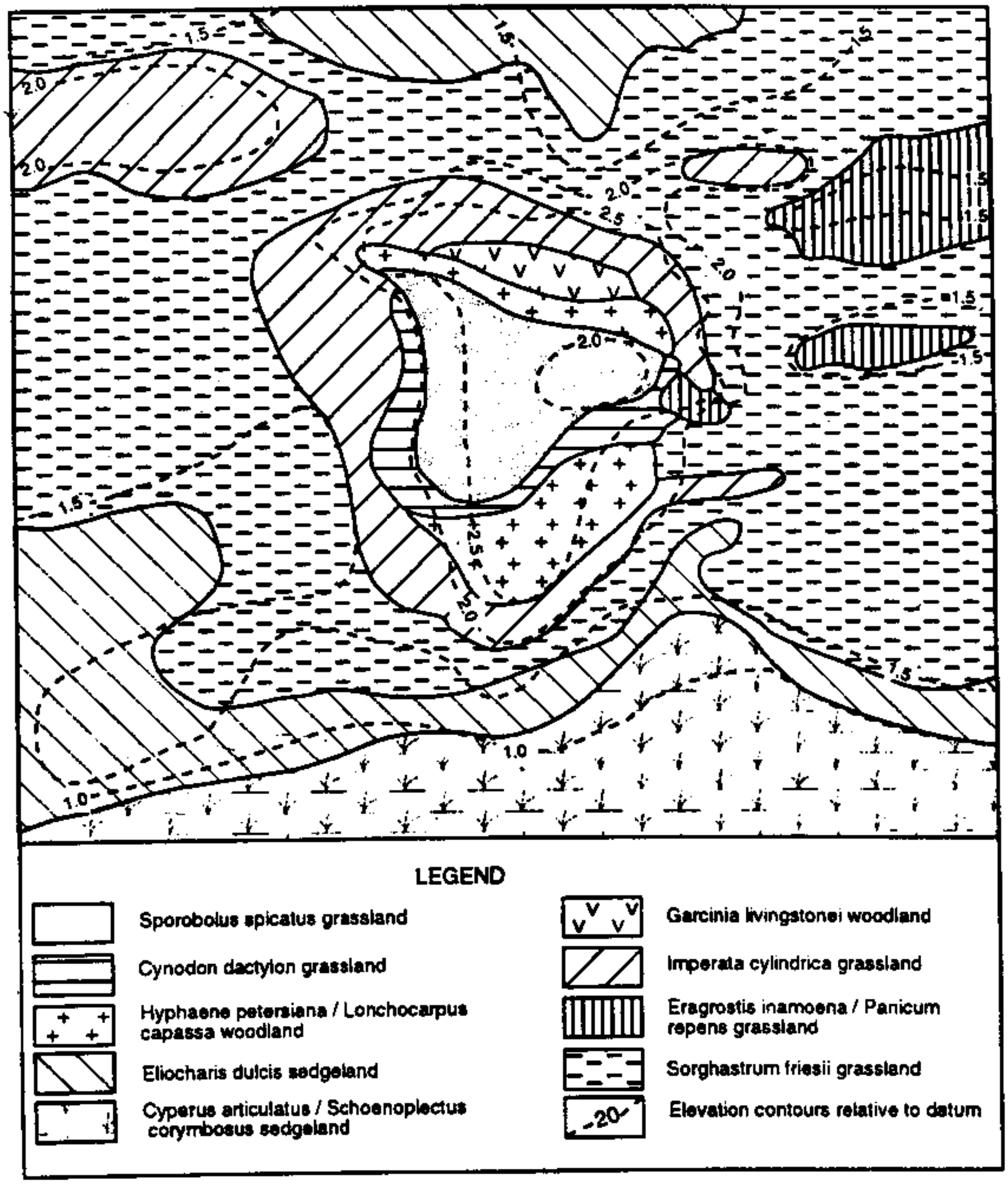

Figure 4: Topography and vegetation distribution of the major plant communities in the lower seasonal swamps near Thokatsebe.

A more detailed study of vegetation distribution in the lower seasonal swamps revealed a similar zonation of plants in relation to elevation (Figure 4). In the low lying areas closest to the Boro River channel, and flooded for the longest duration and greatest depth annually, a sedgeland dominated by *Cyperus articulatus* L. and *Schoenoplectus corymbosus* (Roth. ex Roem. & Schult.) J. Raynal occurs. This gives way to a sedgeland dominated by *Eleocharis dulcis* (Burm. f.) Hensch. with increased elevation. A grassland dominated by *Sorghastrum friesii* (Pilg.) Pilg. occurs on higher lying ground, and immediately surrounding islands the vegetation comprises virtually monospecific stands of *Imperata cylindrica*. In depressions isolated hydrologically from the main river channel, vegetation is dominated by either or a combination of *Eragrostis inamoena* K. Schum. and *Panicum repens* L. The islands are seldom flooded, and are dominated by a mixture of trees including *Garcinia livingstonei* T. Anders., *Hyphaene petersiana* and *Lonchocarpus capassa* Rolfe. The centre of the island has a shallow depression, and is dominated by *Sporobolus spicatus* (Vahl.) Kunth.

FLOODPLAIN AND ISLAND SOILS: THE ROLE OF TERMITES

The four islands depicted in Figure 3 have been studied in detail by McCarthy et al. (1998). The soil profile of each island is shown in Figure 5. The entire floodplain is underlain by clean well-sorted white sand. This white sand is widespread throughout the floodplain and envelops the islands completely. It lacks cohesion when dry, and contains no sedimentary structures that would enable its depositional environment to be determined. However, based on particle shape and surface texture, it was probably deposited under aeolian conditions. A dark grey sandy A-horizon less than 10 cm thick is developed at surface throughout the floodplain and island environments. Roots, organic matter and a small quantity of fine material present in this horizon, imparts some cohesion. The A-horizon grades down to pale grey sand that is generally less than 20 cm thick. Once again this material contains a small quantity of fine material, and is therefore cohesive. Beneath most islands a medium to dark grey sand is developed. It has a greater proportion of fine material than the other soil strata described thus far, and thus has slight to moderate clay-like consistency. It typically has a lens like form beneath islands. Beneath the centre of Hog Island, a dark grey clayey sand is developed. This material has a high proportion of fine material such as clays.

