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Ecological Benefits of Termite Soil Interaction and Microbial Symbiosis in the Soil Ecosystem

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Abstract

Termite activities and their interaction with soil environment have defined and modified ecosystems for ages. Termites, as detrivores, are one of the most important insect groups in the Australian environment whose activities and interactions with soil result in significant temporal and spatial changes, formations or modifications of soil, vegetation and landscape. Their influence is largely through their activities in searching and acquisition of food and construction of nests, galleries, soil sheetings and mounds. Their associated symbiotic relationship with actinomycete bacteria, depending on the species, also influences the soil and contributes to soil rehabilitation and plant diversity. Termite interaction with soil depends on soil type, moisture and organic matter content in different seasons and climatic regions. Other key factors affecting this interaction include termite species, size range and morphological characteristics with in a colony. This paper reviews mechanisms of soil and water transport by individual and colonies oftermites, their preferences and reactions to specific factors, and their effect on selected key soil physical and chemical properties as well as microbial activities.

Keywords: Isoptera, Mound, Symbiosis, Soil physical properties, Soil, Water

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1 Introduction

1.1 Termites

Termites are social insects living in nests or colonies, mostly consisting of multiple generations, ranging from several thousand to several million individuals at maturity, depending on species, availability of food resources, and soil environment [1]. They belong to the order Isoptera of which over 2600 species have been recognized and classified worldwide [1] and 260 species in Australia [2]. They are found in a wide range of terrestrial environments distributed throughout warmer regions of the world—predominantly tropical, subtropical, and temperate regions— and rarely found at altitudes of more than 3000 m [3]. They build various types of nests. Some (e.g., some species of *Amitermes)* have a completely underground existence, apparently without a central nest. Many economically important termites, like *Mastotermes darwiniensis* Froggatt and species of *Coptotermes*, build a central nest in soil, in dead or living trees. Others, like some in the genera *Nasutitermes* and *Microcerotermes,* build arboreal nests but maintain a soil connection using covered shelter tubes running down the trunks' surface [4].

Termites form associations with symbionts. This relationship plays a significant role in the digestion and decomposition of organic matter as well as moderating nutrient dynamics or global cycling through the ingestion and redistribution of minerals [5-9]. The degradation process of wood (mainly cellulose and lignin) from dead or living plants and soil organic matter takes place in the lumen of termites' hindgut or in mound chambers (termitaria). This is accomplished with the help of bacteria and protozoa, living within termite hindguts, and fungi, which are cultivated as 'fungus gardens' or 'fungus combs' by some termites [5, 8, 10-12]**.**

Termites are categorized into two functional or feeding groups depending on their food sources and their effects on soil [1]. Lower (soil-feeding) termites harbor a dense and diverse population of bacteria and cellulose digesting flagellate protozoa in their alimentary tract [1, 11, 13]. They include six of the families in the phylogenic order (excluding family *Termitidae*) [1, 13]. They consume humus and build nests with fecal matter mixed with coarse, inorganic soil particles. Many of these species feed almost exclusively on wood that is decomposed by the interaction of a rich community of organisms. Although wood is an impoverished environment or lower in nutrient content (especially nitrogen and phosphorus), the ability to fix nitrogen overcomes this evident disadvantage for such decomposers [6, 14-17]**.**

The second functional group, higher termites or fungus-growing termites, are the largest family (family *Termitidae*) comprising three fourths of all termite species [6, 8]. They harbor a dense and diverse array of gut bacteria, but normally lack protozoa and have a more elaborate external and internal anatomy and social organization than do lower termites [11]. They are characterized by an exosymbiosis with a fungus (*Termitomyces* sp.) that completes the degradation of litter on which they feed [11]. They enrich their structures with fine, mostly clay particles, and saliva that are rich in easily degradable carbon [18, 19].

1.2 Ecological Benefits of Termite-soil Interaction

Generally, termites create microhabitats, favorable for the development and sustenance of symbiont microorganisms, providing them with optimum security from predators and other interferences, minimum or less extreme fluctuations of wetting and drying cycles, as well as abundant and accessible nutrients [5, 8, 20]. Therefore, termites significantly influence and regulate the structure of soil bacterial and fungal communities, as reported, for instance, with fungus-growing termite species of *Ancistrotermes* and *Odontotermes* [20]**.** French and Ahmed [21] described a network of short dead-end tunnels in irregular sponge-like outer walls of *Coptotermes lacteus* mounds that serve as sites for culturing actinomycetes (particularly actinobacteria) and for trapping excessive moisture from within the mound which would sustain them.

Mounds and other structures built by termites are usually enriched in soil organic matter and fine particles; hence, they could be considered islands of higher fertility in an otherwise less fertile soil [9, 22-24], significantly modifying soil microbial diversity and activity [12, 25-27]**.** Termites were estimated to decompose 20% of total dead plant matter in north Queensland [9] while a similar figure was reported as a minimum percentage of termite removal of animal dung in the Chihuahuan desert ecosystem [28]. Their contribution to organic matter decomposition in tropical and subtropical areas, where their biomass densities can exceed 50 gm^{-2}, is significantly higher than that of grazing mammalian herbivores (biomass densities of 0.013–17.5 gm^{-2}) in similar areas or the direct contribution of all invertebrates in temperate areas [8-10, 29]. Soils surrounding termite mounds also have a massive increase in fertility due to higher nutrient status of materials eroded from mound surfaces [9, 12]**.** Increases in soil nutrient levels by up to seven times have been reported for termites (species of *Amitermes*, *Drepanotermes* and *Tumulitermes*) in north Queensland [30].

