Chapter 9
Termite Preferences for Foraging Sites

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Abstract Termite interaction with soil and its manipulation create spatial variability via the nests and other structures they build using mainly finer materials from surrounding soils. Their preference for particular nesting and foraging conditions profoundly affects the physical as well as microbial properties of soils. Their activities to transport soil and water as well as establish and maintain symbiotic relationship with some microorganisms create suitable nesting and foraging places. They also create fertile area in an otherwise barren landscape. More knowledge on their

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interaction with soil and preferential foraging might help in understanding the conditions under which they are spreading beyond their usual climatic zones. Their potential for improving poor soil conditions into productive ones is also immense. This chapter details termite soil interaction and their preference for foraging sites in different environmental conditions.

Keywords Termite • Soil • Subterranean • Foraging • Symbiosis

9.1 Introduction

Termites are diverse group of social insects living in nests or colonies, mostly consisting of multiple generations, numerically ranging from several thousand to several million individuals at maturity, depending on the species, availability of food resources and soil environment (Kambhampati and Eggleton 2000). They are found in a wide range of terrestrial environments distributed throughout the warmer regions of the world, predominantly tropical, subtropical and temperate regions and rarely found at altitudes of more than 3000 m (Wood 1988). They are important in many ecological systems as they provide basic platforms for vegetation restoration by modifying physical properties of the soil which in turn improve nutrient cycling and ultimately their release (Lal 1988; Palin et al. 2011). They greatly help in carbon cycling, through the transformation, turnover and conservation of soil organic matter and nutrients as well as water (Black and Okwakol 1997; Dawes-Gromadzki 2005; Turner and Soar 2008). In many instances benefits have been obtained from the use of soils from termite mounds as amendments to improve the physical condition of poor soil. Addition into a relatively small space of such soil materials collected from interspersed mounds found throughout farmlands and forest areas resulted in significant improvement of the soil's water holding capacity (Suzuki et al. 2007). In order to address the issues of geographical increase in the spread of termites and their role in soil rehabilitation in mining or other similar areas, termite interaction with soil has been the focus of scientific research for many years. Termite activities that result in significant changes or modification of soil environment are basically due to the following reasons: construction of nest/s, mounds, foraging galleries and sheetings; the search for food and water, their acquisition and transportation once located; the accumulation, breakdown and decomposition of the food material or organic matter with the assistance of symbiotic organisms and feeding the colony; and the control and maintenance of constant humidity and temperature inside their microhabitats or ecosystems. The subsequent changes in the soil environment are observed in the form of transport and movement of soil particles resulting in soil textural change; formation of voids improving the porosity and infiltration while reducing runoff; enrichment of soil with clay materials, organic matter and moisture improving the organic matter content, water holding capacity and soil structure; and sustaining bacterial symbiogenesis.

Termites utilize soil particles selectively, preferring finer particles and building structures which match their ecological, physiological and behavioural needs. The composition and type of structures they build, therefore, reflect these preferences and the species, climate, soil type, moisture, temperature and other factors affecting their environment. In arid and semiarid areas, termite-built structures are so visible and dominant that they form significant part of the landscape and vegetation features, at times forming isolated fertile areas, in an otherwise barren environment, which can benefit other floras and faunas. The chapter outlines the dominant factors in termite preferences for foraging and nesting sites in different environmental conditions that give termites unique characteristics in the global context.

9.2 Selection of Foraging and Nesting Sites

Having successfully coevolved for millions of years, termites form vital component of the ecology (French 1988). They live in complex environments, and thus, individual or combined environmental factors as well as interactions with other predators, pathogens and other inherited genetic traits affect their population dynamics and nesting and foraging behaviours. At the same time, the availability of food and water resources has a spatial or temporal effect adding to the above factors (Campora and Grace 2004; Cornelius and Osbrink 2010).