The mineralogy of typical samples from each of 5 soil strata is shown in Table 1. The overall mineralogy is very simple. It is dominated by quartz, with minor contributions of calcite, limonite and clay minerals (kaolinite and illite). This is related to a combination of depositional setting and the fact that very little clay is introduced into the ecosystem from the catchment. The increase in clay and calcite is consistent with the increase in the contribution of fine-grained material discussed in relation to Figure 5. This information as well as detailed information on soil chemistry (McCarthy et al. 1998) suggest that soils beneath islands are enriched in fine material relative to the surrounding floodplain, particularly of clay minerals and calcite.

All islands in the study area are associated with *Macrotermes michaelseni* termite mounds. Termite mounds consist of a turret that houses a ventilation system, and a pediment which is formed by erosion of the turret by rain (Figure 6). Termites construct their mounds using san grains cemented together with a mortar of fine material mixed with body fluids (McCarthy et al. 1998, Hesse 1955). Initially clay minerals are used, and enrichment by calcite appears to take place subsequently, probably mainly as a result of vegetation processes (McCarthy et al. 1998).

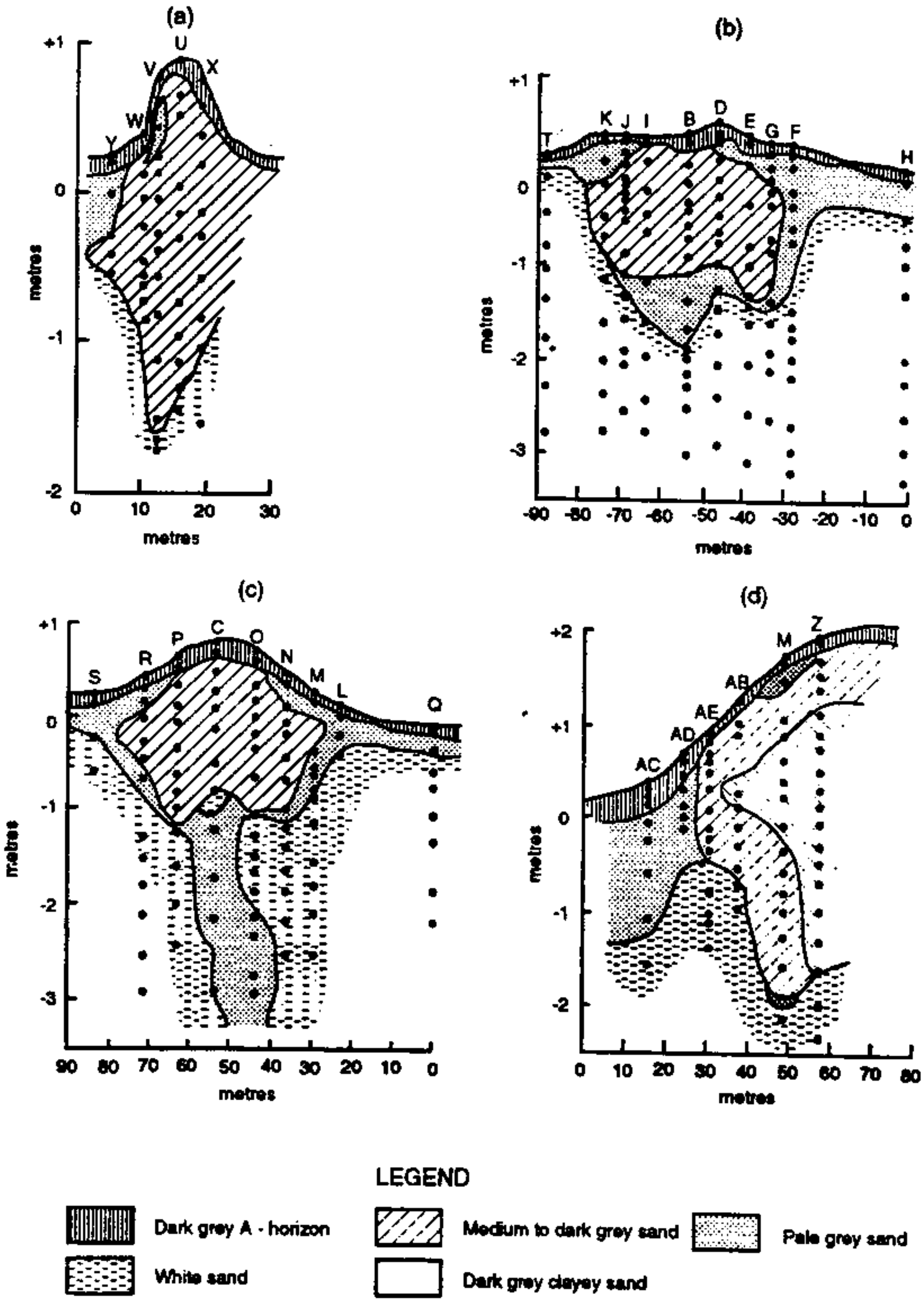

Figure 5: Soil profiles beneath Small Island (a), Imperata Island (b), Phoenix Island (c) and Hog Island (d; from McCarthy et al. 1997).

Table 1. Mineralogy of selected soil samples from the study of islands described by McCarthy et al. (1998). All values are expressed as percentages.

