

The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer

J.M. DANGERFIELD*, T.S. McCARTHY† and W.N. ELLERY‡

*Commonwealth Key Centre for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia.

†Department of Geology, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa

‡Department of Geographical and Environmental Sciences, University of Natal, King George V Avenue, 4001 Durban, South Africa

(Accepted 18th February 1998)

ABSTRACT. Many organisms create or alter resource flows that affect the composition and spatial arrangement of current and future organismal diversity. The phenomenon called *ecosystem engineering* is considered with a case study of the mound building termite *Macrotermes michaelseni*. It is argued that this species acts as an ecosystem engineer across a range of spatial scales, from alteration of local infiltration rates to the creation of landscape mosaics, and that its impacts accrue because of the initiation of biophysical processes that often include feedback mechanisms. These changes to resource flows are likely to persist for long periods and constrain the biological structure of the habitat. The value of ecosystem engineering is discussed as a holistic way of understanding the complexity of tropical ecology.

INTRODUCTION

Many organisms modify the environments in which they occur. This can be through physical changes to abiotic conditions or alterations to the absolute amounts, production and availability of resources. The consequences are that the environment supports a different range of species and populations, with different dynamics, to those if the original organism was not present. Jones *et al.* (1994) and Lawton (1994) have formalised this process by which an organism directly or indirectly modulates the availability of resources for other organisms and called it *ecosystem engineering*. Organisms qualify as either autogenic engineers that change the environment via their own physical structures, or allogenic engineers that transform materials from one physical state to another. Beavers building dams, elephants felling trees, earthworms forming

soil casts would all be examples of allogenic engineering whilst higher plants that grow structures which collect and temporarily store water (eg. Fish 1983) would be autogenic engineers.

Most allogenic and autogenic ecosystem engineering is spatially explicit and frequently contributes to habitat heterogeneity. Consequently the effects of engineering would be seen first as a differential influence on the performance of individuals in their ability to acquire resources. This increased variance in individual performance becomes a component of population dynamics of organisms whose resources have been modified. Secondly, ecosystem engineers would influence the combination of populations present in a habitat and subsequently emergent properties at the community level, particularly succession, ecosystem resilience and stability. When engineers are persistent and widespread they may also have an influence on landscape level patterns in biodiversity (Yair & Rutin 1981). These consequences at higher levels of organisation may be as important to ecosystem function as interactions between species, especially competition, predation, mutualism, parasitism and disease (Jones *et al.* 1994), or patterns of nutrient and energy fluxes (Likens 1992). Also, if communities are tightly organised around engineers, the effects of their loss, for example through disturbance or human impacts, may be large and result in major changes to species composition and fluxes of matter and energy.

Termites, especially species of the genus *Macrotermes* that construct large epigeal nests and extensive underground gallery systems, have major effects on soil chemical and physical properties throughout the tropics and sub-tropics. This paper describes a form of ecosystem engineering by the mound-building species *Macrotermes michaelseni* (Sjöstedt) especially in the distal reaches of the Okavango alluvial fan in northern Botswana. The objective was to assess how the presence of this species influences habitat level heterogeneity and ecosystem function. We argue that the activities of *M. michaelseni* colonies initiate successional sequences and create landscape-level patterns in biodiversity (McCarthy *et al.* 1998) which extends the importance of this species to much larger spatial scales than those associated with local vegetation patterns and that this is likely to occur frequently throughout the species' range. As well as illustrating the importance of invertebrates as potential ecosystem engineers, a discussion of this example addresses questions posed by Jones *et al.* (1994) as to the relevance of ecosystem engineering as a valid conceptual framework to help understand emergent properties of ecosystems.

STUDY SPECIES: *MACROTERMES MICHAELSENI*

Termites account for 40 to 65% of the total soil macrofauna biomass in many tropical ecosystems (Wood & Sands 1978). In African savannas termite standing biomass has been estimated to be between 70 and 110 kg ha⁻¹ (Ferrari 1982, Wood *et al.* 1982, Wood & Sands 1978) and for only one species an annual

turnover of more than 120 kg ha⁻¹ (Darlington 1991). These values are comparable to ungulate biomass in African savannas of 10 to 80 kg ha⁻¹ (Bell 1982) and give some credibility to discussions of the importance of termites in the functioning of savannas (Deshmukh 1989). In most savanna habitats at least one species of the genus *Macrotermes* occurs and colonies are easily recognised by a large epigeal mound that maintains an equitable set of moisture and temperature conditions within the hive (Lüscher 1961). In the moist savannas of southern Africa several *Macrotermes* species are sympatric but with species-specific preferences for particular soil types, whilst in the more xeric habitats *Macrotermes michaelseni* is the most abundant or only species present (Mitchell 1980).

