Sustainability in Plant and Crop Protection

Md. Aslam Khan
Wasim Ahmad *Editors*

Termites and Sustainable Management

Volume 1 - Biology, Social Behaviour and Economic Importance

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Termites and Sustainable Management

Volume 1 - Biology, Social Behaviour and Economic Importance

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Foreword

Insects have been calling attention over years due to their ecological roles. Termites are the most dominant arthropod decomposer and show high diversity. Their abundance in any ecosystem drastically change the below ground biodiversity and are considered to enhance ecosystem productivity. Ecologically, termites act as ecosystem engineers as they influence processes and properties of soil structure as well as organic matter decomposition. They also contribute to the establishment of new soil in eroded areas. Over long periods of time, termites can modify the physical properties of soil. Termites are decisive for the functioning and yield of terrestrial ecosystems thus important for agricultural sustainability. Majority of the termite are helpful to mankind and are one of the effective organisms in food webs.

Despite importance in many ecosystems, destructive activities of termites as a result of their feeding habits cannot be overemphasized. Even though damage control measures have been developed all over the world, termite management is still in infancy, because very little is known about their biology. Therefore, detailed studies related to their biology and behaviour need to be carried out to achieve success in termite management.

This edited volume focuses on the biology, social behaviour and economic importance of this cryptic insect. Different chapters in this book provide valuable information in this regard. The editors of this volume together with the authors of the individual chapters have made a remarkable contribution towards inclusion of information and latest research results in this aspect. This information could be useful for researchers, educators and students for understanding that most of the termite species are not a pest; they play a vital role in the ecosystem as well as for agricultural sustainability. This book comprehensively addresses various issues related to the biology, social behaviour and economic importance of this social insect through the expertise of leading authors worldwide. Finally, this volume in the series *Sustainability in Plant and Crop Protection* is highly innovative in covering together different issues.

I am sure that a new generation of researchers will benefit much from this book. I congratulate the editors and various authors of this volume for such a splendid contribution on this social insect.

Kolkata, India

K. Venkataraman
Former Director,
Zoological Survey of India

Preface

This is the first of two volumes on termites presented in the series Sustainability in Plant and Crop Protection. This book deals with the biology, social behaviour and economic importance of this group of insects. The editors and authors have focussed on many basic and applied aspects of termites, including the main factors underpinning their ecological role and interactions with humans.

The volume includes 12 chapters providing reviews or experimental data on termites' biology. These deal with their systematics, taxonomy and ecology, their interactions with the surrounding environment, and the role of the gut microbiota and pheromones. Termites are described as a significant source of proteins and fat, used as food in some social contexts. Finally, the ecology and the helpful role of termitaria in minerals' exploration are revised, in relation to soil removal and displacement.

Given the large amount of contributions that the editors were able to assemble, several aspects of management have been moved to the second volume on termites, published within this series. It includes chapters spanning from eco-friendly approaches in termite control to management in organic agriculture and biocontrol, or through botanicals and other products.

Since the last decades of the twentieth century, biodiversity conservation and environment protection represent unavoidable steps in many human activities. Although termites are considered only as pests, they are also useful organisms. Only a small fraction of the species in this lineage produce indeed a negative impact on the cultivated field and urban or peri-urban space. On the contrary, many termite groups have a positive impact on the environment, playing a key role in sustaining many ecological processes, including nutrients' recycling and transport, or acting as primary soil engineers.

The present-day challenge is to increase food production by raising the average productivity per unit surface. Most fertile soils are already employed in agriculture, and deforestation has already crossed the acceptable limit. To sustainably increase productivity, we need to effectively expand our knowledge. In particular, we need to increase the expertise about how to replace energy-based production cycles (i.e.

relying on massive use of energy-demanding pesticides or fertilizers) by information-based, more conservative and sustainable approaches.

In this perspective, dealing with a complex and successful group of invertebrates, a compendium of information and data on termites appears very helpful. The amount of information provided is impressive and based on the research data produced by the laboratory and fieldwork of many authors. The scientists, who have contributed to and edited the volume, are at a leading edge in the field, both in terms of their experience and scientific production. Their long-term experience may arouse the reader's interest in their contributions, which are integrated with extensive bibliographies.

The editors' endeavour is highly appreciated in the preparation of these two volumes that were a result of their endless effort and exhaustive support provided to the contributors. These volumes provide a clearer insight on the biology and role of termites, allowing a better comprehension and knowledge about this diverse and fundamental group of invertebrates.

Aurelio Ciancio
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SUPP Series Editor

Preface

Termites play a vital role in the ecosystem by recycling waste material at every stage of decomposition. They have an extraordinary ecological impact, playing a key role in global carbon cycle, decomposition processes and nutrients recycling, as a result of their multi-level co-evolution with microorganisms that allows a superefficient utilization of lignocellulosic materials. They alter soil composition and structure, improve drainage and provide soil aeration due to burrowing activities, enhancing soil fertility when the mounds, rich in minerals and nutrients, are crushed down and incorporated into the soil. Thus, termites are referred as true soil engineers owing to their immense contribution in soil building activity. While in temperate zones termites play a minor ecological role, in the tropics they are the most important invertebrate decomposer.

Termites are an interesting biotechnological model for various industrial applications. These insects have been extensively studied to understand the mechanisms of lignocellulose digestion and their related potential for biofuel production. The termite symbiotic system is a rich resource, promising the discovery of new genes and enzymes. Apart from that, termites are an important food source across sub-Saharan Africa, where they are consumed as delicacies both in rural and urban areas. They are also used in traditional popular medicine. Their ability to withstand adverse environmental conditions is primarily due to their reproduction in large numbers at an astounding rate, along with their social structure. It is, therefore, imperative to study the biology, social behaviour and economic importance of these insects.

This volume comprises 12 chapters in an attempt to bring available information on the biology, social behaviour and economic importance of termites. Chapters in this book dealing with termite identification provide a review on most updated information of their systematics. Ecologically, termites interact with living and non-living surroundings and deliver a wide range of behaviours. In a separate chapter, termite ecology is examined and explored. Termites depend on their gut microbes for digestion of complex polysaccharides of wood into simpler molecules. Information provided on gut microbiome and lignocellulose degradation constitutes an important contribution.

Termite biology and social behaviour have been addressed comprehensively. Trail pheromones are responsible for the orientation and recruitment of nestmates to food sources. Once arriving at a potential food source, termites assess its quality using a different set of cues. A separate chapter on trail pheromones, cues used during foraging and food assessment, with preferences for foraging sites, contributes a wealth of information. Emphasis has been given on reviewing ecological benefits of termites in other chapters. The information with respect to termite species as an edible insect and the overall role played in food and nutrition security in Africa is quite informative. A separate chapter dealing with the importance of termites and termitaria in mineral exploration constitutes a significant step in assessing the economic importance of this insect.

Volume 1 covers the biology, social behaviour and economic importance of this cryptic insect. Volume 2 will focus on the different sustainable methods for the management of notorious termite pest species. We hope that it will be helpful to students, teachers, researchers and industry technicians. We are highly grateful to all the authors for providing their expertise in the form of stimulating contributions. Thanks are due to the head of the Biology Department and dean of the Faculty of Science, Jazan University, Jazan, for their constant support. We are grateful to Dr. Aurelio Ciancio, Bari, Italy, for including this book, in two volumes, dealing with termites and sustainable management in the Springer series “Sustainability in Plant and Crop Protection”. We extend our thanks to the Springer International team for their generous cooperation at every stage of the book production. Md. Aslam Khan acknowledges the Centre for Environmental Research and Studies, Jazan University, KSA, for financial assistance (CERS 7/2013).

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Chapter 1
Termites: An Overview

Md. Aslam Khan and Wasim Ahmad

Contents

Abstract A description of termite biology, distribution and diversity, economic importance, and sustainable management is presented. Liquid termiticide injection to soil, to establish a toxic or repellent chemical barrier against termites, is a traditional method applied for control. Baiting programs have been used successfully to eliminate subterranean termite colonies. Biological approaches along with entomophagy are also effective to manage termite population.

Keywords Termites • Economic importance • Management • Control

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1.1 Introduction

Termites are dominant invertebrate decomposers of dead organic matter in tropical and subtropical regions (Bignell and Eggleton 2000). Their ecological success is often attributed to the combination of a sophisticated social organization with unique ability to feed on recalcitrant plant matters such as wood (Bignell et al. 2011). The phylogenetic position of termites has been long debated. They constitute an ecologically and evolutionary diversified group of social insects that share a common ancestry with cockroaches (Inward et al. 2007a). Termites play an important role in ecosystems, with a major influence on soil chemical and physical structure, plant decomposition, nitrogen and carbon cycling, and microbial activity (Holt and Lepage 2000). While in temperate zones termites play a minor ecological role, in the tropics they are the most important invertebrate decomposer (Bignell and Eggleton 2000; Bignell et al. 2011). In tropical ecosystems, termites often make up over 10% of the total animal biomass and up to 95% of soil insect biomass (Jones and Eggleton 2000) and are considered to enhance ecosystem productivity (Bourguignon et al. 2016). They may reach enormous population density in the tropics, sometimes up to 1000 individuals per square meter (Eggleton et al. 1996). These insects are key species in ecosystems as they recycle a large amount of nutrients, but they are also pests, exerting major economic impacts. Among the eusocial taxa, ants and bees are by far the most studied, whereas termites have received much less attention in spite of their comparable abundance. Similarly, a few termite clades attract the attention of most researchers, while others are almost entirely neglected (Bourguignon et al. 2016). Our global view of the termite world is thus strongly biased toward a few economically important genera that make up approximately 12% of the described termite species (Krishna et al. 2013a) while overlooking other ecologically important and diverse taxa.