In the Chihuahuan desert Elkins et al. [31] reported that removal of subterranean termites caused a complete disappearance of a dominant perennial grass while instigating a chain of changes in soil properties. In the same experiment, termite effects resulted in decreased productivity of dominant shrub in the system while changing the composition of a spring annual plant community. In dry tropical savannas, trees associated with termite colonies remained green throughout the year due to the sustenance of water from termite colonies well into the dry season [32]. Thus, termite modifications have a great impact, in terms of time and space, on the vegetation even after their structures have been abandoned, eroded, or their colonies have been disturbed or destroyed [33]. In the Western Australian wheat belt habitats, favorable environmental conditions in autumn and winter coupled with highly active termites were the most likely reasons for the increase in species richness in the upper soil horizon [34].

Analysis of termite activities becomes imperative if maximum benefit is to be sought with respect to their role in restoring degraded ecosystems [35-37], mitigating effects of climate change, global warming [38], and desertification [31] or if mechanisms in their efficient micro-ecosystems are to be adopted [21]. This paper examines current knowledge pertaining to termite interaction with soil, individually or in colonies, and their role in ecosystem. Termite activities that result in changing soil formation and modification processes in the temporal and spatial senses are discussed along with biological and environmental factors affecting this process.

2 Mechanisms of Termite Soil and Water Transport

2.1 Introduction

Termite activity involves a paramount change in the dynamics of the immediate soil environment [19]. Primarily, it involves sorting out, selective preference and movement of substantial amount of soil particles within or between soil profiles [39] and above the soil surface. This is due to the need for termites to build nests, search for food, foraging galleries, sheetings, and mounds of different sizes, shapes, and architectural complexities, by spending considerable amount of time and energy depending on the species, climate, soil and land use [21, 39-41]. Construction of the termite nest begins with excavation of royal chamber by the founding pair of alates [42]. According to Lee and Wood [8], depending on whether or not they have a concentrated nest system, termites build these structures either by excavation or by construction while the formation of new galleries in those without concentrated nest systems, such as in *Kalotermitidae* and *Termopsinae*, could be linked to their feeding. In all cases, termites use these structures for their physiological function [43] to maintain humidity and temperature, as well as for covering and protecting themselves, their symbionts and their food [44]. No other group of animals have developed the extent of design and dimension that termites have reached in terms of burrowing and molding structures from soil and organic matter [8]. During times of erosion by wind, rain, human activities, and animals, maintenance involves continuous transport of soil into the surface of the mounds to offset the losses [43-45]. This continuous maintenance occurs by adding or reorganizing soil particles making the mound a dynamic structure [32, 43].

Termites usually detect an opening in their mound and immediately start transporting moist soil to cover it to protect the colony from intruders, prevent moisture loss, and maintain humidity inside. This maintenance activity lasts no more than overnight and the new soil material can be identified by its moist dark color and irregular outcrop on the mound structure [21, 43] (Figure 1). Normally a mound grows as the colony grows [8] as a result of additions of soil particles to the mound structure. This usually occurs at a smaller rate, for instance, ranging from 0.3–4.2% of the original size as reported by Lobry de Bruyn and Conacher [41] for *D. tamminensis* in Western Australian open woodland.

Figure 1: Visible new mud or soil deposition on above ground termite mound of *Coptotermes acinaciformis* in Northern Territory collected in less than 14 hours of drilling

2.1 Termite Movement and Soil Transport

Soil is a heterogeneous material composed of solid materials, food or non-food with respect to termites, and interconnected voids containing soil, water, and gas. Termites first travel as far from the nest as possible with the least effort by following existing gaps or preformed tunnels before starting to dig new tunnels [46-48]. This is done in order to save energy and time and hence increase efficiency. According to Evans [46], *C. frenchi* used heterogeneity to their advantage by following gaps in sand quickly to the most distant points and started tunneling at the extremities, thus maximizing the area explored and spreading the network. Similar behavior was also reported for *R. flavipes* and *R. virginicus* by Pitts-Singer and Forschler [48]. Physical guidelines and potential food sources encountered often influence termite foraging behavior. The simplest physical guideline, such as a tine ripping just 300 mm into the soil encouraged *Coptotermes* and *Mastotermes* foragers to use such a "highway" in preference to undisturbed soil (French and Ahmed, unpubl. data). Termites also tunnel extensively along objects they consider as food, and if they are successful, they use it as a starting point to explore more resources in the area [49]. In urban areas, termites use gaps created underneath water or sewer pipes, cables and roots of trees to access building structures [49]. Tucker et al. [50] reported that cracks and gaps wider than approximately 0.7 mm in foundations of building structures were one of the most likely entry points for *R. flavipes* termites.