In Botswana, *M. michaelseni* can be abundant although it is patchily distributed (Mitchell 1980; *pers. obs.* of authors). Favoured areas are those with a high ground-water table, particularly seasonal pans and drainage lines, or where there is some clay accumulation in the soil profile as clay minerals are critical for mound construction (Boyer 1975). *M. michaelseni* is most common in the Okavango Delta in northern Botswana where mature colonies occur at densities of between 0.05 and 6.01 mounds ha⁻¹ (Schuurman & Dangerfield 1997). This inland delta forms part of the Kalahari basin drainage system and is fed by summer rains (December–April) in the river catchment area of central Angola which gives rise to winter floods at the delta's distal end (Ellery & McCarthy 1994).

Each colony is centred on a subterranean nest with a closed system of air passages in an epigeal turret above it (Darlington 1985a). These nests or mounds can be 4 m high and have a basal area of 50 m² (Schuurman & Dangerfield 1996). Mounds appear only when the colony is sufficiently mature and, other than sheets of soil that cover some food items, is the only surface expression of what can be an extensive network of foraging galleries and tunnels below the soil surface. These underground passages radiate from each mound and are used to access foraging areas and transport forage back to the nest (Darlington 1982). Although feeding occurs mostly at night, except on large logs covered with soil and possibly on dead roots underground, transport of material to the nest continues throughout the day (Lepage 1977). Estimates vary but between 1 and 1.5 t ha⁻¹ of plant litter per year are relocated to the central fungus-garden in this way (Lepage 1979). Foraging can extend up to 50 m from the nest with a concentration of both foraging activity and passages around 30–40 m from the nest (Darlington 1982) and an area of between 46–128 m² can be foraged on any one night (Lepage 1979).

Macrotermes michaelseni feeds on standing dead grass and grass litter (Lepage 1981a) or a combination of grass and woody litter (Boutton *et al.* 1983). In the Okavango system, however, it forages extensively on woody litter as well as grass. In *Croton megalobotrys* woodland more than 90% of observed foraging parties were on woody litter from trees of *C. megalobotrys*, *Lonchocarpus capassa* and

Acacia erioloba, and c. 5% were on elephant dung during the late dry and early wet seasons. In *Colophospermum mopane* woodland *C. mopane* woody litter was the main food source (J. M. Dangerfield & G. Schuurman, unpubl. data).

Faeces produced by young workers are moulded into an intricate structure on which a basidiomycete fungus grows and the combined efficiency of termite and fungus activity results in 80% digestion of the cellulose in the food (Wood 1978). The fungus appears to be a nitrogen supplement and energy source for young workers who then feed the nymphs (Rohrmann & Rossman 1980, Veivers *et al.* 1991).

ENGINEERING OF RESOURCES

There are two main ways by which *M. michaelseni* influences the distribution and flow of resources within savannas. The first concerns the consequences of central place foraging, which influences nutrient flow rates and localisation. The second relates to changes in soil composition through non-random selection and relocation of soil particles for mound construction and maintenance, and this influences topography and soil physical properties.

Nutrient resource flows

Evidence from surveys of permanent quadrats suggests that the distribution of foraging by *M. michaelseni* is evenly spread within woodland habitats in the Okavango floodplains (Schuurman & Dangerfield 1994a). Foraging from different colonies covers most of the available area. However, a lack of overt aggression between workers from different foraging parties made it difficult to assess areas foraged by individual colonies (Schuurman & Dangerfield 1994b). Lepage (1981a) observed a similar coverage of a habitat by *M. michaelseni* foragers in Kenyan savanna. The importance of this feeding behaviour for nutrient distribution is clear. Recalcitrant materials are decomposed in centralised locations that result in high concentrations of nutrients.

Some nutrients are temporarily immobilised in the body tissue of termites. There may be more than one million workers, nymphs and soldiers in a mature colony (Darlington & Dransfield 1987), with a fresh biomass of up to 100 kg ha⁻¹ (Darlington 1991). Given a nitrogen content in termite body tissue of 5.6–12.6% (Matsumoto 1976 cited in Wood & Sands 1978) this represents an immobilisation of 5–12 kg ha⁻¹ of nitrogen, c. 1% of that present in the soil pool. This nitrogen is not only temporarily unavailable to plants but it is concentrated in loci that cover less than 2% of the land area. The tendency for existing mounds to become the favoured sites for subsequent establishment of colonies (Collins 1981; Schuurman & Dangerfield 1996, 1997) can perpetuate this nutrient concentration over many decades (Wood *et al.* 1982). Mortality, particularly from ant predation (Lepage 1981b, 1991) and competitive encounters with other termites (Darlington 1982), can be high which contributes to the turnover and redistribution of nutrients.