Soil is one of the most complex and species-rich habitats, hosting a wide range of life forms. Termites form eusocial societies and live in colonies, creating nest systems that may be underground, epigeous, or arboreal. Based on habitat, termites can be grouped into three general categories: subterranean, dry-wood, and damp-wood termites (Paul and Rueben 2005). Subterranean termites live in soil and in wood that is in contact with soil (Fig. 1.1). The name subterranean comes from the strong need of moisture in their environment that is satisfied by nesting inside or in close contact with the soil (Thorne 1998). Subterranean termites are major structural pests causing tremendous amounts of damage (Su and Scheffrahn 1998) and are reported as responsible alone for at least 80% of losses caused by termites (Su and Scheffrahn 1990). Dry-wood termites live entirely in the wood, both nesting and feeding there. Since they have the ability to thrive in wood with low moisture content, they may attack all kinds of dead and dry wood, such as structural timbers, furniture, flooring, and other wooden articles (Myles et al. 2007). Damp-wood termites, however, live inside the wood of varying levels of decay and moisture content.

Fig. 1.1 A live colony of subterranean termite

1.2 Biology and Behavior

A termite colony is usually founded by a pair of alates (winged), the primary reproductives, which produce all the nestmates. In some species, secondary reproductives appear to either replace the primaries or supplement colony reproduction (Haifig et al. 2016). Inside termites' complex society, the individuals are morphologically, physiologically, and behaviorally specialized into distinct castes (Figs. 1.2a, 1.2b, and 1.2c). The castes work together to accomplish specific and complementary tasks within a colony. Division of labor among castes is the key to efficient colony development, survival, and reproduction. It may take 4–6 years for an incipient colony of *Coptotermes formosanus* Shiraki to reach maturity and produce alates (Chouvenc and Su 2014). As social insects, mature *Coptotermes* colonies can reach more than a million individuals (Su and Scheffrahn 1988) with caste polymorphism and polyethism (Chouvenc and Su 2014). They have underground foraging galleries reaching up to 100 m, making detection and control difficult (Su and Scheffrahn 1998). Colonies of the desert subterranean termite, *Heterotermes aureus* (Snyder), have been estimated to include as many as 300,000 individuals around structures in urban environments (Baker and Haverty 2007). Seasonal variation in caste distribution of foraging populations of the subterranean termite, *Reticulitermes flavipes* (Kollar), was recorded. Workers were most abundant in the spring and summer months, and soldiers were most abundant immediately preceding alate flights (Howard and Haverty 1981). In termites, foraging is usually performed by blind castes, and the communication within individuals is mediated mainly by pheromones (Costa-Leonardo and Haifig 2014).

Observation of the behavioral repertoire of some more derived termite species with large colony size and extended nesting type (Abe 1987) remains challenging

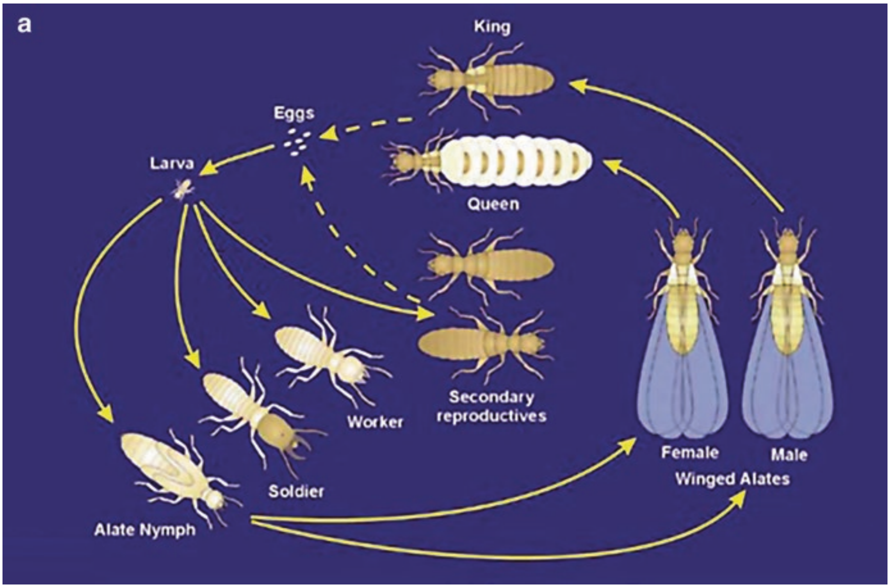

Fig. 1.2a Life cycle of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (*Source*: Su NY; University of Florida, Publication No. EENY121)

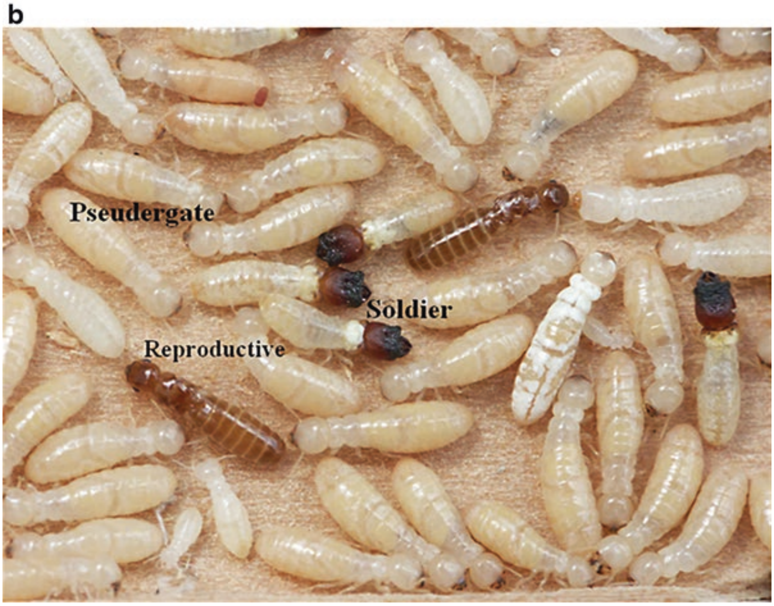

Fig. 1.2b Castes (reproductive, soldiers, and pseudergates – immature reproductives) of the West Indian dry-wood termite, *Cryptotermes brevis* (Walker) (Photo courtesy: Scheffrahn RH, University of Florida)

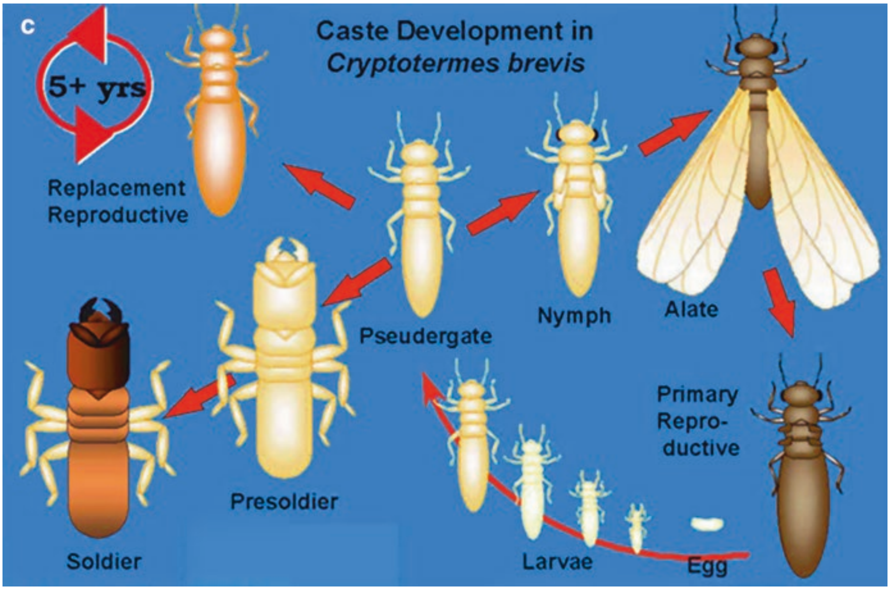

Fig. 1.2c Life cycle of the *Cryptotermes brevis* (Walker) (*Source:* Scheffrahn RH; University of Florida, Publication No. EENY079)

because of the difficulty to maintain live colonies in the laboratory. The problem is to provide a nesting environment that is not overly artificial (possibly resulting in behavioral artifacts), while having a visual on all individuals of the colony, at all times. Researchers and termite control practitioners can only observe termite activity through one or more "windows." This limited view of the diffuse network of tunnels and feeding sites occupied by a termite population is at the heart of the problem of determining the population parameters. An ethogram is the description of an animal's behavior repertoire that forms the basis of ethological studies. Ethograms have been constructed for many animals, including insects (Dinesh and Venkatesha 2013), particularly social insects such as bees (Seeley 1982), ants (Jayasuriya and Traniello 1985), and termites (Rosengaus and Traniello 1991). In social insects, ethograms are particularly relevant in understanding division of labor among individuals in a colony, where caste polyethism and age polyethism can result in optimized growth and fitness for the colony (Seeley 1982). The thorough descriptions of ethograms in termites are rare, owing to their cryptic lifestyle in a closed nest system. There is, therefore, an inherent difficulty in observing the range of behaviors of an entire colony with all castes. Behavioral observations of termites have typically focused on a few fragmentary behaviors, such as feeding (Indrayani et al. 2007) and foraging (Li and Su 2008). According to the origin, relatedness, and number of active reproductives, termite colonies are classified as simple families, extended families, and mixed families (reviewed in Vargo and Husseneder 2011). Simple families are colonies headed by a regular monogamous pair, the royal couple, whereas extended and mixed families present multiple reproductives. In both extended and mixed families, the multiple females may be accompanied by multiple males, because, in termites, polyandry is often associated with polygyny (Roisin and Pasteels 1985). Mixed families can also result from colony fusion (DeHeer and Vargo 2008).