The range of particle sizes that termites can penetrate through a soil medium depends on the mandible and head capsule size of the foraging species and colonies. Termites cannot penetrate soils with particles that are too large for them to pick up in their mouths and move, and with spaces between particles too small for their head capsules to pass through [51, 52]. This observation has led to the development of alternative control methods for termites using graded particles as physical barriers [51, 53-55], such as the nationally accredited granite aggregate product Granitgard (Granitgard Pty. Ltd., Victoria) in Australia for use in regions south of the Tropic of Capricorn, where *M. darwiniensis* are absent [55]. Several physical barriers composed of different soil particle ranges have been reported as effective ways of preventing penetration by different species of termites. Some of these ranges include 1.7–2.36 mm effective against *C. formosanus*, 1–2.36 mm against *R. flavipes* [53] and 1.2–1.7 mm against *R. hesperus* (Ebeling and Pence 1957 cited in [54, 55]. Moreover, as mentioned above, granite screenings of 1.7–2.4 mm acquired national accreditation as physical barriers against *C. acinaciformis* [55]. Su and Scheffrahn [54] also mentioned that in areas where both *C. formosanus* and *Reticulitermes* species occur, two-sized particle barriers (2–2.36 mm and 2.36–2.8 mm) appear to be the only effective means of exclusion.

Laboratory evaluation on the size of minimum foraging hole for *C. formosanus* in Hawaii indicated that termites can travel freely through openings as small as 1.4 mm in diameter, but their activity is negligible at 1.2 mm, and no termites pass a 1.1 mm aperture [56]. Similar dimensions for *C. acinaciformis* in laboratory bioassays in Melbourne were recorded [55]. In field bioassays in Northern Territory, Australia, Lenz et al. [57] examined response of termites to cracks of different widths in concrete structures. They reported minimum values of 3.1 mm for *M. darwiniensis*, 1.5 mm for *C. acinaciformis* and *Heterotermes validus*, 1.4 mm for *Schedorhinotermes intermedius breinl*, and 1.8 mm for *H. vagus*.

Soil texture affects the time it takes for termites to initiate and construct tunnels in different substrates [58]. The coarser the substrate, the lower the number of particles to be removed and the greater the spaces available or created once a particle is removed [59]. This gives termites an advantage during tunneling by reducing the number of individual visits needed for tunnel extension. On the other hand, the presence of finer soil particles fills the gaps and reduces the space in between particles and consequently reduces tunneling rate, as more trips are required to remove the soil particles [59].

In most cases, termites have to maneuver in between or move soil particles when building foraging tunnels. According to the description of Ebeling and Pence, termites build tunnels by using their heads, mandibles, and/or their body to push particles to either side [55]. The buccal cavities are used to carry smaller particles, which are then mixed with saliva and feces to build a very compact and smooth surface by cementing them along the walls of tunnels. At the same time mandibles are used to carry larger soil particles when constructing above-ground shelter tubes or depositing excess ones on surface [50, 53-55]. Although the size of mandibles is only about 0.5 mm, by grasping the edge of a particle, termites can move particles of about 1.0 mm in length [55]. Their actions redistribute soil particles with no or little change in composition. However, most species seem to ingest and then regurgitate finer size fractions while only soil or humus feeding species pass soil particles through their guts. Yet the incorporation of some gravel (5 mm) into above-ground portions of mound or any other structure can give some indication of the size of the workers in the colony [8].

Tunneling activity of termites rearranges soil particles while salivary and fecal products add some organic matter to the packed soil [8]. A compacted soil has reduced volume and hence higher bulk density due to reduced amount of macropores. The closely packed soil particles in the soil medium will be difficult for termites to let loose and carry while the reduced spaces in between provide less room for maneuver [60]. Tucker *et al*. [50] reported slower tunneling rates of termites in the most compacted soil (1.35 $g.cm^3$ of moistened sand at 10% w/w) in the laboratory.

The quantity of soil transported depends on the colonies' type of habitat and season of the year, as colonies in open habitat have been observed to move nearly four times more soil to the surface than those in a wooded habitat [43, 44]. Open habitats have higher evaporation rates due to their exposure to the sun, wind, and dry air [43]. Turner et al. [43] stated that soil transport mostly takes place during rainy seasons and is usually tied to patterns of rainfall. The actual amount transported depends on species and the environment, but estimated figures of 575 kg in the Sonoran desert grassland [61], up to 1059 kg/ha per year in arid areas of North Kenya [44], and more were reported. The abundance, area of coverage, weight, and size of termite mounds give an indication on the amount of soil transported to the surface. Estimates of more than 1,100 mounds/ha in tropical Australia, weighing 62 ton/ha of soil, covering 1.7% of the sampled area [8], and 2400 ton/ha or equivalent to 20 cm deep layer, for *Macrotermitinae* in Congo, covering 33% of the surface (Meyer 1960, cited in [8]) have been reported. Termite mound heights of more than eight meters have been recorded for *Macrotermes* in Ethiopia and *Nasutitermes triodiae* in Australia [8]. Moreover, Wood [3] reported that more than 10,000 kg ha^{-1} could be eroded annually from termite constructions. Holt et al. [45] found termites to be the most abundant insect detrivores near Charters Towers, Queensland, and estimated that in one generation of mounds 20 t/ha of soil would be reworked.

Termites select quality of soil transported depending on the construction they build, be it nest or associated structures - mounds, soil covered runways, subterranean chambers, and galleries. It also depends on climate and habitat, including soil material available needed to match their ecological, physiological, and behavioral needs [3, 62, 63]. This selective transport results in a considerable change of particle size distribution in the soil matrix altering textural composition of the soil [39, 40, 63].