both how much moisture gets into soil and how long it is retained for microbial activity. Porosity, bulk density and infiltration are interrelated properties that, although primarily determined by soil type, are modified by the activities of soil organisms (Lavelle *et al.* 1994). Elkins *et al.* (1986) removed subterranean termites from the Chihuahuan desert and found that on sites with minimal vegetation, infiltration rates in termite free areas were only 58% of those where termites were still active. The result was explained as an increase in bulk density following collapse of termite galleries that previously provided bulk flow into the soil (Elkins *et al.* 1986). At estimated gallery densities of 0.76 m of passage m^{-2} (Darlington 1982), a similar effect on infiltration would be expected from the presence of *M. michaelseni*. An increase in porosity due to extensive subterranean galleries would be mostly trivial in highly porous sands, but at critical times, such as during drought, even small differences may be sufficient to influence plant growth or survival. Given that foraging parties from different colonies appear to cover most of the habitat this impact upon infiltration will have a general spatial expression, unlike the localised effects of nutrient concentrations in nest structures and outwash pediments.

In the seasonally flooded areas of the Okavango Delta mature *M. michaelseni* mounds have tall turrets and steep outwash pediments (Schuurman & Dangerfield 1996) which generally lack vegetation and, consequently, have high runoff potential (Watson 1969). Most mounds are attacked by aardvarks (*Orycteropus afer*) which leave large holes at the base of the mound down which a proportion of runoff enters the main gallery system. However, much of the runoff can be held by the clays at the base of the pediment and a moist zone is present after rain, which also has elevated nutrient levels from erosion of the turret. After several rainfall events or once the soil is saturated these clay rich areas retain moisture for longer than the surrounding soil in between rainfall events. In addition the metabolism of the fungus and several hundred thousand termite workers and soldiers within the nest will contribute to the moisture content of the nest structures. It is, therefore, a combination of moisture retention and elevated nutrients that produces the concentric zonation in vegetation production and composition around mounds (Arshad 1982).

Physical modification of soil properties, in combination with the consequences for moisture availability, are important elements in the zoning of vegetation. In the semi-arid systems, where *M. michaelseni* dominates, such moisture effects are perhaps more important than the changes in nutrients postulated as critical to vegetation composition in areas affected by other *Macrotermes* species (Fanshawe 1968). There is also some evidence that the alteration to runoff and infiltration by termites affects large scale water movements and associations with groundwater. Lee & Foster (1991) reviewed data from studies of *M. bellicosus* in central African savannas and suggested that infiltration around the edge of the mound pediment drains into the area of modified soil beneath the mound through perched water tables (Boyer 1975). This moisture may then return to the nest passively through the heat pump effect of the

turret (Weir 1973) and capillary action through the fines that line the gallery system or actively in the soil particles collected by termite workers for turret and gallery maintenance. This 'wick effect' is important to the accumulation of minerals in the mound (McCarthy & Ellery 1995, Weir 1973).

The transport of clay minerals for mound construction outlined earlier can also have a sorting effect on stony soils. Clay minerals are mined from beneath stones and larger fragments of parent material which subsequently fall to lower levels in the profile and which, over time, create a stone-free A horizon (Darlington 1985b). The vegetation composition and structure that subsequently develops reflects this biotic tillage. The gathering of specific minerals for construction or moisture collection can also reach considerable depths in the soil profile, a much neglected mechanism that extends biotic activity from the upper O and A horizons into the parent material (Richter & Markewitz 1995).

The Okavango Delta

The distal reaches of the Okavango Delta are a mixture of vegetated islands within a floodplain. Islands vary in width from a few metres to many kilometres. Most are, however, less than 10 ha in area with distinct vegetation zonation in relation to size and age (Ellery *et al.* 1993). Topographic surveys, mineralogical and chemical analyses of soils and measurements of vegetation succession on a range of islands and adjacent floodplains (McCarthy *et al.* 1998) suggest that creation of persistent topography above the flood level is critical to the persistence of woody plants and organisms that depend on them. Such topography is first created by the requirement of mature *M. michaelseni* colonies for an epigeal turret that ventilates the fungus garden at the centre of the nest. Woody plants establish on the outwash pediments of termite mounds and then the island expands through carbonate precipitation from groundwater in which solutes are concentrated by transpiration (McCarthy & Ellery 1995, McCarthy *et al.* 1998).

In this example the initial engineering creates a localised topographic feature that is a safe site for woody plant seedlings with a much reduced probability of extended inundation. The undoubted changes in soil chemistry and physical properties also contribute to the quality of the safe site, especially to plant growth, but the fact that areas are now above the mean flood level is most important. These termite-created islands become the foci for biodiversity of woody plant species and the organisms associated with them (Figure 1).