Many species build nests, but it is common to find more than one type of termite living in the same active or abandoned nest (Bandeira 1983). Members of *Inquilinitermes* are obligatory inhabitants found in the nests of *Constrictotermes*, a termite that builds arboreal nests (Melo and Bandeira 2004). Chiu et al. (2015) speculated that the various food sources and their distributions are likely the main selection force for the gallery structures of soil-feeding termites. Studies of the tunneling behavior of marked *C. formosanus* determined that a small number of specific individuals performed most of the work while most of the individuals remained inactive (Cornelius 2012). Study by Cornelius and Gallatin (2015) provided a detailed analysis of the tunneling behavior of workers of the subterranean termite, *C. formosanus*. Chemical communication certainly represents the dominant mean of information exchange in social insects (Richard and Hunt 2013). Chemical mediators of intraspecific communication, the pheromones, are secreted from exocrine glands (Billen 2011) and are perceived by specialized chemoreceptors, located predominantly on the antennae (Wyatt 2003).

Termites' evolutionary success has been linked to their defense mechanisms. They have developed a multitude of active and passive defensive traits. The active defenses comprise morphological (Deligne et al. 1981), chemical (Prestwich 1984; Sobotnik et al. 2010), and behavioral (Sobotnik et al. 2012) adaptations present predominantly in soldiers, while passive defense include cryptic way of life and nest fortification preventing attacks from nonspecialist predators (Noirot and Darlington 2000). Soldiers are recruited for defense in a disturbed area. It was noticed that the disturbed soldiers did not escape in proportion to the workers; rather, there was a modest increase in soldier number (Gautam and Henderson 2012).

1.3 Systematics, Distribution, and Diversity

Termites are traditionally ranked as an insect order (Isoptera), representing a subgroup within Blattodea, with *Cryptocercus* being their sister taxon (Lo et al. 2000; Inward et al. 2007b; Djernaes et al. 2015). Termite systematics is traditionally based on the external morphology of soldiers and alate imagoes[1] (e.g., Holmgren 1912; Emerson 1925; Snyder 1926). However, species with overlapping geographic ranges are notoriously difficult to distinguish morphologically. Fortunately, the worker morphology also allows species identification, especially in soil-feeding taxa, whose digestive tract is highly modified and morphologically distinct among species (Noirot 2001). Despite the wide distribution of *Coptotermes* in the world, and the large body of associated scientific literature for population management, the

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[1] Imago: the last stage attained by an insect at the issue of metamorphosis.

taxonomy of *Coptotermes* remains unsettled, and many species names may be synonyms of others (Chouvenc et al. 2015). Krishna et al. (2013b) listed 110 species names within *Coptotermes* that conformed to the rules of the International Code of Zoological Nomenclature (ICZN). Among them, 69 were regarded as valid in the taxonomic literature, and 42 were listed as subjective synonyms. Moreover, several species currently included in genus *Ruptitermes* Mathews 1977 were initially classified in the genera *Anoplotermes* Fr. Muller 1873 and *Speculitermes* Wasmann 1902 (Acioli and Constantino 2015). Termite experts have also made attempts to solve taxonomic cold cases (http://entomologytoday.org/2015/12/22/termite-experts-attempt-to-solve-taxonomic-cold-cases). The American Museum of Natural History (AMNH) collection of termites is, without question, the largest and most comprehensive in the world for these insects and fully global in scope. The collection consists of over a million specimens belonging to about 80% of the world's species (excluding the plethora of species recently described from China). A reference library on termites contains the most comprehensive archive of original publications on the systematics of Isoptera (http://www.amnh.org/our-research/invertebrate-zoology/collections/isoptera).

Although the presence of the soldier caste is a synapomorphy[2] of all termites (Roisin 2000), the soldier to worker ratio decreases in soil-feeding termites compared with their wood-feeding relatives (Haverty 1977). Soldierless termites (Termitidae, Apicotermitinae) constitute about one third of the termite diversity in African and South American rainforests (Eggleton 2000). Because they lack the soldier caste, species identification must be based on alate imagoes, when collected, and on workers and requires the dissection and close examination of their digestive tube (Noirot 2001). An excellent review on poorly known and ecologically dominant soldierless Apicotermitinae is presented by Bourguignon et al. (2016).

Although human transport of termite-infested material is the primary method of expansion to new regions, natural dispersal occurs slowly through the annual nuptial flights of alates. Alates of *C. formosanus* generally swarm from April through June to give rise to new colonies (Henderson 1996). Average recorded alate flight was 621 m, and the longest flight was 1.3 km distant from the parent colony (Mullins et al. 2015). Therefore, alate dispersal plays an important role in the spread of *C. formosanus* in areas where it has become established and in the reinvasion of areas where colonies have been eliminated through treatments. *C. formosanus* is endemic to China and Taiwan and has spread to many temperate and subtropical regions (Evans et al. 2013). It is now found throughout the southeastern United States and is responsible for more than $1 billion of structural damage each year in this country alone (Corn and Johnson 2013). *Coptotermes gestroi* (Wasmann) is native to Southeast Asia and has spread in many tropical regions, being potentially the most ubiquitous and destructive subterranean termite pest in the world (Evans et al. 2013). Both species have distinct ecological requirements (Grace 2014), but there are now established populations in many non-native areas due to human activity

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[2] Synapomorphy, presence of a shared derived character that characterizes a clade from other lineages.

(Hochmair and Scheffrahn 2010). *C. formosanus* probably became established in Florida in the early 1970s, remained undetected until the first reported record (Koehler 1980) in Hallandale (Broward County), and has since been found in most urban localities throughout Florida (Scheffrahn 2013).

Reticulitermes Holmgren, 1913, is a Holarctic genus of subterranean termites (Isoptera: Rhinotermitidae) that is widespread and abundant in temperate regions where their biomass can approach that of many termite taxa living in tropical regions (Bignell and Eggleton 2000). Human commercial activities unwittingly transport termites to their nonendemic areas. This is evidenced by the appearance of *Reticulitermes* infestations in Hallein (Austria), Hamburg (Germany), Devon (England), and Toronto (Canada) (Gay 1969; Su and Tamashiro 1987; Jenkins et al. 2001). Thus subterranean termites will continue to be a worldwide problem for urban and suburban property owners (Forschler and Jenkins 2000). There is also mounting evidence that warming environments resulting from climate change can be an important factor for altering the species distribution (Chunco 2014).

Termite faunal structure is determined by climatic and vegetational characteristics. Termite species richnesses, abundances, diversity, and trophic structures, however, differ between the two kinds of ecosystems. Greater species richness (Eggleton et al. 1997; Vasconcellos et al. 2010) and density (Bignell and Eggleton 2000) have been observed in humid forests than in arid or semiarid environments. Differences related to feeding groups are also observed, with humus-consuming species being more abundant and vulnerable to environmental alterations in humid forests (Eggleton et al. 1997; Vasconcellos 2010). Xylophagic species constitute the most abundant and vulnerable group in dry tropical forests (Vasconcellos et al. 2010). The structure of the termite fauna can vary considerably between areas in the same ecosystem, after exposure to different degrees of anthropogenic alterations (Vasconcellos et al. 2010). The modification of natural areas to form agroecosystems, for example, can result in significant loss of species richness, abundance, and diversity (Bandeira et al. 2003).

1.4 Invasive Termites

The invasion of a new habitat by an introduced species may depend on a number of factors such as the suitability of the abiotic environment (Blackburn and Duncan 2001), the ability of the species to adapt to the novel environment (Sax and Brown 2000), and the interaction between the invader and the recipient community (Holway 1998). *Coptotermes* is a termite genus that is ecologically successful. Two species, the Formosan subterranean termite, *C. formosanus*, and the Asian subterranean termite, *C. gestroi*, are particularly invasive (Chouvenc et al. 2015). They have spread far beyond their native range with the help of human maritime activities (Scheffrahn and Crowe 2011; Rust and Su 2012). These two species contribute in large part to the annual $40 billion cost associated with termite damage and control around the world (Rust and Su 2012). Whereas *C. formosanus* has a warm temperate/

subtropical distribution, *C. gestroi* has a tropical distribution (Cao and Su 2016). In the New World, *C. formosanus* has invaded most of the southeastern United States, whereas *C. gestroi* has invaded areas of Brazil, most of the Caribbean, and, more recently, parts of south Florida (Su et al. 1997; Scheffrahn et al. 2015). One of the reasons for the success of termite species comes from their ability to adapt to disturbed environments and display a high behavioral plasticity at the colony level, with efficient task division (Du et al. 2016). Chouvenc et al. (2016) reported that the risk for structures in metropolitan southeastern Florida with known *Coptotermes* infestations increased from 0.49% to 7.3% (from year 2000 to 2015), with some species distributional overlap. In addition, several localities that had *Coptotermes* records before 2000 have registered an increased density of termite infestation and swarming activity. It is expected that the distribution and structural infestations by *Coptotermes* will continue to increase in the years to come, with an estimated 50% of all structures in southeastern Florida at risk by 2040.