	Dark grey A-horizon	White sand	Pale grey sand	Medium to dark grey sand	Dark grey clayey	Termite mound
Quartz	93.2	95.4	95.6	83.6	73.0	76.0
Calcite	0.6	0.5	0.5	4.3	14.8	9.5
Kaolinite	3.4	2.6	2.7	6.5	4.1	5.1
Illite	1.0	0.9	0.7	2.4	4.0	3.2
Limonite	0.6	0.5	0.5	1.9	2.0	1.8
Organics	1.2	0.0	0.0	1.4	2.1	4.4

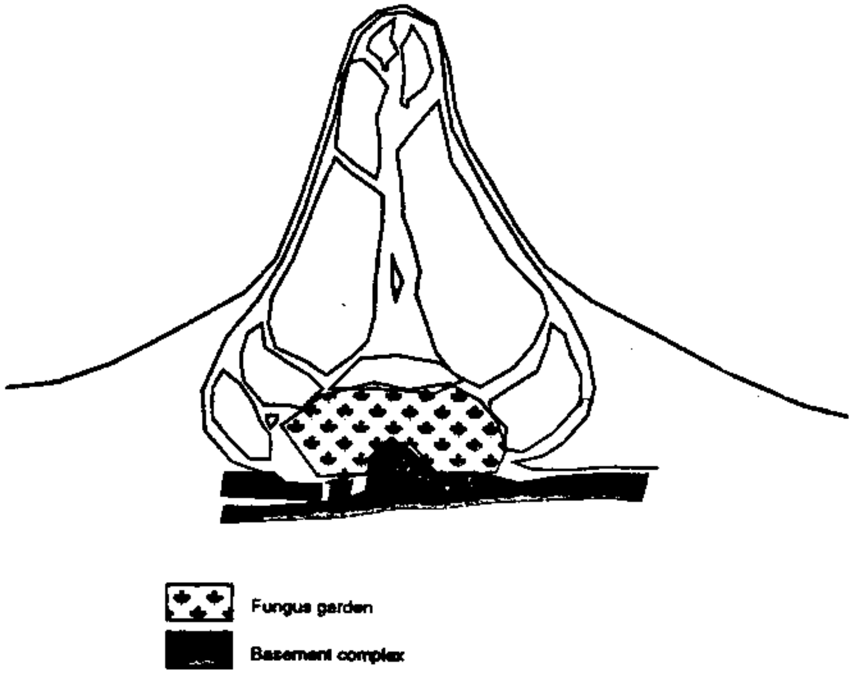

Figure 6: Schematic cross-section through a termitarium (from McCarthy et al. 1997).

We therefore believe that construction of termite mounds by *Macrotermes michaelseni* within floodplain habitats is accomplished by focussing clay minerals locally on the floodplain. This is important ecologically for many reasons, but the most important of these is the creation of a microhabitat free of flooding that enables growth of trees. Furthermore, nutrient enrichment associated with termite activity results in mammals spending a disproportionate share of their time in these areas (cf. Milton and Dean 1990), a process promoting dispersal of seeds of woody plants to these sites. Mounds are therefore colonised by trees, and once trees colonise a mound, their role in modifying floodplain morphology becomes dominant.

MODIFICATION OF FLOODPLAIN MORPHOLOGY BY VEGETATION

The role of vegetation in mima mound creation has traditionally been centered on the increased sedimentation of airborne dust that is considered to take place beneath individual trees or clumps of trees (van der Merwe 1940, Collins 1975). In contrast to this, we propose that trees modify floodplain morphology as a consequence of the precipitation of calcite below ground, due to high rates of transpiration relative to that in the surrounding floodplains.

Larger islands in the present study area as well as in other areas of the Okavango Delta are characterised by a distinct zonation of species from the fringe to the interior (Ellery et al. 1993, McCarthy et al. 1993). Typically the outer edge is dominated by a lush broad-leaved evergreen fringe. This gives way to deciduous trees with members of the genus *Acacia*, as well as the ivory palm *Hyphaeae petersiana*. The central regions are typically dominated by a short grassland dominated by *Sporobolus spicatus*, or they may even be completely barren.

Island topography, features of soil chemistry, groundwater elevation and conductivity, and the broad zonation of vegetation on an island in the Okavango Delta are indicated in Figure 7 (Ellery et al. 1993). Islands are typically atoll shaped, with a rim of high lying ground around a central depression. The concentration of calcium in soils is highest in regions of high elevation. However, the concentration of sodium is greatest in the centre of the island. close to and at the soil surface. High sodium concentrations at the soil surface are toxic to vegetation, and only the hardy grass *Sporobolus spicatus* is able to survive these conditions.

The groundwater table beneath islands is generally lower than in the surrounding swamp. Groundwater has a low conductivity close to island edges, but the concentration of dissolved solids increases dramatically towards the centre, increasing conductivity. It appears to be this combination of soil and groundwater chemistries that determines distribution of vegetation on islands in the Delta.

However, island topography as well as groundwater and soil chemistry, are the products mainly of vegetation processes in the island fringe. Plants generate strong abiotic environmental gradients in the subsurface soils and groundwater, and are even associated with the creation of topographic relief

The concentration of sodium in waters of the Okavango Delta is highly correlated with conductivity (Figure 8a). Sodium is therefore soluble over the entire range of total dissolved solid concentrations that occur in the ecosystem as a consequence of evapotranspirational water loss, and can therefore be regarded as a conserved constituent. Water entering the ecosystem has very low concentrations of dissolved solids, and as the concentration of dissolved solutes increases within the ecosystem as a consequence of evaporation and transpiration, the concentration of sodium increases. However, the same does not apply to calcium (Figure 8b). The plot of calcium concentration in relation to sodium concentration suggests that at low concentrations of dissolved solids, calcium concentration increases in proportion to the concentration of dissolved solutes that takes place as a result of evapotranspirational water loss. Thus, if 10 g of calcium is dissolved in 1000 litres of water, giving a concentration of 10 ppm, and this volume is evaporated down to 100 litres, 10 g of calcium remains in solution, giving a concentration of 100 ppm. However, as evaporation continues, calcium starts to precipitate out of solution as calcium carbonate. Therefore, with continued evaporation to 10 litres, 9.3 g of calcium