In the proximal reaches of the Delta there is sufficient water for permanent swamps that vary in extent with the seasonal flood. Here the effect of termite mounds on plant diversity is enhanced because the flooded back-swamp areas contain fewer plant species than the seasonally inundated grasslands of the distal reaches. The greater diversity, particularly of palatable plants, on islands initiated by *M. michaelseni* encourages many invertebrate, bird and mammal species to seek islands as refuges or sources of food. The many interactions that

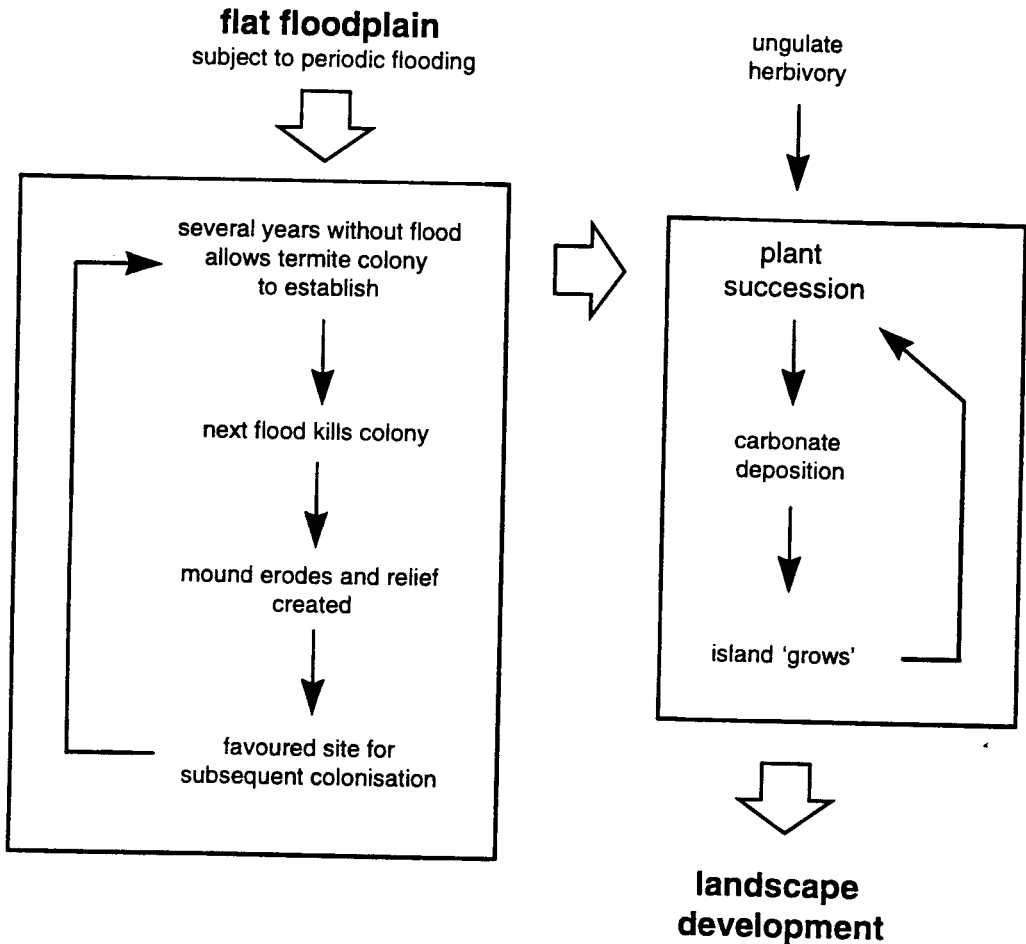


Figure 1. Sequence of events and feedback mechanisms in the formation of islands on the floodplain of the Okavango Delta, Botswana.

subsequently develop include several positive feedback mechanisms of nutrient enrichment and seed dispersal that contribute to succession (McCarthy *et al.* 1998). The combination of the initial creation of safe sites and subsequent reinforcement by physical processes of carbonate deposition (McCarthy *et al.* 1986) and biological succession (McCarthy *et al.* 1998) defines the structure and scale of the Delta's landscape.

ENGINEERING IMPACTS AT LARGER SCALES

The impact of *M. michaelseni* mounds on local topography and nutrient status can persist for long periods, perhaps centuries, even after major habitat disturbance. For example, fire is frequent in seasonal savannas and may have dramatic impacts on local species composition (see papers in Booysen & Tainton 1984) but *Macrotermes* colonies remain relatively unaffected by the fire itself and probably only temporarily influenced by the reduction in food supply because of their flexibility in food selection. There is no doubt that the combination of increased forage quality due to high soil nutrient status around mounds, contributes to increased grazing pressure by ungulate mammals

(McCarthy *et al.* 1998). The fuel load around termite mounds is therefore always low and the moisture content of the vegetation relatively high, hence fire seldom affects the vegetation on or surrounding mounds in floodplain habitats. Similarly Brinn (1990) established that nutrient heterogeneity in soils of arable fields derived from savannas in which mound building *Odontotermes latericius* and *O. badius* were abundant was due to past termite effects and produced variability in crop production within a field. Once termites have engineered a soil the changes in nutrient fluxes appear to persist well beyond the lifetime of the colony.