1.5 Termite-Gut Microbiota

Gut-associated microbes of insects are postulated to provide a variety of nutritional functions. The diet of termites is diverse, with cellulose as the main food resource exploited (Moore 1969; Lima and Costa-Leonardo 2007). However, termites are deficient in enzymes that decompose cellulose and lignin, which provide them with extra carbohydrates (Williams 1965). For this reason, they require the aid of symbiotic microorganisms in their feeding channel to digest these compounds. Termite-gut microbiota is very diverse and comprises many phylogenetic lineages that have been extensively documented in recent decades (Ohkuma and Brune 2011). The gut of these insects is a specialized habitat for bacteria, archaea, and protists which make them highly efficient decomposers (Eggleton 2011). Based on feeding ecology, termites can be grouped as the higher termites and the lower termites. Lower termites (all families except Termitidae) harbor in their gut a dense and diverse population of prokaryotes and flagellated protists (Ohkuma 2003). Protozoan symbionts residing in lower termites are responsible for lignocellulose digestion in this group. Digestion of cellulose and hemicellulose is attributed to a consortium of termite, bacteria, and protist-derived cellulases that ultimately liberate carbon in plant tissues (Scharf et al. 2011). Higher termites (Termitidae) lack flagellates and harbor only prokaryotes in their highly structured guts. However, recently, a low-abundant ciliate has been detected in the guts of higher termite species (Rahman et al. 2015). Lower termites predominantly feed on dead wood (with few exceptions). The diversification of feeding habits is high in Termitidae. The symbionts are not transmitted vertically (from mother to offspring) but become established by a gradual process allowing the offspring to have access to the bulk of the microbiota prior to the emergence of workers and, therefore, presumably through social exchanges with nursing workers

(Diouf et al. 2015). The acquisition of genetic data in termites and their gut microbial community has been of recent interest to the scientific community. This is mostly due to the development and accessibility of new sequencing technologies such as 454 pyrosequencing and Illumina sequencing (Scharf 2015).

1.6 Feeding Groups

Termites have also been classified into several functional feeding groups: soil feeders, soil/wood interface feeders, wood feeders, litter foragers, epiphyte feeder, grass feeders, and some other minor feeding groups (Collins 1984). Although several classifications into feeding groups have been proposed (Inward et al. 2007a), the fundamental differential trait lies in the distinction between wood- and soil-feeding groups (Bourguignon et al. 2009). Wood-feeding termites feed on sound dead wood and true soil-feeding termites feed on soil organic matter in mineral soil, with no visible plant remains. Soil-feeding termites were found in the surface horizon of soil (Inoue et al. 2001), in the intermediate organic matter between wood and topsoil (Souza and Brown 1994), and in the mounds of other termite species (Eggleton and Bignell 1997). These termites increase the polysaccharide content of soil (Garnier-Sillam and Harry 1995) and facilitate its humification process (Brauman 2000). Most soil-feeding termites build subterranean and diffuse gallery systems that are difficult to observe. The high diversity of soil-feeding termites indicates soil feeders as a successful feeding guild of termites (Brauman et al. 2000).

1.7 Biotic and Abiotic Factors

Biotic and abiotic factors play a role in the successful establishment of invasive species. Among the abiotic factors, moisture and temperature play a vital role in determining which areas are the most suitable for establishment. Given the importance of these factors, a fluctuation in either moisture or temperature will impact the overall termite consumption and survival. Humidity directly affects temperature and vegetation structure, which strongly influence the termite assemblage structure. The workers and soldiers, which comprise a large proportion of the colony's population, have a soft integument that makes them extremely vulnerable to desiccation (Moore 1969). Surrounding moisture is of utmost importance for the survival of subterranean termites, which are highly susceptible to desiccation, making moisture a critical factor for survival. Many studies have examined the influence of moisture on the tunneling and feeding behavior of subterranean termites (McManamy et al. 2008; Gautam and Henderson 2011) which have a relatively soft cuticle that readily desiccates (Moore 1969). As a survival strategy, subterranean termites always associate with moist and humid environments. Moisture can be obtained from many sources, including metabolic breakdown of sugars (food source) and wet food materials (Pearce 1997).

Barriers of dry soil affect the ability of termites. Cornelius and Osbrink (2011) observed high significant effect on the ability of termites to colonize food located in dry sand. They reported that only one feeding station located in dry sand was colonized by termites, compared with 11 feeding stations located in moist sand. Delaplane and LaFage (1989) reported that *Coptotermes formosanus* Shiraki preferred wet wood blocks over dry blocks. Behr et al. (1972) also showed a positive correlation between wood moisture level and the feeding by *Reticulitermes flavipes* (Kollar).

Temperature is another important factor that determines the geographic distributions, feeding, and survival of species. It was believed that soil temperature has more effect on activity of subterranean termites than air temperature (Ettershank et al. 1980). Sen-Sarma and Mishra (1968) studied the seasonal activity variation of *Microcerotermes beesoni* Snyder in North India and indicated that soil temperatures determined termite activity levels in different seasons. Evans and Gleeson (2001) documented similar observations from the study of another subterranean termite species, *Coptotermes lacteus* (Froggatt), in Australia. Haverty et al. (1974) noted that foraging intensity of *Heterotermes aureus* (Snyder) increased in spring and fall but decreased during the winter months in desert grassland. *Reticulitermes* sp. preferred significantly lower temperatures than *Coptotermes* sp. (Cao and Su 2016). The highest survival (Fei and Henderson 2002) and the highest feeding rate (Nakayama et al. 2004) for *C. formosanus* were reported at 30 °C.

Fire strongly affects habitat resources used by termites, such as plant biomass and dead wood (Haslem et al. 2011), and therefore may indirectly modify their communities. However, termites appear to be resistant to the effects of fire at multiple spatial scales (Avitabile et al. 2015). Termites are common in fire-prone landscapes, including savannas worldwide (Davies et al. 2010) and arid and semiarid woodlands (Abensperg-Traun et al. 1996). In general, altitude and species richness correlate negatively for several organisms (McCain 2009). However, Diehl et al. (2015) found no significant correlation between termite species richness and altitude.

1.8 Economic Importance

The economic importance of termites is twofold, extremely beneficial and extremely injurious to man. These small creatures are a part of the natural ecosystem and contribute significantly to most of the world ecosystems. The significance of termites for ecosystem functioning is widely acknowledged and receives considerable attention from the scientific community, with much effort applied to disentangling their specific contributions to ecosystem functioning (Davies et al. 2014b). Termites are important in both dry and humid tropical forests, where they are consumers of the plant necromass, helping in the processes of nutrient cycling and soil formation (Lee and Wood 1971; Vasconcellos and Moura 2010). A great role in the cycles of biogenic elements in tropical forest ecosystems belongs to termites that consume up to 50% of the leaf litter (Brauman 2000). They are often referred to as ecosystem engineers because they shape the environment through their action. Bonachela et al.

(2015) reported that in many arid ecosystems, termite nests impart substrate heterogeneity by altering soil properties, thereby enhancing plant growth. Furthermore, they noticed that mound-field landscapes are more robust to aridity, suggesting that termites may help stabilize ecosystems under global change. Termite mounds shape many environmental properties, as their soils differ from surrounding "matrix" soils in physical and chemical composition, which enhance vegetation growth (Sileshi et al. 2010), creating "islands of fertility" (Sileshi et al. 2010; Davies et al. 2014a). The increased soil fertility and moisture found near termite mounds can have pronounced effects on vegetation communities and their productivity (Sileshi et al. 2010). Previous studies have found that woody vegetation growing on termite mounds increased density (Moe et al. 2009), tree height (Levick et al. 2010), species richness (Traore et al. 2008), functional diversity (Joseph et al. 2014), and reproductive output (Brody et al. 2010).

Termites have long been studied because of their uncommon diet and complex hindgut microbiota. Researchers have discovered that enzymes found in a termite's digestive system could aid in biofuel production from woody biomass (see Chap. 5 for more details). The lignocellulolytic system in wood-feeding termites has some unique system advantages and can potentially serve as a model system to improve our current biomass bioconversion technology for fuels and chemicals (BenGuerrero et al. 2015). The termitaria are formed from materials burrowed from deep-seated environments upward by termites and are residual in character. The use of termite mound samples is an appropriate media in the search for concealed mineralization in complex regolith environments (Arhin et al. 2015). Affam and Arhin (2006) recognized termite mounds as a good geochemical sample media for gold exploration, and its validation has been confirmed by Arhin and Nude (2010) in northern Ghana.

Termite species, however, gain pest status when they damage building materials or agronomic and forestry commodities. As the principal food of some of the termite castes is cellulose, they cause economic losses by directly injuring and destroying both living and dead vegetation, buildings, bridges, dams, etc. Many subterranean termite species are considered "urban pests" due to their tendency to attack man-made structures (Rust and Su 2012), and some are now invasive throughout the world, increasingly causing structural damage (Evans et al. 2013). Subterranean termites, particularly members of the genera *Coptotermes* and *Reticulitermes*, represent the most widespread and economically important structural insect pests in the urban environment (Gay 1969; Su and Scheffrahn 1990). Twenty-three species in the genus *Coptotermes* are among the most significant termite pests worldwide for man-made structures. *C. formosanus* and *C. gestroi* are of particular economic importance (Rust and Su 2012) due to their ecological success and invasive ability (Evans et al. 2013). Termites cause tree damage in public areas, thus threatening people safety. Infested living trees can ultimately lead to their felling and death. *Coptotermes formosanus* attacks structural wood as well as living trees (Henderson 2001).