Usually termite mounds show higher contents of clay and silt particles than their surrounding soils [39, 61, 63-69]. This is due to their preference for entirely finer (<0.5 mm) clay, silt, and sand particles from topsoil to build their nests and specifically use them as cementing materials, particularly in the royal chamber and nursery. It can also be a result of selecting clay-rich subsoil [39, 70]. According to Millogo et al. [71] termites can also transform clay, K-feldspar into kaolinite, use it as a cementing agent during mound construction, and synthesize organo-metal complexes. They reported termite mound in Burkina Faso consisting of 76% quartz, 21% kaolinite and 3% K-feldspar in percentage weight. Most literature results show higher proportions of clay in termite structures—mound, nest, gallery, and sheetings—compared to relatively untouched surrounding soil (control) (Table 1). However, valid comparisons could not be made between different studies due to differences in species, environment, sampling technique, number and location of sampling points and their inadequate description, as well as lack of detailed soil classification [69].

Large quantities of coarse-grained sand are transported from the nest to the top and outside part of mounds resulting in the proportion of sand increasing upward from the mound base [32, 63]. This is indeed manifested in the increased sand: silt + clay ratios in the same direction [39]. In a study to assess the difference between two morphologically similar termite species in sorting out soil constituents during their nest-building activities, Arshad [39] reported sand: silt + clay ratios of maximum 0.75 at the top of an open mound decreasing to 0.39 and 0.28 at nursery and royal chambers of the mound, respectively, and values of 0.52, 0.25, and 0.21 at another site. In the same experiment similar trends were observed with closed mounds. In some cases, distinctive stony layers or stone lines are formed as residual materials in subsoil [69] after termites have transported all sand, silt, and clay particles to the top soil.

Table 1: The impact of termite activity on soil texture; values based on the comparisons of termite structures or constructions with the immediate surrounding soils.

Reference (Termite Species)	Sample Location	Soil Texture (%)		
		Total Sand	Silt	Clay
Watson [64] (*Macrotermes bellicosus*)	Mound (0-38)	68.0	15.0	17.0
	Soil (0-10)	90.0	5.0	5.0
Watson [64] (*Odontotermes badius*)	Mound (0-30)	57.0	20.0	23.0
	Soil (0-30)	83.0	8.0	9.0
Lee and Wood [8] (*Amitermes laurensis*)	Mound (internal)	59.0	5.0	24.0
	Soil (0-20)	91.0	4.0	4.0
Lee and Wood [8] (*Drepanotermes rubriceps*)	Mound (internal)	75.0	5.0	20.0
	Soil (0-10)	75.0	4.0	9.0
Lee and Wood [8] (*Nasutitermes exitiosus*)	Mound (external)	60.0	5.0	33.0
	Soil (0-12)	86.0	6.0	7.0
Lee and Wood [8] (*Nasutitermes triodiae*)	Mound (internal)	59.0	12.0	23.0
	Soil (0-6)	77.0	14.0	9.0
Watson [72] (*Macrotermes falciger*)	Mound	59.0	12.0	29.0
	Ah horizon	90.0	5.0	5.0
Holt et al. [45] (*Amitermes vitiosus*)	Mound	64.7	7.8	27.5
	Soil (0-20)	74.7	7.7	17.6
Arshad [39] (*Macrotermes michaelseni*)	Mound (2-35)	33.0	14.0	53.0
	Soil (7-35)	44.0	20.0	36.0
Arshad [39] (*Macrotermes subhyalinus*)	Mound (25-50)	42.0	10.0	48.0
	Soil (7-35)	44.0	20.0	36.0
Sheikh and Kayani [70] (*Odontotermes Iokanadi*)	Mound (60-75)	65.0	26.0	8.7
	Subsoil	69.0	25.0	5.4
Sheikh and Kayani [70] (*Odontotermes obesus*)	Mound (100-1 15)	52.0	38.0	9.8
	Subsoil	56.0	38.0	5.6
Wood et al. [65] (*Cubitermes oculatus*)	Mound	61.0	19.6	19.8
	Topsoil (0-5)	77.0	12.0	10.9
Wood et al. [65] (*Cubitermes severus*)	Mound	25.0	52.0	23.4
	Topsoil (0-5)	35.0	47.0	18.3
Wood et al. [65] (*Mnervitermes*	Mound	62.0	18.0	21.0

geminatus)	Topsoil (0-5)	92.7	12.0	7.0
Arshad et al. [73] (*Macrotermes michaelseni*)	Mound crust	48.0	14.0	38.0
	Topsoil	67.0	15.0	18.0
Arshad et al. [73] (*Macrotermes herus*)	Nursery	30.0	28.0	42.0
	Topsoil	59.0	16.0	25.0
Asawalam et al. [74] (*Nasutitermes* sp)	Mound	74.0	7.0	19.0
	Soil	93.0	1.0	6.0
Asawalam and Johnson [67] (*Nasutitermes* sp)	Mound	42.2	32.8	25.0
	Mound	59.2	8.8	32.0
	Control	64.2	16.8	19.0
Jouquet et al. [18] (*Odontotermes nr. Pauperans*)	Galleries (top-soil)	74.2	18.9	5.9
	Control (top-soil)	74.3	19.8	6.0
	Galleries (deep-soil)	57.5	24.6	17.9
	Control (deep-soil)	70.0	15.0	15.0
Jouquet et al. [18] (*Odontotermes nr. Pauperans*)	Fungus-comb Wall (top-soil)	74.9	18.9	6.2
	Control (top-soil)	74.3	19.8	6.0
	Fungus-comb Wall (deep-soil)	60.4	21.6	18.1
	Control (deep-soil)	70.0	15.0	15.0