Such long term effects may contribute to the relatively low levels of organic carbon recorded in many savanna soils (Woomer *et al.* 1994). Jones (1990) proposed that significant proportions of carbon volatilisation on some sites is due to the rapid and efficient turnover of litter by termites which causes the soil carbon pool to be bypassed and reduces carbon buildup. Over geological time such a process, along with more tangible effects of fire, high mean temperatures, sand content of soil and seasonality (R. J. Scholes, *pers. comm.*) could have major influences on the accumulation and spatial distribution of recalcitrant soil carbon. At such long time scales these changes may constrain the evolution of organisms within the system by affecting absolute levels of resources. Such systems may also restrict invasion to those species already able to compete for sparse nutrients. These larger scale properties are those of most interest when land use change places pressures and perturbations on ecosystems.

IS ECOSYSTEM ENGINEERING A VALID CONCEPT?

Jones *et al.* (1994) list several advantages to thinking of organisms in terms of their impacts as ecosystem engineers, specifically as an alternative to a focus on trophic transfers or their intrinsic properties. We agree that termites are a prime example of allogenic ecosystem engineers and that consideration of an invertebrate as a modulator of resource flows is valuable to help answer questions of how ecosystems are structured and maintained. In the case of the Okavango Delta a flat floodplain has developed local topography and vegetation pattern because of the initial soil transport and nutrient changes associated with mound construction by *M. michaelsoni* (McCarthy *et al.* 1998). The spatial heterogeneity created also helps to understand processes that maintain local diversity, such as meta-population dynamics and dispersal, and at what scale they operate. A similar example of the impact of termite mounds on alpha diversity is that at least half the woody plant species in a miombo woodland site in southern Zambia were only found on mounds of *M. falciger* (Timberlake 1995). The real advantage to thinking of ecosystem engineers, in addition to traditional approaches, is that consideration of state and resource modulations often leads to the identification of feedback mechanisms, those internal processes that may either confer stability on a system or facilitate successional sequences.

In the Okavango Delta the higher nutrient availability on termite mounds creates concentrations of palatable plants, these attract ungulates which import more nutrients but also aid the dispersal of woody plant species (McCarthy *et al.* 1998). Establishment of these woody plants attract further mammal and bird species, a positive feedback that results in a local succession of plant and animal species. Should a high flood saturate the soil and kill a large number of *M. michaelseni* colonies within the distal floodplain, knowledge of how the soil nutrient status and physical expression has been engineered allows us to predict the pattern of vegetation development in the temporary absence of termites.

A related but frequently neglected aspect of ecosystem development is that once a resource flow has been engineered the original pathway may be lost entirely. The concentration of clay minerals into a locally rich patch, and the subsequent heterogeneity in CEC created, is a persistent feature. The organisms within the ecosystem are now constrained by this nutrient distribution. This is familiar in terms of external abiotic disturbances such as fire or drought but rarely considered as the consequence of biotic activity.

Clearly the removal of *M. michaelseni* from parts of the Okavango Delta would be a useful test of how important engineers are to ecosystem stability. Results of a preliminary removal experiment suggest that there might be some compensation in activity by other termite groups when *M. michaelseni* abundance is reduced and that any significant impact on processes may take several years before there are observable effects on ecosystem properties (J. M. Dangerfield & G. Schuurman, unpubl. data). Similarly the addition of nutrients without the presence of mounds or the construction of artificial mounds would test the degree of synergism between elevation and nutrient availability that are created by a *M. michaelseni* mound. Few such experimental tests have been attempted but would be a productive way forward.

Traditionally, conservation biology has taken an organism centred approach to the problem of declining diversity (see discussion by Caughley 1993). Rare and endangered species, or more strictly populations of these species, are the focus of research and active management. For example, the conservation, usually through protection, of charismatic mammals can protect large enough tracts of habitat for all other species. Walker (1995) and Smith *et al.* (1993) suggest that preservation of processes is really the key to ensure ecosystem persistence and hence a conservation of functional types has a better chance of success in conserving diversity. In the seasonal swamps of the Okavango Delta preservation of ecological process is inextricably linked to the persistence of *M. michaelseni*. In the permanent swamps at the proximal end of the Delta, *M. michaelseni*, the giant sedge (*Cyperus papyrus*) and hippopotamii (*Hippopotamus amphibius*) are equally critical ecosystem engineers. A mechanism toward preservation of process, which has been a rather abstract concept to define and, therefore, assign management objectives and strategies to, might be to focus

on the maintenance of those engineers that have impacts at ecosystem or landscape scales.