Once a colony of *C. formosanus* is established in an area, it soon invades nearby areas while searching for food and gradually spreads to new locations (Fig. 1.3). This termite lives a cryptic lifestyle where workers and soldiers forage through tunnels and galleries originating from their nests. Unlike subterranean *Reticulitermes*

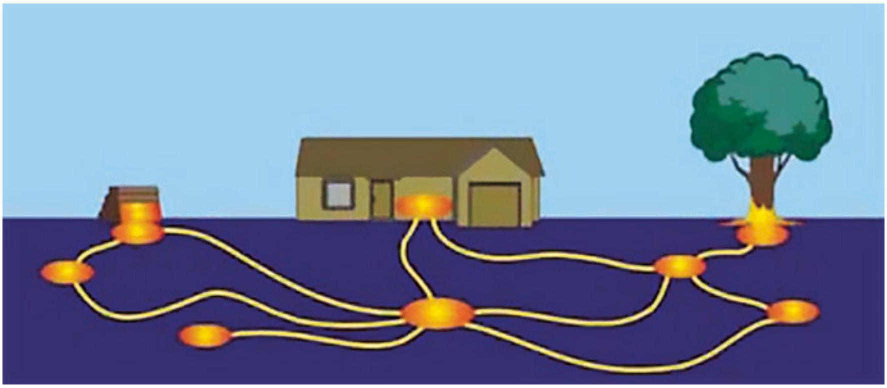

Fig. 1.3 A single colony of the Formosan subterranean termite *Coptotermes formosanus* Shiraki may contain several million individuals that forage up to 100 m in soil (*Source*: Su NY; University of Florida, Publication No. EENY121)

sp., *C. formosanus* has a large colony size and aggressive feeding behavior (Tamashiro et al. 1980). In Japan and the United States, *C. formosanus* and in Australia *C. acinaciformis* (Froggatt), as well as *Mastotermes darwiniensis* Froggatt, are economically important species (Alexander et al. 2014). However, subterranean termite *R. flavipes* (Kollar) is the most common and widely distributed termite pest species in the United States (Scheffrahn et al. 1988; Wang et al. 2009). Termites are selective in which types of wood they feed on. Wood species vary in chemical makeup and structure providing a number of possible cues that termites could use in food selection. Natural compounds such as sugars, amino acids, urea (Castillo et al. 2013), and phosphates (Botch et al. 2010) were previously found to increase termite feeding. It has also been suggested that wood fiber density also plays an important role in food selection.

Economic losses associated with termite damage in the United States and Japan are around 1000 and 800 million US$ a year, respectively (Verma et al. 2009), and Japan may be the third largest user of pesticides for structural pest control in the world. In Europe, the losses caused by termites are estimated at 313 million US$ per year (Eggleton 2000). Economic losses due to termite in India have been estimated around 35.12 million US$ (Joshi et al. 2005). However, in Malaysia 8–10 million US$ is spent toward termite treatment every year (Lee 2002). The global economic impact of termite pests is estimated to be at least $40 billion (Rust and Su 2012).

1.9 Prevention and Control

For decades, soil treatment with liquid termiticides has been the dominant method used in subterranean termite control programs. The traditional method is by injection of liquid termiticide to the soil to establish a toxic or repellent chemical barrier against termites. Barrier treatments first were developed in the 1940s and have changed very little since then (Lewis 1997). These treatments are labor-intensive and require a relatively large amount of insecticide to achieve the required concentration levels in the soil. Liquid termiticides are either neurotoxins or inhibitors of mitochondrial respiration. There are six main insecticide classes, i.e., organophosphate, carbamate, pyrethroid, neonicotinoid, phenylpyrazole, and avermectin, of termiticides used currently in the field (Chen et al. 2015).

The use of proper application method of termiticides is important to reduce their negative impact to the environment. Though treatments result in varying degrees of success depending on the skills of the applicator, type and dosage of chemical used, and degree of infestation, it is extremely difficult to obtain a continuous and uniform distribution of insecticide at the correct soil concentration, around infested structure (Forschler and Lewis 1997).

Termite control exploits their eusociality to deliver the insecticide. When termites forage in termiticide-treated areas, they acquire the active ingredient and inadvertently share it with unexposed nestmates, a process known as horizontal transfer. Subsequently, horizontal transfer results in secondary mortality in situations where a lethal dose of the active ingredient is transferred from the exposed donor termites to the unexposed recipient termites. Transfer of pesticides among termites (mainly through grooming) has been reported for various products, e.g., imidacloprid, indoxacarb, ivermectin, and chlorpyrifos (Valles and Woodson 2002; Shelton and Grace 2003; Hu et al. 2005).

It is established that, unlike repellent soil termiticides, nonrepellent, delayed action termiticides have impacts beyond the treated area. Nonrepellent termiticides are slow-acting insecticides that are not detected by termites when they forage through treated soil. One important advantage of a nonrepellent termiticide is the potential greater “coverage” as termites do not detect the chemical presence and do not die too quickly after walking across the treatment (Thorne and Breisch 2001). This opens the door for possible alternative treatment methods to incorporate into integrated pest management strategies that reduce the amount of chemicals applied. Presently, nonrepellent and relatively slow-acting liquid termiticides represented by imidacloprid (Premise®), fipronil (Termidor®), chlorfenapyr (Phantom®), indoxacarb (Aperion™), and chlorantraniliprole (Altriset™) are soil termiticides widely used for the prevention and treatment of structural infestations of subterranean termites (Potter and Hillery 2002; Remmen and Su 2005; Gautam et al. 2014).

Together with prevention and control strategies, early detection of termite infestations would enable the determination of infestation extent and the delineation of areas for future treatment procedures (Su and Scheffrahn 2000). Visual inspection is the normal procedure for dry-wood termite detection, although it is not 100% effective, so it should be accomplished with other sophisticated methods, such as moisture meters, electronic odor devices, acoustic emission detectors, or infrared heat detectors, for enhancing the reliability of termite detection (Evans 2002; Oliver-Villanueva and Abian-Perez 2012). Throughout the world, chemical termiticides are going to be replaced by baits, microwave, and sensor technology. Termite detection radar, moisture meter, and remote thermal sensor with laser are available throughout the world. These can detect termites underground and use fewer chemicals than traditional methods (Manzoor 2013). Therefore, nondestructive detection methods together with traditional visual inspections are advisable, since the integrity of wooden elements is maintained.

Popular control practices involve the use of nonrepellent termiticides and baiting systems (Henderson 2001). Subterranean termite colonies have extensive underground gallery systems, and it is difficult to eliminate entire colonies using soil insecticides. Baiting programs have been used successfully to eliminate subterranean termite colonies (Su et al. 1995; Eger et al. 2012). The goal of a baiting system is to eliminate the entire termite colony from an area with the least possible cost and harm to nontarget organisms in the environment (Su and Scheffrahn 1998). Baiting systems depend on the exploitation of foraging behavior of subterranean termites, where a subset of individuals from a colony feed on the cellulosic food material impregnated with slow-acting toxicants and introduce the toxicants to the colony (Su and Scheffrahn 1998). The success of baiting system is more variable than that of the liquid soil termiticides (Lewis 1997). Environmental factors such as temperature, humidity, soil type, and soil moisture affect termite activity at bait stations (Messenger and Su 2005; Ruan et al. 2015). Seasonal variations in caste distribution of foraging populations could also influence feeding and foraging behavior of termites on baits. Although baiting is the most environmental friendly way of controlling termites, about two thirds of the treatments by pest control companies rely on the use of liquid insecticides in soil (Curl 2004). Although insecticide resistance is extremely rare among social insects, it is nonetheless important to search for new alternatives of conventional insecticides used in termite control.

Biological alternatives for termite control include botanicals (essential oil, seed, bark, leaf, fruit, root, wood, resin), as well as fungal, bacterial, and nematode approaches (Verma et al. 2009). The active component from biomass can be extracted to prepare efficacious and potent biocidal formulations. Phytophagous insects use plant volatiles to recognize their host plants. Therefore, the use of essential oils as a nonhost volatile emission to repel insect pests is a viable alternative for control (Mauchline et al. 2005). Numerous studies have documented the natural resistance of certain wood species to termite attack. Cornelius and Osbrink (2015) reported that toxic chemical components of teak hold the most promise as wood preservatives.

Termites are frequently preyed upon by ants in tropical forests, and most termite species are likely to be affected by ant predators (Goncalves et al. 2005). They exhibit several adaptations to avoid predation, including chemical defense, mandible snapping, and fighting with large, smashing mandibles (Prestwich 1984; Legendre et al. 2008). Some species of ant, including those from the genera *Centromyrmex* (Bolton and Fisher 2008), *Megaponera* (Dejean et al. 1999), *Anochetus* (Schatz et al. 1999), *Tetramorium* (Longhurst et al. 1979), and *Paltothyreus* (Dejean et al. 1993), specialize on particular termite taxa, while species from a wide range of genera are known to predate termites opportunistically, to a greater or lesser extent (Dejean et al. 1999). Other species, such as *Dorylus* (*Anomma*) driver ants, only feed on alates during swarming (Schoning and Moffett 2007). Furthermore, there is substantial (correlational) evidence that the nest density of termites is limited by the abundance of both dominant (Pequeno and Pantoja 2012) and non-dominant ant species (Ellwood et al. 2002). Several spider species have specialized to feed on prey that is highly aggregated, including termites and ants (Haddada et al. 2016). Wesolowska and Haddad (2002) reported *Heliophanus (Heliocapensis) termitophagus* n. sp., a jumping spider in or on the termitaria of *Trinervitermes trinervoides* (Sjostedt) that fed mostly on workers of *T. trinervoides*. Petrakova et al. (2015) reported that the spider *Ammoxenus amphalodes* is a monophagous prey specialist, specifically adapted to feed on harvester termites, *Hodotermes mossambicus* (Hagen). The spiders attacked the lateral side of the thorax of termites and immobilized them within 1 min. The paralysis efficiency was independent of the predator/prey size ratio. However, its role as a biocontrol agent against termites is limited, due to an insufficient numerical response.