Soil provides a medium for termite nesting and foraging, food storage and consumption and moisture reservoir and serves as a protection against extreme temperatures. Termites build elaborate networks of underground tunnels and soil covered tubes to access resources as well as secure protection from predators and severe environmental situations while foraging (Lee and Wood 1971; Lee and Su 2010). They use microbial actinomycete as cues and follow them in the soil to locate food sources and moisture (Kurtböke et al. 2014). Soil moisture, soil type and particle size distribution play a major role in determining the foraging behaviour of individual termites (Haverty et al. 1974; Haverty and Nutting 1976; Lax and Osbrink 2003; Campora and Grace 2004). Although termites are very skilled in modifying the soil and water characteristics of their environments (Konate et al. 1999), they are also selective in their preference of some environmental conditions during their nesting or foraging activities (Haverty and Nutting 1976). They nest in a suitable place, build tunnels or foraging galleries above or below the ground to transport food and water to and from the nest. It means that they have to deal with different soil types in one or different places, move lots of soil particles or manoeuvre in between different size ranges and mixtures, moisture content, temperature and bulk densities among many other variables (Smith and Rust 1991; Turner 2006; Li and Su 2008; Cornelius and Osbrink 2010). Their success in tunnelling through the substrate as well as transporting moisture to the food source or drier substrates can, thus, be determined by the presence of different soil types within the foraging range of a specific colony (Cornelius and Osbrink 2010). Soil and moisture are, therefore, critical to termites in terms of their selection for nesting and foraging sites.

9.2.1 Soil

Although temperature and moisture play a big role, the effect of soil on termites distribution is one of the most noticeable ones (Cookson and Trajstman 2002). It is well recognized that long-distance commercial trading of timber and wood has been one of the prime reasons for the expansion of subterranean termites. Lax and Osbrink (2003) could not establish any particular preference of the termite population in New Orleans City Park for a particular food source or soil type. However, rainforest as well as extensive bauxite soils were inhospitable areas for the *Mastotermes darwiniensis*, while vertisols discouraged survival of mound-building termites in Queensland and Northern Territory in Australia (Holt et al. 1993). Thus, extraordinarily enough, the black earths of inland northern Australia are nearly devoid of termites although nearby sandy-desert steppe soils contain rich fauna. The sclerophyll forests, woodlands and savannahs are environments where majority of termites are found. Arid regions have a small number of termites. However, some are actually restricted to such regions (Lee and Wood 1971). Eucalyptus communities are the only communities synonymous with termite richness. Despite this fact, in mallee growing on deep sand, dominated by such communities, the species *Coptotermes acinaciformis* are absent due to the lack of clay soils vital for mound building (Gay and Calaby 1970).

In laboratory conditions, termite foraging preferences activities vary according to the type and amount of soil particles presented. For instance, when concentrations of sand particles were increased, termites increased their tunnelling activities (Houseman and Gold 2003). Termites are also more likely to aggregate in moist topsoil and clay (mainly fine textured soils) as they can retain moisture in their galleries for a long period of time and avoid dehydration as a result of evaporation from the soil. However, soils with more organic matter like peat moss and potting soil are preferred when they move from a moist soil to a dry soil mainly due to the higher water retention capacity of these soils and the fact that the water is readily available in such soils (Cornelius and Osbrink 2010). Cornelius and Osbrink (2010) also observed that *C. formosanus* termites 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 while those in replicates with clay and topsoil built shelter tubes up on the sides of the tanks. Shelter tubes enabled them to forage up the sides of plastic container while providing 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 the construction of the protective cover of a shelter tube.

C. acinaciformis were presented with four soil types (fine sand, topsoil, peat and potting) in a laboratory set-up to study if moisture would be a significant factor. At lower moisture levels of 0 and 5%, termites preferred fine sand. Topsoil was preferred at moisture levels of 10, 15 and 20%. Peat soil was the least preferred soil type, and in most cases opening holes beneath tubes containing peat were either sealed for most of the time or opened with no or little penetration and termite activity (Ali et al. 2014). They also reported that termites penetrated earlier, constructed distinct tunnels and tunnelling branches in fine sand, most of the time starting from top to bottom, and covered them with dark clay particles transported from nesting jars.