CONCLUSIONS

Macrotermes michaelseni is the consummate allogenic ecosystem engineer. The activity of colonies modifies resource flows directly by relocating nutrients and soil particles as well as indirectly through effects on soil properties and feedback mechanisms. The landscape pattern of islands surrounded by inundated grasslands over more than 20,000 km² of the Okavango floodplain is initiated by this engineer. Although often masked by other factors, such engineering must impact on community properties wherever mound building termites occur. We would suggest that the extensive literature on how termites modify soils and nutrient cycling in Africa (Hulugalle & Ndi 1993, Jones 1990, Pomeroy 1983), North America (Elkins *et al.* 1986), Australia (Holt & Coventry 1990, Lobry de Bruyn & Conacher 1990) and Asia (Lal 1987) might be reconsidered in the light of the termites as ecosystem engineers.

The idea that one species can be central to the current structure and dynamics of an ecosystem is not new but the concept of an engineer, an organism that modifies resource flow and drives or becomes part of feedback mechanisms, is a powerful way to consider ecological assemblages. As ecologists continue to consider interactions (Thompson 1996) and functions (Martinez 1996) of ecosystems as important elements of conservation and management strategies, an eye toward the organisms that modify these processes would be rewarding.

ACKNOWLEDGEMENTS

We are grateful to Gregor Schuurman, Bob Scholes and David Bignell for helpful discussions. John Lawton, Andy Beattie, Ian Oliver, Jo Darlington and two anonymous reviewers made helpful comments on an earlier version of this paper. The Okavango Research Centre, University of Botswana, provided travel funds to facilitate part of this work which began when one of us (JMD) was in the Department of Biological Sciences, University of Botswana. This contribution is Key Centre for Biodiversity and Bioresources paper no. 257.

LITERATURE CITED

- ARSHAD, M.A. 1981. Physical and chemical properties of termite mounds of two species of *Macrotermes* (Isoptera, Termitidae) and the surrounding soils of the semi-arid savannah of Kenya. *Soil Science* 132:161–174.
- ARSHAD, M. A. 1982. Influence of the termite *Macrotermes michaelseni* (Sjost) on soil fertility and vegetation in a semi-arid savannah ecosystem. *Agro-ecosystems* 8:47–58.
- BELL, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. Pp.192–216 in Huntley, B.J. & Walker, B.H. (eds). *Ecology of tropical savannas*. Springer-Verlag, Berlin.