Entomophagy, the practice of using insects as a part of the human diet, has played an important role in the history of human nutrition in Africa, Asia, and Latin America (Srivastava et al. 2009). However the use of insects by human in medicine is known as entomotherapy. People from different parts of the world use termites as food (for humans and livestock) and as a source material for popular medicine (Figueiredo et al. 2015). Kinyuru et al. (2013) reported that different edible termites from Western Kenya contain about 45% fat and 35% dry matter. Research continues to focus on suitable termite control measures that are both effective and environmentally benign. Ultimately there is a dire need to develop strategies for sustainable termite management locally that would save money and protect the environment.

1.10 Conclusion

The cryptic nature and social organization of termites represent a primary reason why termite infestations can be difficult to study and control. Once a subterranean colony is established in an area, it soon invades nearby areas while searching for food and gradually spreads to new locations. Labor-intensive soil treatment with liquid termiticides has been the dominant method used in subterranean termite control programs. There is a dire need to develop strategies for sustainable termite management, focusing on goals of least possible cost and harm to nontarget organisms, in the environment.

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Chapter 2
Termites Identification

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Contents

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Abstract There have been several attempts by taxonomists to identify and trace the phylogeny of termites over the course of time. Termites were previously classified under the order Isoptera because of the equal size of front and hind wings of adult. They are considered as a sister group of primitive wood-dwelling cockroaches and mantids, hence classified under the same superorder, Dictyoptera. However, a molecular phylogenetic study by Inward et al. (Biol Lett 3:331–335, 2007) proved that termites are social cockroaches. The study showed that termites nest within the cockroaches in the phylogenetic tree. Also, wood roach *Cryptocercus* forms a sister group with termites. Hence, termites are reclassified under the order Blattodea and epifamily Termitoidea. At present, 3106 living and fossil termite species have been identified across the world, representing 330 living and fossil genera, under 12 families. In general, the termites can be grouped according to the presence/absence of protozoan in the gut, feeding, and nesting behavior. Only 10% of termite species act as pests either in forest, urban, or agricultural areas. Asian termite pests mainly belong to the family Rhinotermitidae and Termitidae, with species of the genera *Coptotermes*, *Macrotermes*, and *Schedorhinotermes*. They cause serious damages to buildings, crops, and even in plantation forests.

Keywords Taxonomy • Isoptera • Blattodea • Cockroaches • Termitoidea

2.1 Introduction

Taxonomy is the branch of science that comprises nomenclature, classification, and construction of identification key for particular groups of organisms (Quicke 1993). This branch is very important in science because relationship between organisms and its contemporaries can be understood through taxonomy. The combination of traditional taxonomy with theoretical and practical aspects of evolution, genetics, and speciation is known as systematics. These branches have been extensively developed for many insects and especially termites.

Classification of organisms began with introduction of the modern system for naming organisms, known as the binomial nomenclature, by Carl Linnaeus who published the first edition of *Systema Naturae*, a publication related to classification of living forms in 1735 (Krishna et al. 2013a). Since then, he published many editions explaining the classification of organisms. Classification of termites was first explained in his 10th edition of *Systema Naturae* in 1758 (Krishna et al. 2013a). Continuously, taxonomists such as Daniel Rolander, Johann C. Fabricius, Henry Smeathman, Daniel C. Solander, Thomas S. Savage, Johann G. Konig, Carl De Geer, Vincenz Kollar, Pierre A. Latreille, John O. Westwood, Francis Walker, and Gaspard A. Brulle have contributed to the classification of termites, which resulted in the creation of an order specific for termites, Isoptera, in 1832 (Krishna et al. 2013a).

The term Isoptera was derived from the Greek words, *iso*s meaning equal and *pteron* meaning wing, where the adult termites have front wings and hind wings of equal size. Termites, which are also known as “white ants” among the public, however, have no close phylogenetic relationship with ants. Termites are considered as a sister group with a primitive group of wood-dwelling cockroaches and mantids, hence classified under the same superorder Dictyoptera, order Blattodea, and epifamily Termitoidea (Inward et al. 2007).

At present, 3106 living and fossil termite species have been identified across the world, consisting of 330 living and fossil genera and 12 families (Krishna et al. 2013a). However, Mahapatro et al. (2015) mentioned that latest literature reveals record of about 3138 species (fossil and living) worldwide. A constant flow of first descriptions is still increasing this number significantly. Among this, only 10% of termite species are known as pests either in forest, urban, or agricultural areas, such as *Coptotermes* sp. and *Macrotermes* sp., which have caused serious damages to buildings, crops, and even in plantation forests.

2.2 Termite Classifications

There were several attempts made by taxonomists to identify and trace the phylogeny of termites over the course of time. A French entomologist, Gaspard A. Brulle (1809–1873), introduced the term "Isopteres" in 1832, based on equal wings. This classification distinctly differentiated termites from other insects such as Orthoptera, Neuroptera, and Hemiptera. Soon after, this view was adapted and accepted by other taxonomists as order Isoptera (Krishna et al. 2013a).

On the other hand, phylogenetically, the order Isoptera is said to be a sister group with a primitive group of wood-dwelling cockroaches (Blattodea) (Thorne et al. 2000). This is based on the similarity between termites and cockroaches, both the groups being hemimetabolous.[1] Termites have styli in the rear end of the abdomen as in cockroaches (Harris 1957). Furthermore, they enclose their eggs in a specialized case known as "ootheca," similar to cockroaches (Triplehorn and Johnson 2005). Termites are now grouped under the superfamily Blattidae and epifamily Termitoidae (Table 2.1) (Eggleton et al. 2007; Zhang 2011).

Most commonly accepted classifications of termites were proposed by Synder (1949) and Emerson (1955). Synder (1949) produced the "Catalog of termites (Isoptera) of the world," in which he listed about 1773 living and fossil species of

Table 2.1 Classification of termites (Zhang 2011)

Kingdom	:	Animalia
Phylum	:	Arthropoda
Class	:	Insecta
Subclass	:	Pterygota
Superorder	:	Dictyoptera
Order	:	Blattodea
Superfamily	:	Blattoidea
Epifamily	:	Termitoidea

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[1] Hemimetabolous = insect gradual development through three stages (egg, nymph, and imago), without pupae.

153 living and fossil genera and 6 living and fossil families. Few changes were made at the family, subfamily, and generic level with revisions produced by Krishna (1970), Harris (1971) and Roonwal and Chhotani (1989). The most updated revision of termite classification was given by Krishna et al. (2013a), who published the seven volumes of the *Treatise on the Isoptera of the World*. The termites were classified into 12 families, with 9 living families and 3 fossil families (Table 2.2), with 330 living and fossil genera and about 3105 living and fossil species, worldwide. Of these, three families are commonly found in Southeast Asia, namely, Kalotermitidae, Rhinotermitidae, and Termitidae.

2.2.1 Kalotermitidae

The morphology, nesting behavior, and social organization of the family Kalotermitidae indicate that it is a primitive group of termites (Krishna 1961). They only feed on damp or decay wood and are referred to as dry-wood termites (Eggleton 2000). Kalotermitidae also are believed to be a sister group to the family Rhinotermitidae and Termitidae. This family is believed to have evolved from the family Mastotermitidae. They are considered as an "evolutionary dead end." This family consists of 21 living genera with 456 species (Krishna et al. 2013b).

They have no distinct nest structures (Tho 1992). In this family the galleries excavated within the wood act as nests. They also consist of small colonies. A distinct soldier caste is present in the colony, but there is no true worker caste (Tho 1992). The role of the worker is carried out by the pseudergates or pseudoworkers, which are morphologically still larva-like, but behaviorally more like workers of higher termites. Many species in this family act as pests and cause serious damage

Table 2.2 Termite families and genera

Families	Subfamilies	Number of genera
†Archeorhinotermitidae	–	†1
Archotermopsidae	–	3 and †1
†Cratomastotermitidae	–	†1
Hodotermitidae	–	3
Kalotermitidae	–	21 and †8
Mastotermitidae	–	1 and †7
Rhinotermitidae	6	12 and †1
Serritermitidae	–	2
Stolotermitidae	2	2 and †1
Stylotermitidae	–	1 and †2
Termitidae	8	236 and †1
†Termopsidae	–	†1

The symbol '†' refers to a fossil family or genera
Krishna et al. (2013a)

to the forest product. *Cryptotermes cynocephalus* Light and *C. domesticus* (Haviland) are the examples of two common species found in Malaysian forest (Homathevi 2003).

2.2.2 *Rhinotermitidae*

The Rhinotermitidae is a relatively primitive family (Tho 1992) and referred to as damp-wood termites. The family has a worldwide distribution and is considered to have its origin in the Oriental region (Tho 1992). It is believed to have evolved from an extinct ancestral Hodotermitidae. Moreover, this is the most important family of lower termites in Malaysian forest and commonly found in standing or fallen trunks and limbs (Homathevi 2003). There are six subfamilies identified (Tho 1992; Engel et al. 2011): Coptotermitinae, Heterotermitinae, Psammotermitinae, Termitogetoninae, Stylotermitinae, and Rhinotermitinae (Eggleton 2000), comprising 12 genera with 315 living and 18 fossil species (Krishna et al. 2013c). Several of the common genera found in Malaysian forest are *Heterotermes*, *Coptotermes*, *Termitogeton*, *Prorhinotermes*, *Parrhinotermes*, and *Schedorhinotermes* (Thapa 1981; Tho 1992). *Coptotermes curvignathus* Holmgren is an important pest species found in this family that infests rubber and pine trees (Homathevi 2003).