Termites move soil particles to transport soil and moisture, build foraging galleries underground or on surfaces such as walls, pipes, glasses, plastic, etc. and cover surfaces to create dark and moist environments (Cornelius and Osbrink 2010). The creation of tunnels usually includes processes of excavation, loading, transportation and deposition of soil particles (Lee and Wood 1971). The texture of a soil determines the time it takes for termites to initiate and construct foraging galleries in different environments or substrates (Cornelius and Osbrink 2010). The coarser the texture of the substrate material, the lower the amount of soil particles to be removed and the greater the spaces available or created once a particle is removed (Houseman and Gold 2003). As this minimizes the number of particles to be removed and thus reduces the number of individual termite visits required to extend the tunnel, it gives the termites an advantage during tunnelling. The presence of finer soil particles on the other hand reduces the amount of empty space in between the particles by filling the gaps and consequently reducing the tunnelling rate as more trips are required to remove the soil particles (Houseman and Gold 2003). Tunnelling or foraging activity of termites reorganizes soil particles, whereas the addition of salivary and faeces products adds some organic matter to the packed soil (Lee and Wood 1971). As a result of reduction of the amount of macropores, compacted soil has reduced volume and hence higher bulk density. This in turn decreases the amount of available space for water movement. The tightly packed soil particles in the soil medium will be hard for termites to detach and carry, while the reduced spaces in between the packed particles provide less room for manoeuvring (Nobre et al. 2007). A slowdown in tunnelling rates of termites was reported by Tucker et al. (2004) in the most compacted soil (1.35 $g.cm^3$ of moistened sand at 10% w/w) in the laboratory.

The amount of soil transported by termite colonies depends on the colonies' type of habitat and season of the year, as it has been observed by colonies in open habitat moving nearly four times as much soil to the surface as those in a wooded habitat (Bagine 1984; Turner et al. 2006). Because of their exposure to the heat of the sun, wind and dry air, open habitats have higher rates of evaporation (Turner et al. 2006). Turner et al. (2006) reported that most of the soil transport happens during rainy seasons, and usually it is tied to the patterns of rainfall. The actual amount of soil transported depends on the termite species and the environment that they inhabit, but estimated ranges of 575 kg in the Sonoran Desert grassland (Nutting et al. 1987), up to 1059 kg of soil per hectare per year in arid areas of North Kenya (Bagine 1984) and 13 tons per hectare per year were reported (Sarcinelli et al. 2009). The abundance of termite mounds, their area of coverage, weight and size give an indication on the amount of soil transported to the surface. For instance estimates of more than 1100 mounds/ha for mounds in tropical Australia, weighing 62 ton/ha of soil and covering 1.7% of the sampled area (Lee and Wood 1971), and 2400 ton/ha of soil or equivalent to 20 cm deep layer, for *Macrotermitinae* in Congo, covering

33% of the surface (Meyer 1960 cited in Lee and Wood 1971) have been reported. Mound heights of greater than 8 m have been documented for *Macrotermes* species in Ethiopia and *Nasutitermes triodiae* in Australia (Lee and Wood 1971). Moreover, Wood (1988) reported that more than 10,000 kg ha^{-1} could be eroded from termite constructions every year.

The quality of soil termites transport depends on the construction they build, be it the nest or associated structures, such as epigeal mounds, soil covered runways, subterranean chambers and galleries. It also depends on the climate and their particular habitat, including the soil material available needed to match their ecological, physiological and behavioural needs (Harris 1956; Wood 1988; Konate et al. 1999). This preferential transport results in a significant change of the particle size distribution in the soil matrix altering the textural composition of the soil (Arshad 1981; Lal 1988; Konate et al. 1999).

Most of the time termite mounds exhibit higher contents of clay and silt particles than their surrounding soils (Watson 1969; Arshad 1981; Wood et al. 1983; Nutting et al. 1987; Lobry de Bruyn and Conacher 1990; Konate et al. 1999; Rogers et al. 1999; Asawalam and Johnson 2007; Adekayode and Ogunkoya 2009). In an experiment to study the soil texture, the structure and the soil water regime at different depths in a termite mound and in comparable surrounding areas, clay contents in the top 0–0.10 m and 0.20–0.30 m soil layer were three times as much on the mound (23% and 29%, respectively) than in the control area (8% and 10%) (Konate et al. 1999). While in another study, mound surfaces in fallow and forest areas were 31.5% and 18.8% higher, respectively, while those under cropping showed 16% higher clay content than their surrounding soils (Hulugalle and Ndi 1993). This is related to the termite preference of entirely finer (<0.5 mm) clay, silt and sand particles from the topsoil to build their nests and specifically use them as cementing materials, especially in the royal chamber and the nursery. It can also be as a result of selecting clay rich subsoil (Arshad 1981; Sheikh and Kayani 1982). Table 9.1 summarizes some literature results on the effect of termite activities on soil texture in comparison with control (surrounding) soils. Most of the numbers show higher proportions of clay in termite constructions—mound, nest, gallery and sheetings—as compared to the control or relatively intact surrounding soil. Millogo et al. (2011) reported that termites transform K-feldspar into kaolinite and use it as a cementing agent during mound construction and synthesize organometal complexes. At the same time, they investigated the mineralogy, microstructure and physical characteristics of a termite mound in Burkina Faso and reported that it consisted of 76% quartz, 21% kaolinite and 3% K-feldspar in percentage weight as well as organic matter.