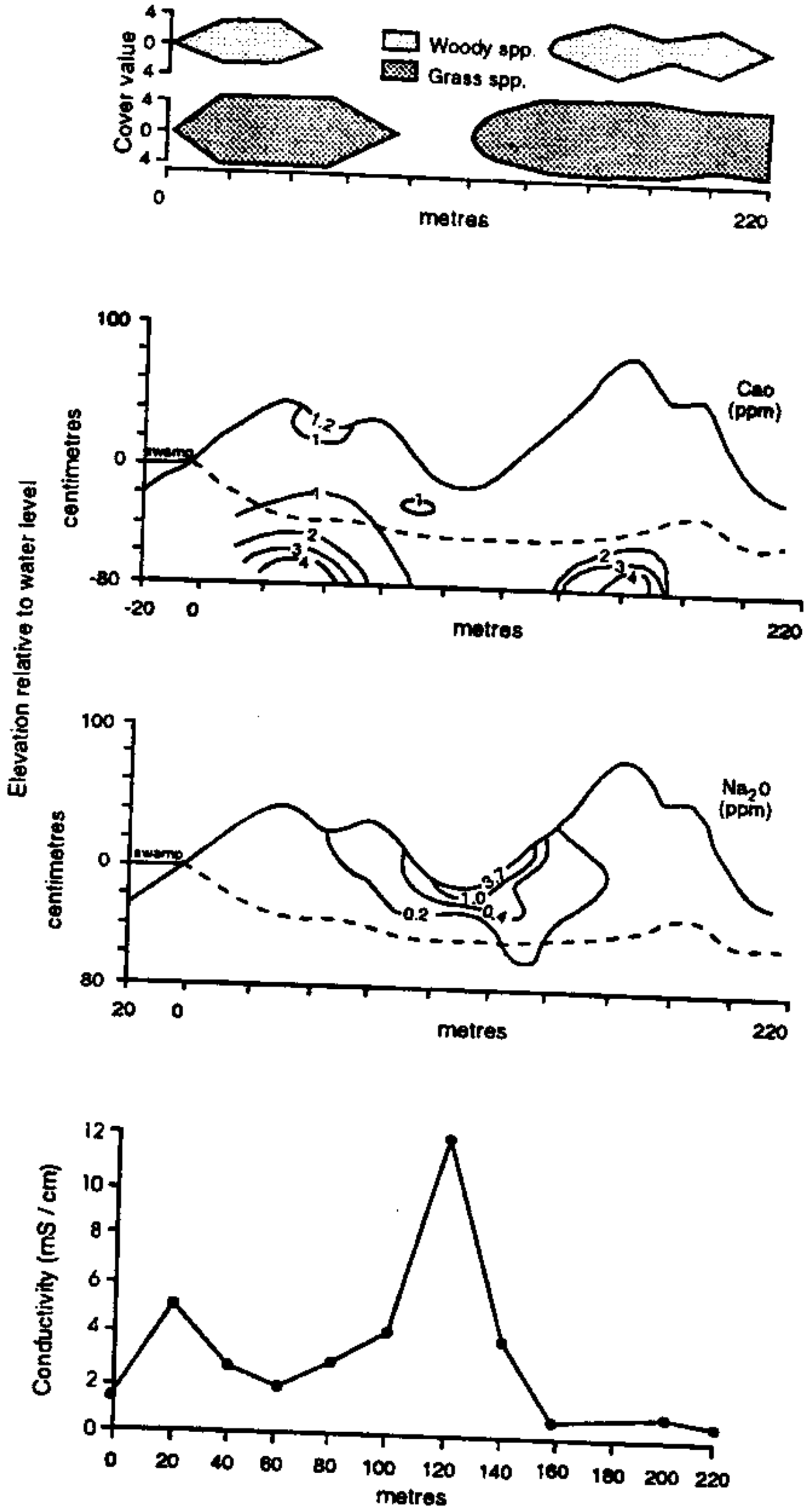

Figure 7: Typical island cross section and water table elevation in the middle and lower reaches of the Okavango Delta showing the zonation of vegetation (a), concentration of calcium as CaO (b) and sodium as Na_2O (c) in the soil, and the electrical conductivity of groundwater (d). (from Ellery et al. 1993).