2.2.3 *Termitidae*

Family Termitidae originated from Rhinotermitidae ancestors and initiated a spectacular adaptive radiation comprising about 75% of termite fauna in the world (Krishna 1970; Wilson 1971). About 85% of the identified Termitidae species are found in Oriental, Ethiopian, and Neotropical zoogeographic regions. In Nearctic and Palaearctic regions, only 17 and 13 species are recorded, respectively. This family is further divided into eight subfamilies, viz., Apicotermitinae, Cubitermitinae, Foraminitermitinae, Macrotermitinae, Nasutitermitinae, Sphaerotermitinae, Syntermitinae, and Termitinae, consisting of 238 living and 1 fossil genus, with 2027 living and 34 fossil species (Krishna et al. 2013d).

2.3 Group of Termites

Other than taxonomic classification, termites are also categorized into general groups, according to the presence or absence of protozoan in the gut, feeding and nesting behaviors, and few other common characteristics.

2.3.1 Lower and Higher Termites

Termites are classified into “lower” termite and “higher” termite, a terminology that refers to their evolutionary level, both as concerns behavior and anatomy. In general, this grouping refers to the symbiotic relationship between termite and protozoans during the digestion process. It is known that digestion in termites is assisted by symbiotic flagellates or symbiotic protists and bacteria living in their gut (Krishna et al. 2013a). This led to their grouping into two categories, which are the “lower” and “higher” termites.

The presence of protists and bacteria is observed in “lower” termites which comprise all the termite families except Termitidae (Carpenter 1989). Presence of symbiotic flagellate protozoans in this group enables the digestion of cellulose in the gut, with the digested food passed on to other colony members by trophallaxis, a transfer process through oral or anal feeding (Mc Gavin 2001).

The family Termitidae is classified as “higher termite” due to the capability to degrade cellulose without symbiotic protists in their gut (Watson and Sewell 1985; Ohkuma 2003). The “higher termites” have a more complex and developed social structure. They also build a more complex and varied nest, compared to “lower” termite (Wheeler 1995).

2.3.2 Feeding Group

Termite foods consist of plant tissues in all stages of decay and also living plants, for certain species. The consumption of plants could be such as standing dead branches, highly decomposed flaky detritus mixed with mineral soil, living shoots and roots, and surface litters of woody twigs, branches, and leaves (Wood 1976; Wardle 1987). Hence, the termites can also be grouped according to their feeding habit and be divided into several types of feeding groups such as wood feeders, soil feeders, litter forages, soil-wood interface feeders, and micro-epiphyte feeders (Eggleton et al. 1997).

Wood feeders feed on wood and woody litters, inclusive of dead branches still attached to trees (Bignell and Eggleton 2000). Termites of this feeding group are the primitive ones (Eggleton et al. 1997). Most “lower” termites are wood feeders. In “higher” termites, wood-feeding species can be found in all subfamilies of Termitidae, except the Apicotermitinae (Bignell and Eggleton 2000). Termite genus *Bulbitermes* is an example of wood feeder (Syaukani and Thompson 2011), although not feeding on living trees but only on dead and decaying woods (Chey 2012).

Another feeding group is the soil feeders, which feed on the upper mineral soil. These types of feeders are only found in Apicotermitinae, Termitinae, and Nasutitermitinae (Bignell and Eggleton 2000). Litter forages, on the other hand, are termites that hunt for leaf litter and small woody items which can be found in different levels of the decaying process. These termites take back the food and store them temporarily in their nest (Eggleton et al. 1997). Examples of litter feeders can be found in the subfamily Macrotermitinae, Apicotermitinae, Termitinae, and Nasutitermitinae (Bignell and Eggleton 2000).

Soil-wood interface feeders feed on highly decayed wood which has turned into friable and soil-like wood. They are also known as "intermediate feeders." They are found only in Termitinae, Apicotermitinae, and Nasutitermitinae (Bignell and Eggleton 2000). Lastly, the micro-epiphyte feeders usually look up for mosses, lichens, or fungi on tree barks as their food source (Eggleton et al. 1997). *Hospitalitermes* in Southeast Asia, *Constrictotermes* in South America, and *Grallatotermes* in East Africa are examples of micro-epiphyte feeders (Bignell and Eggleton 2000).

In addition, according to Krishna (1970), termites also include another feeding group, the grass feeder. These species consume dung and may sometimes scavenge vertebrate corpse and are usually found at savanna and desert. These feeders play an important role in the Northern Australia's savanna ecology by processing larger amount of biomass (Termites 2001). Examples are mainly species from the family Hodotermitidae (Krishna 1970).

2.3.3 Nesting Group

Nest building is a natural behavior, often resulting in species-specific architectural behavior (Emerson 1938). All termite species build a nest to house the colony members and protect them (Bignell and Eggleton 2000). The nests range from simple and small excavations to huge subterranean and epigeal systems (Harris 1957). The nesting behavior of termites can be classified into four different nester groups: arboreal, wood, hypogeal or subterranean, and epigeal (Bignell and Eggleton 2000). This behavior is classified according to their habitat, where termites can be found wherever there is timber, decaying wood, epiphytes, and soil.

Arboreal nesters build tree nests made of carton (Fig. 2.1). The genus *Bulbitermes* is an example of arboreal nester. They live in arboreal "stercoral carton" nest

Fig. 2.1 Arboreal nest of *Bulbitermes sarawakensis*

(Lommen et al. 2004). The nest is rounded or elongated in structure and located on a tree trunk, a branch, or in a bush (Weesner 1965). The termites forage through covered runways or "galleries" which connect the nest to the ground (Bignell and Eggleton 2000; Lommen et al. 2004; Chuah 2005). The runways act as protection for the foraging *Bulbitermes* workers and soldiers, sheltering them from attacks by their main invertebrate enemies such as ants (Lommen et al. 2004; Chuah 2005). Other arboreal nesters can be found in genera *Hospitalitermes*, *Nasutitermes*, and *Microcerotermes*.

Beside arboreal nesters, there are several types of nest which could be found among other termite species. Wood nesters (Fig. 2.2) have been identified in Rhinotermitidae and Termitidae (subfamily Termitinae and Nasutitermitinae), which live in or around standing trees or dead logs, without any connection to soil (Bignell and Eggleton 2000).

Hypogeal or subterranean nesters include termites that build their nest below the ground. The most famous example of this nester is the genus *Apicotermes*. The subterranean nest could grow to the size of a football (Bignell and Eggleton 2000; Noirot and Darlington 2000).

Other than that, epigeal nesters are the colony of termites found on the ground, freestanding, or against the side of trees. In this case the nest is known as mound (Fig. 2.3). The mound could vary widely within a genus (Bignell and Eggleton 2000). *Odontotermes grandiceps* Holmgren, *Macrotermes malaccensis* (Haviland), and *Dicuspiditermes* sp. are the examples of termites that build epigeal nests (Noirot and Darlington 2000).

Fig. 2.2 Wood nest of *Bulbitermes* sp.

Fig. 2.3 Nest of *Dicuspiditermes* sp.

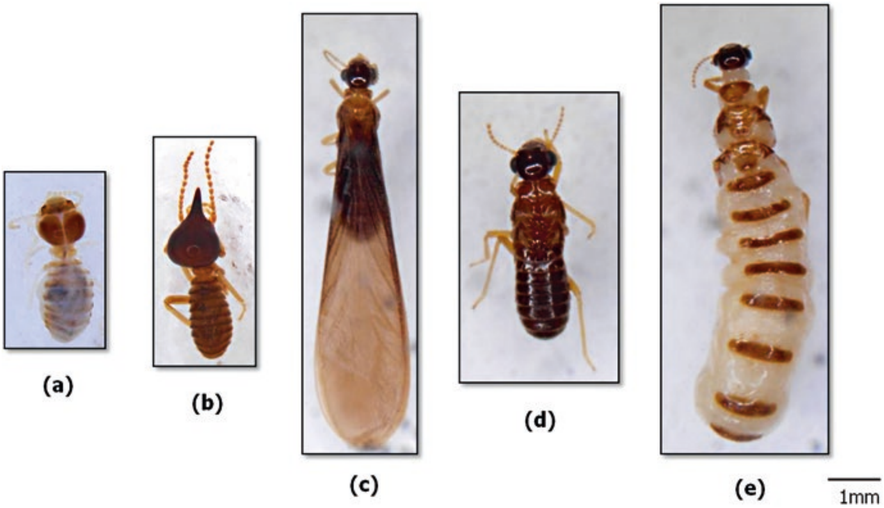

Fig. 2.4 Colony structure of a *Bulbitermes sarawakensis*: (**a**) worker, (**b**) soldier, (**c**) winged reproductive (**d**) king and (**e**) queen

2.4 Identification of Termite Caste

Termites are social insects, like members of the distinct order Hymenoptera such as ants, bees, and social wasps. In general, their social system is formed by three main castes: reproductive (a queen and a king), soldiers, and workers (Fig. 2.4). In addition, there will be a large number of young immature forms in all stages and of all castes (Harris 1957). The number of individuals of each caste varies among species and also depends on the age and size of the colony (Bignell and Eggleton 2000).

2.4.1 Reproductive

Reproductive individuals (also known as alates or royal pair, the king and queen) play an important role. The royal pair can live longer, as long as 50 years (Gibb and Oseto 2006). The king and queen morphology shows wings during their early life, which are lost after dispersing from the original colony (Lewis 1997). They will shed their wings and pair off to search for a suitable harborage to build up a new colony (Ackerman et al. 2009). Figure 2.5 shows the structural morphology of termite imago heads. This structure can be used to identify adult reproductive termites.