Large amounts of coarse-grained sand are transported from the nest to the top and outer part of the mounds with the resulting proportion of sand increasing upwards from the base of the mound (Konate et al. 1999; Turner 2006). This is indeed manifested in the increase of sand: silt + clay ratios in the same direction (Arshad 1981). In a research to study the difference between two morphologically similar termite species in sorting out soil constituents during their nest-building activities, Arshad (1981) reported that sand/silt + clay ratios of maximum 0.75 at the

Table 9.1 Comparisons of soil textural changes between termite constructions and surrounding soils (Ali et al. 2013)

Reference (termite species)	Soil sample location	Soil texture (%)		
		Total sand	Silt	Clay
Watson (1969) (*Macrotermes bellicosus*)	Mound (0–38)	68.0	15.0	17.0
	Soil (0–10)	90.0	5.0	5.0
Watson (1969) (*Odontotermes badius*)	Mound (0–30)	57.0	20.0	30.0
	Soil (0–30)	83.0	8.0	9.0
Lee and Wood (1971) (*Amitermes laurensis*)	Mound (internal)	59.0	5.0	24.0
	Soil (0–20)	91.0	4.0	4.0
Lee and Wood (1971) (*Drepanotermes rubriceps*)	Mound (internal)	75.0	5.0	20.0
	Soil (0–10)	75.0	4.0	9.0
Lee and Wood (1971) (*Nasutitermes exitiosus*)	Mound (external)	60.0	5.0	33.0
	Soil (0–12)	86.0	6.0	7.0
Lee and Wood (1971) (*Nasutitermes triodiae*)	Mound (internal)	59.0	12.0	23.0
	Soil (0–6)	77.0	14.0	9.0
Watson (1977) (*Macrotermes falciger*)	Mound	59.0	12.0	29.0
	Ah horizon	90.0	5.0	5.0
Holt et al. (1980) (*Amitermes vitiosus*)	Mound	64.7	7.8	27.5
	Soil (0–20)	74.7	7.7	17.6
Arshad (1981) (*Macrotermes michaelseni*)	Mound (2–35)	33.0	14.0	53.0
	Soil (7–35)	44.0	20.0	36.0
Arshad (1981) (*Macrotermes subhyalinus*)	Mound (25–50)	42.0	10.0	48.0
	Soil (7–35)	44.0	20.0	36.0
Sheikh and Kayani (1982) (*Odontotermes iokanadi*)	Mound (60–75)	65.0	26.0	8.7
	Subsoil	69.0	25.0	5.4
Sheikh and Kayani (1982) (*Odontotermes obesus*)	Mound (100–115)	52.0	38.0	9.8
	Subsoil	56.0	38.0	5.6
Wood et al. (1983) (*Cubitermes oculatus*)	Mound	61.0	19.6	19.8
	Topsoil (0–5)	77.0	12.0	10.9
Wood et al. (1983) (*Cubitermes severus*)	Mound	25.0	52.0	23.4
	Topsoil (0–5)	35.0	47.0	18.3
Wood et al. (1983) (*Mnervitermes geminatus*)	Mound	62.0	18.0	21.0
	Topsoil (0–5)	92.7	12.0	7.0
Arshad et al. (1988) (*Macrotermes michaelseni*)	Mound crust	48.0	14.0	38.0
	Topsoil	67.0	15.0	18.0
Arshad et al. (1988) (*Macrotermes herus*)	Nursery	30.0	28.0	42.0
	Topsoil	59.0	16.0	25.0
Asawalam et al. (1999) (*Nasutitermes* sp.)	Mound	74.0	7.0	19.0
	Soil	93.0	1.0	6.0
Asawalam and Johnson (2007) (*Nasutitermes* sp.)	Mound	42.2	32.8	25
	Mound	59.2	8.8	32.0
	Control	64.2	16.8	19.0