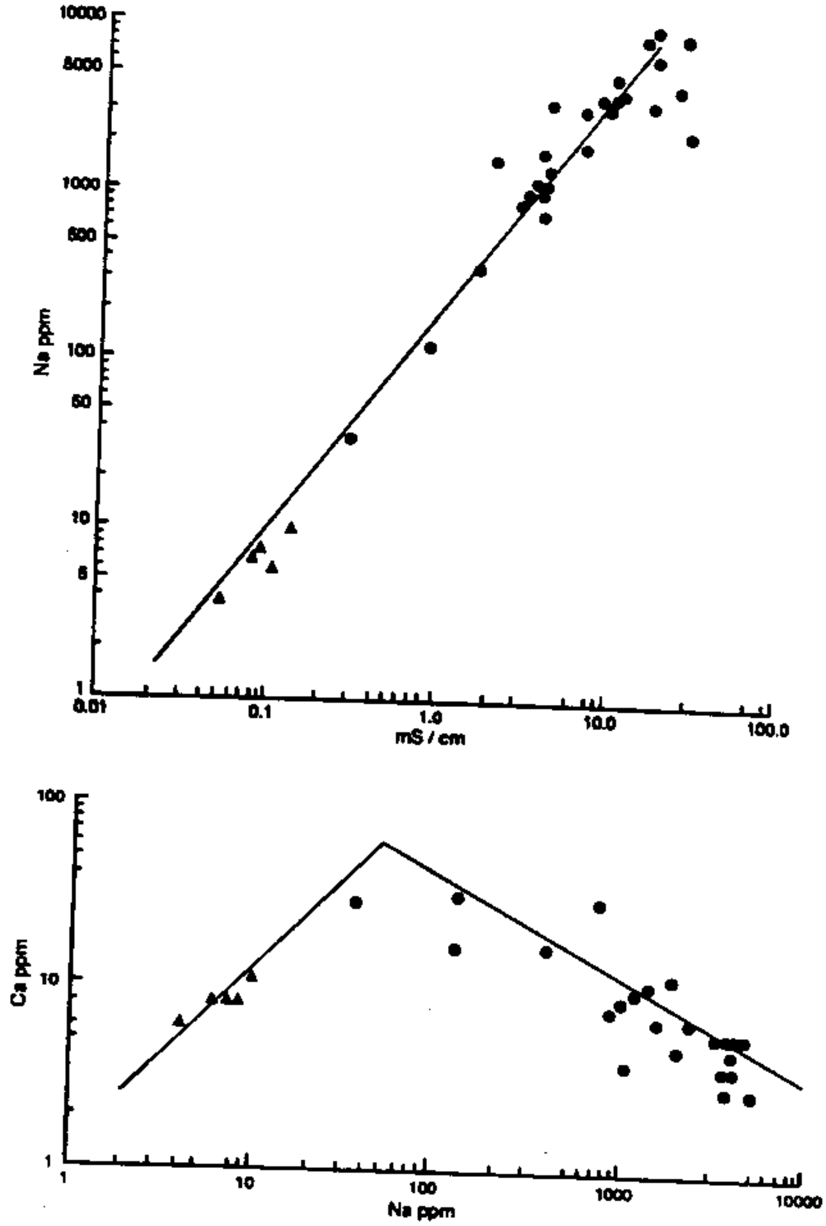

Figure 8: Plot of sodium against electrical conductivity (a) and calcium against sodium (b) for water samples in the Okavango Delta (from McCarthy et al. 1993).

carbonate ($CaCO_3$) will have precipitated out of solution while 0.7 g remains in solution, giving a calcium concentration of 70 ppm.

Examination of a typical conductivity profile beneath an island in the permanent swamps provides an indication of a marked increase in concentration of dissolved solids that occurs beneath islands (Figure 9). In order to achieve the conductivity profile indicated beneath the surface of this particular island, assuming that groundwater is derived ultimately from swamp water, enrichment would have to be 180 fold. This requires that 1000 litres of water be reduced to 5.5 litres (McCarthy et al. 1993), while solutes remain in the residual solution.

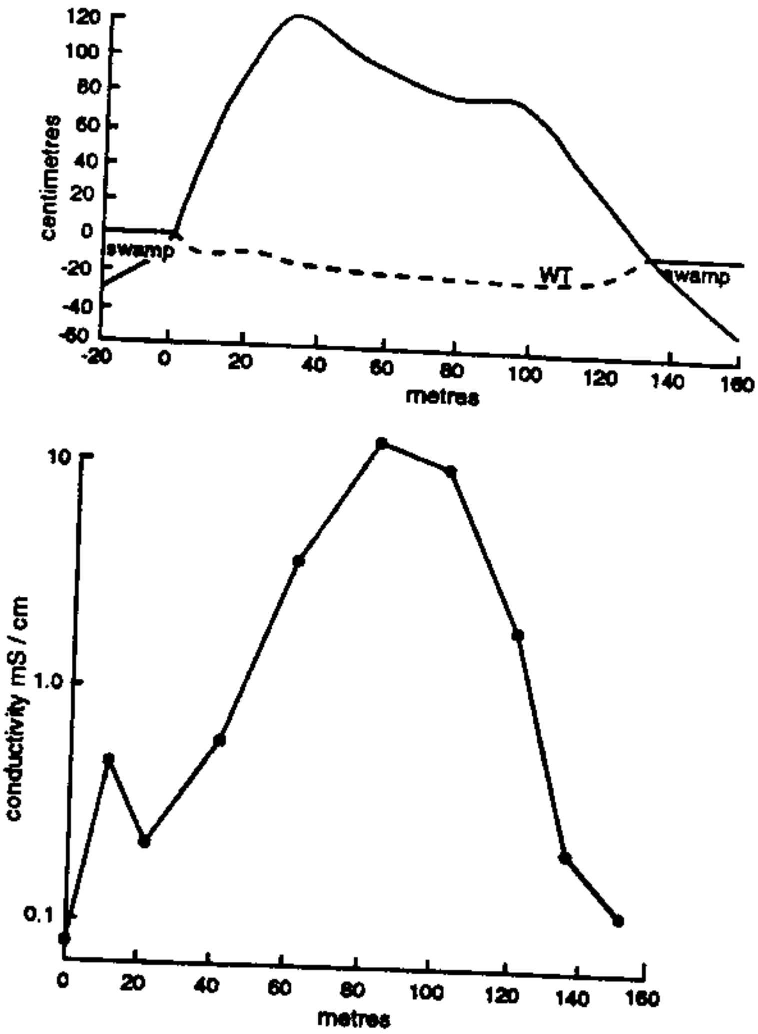

Figure 9: Island topography and water table elevation (a) and groundwater electrical conductivity (b) for an island in the middle reaches of the Okavango Delta (from McCarthy et al. 1993).

An indication of processes responsible for this increase in concentration of dissolved solutes beneath islands was provided in a study in which the depth to water table was accurately measured over a 24 hour period (Ellery et al. 1993, Figure 10). Results are plotted relative to readings taken at 5:50 a.m. In the centre of the island, the elevation of the water table remained fairly constant, but the change in elevation of the water table increased progressively with stations closer to the island edges, such that at the edges the variation was in excess of 6 cm. Furthermore, the elevation of the water table was lowest in the afternoon. Water loss was greatest in the area where the cover-abundance of woody plants was greatest, and it seems clear that woody plants, particularly those in the broad-leaved evergreen fringe are responsible for this loss of water. The following morning all of the water levels had returned to what they were at start of experiment as a result of recharge from the surrounding swamp. Plants are selective in what solutes they remove from water, and appear to be leaving most of them behind. For this reason the concentration of dissolved solutes increases as water migrates from the swamp into the island centre (McCarthy and Ellery 1994).