Termites have a high degree of selective nature, utilizing certain soil particle sizes for specific parts within their structures and favoring finer (clay) particles when provided with more than one soil type [18, 66, 75]. However, no such selection was observed when termites were restricted to use only top soil material [18] or when they were limited in their distribution to a particular ecological niche with limited variation in soil and climate [62]. In another experiment in central Amazonia, termite mounds showed lower clay content than their control soil due to a high clay percentage originally in the mound that they did not have to preferentially select clay particles in
their construction activities [75]. Ackerman *et al*. [75] also cited the presence of smaller gradient in mineral texture along the depth of soil profile in plateau soils, which limited their choice of particle sizes. The high clay content gives the mound a high shrinking/swelling capacity [63] as well as high moisture holding capacity [40, 69]. However, although termites are selective and active in all soil types, in general the presence of both deep and top soils in their immediate environment helps stimulate their building activity [18].

2.2 Soil Moisture Transport

In order to provide the nest with water and maintain the colony's water balance, termites link together soil and water transport in the form of moisture in the salivary glue they use to stick in place freshly deposited soil. Usually patterns of soil and water movement follow patterns of rainfall although it is probably intended to regulate the colony's water balance [43]. As indicated above, more water is transported through termite mounds in open habitats (such as *Macrotermes michaelseni* in northern Namibia) [43]. Furthermore, Turner *et al*. [43] estimated water transported in one season to be 25kg and 6kg for termites in open and wooded habitats, respectively. Most colonies ensure presence of enough water in nests and maintain it by constructing large foraging galleries that go deep below ground while using fungus, fecal carton and clay to absorb and retain the moisture [32, 65].

The area of influence of termite activity can range as far as 70 m from the nest in the form of a network of foraging tunnels (Abe and Darlington 1985, cited in [32]) and as deep as 100 m in the form of vertical transport of water and soil (Lepage 1974, cited in [32]). This enables them to not only gather a massive amount of water, but also retain it in the subsequently more porous and clay-rich soils relative to the surrounding parent material [43]. Turner et al. [43] noted that the difference in water potential between nest soil and surrounding soil can also drive water to the nest from nearby perched water tables in the soil, depending on the soils' hydraulic conductivity. Other termite species use and control water released from their bodies and the microbes' metabolism or respiration in the mound and maintain high humidity in the nest [21], although no water loss data are available to analyze their impact on the water balance [3].

Termite mounds are made somehow impermeable to prevent nest flooding [66]. This impermeable layer promotes runoff in the events of rainfall distributing the water in a radial manner to surrounding soils, which are relatively porous due to extensive foraging activity of termites. The distributed water infiltrates the porous soil and is redistributed into the soil profile, charging perched and permanent reservoirs of ground water, from which the termite colonies can then extract during dry periods to balance water lost to evaporation throughout the year. The types of construction and transport activities of water and soil required to maintain this balance (maintain nest humidity) depend on evaporative demand of the habitat they live in. In dry environments, due to high evaporative demand, mounds with low evaporative conductance are constructed along with increased transport of soil water to the nest. In wet environments, however, the balance is maintained by building mounds with higher evaporative conductance coupled with rapid transport of wet soil from nest to the mound surface [32, 43].

The above observations of Turner and colleagues are based on observations of the *Macrotermes* species in Africa. However, Australian mound-building termites of *Rhinotermitidae* and *Schedorhinotermes* maintain high humidity in their mounds using closed and unique mound architecture [21]. They construct numerous short closed-end tunnels inside irregular sponge-like zones that serve to "trap" excess moisture from within the mound, and thus avoid moisture dripping down into the mound center. Thus they control and use excess moisture produced all year round from the mound microorganisms' and their own respiration products. Termites always use moist soil to repair their mound or extend it by plastering new materials, even during periods when surrounding soils are dry. This is probably because of readily available stored moisture in the mound, which they can quickly use during the repairing process. This is more efficient in terms of time and energy rather than carrying moisture from below the ground level, as mentioned by Turner *et al*. [43] in the above paragraph [21, 76]. The influence of termites on dynamics of soil water balance, however, is more extensive than just mound soils, largely due to extensive networks of subterranean galleries and chambers and wide area of influence of termite activity (McKay and Whitford, 1988, cited in [23]).

Soil water balance in ecosystems is controlled by soil water storage capacity, and the different processes driving water flow in the soil-plant-atmosphere continuum: namely, precipitation (and irrigation), surface runoff, evapotranspiration (soil evaporation + plant transpiration), and drainage below rooting zone [63, 77, 78].
The most commonly used soil water balance equation of an ecosystem, in a typical time period, is given as [63, 78, 79]:

$$ET = P - R - \Delta S - D$$

where ET is Evapotranspiration, P is precipitation, R is runoff, ΔS is change in soil water content or storage, and D is deep drainage. Components ET and P are always positive, but the others can be positive or negative. If R is negative, it implies run on from the surrounding areas. Negative S indicates depletion of soil-water reserves, and negative D means upward flow from groundwater. At the same time, assuming that any water remaining on the surface infiltrates into the soil, the infiltration (I) occurring during a rain event is given as [77, 79]:

$$I = P - R \qquad \text{or} \qquad I = ET + \Delta S + D$$

Total ET is defined as the amount of water lost to the atmosphere through evaporation from soil surface, and transpiration or water use from vegetation. In arid and semi-arid areas, ET plays a major role in driving soil water balance of ecosystems. As can be concluded from the equation above, an increase in the amount of water infiltrated, drained, and/or retained deeper in the soil limits the amount of water exposed to the atmosphere for ET. Termite-modified soils have an increased infiltration rate, water holding capacity, and drainage due to improved porosity and structural stability of soil [31, 79]. Extreme dry conditions in these environments accelerate water diffusion or capillary rise from deeper layers in which the drained water has been protected from ET [79]. The dry conditions also accelerate termite activities to draw water from deeper layers which ultimately affect the water balance of the system [32].
Black and Okwakol [23] cited in their literature that some workers reported that soil-water balance is perhaps one of the most essential determinants of vegetation structure. Many dominant termite species have been described as ecosystem engineers and keystone species, due to their extensive impact in modifying or changing availability and concentration of resources for other organisms [32, 33], and due to their role as consumers, maintaining structural and functional integrity of ecosystems [31], respectively.

3 Effect of Termite Activity on Soil Physical Properties – Texture and Moisture

3.1 Introduction

Termite activities to construct mounds and maintain them structurally, provide food and water to the nest, and maintain the moisture and temperature content concurrently involve modifications or changes to the physical and chemical properties of the soil [43, 63, 79].

The impact of termite activities on selected soil physical properties: texture, structure, infiltration, runoff, and soil water storage is discussed below.

3.2 Effect on Soil Texture

The continual transport, erosion, and reconstruction of mounds and nests disturbs soil profiles, consequently causing redistribution of soil particles, and changing soil texture, which is more clearly evident than any other change in chemical property [3, 67, 80]. The preferential use of finer particles to construct nests, mounds, and galleries results in a higher content of finer soil texture of the mound material, as much as two to three fold [63], compared to that of the surface layer of top soil [40]. This may result in a marked textural variability in areas where mound density is high [39, 81].

Termites use their saliva and other body wastes to cement soil particles together when constructing their mounds with finer particle sizes. By choosing higher proportions of kaolinite with some chlorite and montmorrillonite, they ensure that mound surfaces remain harder because clay particles fill in between sand grains [21]. When compared to mounds, however, construction of feeding galleries and burrowing channels improves soil porosity and water transmission properties in which the macropores would otherwise be extensively reduced or eliminated during packing and remolding process in mounds. The resulting high bulk density associated with the mound's massive structure and low total porosity, even in abandoned ones, inhibits plant growth due to its poor physical condition, higher compaction, and impermeability [40, 66, 80]. In contrast, the feeding galleries and burrowing channels formed, the resulting soil structure and structural stability, porosity coupled with changes in the decomposition processes and chemical fertility improve the amount and rate of water infiltration into soils and its storage for plant use [40, 80].

3.3 Effect on Soil Moisture

Termites create numerous voids on sealed soil surface by their extensive subterranean excavation and construction of feeding galleries, channels and foraging holes, thereby significantly increasing infiltration by a factor of two to three [82, 83] or even as much as tenfold [83]. Not only would macropores help increase infiltration rate depending on their stability and connectivity to the surface and to each other, but also help in intercepting runoff water due to some roughness created on the surface [31, 40]. In fact, the ability of macropores to intercept running water is one of the critical factors in the infiltration process [83]. In other words, termite activity increases the time until ponding or surface storage is formed and therefore delays formation of runoff. Their interconnectivity also helps in the continuity of infiltration even after the soil surface has become saturated and thus increases water availability [84].

Termites transport finer particles to the soil surface enriching the nest surroundings with fine particles [63] as well as constructing the mound. The relative compactness and higher clay content of the mound increases its water holding capacity by decreasing its porosity, or increasing the proportion of micropores. The same structure, therefore, discharges as runoff most of the rainwater to the surrounding soil [40]. It is also responsible for shrinking/swelling capacity of the mounds which in dry areas help increase water infiltration into the mound and its deep percolation [63]. Infiltrated water is readily available to plants when it is stored in micropores. As water stored in the soil is related to the amount of water input by infiltration, termite-modified soil structure ultimately increase soil water stored [79]. Mando [79] also reported that termite modification resulted in an increase in soil-water content of up to 50 mm in the driest year in crusted Sahelian soils.

4 Soil and Moisture Factors Affecting Termite Interaction with Soil

4.1 Introduction

Termites form an essential component of the ecology having successfully coevolved for millions of years [85]. They live in complex environments, and thus, environmental factors and interactions with other predators and pathogens, availability of food and water resources, and other genetic behaviors affect their population dynamics and behaviors of nesting and foraging, spatially or temporally, separately or in combination [58, 86].

Termites can modify degraded environments in a relatively short period of time by improving the soil and water characteristics [63]. However, they are selective in their choice of certain environmental conditions during their nesting or foraging activities [87]. They nest in relatively moist places and create tunnels or foraging galleries above or beneath the ground to transport food and water. This means that they have to deal with different soil types in one or different places, move lots of soil particles or maneuver in between different size ranges and mixtures, moisture content, temperature, and compaction levels or bulk densities among many other variables [32, 52, 58, 88].