(continued)

Table 9.1 (continued)

Reference (termite species)	Soil sample location	Soil texture (%) Total sand	Silt	Clay
Jouquet et al. (2002) (*Odontotermes nr. pauperans*)	Galleries (topsoil)	74.2	18.9	5.9
	Control (topsoil)	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. (2002) (*Odontotermes nr. pauperans*)	Fungus-comb wall (topsoil)	74.9	18.9	6.2
	Control (topsoil)	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

top of an open mound decrease to 0.39 and 0.28 at the nursery and royal chambers of the mound, respectively, and values of 0.52, 0.25 and 0.21 at another site. With closed mounds, on the other hand, sand/silt + clay values of 0.56, 0.45, 0.39 and 0.59, 0.33, 0.27 were reported for two different sites, respectively. In some cases, after termites have transported all the sand, silt and clay particles to the topsoil, distinctive stony layers or stone lines are formed as residual materials in the subsoil (Lobry de Bruyn and Conacher 1990).

Termites show a high tendency of preferential nature of utilizing certain soil particle sizes for specific sections within their structures and therefore favouring finer (clay) particles when provided with more than one soil type (Rogers et al. 1999; Jouquet et al. 2002; Ackerman et al. 2007). However, no such preference was witnessed when termites were limited to the use of only topsoil material (Jouquet et al. 2002) or when they were restricted in their distribution to a particular ecological niche with limited variation in soil and climate (Harris 1956). In another case in an experiment in central Amazonia, due to a high percentage of clay originally in the mound that they did not have to preferentially select clay particles in their construction activities, termite mounds showed lower clay content than their control soil (Ackerman et al. 2007). Ackerman et al. (2007) also mentioned the presence of low gradient in mineral texture along the depth of the soil profile in the plateau soils which restricted the termites' selection of particle sizes. The high clay content gives the mound a high shrinking/swelling capacity (Konate et al. 1999) as well as high moisture holding capacity (Lal 1988; Lobry de Bruyn and Conacher 1990). However, in general, the presence of both deep and topsoils in their immediate environment helps stimulate termite-building activity, although they are selective and active in all soil types (Jouquet et al. 2002).

9.2.2 Moisture

Soil moisture is an important environmental factor that determines termite behaviour and preference for a nesting or foraging places, pattern, rate, area, number and direction of movement and tunnelling within the soil (Ahmed 2000; Su and Puche 2003; Green et al. 2005; Cornelius and Osbrink 2010; Wong and Lee 2010). It determines the probability and severity of infestations mainly because it attracts termite movement in soil and increases their foraging activity in soil depth (Ahmed 2000). It is one of the reasons why most infestations are located at sites of higher moisture contents in structures, buildings or even agricultural stations (Arab and Costa-Leonardo 2005; Green et al. 2005).

Termites are susceptible to desiccation due to their thin and porous epidermis. Humidity and moisture are, therefore, critical, their availability and maintenance affecting termite interaction with soil as well as feeding and tunnelling behaviours. The ability of termites to transport water into dry soils is influenced by the water holding capacity of the soil which in turn determines the availability of free water for termites (Ahmed 2000; Cornelius and Osbrink 2010). Cornelius and Osbrink (2010) observed that termites could not successfully colonize woodblocks located on dry clay substrates because water molecules hold more tightly to fine particles of clay when compared to the coarser particles of sand. In fact moisture is so critical that dry soil has been used as a barrier against termite penetration (Cornelius and Osbrink 2011).

Location and number of termites are higher in places with higher moisture content as compared to lower moisture content (Ahmed 2000; Wong and Lee 2010). In an experiment to see the effects of different moisture levels of a sand substrate on the behaviour of laboratory groups of termites (*M. crassus* and *C. gestroi*), Wong and Lee (2010) discovered a higher number of termites in 20% moisture level dishes than in lower moisture content dishes. However, due to saturation of the sand substrate with water, less activity and presence of the species were 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* (Ahmed 2000).