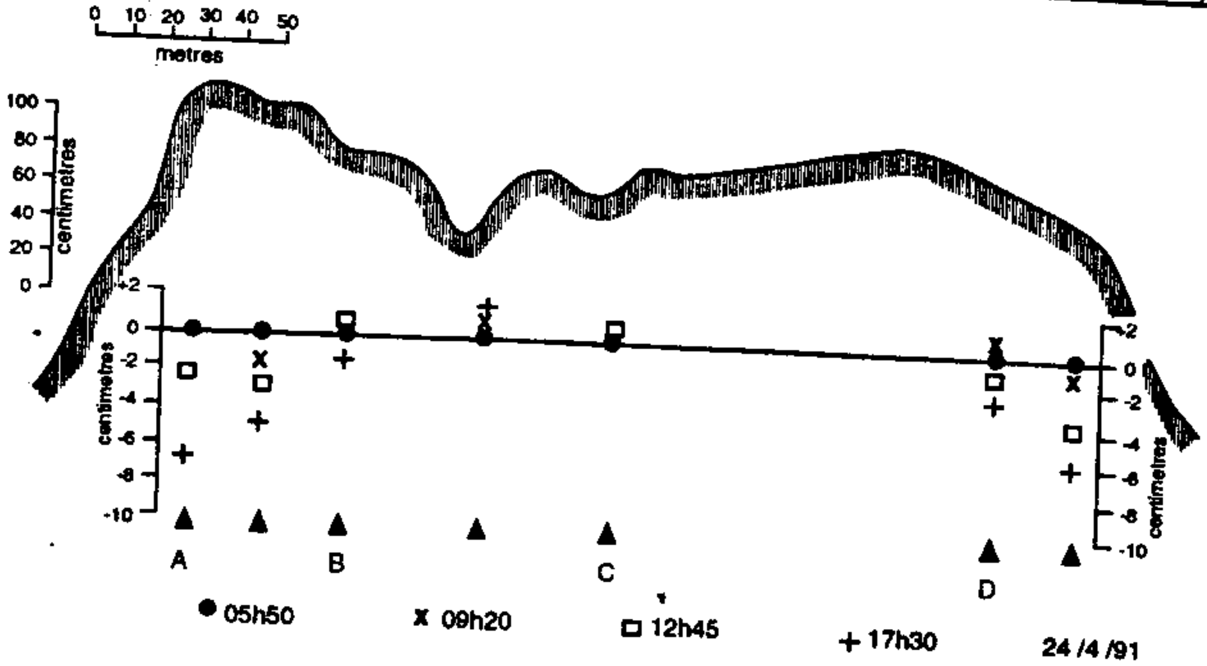

Figure 10: Relative change in water table elevation over a diurnal cycle. The elevation of the water table at 05: 50 is used as reference (from Ellery et al. 1993).

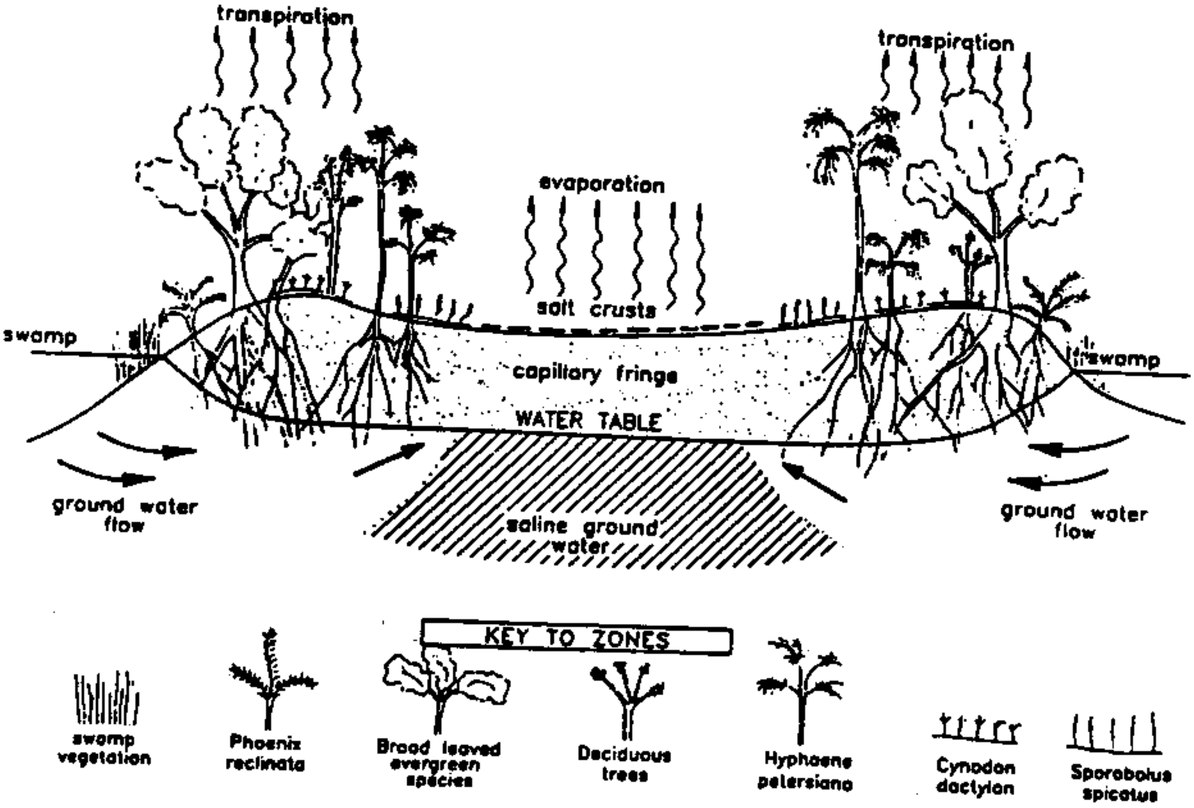

Figure 11: Diagram summarising the most important processes of water loss from islands in the Okavango Delta which contribute to observed variations in groundwater and soil chemistry.

The processes that take place on islands in the Okavango Delta are summarised in Figure 11. Illustrated is a typical atoll shaped island with a dense fringe of trees transpiring large quantities of water, but leaving dissolved constituents behind. Water moves from the surrounding swamp to replace transpired water. Evaporation from the soil surface in the capillary zone is also clearly an important process, leaving behind salt crusts and saline surface soils. As water moves from the surrounding swamp to replace water lost to the atmosphere, its conductivity increases, and calcite precipitates in the soil causing swelling. This swelling causes both vertical and lateral growth of the island. Vegetation processes therefore contribute enormously to shaping the morphology of floodplain environments as well.