- BOOYSEN, P. de V. & TAINTON, N. M. (eds) 1984. *Ecological effects of fire in South African ecosystems*. Springer-Verlag, New York. 435 pp.
- BOUTTON, T. W., ARSHAD, M. A. & TIESZEN, L. L. 1983. Stable isotope analyses of termite food habits in East African grasslands. *Oecologia* 59:1-6.
- BOYER, P. 1975. Action de certains termites constructeurs sur l'évolution des sols tropicaux. III. Les différents aspects de l'action de *Bellicositermes* sur les sols tropicaux. - *Annales des Sciences Naturelles Zoologie (Paris) Série 12*. 17:447-504.
- BRINN, P. J. 1990. *Termite modification of soils in south eastern Botswana*: Report to Land & Water Management Project. Unpublished Report, Natural Resources Institute, Chatham. 43 pp.
- CAUGHLEY, G. C. 1993. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- COLLINS, N. M. 1981. Populations, age structure and survivorship of colonies of *Macrotermes bellicosus* (Smeathman) (Isoptera: Macrotermitinae). *Journal of Animal Ecology* 50:293-311.
- DANGERFIELD, J. M. 1991. Soil modification by *Cubitermes sankurensis* (Wassman) (Isoptera: Termitidae) within a Miombo woodland site in Zimbabwe. *African Journal of Ecology* 29:267-269
- DARLINGTON, J. P. E. C. 1982. The underground passages and storage pits used in foraging by a nest of the termite *Macrotermes michaelseni* in Kajiado, Kenya. *Journal of Zoology (London)* 198:237-247.
- DARLINGTON, J. P. E. C. 1985a. The structure of mature mounds of the termite *Macrotermes michaelseni* around Kajiado, Kenya. *Insect Science and its Applications* 6:149-156.
- DARLINGTON, J. P. E. C. 1985b. Lenticular soil mounds in the Kenya highlands. *Oecologia* 66:116-121.
- DARLINGTON, J. P. E. C. 1991. Turnover in the populations within mature nests of the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux* 38:251-262.
- DARLINGTON, J. P. E. C. & DRANSFIELD, R. D. 1987. Size relationships in nest populations and mound parameters in the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux* 34:165-180.
- DESHMUKH, I. 1989. How important are termites in the production ecology of African savannas? *Sociobiology* 15:155-168
- ELKINS, N. Z., SABOL, G. V., WARD, T. J. & WHITFORD, W. G. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia* 68:521-528.
- ELLERY, W. N. & McCARTHY, T. S. 1994. Principles for the sustainable utilisation of the Okavango Delta ecosystem, Botswana. *Biological Conservation* 70:159-168
- ELLERY, W. N., ELLERY, K. and McCARTHY, T. S. 1993. Plant distribution on islands of the Okavango delta, Botswana: determinants and feedback interactions. *African Journal Ecology* 31:118-134.
- FANSHAWE, D. B. 1968. The vegetation of Zambian termitaria. *Kirkia* 6:169-179.
- FERRAR, P. 1982. Termites of a South African savanna IV. Subterranean populations, mass determinations and biomass estimations. *Oecologia* 52:147-151.
- FISH, D. 1983. Phytotelmata: flora and fauna. Pp. 1-27 in Frank, J. H. & Lounibos, L. P. (eds). *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, NJ.
- HOLT, J. A. & COVENTRY, R. J. 1990. Nutrient cycling in Australian savannas. *Journal of Biogeography* 17: 427-432.
- HULUGALLE, R. & NDI, J. N. 1993. Soil properties of termite mounds under different land uses in a Typic Kandiodult of Southern Cameroon. *Agriculture, Ecosystems Environment* 43:69-78
- JONES, C. G., LAWTON, J. H. & SHACHAK, M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- JONES, J. A. 1990. Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *Journal of Tropical Ecology* 6:291-305.
- LAL, R. 1987. *Tropical ecology and physical edaphology*. J. Wiley & Sons, New York. 732 pp.
- LAVELLE P., DANGERFIELD J. M., FRAGOSO C., LOPEZ-HERNANDEZ D., ESCHENBRENNER V., BRUSSARD L. & PASHANASI B. 1994. The relationship between soil macrofauna and tropical soil fertility. Pp. 137-169 in Wooster, P. L. & Swift, M. J. (eds). *The biological management of tropical soil fertility*. J. Wiley & Sons, Chichester.
- LAWTON, J. H. 1994. What do species do in ecosystems? *Oikos* 71:367-374.
- LEE, K. E. & FOSTER, R. C. 1991. Soil fauna and soil structure. *Australian Journal of Soil Research* 29:745-775.
- LEPAGE, M. 1977. Foraging and food consumption of *Macrotermes subhyalinus*. Proceedings. VIIIth International Congress IUSSI, Wageningen, pp. 249-252.
- LEPAGE, M. 1979. La récolte en strate herbacée de *Macrotermes* aff. *subhyalinus* (Isoptera:Macrotermitinae) dans un écosystème semi-aride (Kajiado-Kenya). Comptes Rendu Université Institut d'Étude d'Insecte sociale, sect. Française, Lusanne. Pp. 145-151.
- LEPAGE, M. 1981a. L'impact des populations récoltantes de *Macrotermes michaelseni* (Sjostedt) (Isoptera:Macrotermitinae) dans un écosystème semi-aride (Kajiado, Kenya) II. Nourriture récoltée, comparaison avec les grands herbivores. *Insectes Sociaux* 28:309-319.
- LEPAGE, M. 1981b Etude de la prédation de *Megaponera foetens* (F.) sur les populations récoltantes de *Macrotermitinae* dans un écosystème semi-aride (Kajiado, Kenya) II. Nourriture récoltée, comparaison avec les grands herbivores. *Insectes Sociaux* 28:247-262.