Generally termite activities increase with the increase in soil moisture (Arab and Costa-Leonardo 2005; Wong and Lee 2010) unless the soil is saturated which drastically limits their movement (Wood 1988; Ahmed 2000; Su and Puche 2003). Termites primarily concentrate their early tunnelling activities in areas of higher moisture levels. The rate of tunnelling, distance and area they explore increases with the increase in the moisture content (Su and Puche 2003). After being released into a homogenous sand-filled arena in a laboratory condition, termites of the Australian *C. frenchi* species tunnelled slowly in the dry part of the substrate before concentrating and increasing their tunnelling activity by about five times after discovering the wet sand (Evans 2003). Su and Puche (2003) observed a positive correlation between tunnelling activity of termites and moisture content and reported a 1% increase in moisture content resulting in an increase of tunnelling areas at 6.26 cm^2 and 7.17 cm^2

for termite species of *C. formosanus* and *R. flavipes,* respectively. In an experiment done by Arab and Costa-Leonardo (2005), it was reported that *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 (2010) reported the species *M. crassus* and *C. gestroi* tunnelled significantly further in sand with 20% moisture than compared with sand with 0% moisture.

A consistently humid microclimate and soft food for easy consumption, with the help of symbiotic organisms, are ideal environments to a successful termite colony, more so if it is established on dry soils or substrates (Ahmed 2000; Su and Puche 2003; Arab and Costa-Leonardo 2005; Wong and Lee 2010). As mentioned in Sect. 9.3.1 in more detail, nonstop transport and maintenance activities ensure constant supply and presence of moisture. As aggressive as termites can be in their tunnelling, some of the moisture is also used to conquer drier soils or substrates or access food resources located in such environments (Ahmed 2000; Evans 2003; Wong and Lee 2010).

Excessive moisture in the soil coupled with extended periods of rainfall result in dramatic reduction of subterranean termite population while at the same time reducing their foraging activities (Forschler and Henderson 1995). It has been reported that frequent flooding in some areas resulted in the elimination of a *Reticulitermes* species (Snyder cited in Gautam and Henderson 2011). Cornelius et al. (2007) observed a shift in the foraging range of *C. formosanus* subterranean termite species probably as a result of flooding due to hurricane Katrina. Termites would not prefer foraging in saturated soil conditions if they are provided with soils of different moisture ranges. Saturated conditions especially in clay-dominated nesting or foraging areas prevent termites from moving freely and also affect the oxygen and nitrogen levels needed for survival (Ahmed 2000). Foraging galleries and nests are made from water-resistant materials to prevent flooding. While most of the time they remain structurally intact, they may lose their integrity once they become flooded (Cornelius et al. 2007).

In built-up areas, urbanization and human manipulation of certain natural environments through irrigation and landscaping have created environments favourable to termite presence and activity due to the influence these practices have on water content, relative humidity and temperature. In data from an Australia-wide termite survey conducted during 1994–1998, initiated by Dr. John French of CSIRO, to determine the influence of type of location and house construction on termite activity, the age of a house was considered as the major factor in determining the existence of termites (Cookson and Trajstman 2002). Regular fluctuations in termite foraging activity due to seasonal changes in temperature and moisture conditions were reported in some cases (Haverty et al. 1974; Lax and Osbrink 2003), two factors which termites are susceptible of (Abensperg-Traun 1998). In fact temperature is the most important factor affecting termite distribution. The next important factor is rainfall, while soil type and vegetation seem to have lesser impact within the dominant effects of temperature and moisture (Cookson and Trajstman 2002). However, the presence of warm, humid and moist environments around housing structures and buildings as well as some agricultural areas has created a consistently conducive environment where termites can remain active throughout the year and cause attack and damage to timber in service. Moreover, warmer conditions expanding towards the higher latitudes of the globe as well as increased storms in the other parts of the world as a result of climate change are apparently increasing the territorial distribution of termites (Peterson 2010). Extreme drought conditions can also restrict termite activity, as has been observed in New Orleans from October 2005 to June 2006, but once favourable conditions come back, such as steady rainfall immediately following the drought, they can increase their activities dramatically (Cornelius et al. 2007).