Regular fluctuations in termite distribution and foraging activity occur due to seasonal changes in temperature and moisture conditions [89, 90], two factors that termites are susceptible of [91]. The next important factor is rainfall while soil type and vegetation seem to have lesser impact within the dominant effects of temperature and moisture [92]. However, the presence of warm, humid and moist environments around housing and other structures as well as some agricultural areas through heating, irrigation and landscaping has created a consistently conducive environment where termites can remain active throughout the year. Moreover, warmer conditions expanding toward higher latitudes of the globe as well as increased storms in other parts of the world because of climate change is apparently increasing territorial distribution of termites [93]. Severe drought conditions though can limit termite activity, as has been observed in New Orleans from October 2005 to June 2006, but once favorable conditions return such as steady rainfall immediately after the drought, they can increase their activities dramatically [94].

Dry conditions along with occasional fires have been features of many forests for years. On March 1965, two radiata pine plantations in the Moss Vale area of New South Wales, Australia, were subjected to crown and ground fires, and over 1,874 acres were destroyed or damaged. In severely burnt plots, pine needle litter was completely destroyed and the number of soil microfauna was reduced compared with those in lightly burnt plots. The first and most frequently collected insects in all plots were subterranean termites (*Coptotermes* and *Heterotermes* spp.), ants, and carabid and scarabid beetles. Within 24 hours of the crown fire passing a plot, termites were found attacking burnt logs and old stumps. Insects present in the area before the fire would have been destroyed, except for termites and cicadas insulated by the soil [95]. The primary recolonizers would live on plant debris and vegetation, but predacious insects could only thrive when prospective food base was well established. This follows the idea of life systems [96], showing that a population and its environment are interdependent elements which function together as a system. However, Peterson [97] noted that severe wildfire incidents have drastic impact on their populations by burning termites themselves and surrounding soil and organic materials causing direct mortality to the population, converting the cellulose to indigestible materials and altering the soil.

4.2 Soil Type

Soil provides a medium of moisture reservoir and serves as a protection against extreme temperatures. Termites follow microbial actinomycete cues in soil to find food sources and moisture. They encounter different materials in their immediate environment which can profoundly influence their tunneling behavior and choice of nests. The presence of different soil types within the foraging range of a particular colony can, thus, determine their success in tunneling through the substrate as well as moving moisture to the food source or drier substrates [58].

One of the most noticeable effects of soil on termites is its effect on their distribution although in a lesser impact compared to temperature and moisture [92]. Long distance commercial trading of wood and timber has been one of the primary reasons for the expansion of subterranean termites. Lax and Osbrink [90] reported that no particular preference for a specific food source or soil type could be established for the termite population in New Orleans City Park. However, rainforest soils and extensive bauxite soils have been described as no-go areas for the *M. darwiniensis* while Vertisols, which are characterized by heavy swamp after rain and deep and wide cracking during dry conditions, were also reported to discourage survival of mound-building termites in Queensland and Northern Territory [98]. Thus, interestingly enough, black earths of inland northern Australia are virtually devoid of termites although adjacent sandy-desert steppe soils have abundant fauna. The majority of termites are found in the sclerophyll forests, woodlands, and savannahs. Arid regions have few termites, but some are apparently confined to such regions [8].

The ability of termites to transport water into dry soils is influenced by water holding capacity of a soil which can determine availability of free water for termites [58, 99]. Cornelius and Osbrink [58] observed that termites could not successfully colonize wood blocks located on dry clay substrate because water molecules hold more tightly to fine particles of clay than to coarser particles of sand.

Termites are more likely to aggregate in moist top soil and clay (mainly fine texture) as they can retain moisture in their galleries for extended periods of time and avoid dehydration due to evaporation from the soil. However, soils with more organic matter like peat moss and potting soil are chosen when termites move from a moist to dry soil due to the higher water retention capacity of these soils and the fact that the water is readily available [58]. Cornelius and Osbrink [58] also observed that *C. formosanus* termites in replicates with clay and top soil built shelter tubes up the sides of the tanks while those in sand replicates not only built shelter tubes into the air with no contact with the tank walls but also spread the sand particles all over the surface to help them move up the tank walls. Shelter tubes allowed them to travel up the sides of plastic tanks and provide protection from dehydration. Termites climbed up the tank using the sand particles spread on the wall but were exposed to the air. However, because the tanks were kept in an incubator with 97% relative humidity, the sand particles may have maintained their moisture content and allowed termites to obtain moisture easier than in soil or clay, thus successfully climbing without constructing shelter tube.

4.3 Soil Moisture

Soil moisture determines termite behavior and preference for nesting or foraging places, pattern, rate, area, number, and direction of movement and tunneling within soil [58, 99-102]. It determines the probability and severity of infestations mainly because it attracts termite movement in soil and increases their foraging activity in soil depth [99]. It is one of the reasons why most infestations are located at sites of higher moisture contents in structures, buildings or even agricultural stations [101, 103].