IMPLICATIONS FOR MIMA MOUNDS

We believe that these studies have an important bearing on the origin of mima mounds. The first, and perhaps the most significant feature of this work, is that transpiration by woody plants results in precipitation of calcite, a process which causes a volume expansion in soils on the floodplain and leads to vertical and lateral growth of "islands". The association of calcrete with mima mounds has been widely reported as mentioned in the introduction, but the significance of calcrete precipitation as a formative process of mima mounds has been entirely overlooked. As an aggradational process in the Okavango Delta, it is clearly very important (McCarthy and Metcalfe 1990, McCarthy et al. 1991, McCarthy et al. 1993, McCarthy and Ellery 1994, 1995), and results in similar features to those described as mima mounds.

It would appear at the outset that mima mounds are only likely to form in areas with a high water table where potential evapotranspiration is much greater than rainfall. Atmospheric (evaporative) demand for water appears to be a prerequisite to the formation of mima mounds based on our understanding. Where rainfall is exceptionally high and equals or exceeds evaporation, dissolved solutes would probably be leached into deeper horizons, and would not accumulate in the root zone.

An important feature of mound building by the vegetation processes in the Okavango Delta is spatial variation in rates of transpiration. Because transpiration causes precipitation of chemicals in the soil, and accounts for aggradation, the greater the spatial variation in transpiration rate within the system, the more significant vegetation processes are in contributing to mound formation. Furthermore, the actual spatial variation in transpiration rate and the underlying causes of this variation, are likely to determine the spatial arrangement and size of mounds within a system.

A prerequisite to the establishment of woody plants in the Okavango Delta is the presence of a habitat free of flooding. This is often provided by termite mounds. However, any elevated area would be colonised by woody plants, and once colonised, would be subjected to aggradation by precipitation of calcite in the soil. In the Okavango Delta such habitats are afforded by depositional features such as scroll bars or by the inverted topography caused by channel abandonment (Ellery et al. 1989, McCarthy et al. 1988). Alternatively, they may arise as a consequence of tectonic activity (McCarthy et al. 1993).

Spatially, the association of trees and termite mounds in the Okavango Delta is widespread, and as such the importance of termites in initiating vegetation processes that contribute to mound building is very important. The mound features are therefore determined to a large degree by the distribution of termite mounds in the first place, and by whatever determines this - whether it is competition or other features of organism behaviour.

In contrast to other studies, we recognise that it is a combination of processes that contributes to mound creation and aggradation. Furthermore, the relative contribution of different processes changes as islands increase in size and therefore age (Figure 12). Initially the role of mound building organisms or processes contribute most to the volume of material present in the mound. In the case of the Okavango Delta, termites are particularly important, but fluvial and tectonic landforms may also be utilised. In the case of termites, island growth is initiated by collecting material suitable for construction. Termites are highly selective for particles in particular size classes that afford cohesive strength to the mound. This creates a microhabitat suitable for colonisation by woody plants, both by offering elevated sites free of flooding, and also by increasing the probability of recruitment.

Once woody plants have established on a mound, the role of vegetation in causing the subsurface precipitation of calcite becomes increasingly important. Furthermore, the role of trees in promoting deposition of wind borne dust may be important. The importance of evaporation and deposition of trona on the soil surface may contribute a small quantity of chemical sediment, but this is not a permanent feature as trona is extremely soluble and would be leached from the soil in the long-term.

We further believe that our model may be widely applicable. However, the contribution of each of the role players may vary appreciably. The importance of transpirational processes to aggradation is related to the spatial heterogeneity in rates of transpiration that is capable of appearing at a particular site. Sites with a climate not conducive to the establishment of trees, such as areas that are within a grassland biome, may therefore be dominated by processes related to the activities of burrowing animals rather than by chemical precipitation induced by transpiration. Furthermore, areas dominated entirely by trees are not likely to exhibit spatial differences in transpiration rate.

It is also likely that the importance of transpiration in contributing to overall aggradation would appear to increase in proportion to the contribution of dissolved chemicals from an external source, such as a catchment (Figure 13). In the absence of an external source of dissolved chemicals, such as in areas where rainfall contributes most to the water balance of an ecosystem, the importance of mound building organisms to overall aggradation may be greater than in environments which receive higher quantities of dissolved chemicals from external sources. However, even in areas in which rainfall dominates the water balance, lateral transfer of solutes will occur if transpiration rates are spatially heterogeneous, provided that the water table is sufficiently high to be within the root zone.

In the case of the Okavango Delta, calcite is the most important chemical constituent involved in mound growth. However, this is a function of ground water chemistry. Where ground water chemistry is different, other precipitates could become important, notably silica or iron oxides, which could produce mounds dominated by silcrete or iron laterite soils.

The contribution of externally derived water plus dissolved solutes also has a bearing on the size and spatial arrangement of mound structures that are likely to be created. Where rainfall dominates, weathering and solution/precipitation processes are likely to