9.3 Modification of Foraging Sites

9.3.1 Transport of Soil and Water

Termites link water transport to soil transport. They modify their preferred or selected foraging or nesting sites to suit their colony's needs. It is for this reason that modification by soil and water transport was explained together with their preference for specific soil or water demands in their foraging sites. They transport water from moist areas to the relatively drier substrate and improve their microhabitat by creating and maintaining a humid environment while softening their food material for easy consumption (Ahmed 2000; Evans 2003; Su and Puche 2003; Arab and Costa-Leonardo 2005; Wong and Lee 2010). They build galleries in dry soils using moisture carried from wetter soils and retain it in the galleries during evaporation and hence maintain continuous supply (Evans 2003). This helps them forage to and colonize food sources located in dry soils, and it determines their success in conquering new areas (Wong and Lee 2010). Two weeks after successfully establishing their foraging activities in their favourite soil moisture range (10–20%), Ahmed (2000) reported that *C. acinaciformis* conquered drier moisture ranges of 2.5% and 5% in a laboratory apparatus. After conquering places of higher moisture content, termites modify or control drier environments cancelling the effect of any moisture gradient due to drying (Ahmed 2000; Su and Puche 2003; Arab and Costa-Leonardo 2005). Wong and Lee (2010) attributed the success of *Coptotermes gestroi* over other species to their efficiency in carrying moisture into their food irrespective of the moisture content of the sand while being aggressive in their tunnelling.

When termites detect an opening in their mound, they immediately start transporting moist soil to cover it and protect the nest and colony from intruders, prevent moisture loss and maintain the humidity inside (Fig. 9.1). This maintenance is usually finished overnight, and the transported soil is recognized by its moist dark colour and irregular outcrop on the mound structure (Turner et al. 2006; French and Ahmed 2010). Basically mounds grow as the colony grows by adding soil particles to the mound structure (Lee and Wood 1971). This could be slow as reported by Lobry de Bruyn and Conacher (1995) for the *D. tamminensis* at a rate ranging from 0.3 to 4.2 % of the original size in an open woodland in Western

Fig. 9.1 Visible new soil deposition transported overnight around an intrusive section of hempcrete inserted into the top of the above-ground termite mound of *Coptotermes acinaciformis* in the Northern Territory (J.R.J French, personal communication)

Australia. The addition of soil during mound building and repair at the same time offsets the amount lost to the surrounding due to erosion, unlike in the abandoned ones where erosional forces can continue eroding and distributing the soil particles (Holt et al. 1980).

9.3.2 Establishment and Maintenance of Symbiotic Relationship

The association of termites with their symbionts is well recognized, and via this relationship they play an important role in the digestion and decomposition of organic matter. Through the ingestion and redistribution of minerals, they also moderate nutrient dynamics or global cycling (Lee and Wood 1971; Bignell et al. 1978; Holt and Coventry 1990; Radek 1999; Lavelle et al. 2001). The process of breaking down the woody plant components (mainly, cellulose and lignin) consumed from dead or living plants and soil organic matter takes place in the lumen of the termites' hindgut or in mound chambers (termitaria). This is basically with the help of symbionts—bacteria and protists (while sustaining bacterial symbiogenesis (Margulis 1998; Margulis and Sagan 2002)) which live within the hindgut of the termite—and fungi, which are cultivated as 'fungus gardens' or 'fungus combs' by some termites, respectively (Lee and Wood 1971; Bignell et al. 1978; O'Brien and Slaytor 1982; Breznak and Brune 1994; Lavelle 1997).

Termites are classified into two feeding or functional groups based on their food sources and their effects on the soil (Kambhampati and Eggleton 2000). The lower termites, also called the soil-feeding termites, harbour a dense and diverse population of bacteria and cellulose digesting, flagellate protozoa in their alimentary tract on which they depend for their cellulose digestion (O'Brien and Slaytor 1982; Kambhampati and Eggleton 2000; Eggleton 2001). They include the six families in the phylogenic order, namely, *Mastotermitidae*, *Kalotermitidae*, *Hodotermitidae*, *Termopsidae*, *Rhinotermitidae*, and *Serritermitidae* (Kambhampati and Eggleton 2000; Eggleton 2001). These termites feed on humus and build their nests using faecal matter mixed with coarse, inorganic soil particles. Many species of lower termites feed almost exclusively on wood decomposed by the interaction of a rich community of organisms. The collective action of the microbial enzymes and those of the endosymbionts of the termites ensure the decomposition of available woody components. Although wood is poorer in nutrient content (especially nitrogen and phosphorus) than other plant materials, the capacity to fix nitrogen overcomes this apparent disadvantage for such decomposers. In these circumstances the fresh input of nutrients by nitrogen fixation is most important ecologically. It may be concluded that wood which is capable of microbial or termite attack may not be an impoverished environment so much as a variably inadequate environment, with nitrogen-fixing bacteria involved in wood decomposition (French et al. 1976; Waughman et al. 1981; Radek 1999; Kurtböke and French 2008; French and Ahmed 2011).