- LEPAGE, M. 1984. Distribution, density and evolution of *Macrotermes bellicosus* nests (Isoptera: Macrotermitinae) in the north-east of the Ivory Coast. *Journal of Animal Ecology* 53:107–117.
- LEPAGE, M. 1991. Predation on the termite *Macrotermes michaelseni* reproductives and post settlement survival in the field (Isoptera: Macrotermitinae). *Sociobiology* 18:153–166.
- LIKENS, G. E. 1992. *The ecosystem approach: its use and abuse*. Ecology Institute, Oldendorf/Luhe. 166 pp.
- LOBRY DE BRUYN, L. A. & CONACHER A. J. 1990. The role of termites and ants in soil modification: a review. *Australian Journal of Soil Research* 28:55–93
- LÜSCHER, M. 1961. Air-conditioned termite nests. *Scientific American* 205:138–145.
- MARTINEZ, N. D. 1996. Defining and measuring the functional aspects of biodiversity. Pp. 114–148 in Gaston, K. (ed.) *Biodiversity*. Blackwell Scientific Publications, Oxford.
- McCARTHY, T. S. AND ELLERY, W. N. 1995. Sedimentation on the distal reaches of the Okavango fan, Botswana, and its bearing on calcrete and silcrete (ganister) formation. *Journal of Sedimentary Research* A65:77–90.
- McCARTHY, T. S., ELLERY, W. N. & DANGERFIELD, J. M. 1998. The role of soil biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes and Landforms* 23:291–316.
- McCARTHY, T. S., McIVER, J. R. & CAIRNCROSS, B. 1986. Carbonate accumulation on islands in the Okavango Delta. *South African Journal of Science* 82:588–591.
- MITCHELL, B. L. 1980. Report on a survey of the termites of Zimbabwe. – *Occasional papers National Museum, Rhodesia, B., Natural Sciences*. 6:187–323.
- MERMUT, A. R., ARSHAD, M. A. & ARNAUD R. J. St. 1984. Micropedological study of termite mounds of three species of *Macrotermes* in Kenya. *Soil Science Society of America* 48:613–620.
- POMEROY, D. E. 1976. Some effects of mound building termites on soils in Uganda. *Journal of Soil Science* 27:377–394.
- POMEROY, D. E. 1983. Some effects of mound-building termites on soils in Kenya. *Journal of Soil Science* 34:555–570.
- RICHTER, D. D. & MARKEWITZ, D. 1995. How deep is soil? *Bioscience* 45:600–609.
- ROHRMANN, G. F. & ROSSMAN, A. Y. 1980. Nutrient strategies of *Macrotermes ukuzii* (Isoptera: Termitidae). *Pedobiologia* 20:61–73.
- SCHOLES, R. J., DALAL, R. & SINGER, S. 1994. Soil physics and fertility: the effects of water, temperature and texture. Pp. 117–136 in Wooster, P. L. & Swift, M. J. (eds.). *The biological management of tropical soil fertility*. J. Wiley & Sons, Chichester.
- SCHUURMAN, G. & DANGERFIELD, J. M. 1994a. *Abundance, distribution and feeding ecology of fungus growing termites of the genus Macrotermes in Moremi Game Reserve*. Second Quarterly Report, Department of Wildlife & National Parks, Gaborone. 19 pp.
- SCHUURMAN, G. & DANGERFIELD, J. M. 1994b. Assessment of intraspecific aggression in *Macrotermes michaelseni* (Isoptera: Macrotermitinae). *Sociobiology* 24:1–6
- SCHUURMAN, G. & DANGERFIELD, J. M. 1996. Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (Isoptera: Macrotermitinae). *Sociobiology* 27:29–38
- SCHUURMAN, G. & DANGERFIELD, J. M. 1997. Dispersion and abundance of *Macrotermes michaelseni* colonies: a limited role for intraspecific competition. *Journal of Tropical Ecology* 12:39–49.
- SMITH, T. B., BRUFORD, M. W. & WAYNE R. K. 1993. The preservation of process: the missing element of conservation programs. *Biodiversity Letters* 1:164–167.
- THOMPSON, J. N. 1996. Evolutionary ecology and the conservation of biodiversity. *Trends in Ecology and Evolution* 11:300–303.
- TIMBERLAKE, J. R. 1995. Botanical assessment of the Kalomo study area. Pp. 20–23 in Cotterill F. P. D. (ed.) *SAVSKILL: a method to measure and monitor biodiversity in central African savannas*. Biodiversity Foundation for Africa, Bulawayo.
- VEIVERS, P. C., MUHLEMANN, R., SLAYTOR, M., LEUTHOLD, R. H. & BIGNELL, D. E. 1991. Digestion, diet and polyethism in two fungus-growing termites: *Macrotermes subhyalinus* Rambur and *M. michaelseni* Sjoestedt. *Journal of Insect Physiology* 37:675–682.
- WALKER, B. H. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* 9:747–752
- WATSON, J. P. 1969. Water movement in two termite mounds in Rhodesia. *Journal of Ecology* 57:441–451.
- WEIR, J. S. 1973. Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus* (Rambur). *Journal of Animal Ecology* 42:509–520
- WOOD, T. G. 1978. Food and feeding habits of termites. Pp. 55–80 in Brian, M. V. (ed.) *Production ecology of ants and termites*. Cambridge University Press, Cambridge.
- WOOD, T. G. & SANDS, W. A. 1978. The role of termites in ecosystems. Pp. 245–292 in Brian, M. V. (ed.) *Production ecology of ants and termites*. Cambridge University Press, Cambridge
- WOOD, T. G., JOHNSON, R. A., BACCHUS, S., SHITTU, M. O. & ANDERSON, J. M. 1982. Abundance

- and distribution of termites (Isoptera) in a riparian forest in the southern Guinea savanna vegetation zone of Nigeria. *Biotropica* 14:25-39.
- WOOMER, P. L., MARTIN, A., ALBRECHT, A., RESCK, D. V. S. & SCHARPENSEEL, H. W. 1994. The importance and management of soil organic matter in the tropics. Pp. 47-80 in Woomer, P. L. & Swift, M. J. (eds). *The biological management of tropical soil fertility*. J. Wiley & Sons, Chichester.
- YAIR, A. & RUTIN, J. 1981. Some aspects of the regional variation in the amount of available sediment produced by isopods and porcupines, northern Negev, Israel. *Earth Surface Processes and Landforms* 6:221-234.