Termites always follow decay, which is found in “wound affected wood” in trees. According to Shigo [104], who postulated in his theory of Compartmentalization of Decay in Trees (CODIT), the starting process for decay are usually wounds in trees. These wounds can be caused by agents like insects, birds, other animals, wind, ice, snow, temperature extremes, fire, chemicals and people and their activities. Wood discoloration, as a result of the tree response to the wound by chemical reaction and by plugging, and decay, due growth of infecting pioneer microorganisms, such as fungi, and their digestion of cell wall follow. Termites, especially in the early stages, follow the model perfectly, by attacking and feeding on vastly decayed dead cells (xylem cells) after decay organisms have fruited, and probably assisted by soil actinomycete bacteria that lead them onto a prepared wood source, while keeping relatively thinner, younger, and outer part of the woody stem (sapwood living cells) intact. Nevertheless, eventually all the decay-causing microorganisms and termites will break down all the organic matter [14, 15]. The microbial degradation, particularly by actinomycete bacteria that degrade ligno-celluloses softens wood fibers, makes it easy to masticate and with an ambient high humidity it creates perfect environment for the digestion of cellulose material. Termites consume resources at such a location with adequate moisture level and maintain it regardless of the distance to their harborage as they bring in their own moisture, in each mouth of the foraging and attacking termite workers [21]. They need constant hydration as they are susceptible to desiccation due to evaporation of water from the soils or contact with their surrounding soil or other particles [58].

Location and number of termites in a particular place is higher in higher moisture content as compared to a lower moisture content [99, 102]. In an experiment to see the effect of different moisture levels of a sand substrate on the behavior of laboratory groups of termites (*M. crassus* and *C. gestroi*), Wong and Lee [102] discovered higher number of termites in 20% moisture content dish than in lower moisture content. However, due to saturation of the sand substrate with water less activity and presence of the species was observed in 25% moisture level dishes. A medium range of 10–15% moisture was reported as the preferred range to attack baits located at the top end of a sand substrate for *C. acinaciformis* [99].

Generally, termite activities increase with increase in soil moisture [100, 102, 103] unless the soil is saturated which drastically limits their movement [3, 99, 100]. Termites primarily concentrate their early tunneling activities in areas of higher moisture levels. Their rate of tunneling, distance and area they explore increase with increase in moisture content [100]. After being released into a homogenous sand filled arena in a laboratory condition, termites species of *C. frenchi* tunneled slowly in the dry part of the substrate before concentrating into and increasing their tunneling activity by about five times after discovering the wet sand [46]. Su and Puche [100] observed a positive correlation between tunneling activity of termites and moisture content and reported a 1% increase in moisture content resulting in an increase of tunneling areas at 6.26 cm^2 and 7.17 cm^2 for termite species of *C. formosanus* and *R. flavipes,* respectively. In an experiment conducted by Arab and Costa-Leonardo [103], it was reported that termites of the *C. gestroi* explored more areas at soil moisture content of 15% and above in a sand substrate by building more secondary tunnels. Wong and Lee [102] reported the species *M. crassus* and *C. gestroi* tunneled significantly further in sand with 20% than 0% moisture.

Termites transport water from higher moisture content to their substrate and improve the microclimate by creating and maintaining a humid environment as well as softening their food material for easy consumption [46, 99, 100, 102, 103]. They construct galleries in dry soils using moisture carried from wetter soils and retain it in the galleries during evaporation from the soils and hence maintain continuous supply [46]. This helps termites colonize food sources located in dry soils and depending on the species, it determines the success of a colony to move to a new area [102]. After successfully establishing their foraging activities in their favorite range (10–20%), Ahmed [99] reported that *C. acinaciformis* conquered drier moisture ranges of 2.5% and 5% after two weeks. Wong and Lee [102] attributed the success of *C. gestroi* over other species to their efficiency in carrying moisture into their food irrespective of the sand moisture content, while being aggressive in their tunneling. After conquering places of higher moisture content, being a species not favoring feeding and harboring at a single area, termites can modify or control drier environments cancelling the effect of any moisture gradient due to drying [99, 100, 103].

5 Conclusion

The interaction between termites and their soil environment has been a focus of research for many years. This brief review explains the significance of termites in modifying selected soil physical properties and their ability to moderate the soil water balance. The main termite activities that result in significant changes or modification of soil environment include the construction of nest/s, galleries, sheetings, and mounds; the search for food and water as well as their acquisition and transportation; the accumulation, breakdown, and decomposition of food material or organic matter with the help of symbiotic organisms and feeding of the colony; and the control and maintenance of constant humidity and temperature inside their micro ecosystems. The resulting changes are transport and movement of soil particles that significantly change soil texture, creation of voids that improve porosity and infiltration while reducing runoff, and enrichment of soil with clay materials, organic matter and moisture that improve the soil's water holding capacity, organic matter content and soil structure.

Most literature concerning termite-soil interactions compare termite-modified soil with relatively intact surrounding soil where no significant termite activity exists. It is vital to mention that research comparisons have been difficult because of differences in species of termites and their environments, quantity and location of sampling points, their insufficient description, sampling methods, and lack of detailed soil classification or description. It might be interesting to see if termites of the same species affect soil properties differently in different climatic regions.

Termites utilize soil particles selectively, favoring finer particles and making constructions that match their ecological, physiological, and behavioral needs. The composition and kind of structures they build, therefore, reflect the species, climate, soil type, moisture, temperature, and other factors affecting their environment. In some arid and semi-arid areas, these structures are so conspicuous and dominant that they become part of the main landscape and vegetation features, creating fertile areas in an otherwise harsh environment, which can benefit other flora and fauna inhabiting these areas. The potential and ability of termites to conquer harsh environments and their resilience during high levels of disturbance is as impressive as the sophistication and beauty of their structures. Thus, in order to benefit from this potential, it is imperative that we increase our understanding of their activities and interactions with the soil.

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