The second group, higher termites (family Termitidae) or fungus-growing termites, are the biggest family comprising three fourths of all termite species (Lee and Wood 1971; Radek 1999). They host a dense and diverse collection of gut bacteria but most typically lack protists and have a more intricate external and internal anatomy and social organization than do the lower termites (O'Brien and Slaytor 1982). They are characterized by an exosymbiosis with a fungus (*Termitomyces* sp.) which finishes the degradation of the litter on which they feed (O'Brien and Slaytor 1982). They enrich their structures with fine or mostly clay particles as well as saliva which are rich in easily degradable carbon (Holt and Lepage 2000; Jouquet et al. 2002).

Generally termites create a number of microhabitats, favourable for the development and sustenance of the symbiont microorganisms, with the establishment of optimal security from predators and other interferences, minimum or no extreme fluctuations of wetting and drying cycles, as well as abundant and accessible nutrients (Lee and Wood 1971; Bignell et al. 1978; Jouquet et al. 2005). Therefore, termites considerably influence and regulate the structure of soil bacterial and fungal communities, as reported, for instance, with the fungus-growing termite species of *Ancistrotermes* and *Odontotermes* in the West African Savanna (Jouquet et al. 2005) and *Cubitermes nikoloensis* (Diaye et al. 2003). French and Ahmed (2010) described a network of short dead-end tunnels in the irregular sponge-like outer walls of *Coptotermes lacteus* mounds that serve as places for culturing actinomycetes and for trapping excessive moisture from within the mound which would sustain the symbiotic microorganisms (particularly *Actinobacteria*) within the mound materials and within themselves and are used in repairing mound walls.

In North Queensland, termites have been estimated to decompose 20% of the total dead plant matter (Holt and Coventry 1990), while a similar figure was reported as a minimum percentage of termite removal of animal dung in the Chihuahuan Desert ecosystem (Whitford 1982). In tropical and subtropical areas, where their biomass densities can exceed 50 gm^{-2}, the contribution of termites to organic matter decomposition 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 (Lee and Wood 1971; Collins 1984; Holt and Coventry 1990; Breznak and Brune 1994).

Mounds and other structures built by termites are usually enhanced in soil organic matter and fine particles and hence could be considered as islands of better fertility in an otherwise low fertile soil (Holt and Coventry 1990; Black and Okwakol 1997; Dawes-Gromadzki 2005; Turner and Soar 2008) significantly modifying soil microbial diversity and activity (Lavelle 1997; Brauman 2000; Diaye et al. 2003; Duponnois et al. 2006) as well as the plant symbiotic microflora (Diaye et al. 2003). Soils adjacent to termite mounds also have a massive increase in fertility due to the higher nutrient status of materials eroded from mound surfaces (Holt and Coventry 1990; Lavelle 1997). Increases in soil nutrient levels by up to seven times have been reported for termites (species of *Amitermes*, *Drepanotermes* and *Tumulitermes*) in North Queensland (Coventry et al. 1988).

9.4 Conclusion

Termite interaction with soil and foraging behaviour in different environmental conditions depend on their genetics and prevalent conditions in their immediate environment (soil type, soil moisture content, etc.). Termites utilize soil particles selectively, favouring finer particles and building constructions that match their ecological, physiological and behavioural needs. Soil and moisture play a big role in terms of termite preference for nesting and foraging site. However, they also need to work hard to maintain optimum soil and moisture conditions by transporting soil and water as well as establishing and maintaining symbiotic relationships with preferred microorganisms. This knowledge has become imperative as they are spreading into areas previously thought of as inhabitable with the help of urbanization and other human activities. At the same time, they have been useful in turning barren lands into productive ones.

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