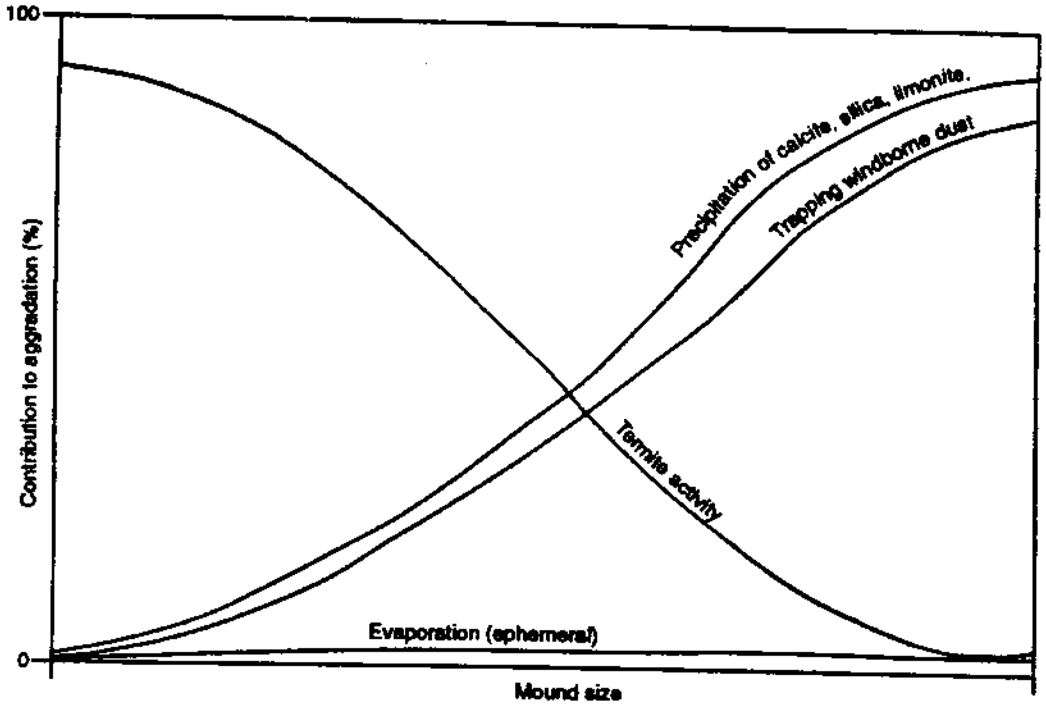

Figure 12: Hypothesised relationships between factors that contribute to mound aggradation and mound size.

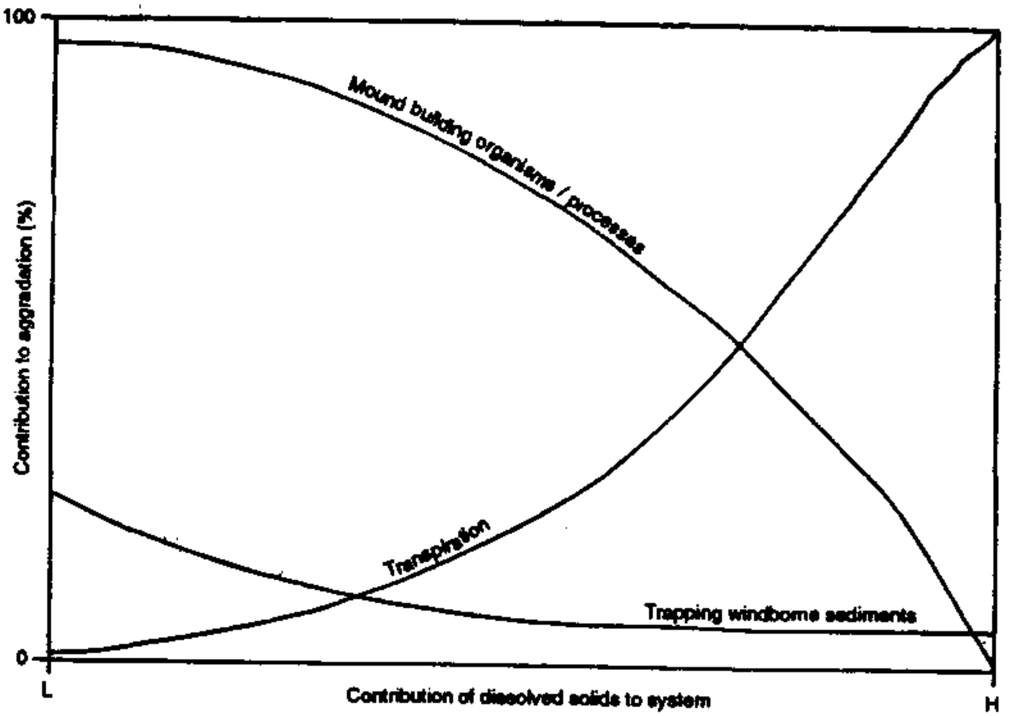

Figure 13: Hypothesised relationships between the contribution of transpiration, mound building organisms and windborne sediments and the contribution of dissolved solutes to a wetland (see text for details).

result in local (internal) redistribution of solutes, and mounds are likely to be closely related to the initial spacing of mounds by mound building organisms or other mound building processes. Furthermore, they are likely to be small, and of approximately equal sizes. However, where the water balance is dominated by inflow from an external source area, mounds are likely to be larger, less uniform in size, and may even be the product of coalescence of several mounds. As such the final mima mound structures are likely to extend well beyond the limits of the initial mounds produced by mound building organisms or processes. We therefore predict that small, evenly spaced mounds will occur in ecosystems which receive their water supply primarily as rainfall, and that as the contribution of surface and/or groundwater increases, individual mounds will not be detectable, but that, accretionary features will be extensive and include several to many initial mounds.

CONCLUSIONS

This paper has highlighted aspects of studies in a wetland in southern Africa where chemical aggradation is a dominant process, and which is the result of vegetation processes which cause the precipitation of dissolved chemicals below ground. This causes a volume increase in the soil, and is associated with the creation of topographic relief Spatial variability in transpiration rate is the primary cause of topographic heterogeneity. We suggest that mima mounds in general are the product of spatial differences in transpirational water loss from the system. The importance of mounds of any type in initiating spatial differences in transpiration rates is crucial, and we recognise that any biotic or abiotic process contributing to the formation o an initial mound that is suitable for woody plant establishment, could potentially give rise to mima mound topography. We further recognise several other important processes that may contribute to the size and spatial distribution of mounds, including the overall variation in transpiration rates that occur spatially, which may be determined by climate, as well as the source and quantity of dissolved chemicals introduced into an area. Where transpiration rates do not vary substantially in space, mima mounds are likely to be the product of processes other than the precipitation of dissolved substances in the soil as a consequence of transpiration. Furthermore, where the input of externally derived dissolved solutes is small, such as in systems that are dominated by rainfall, mounds are likely to be small and evenly spaced. As such they are likely to reinforce the initial topography created by processes other than vegetation processes. However, where there is an external source of dissolved chemicals, mounds are likely to be larger and less distinct. As such their association with an initial mound is not likely to be clear.

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