2.4.2 Worker

The colony contains high numbers of workers compared to the other castes. The blind workers are also the wingless form of sterile adults. They are also known as helpers or neuter caste (Pearce 1997; Miura et al. 1998), because they give up their

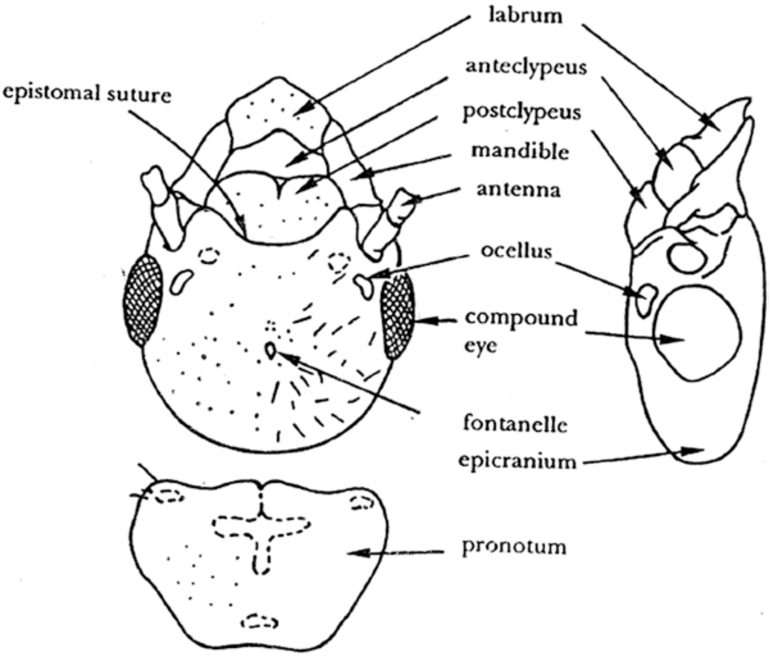

Fig. 2.5 The morphology of termite based on imago head (*Source*: Tho YP; Malayan Forest Records, Forest Research Institute Malaysia, No. 36)

own reproduction to support a number of reproductive individuals. Basically, the workers provide food for the colony, care for the egg-laying queen, and construct new tunnels and chambers (Higashi et al. 2000; Gibb and Oseto 2006). Workers also protect their colony in the absence of soldiers. They use their robust and unspecialized mandibles to attack ants or termites from other colonies, which are their main predators (Noirot and Darlington 2000).

Workers of different termite genera could be identified using mandible characters. The mandible is also useful to differentiate various feeders such as wood, epiphyte, litter, or fungus feeders from soil feeders. Figure 2.6 shows the structure of imago-worker mandibles of soil-feeding termites. The workers and alates have similar mandibles. These have right and left parts which differ in morphology (Fig. 2.6). The left mandible is made up of an apical tooth, a first marginal tooth, a first plus second marginal tooth, a third marginal tooth, a molar tooth, and a molar prominence. The right mandible includes an apical tooth, a first and second marginal tooth, an apical thickening, a molar plate, and a basal notch.

The termite gut structure could also be used to identify the feeding groups (Fig. 2.7). The in situ gut characters and the enteric valve characters can be used to separate the worker caste at a generic level (Ahmad and Akhtar 1981). The in situ gut character (together with the seating of enteric valve) and mandible characters are most suitable for separating genera (especially for the soil-feeding *Capritermes* complex). However, although the enteric valve character is a useful aid for species separation within genera, the use of the enteric valve characters is often limited in small specimen collections.

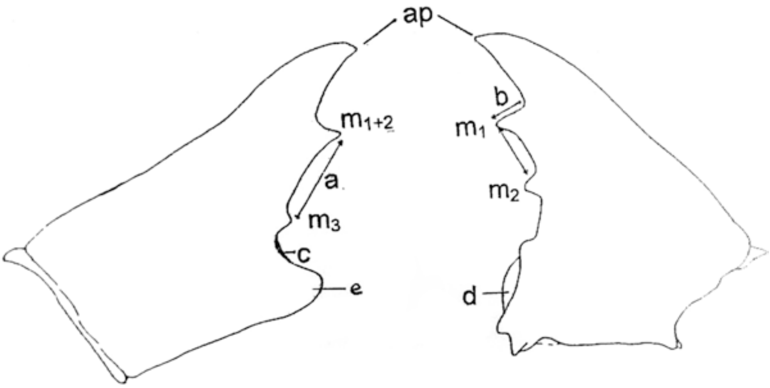

Fig. 2.6 The structure of imago-worker mandibles of soil-feeding termite, left and right: *ap* apical teeth, m_{1+2} fused first plus second left marginal tooth, m_3 third left marginal tooth, m_1 first marginal tooth, m_2 second right marginal tooth, *a* posterior cutting edge, *b* anterior cutting edge, *c* subsidiary tooth, *d* molar prominence, *e* molar plate

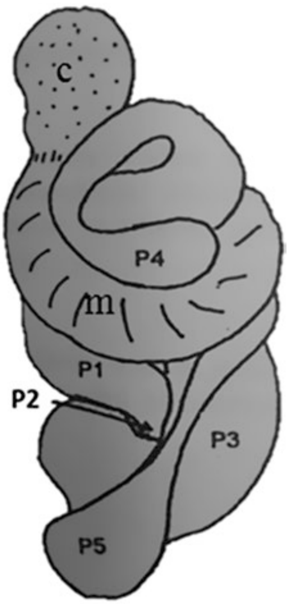

Fig. 2.7 Configuration of the digestive tube in situ, dorsal view: *Termes* spp. *c* crop, *m* mesenteron, *p1* first proctodeal segment, *p2* enteric valve, *p3* third proctodeal segment, *p4* colon, *p5* rectum

2.4.3 Soldier

Termite soldiers are also a wingless form of sterile adults as workers. They usually have stout, triangular, and well-developed mandibles (Harris 1957). In addition, dimorphic soldiers (major and minor soldier) are present in certain termite species, such as in genera *Macrotermes* and *Schedorhinotermes* (Thapa 1981). They play an important role in defending the colony and nest from being attacked by other insects (Gibb and Oseto 2006). They also protect the colony through defensive secretions using the "fontanelle" on their head. In specialized subfamily Nasutitermitinae, the mandibles are replaced with the "nasus," an elongated projection of the "fontanelle" (Tho 1992) (Fig. 2.8).

2.5 Important Asian Termite Pest Species

According to the world termite population, only 10% of their species were identified as pest (Lewis 1997). Wood-feeding subterranean termites are considered as the most destructive insects in the world, because their feeding activity can damage the wooden structures (Hodgson and Roe 2008). This species remains hidden in wood or underground which makes it difficult to find the colony. The estimated number of the pest species is approximately 80 (Grace 2013). Furthermore, some species are closely related to dry-wood termite, Kalotermitidae, and damp-wood species, Termopsidae (Hodgson and Roe 2008).

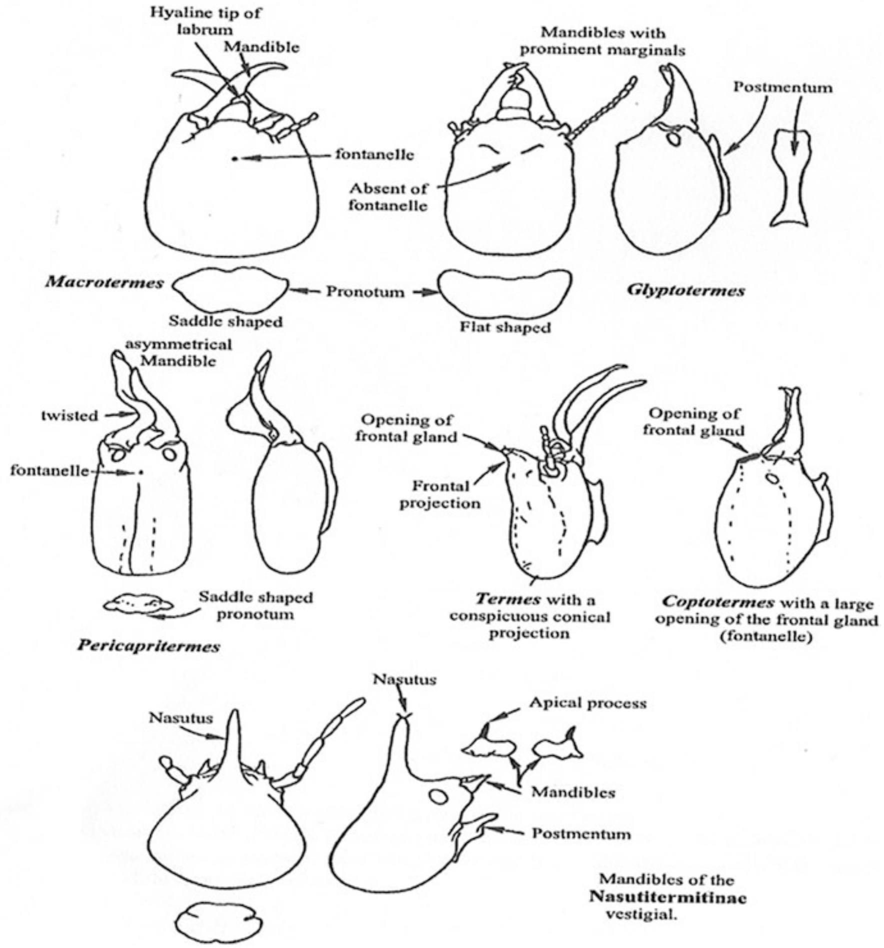

Fig. 2.8 Major characteristics of soldier head (*Source*: Tho YP; Malayan Forest Records, Forest Research Institute Malaysia, No. 36)

Asian pests mainly belong to the family Rhinotermitidae and Termitidae, which consist primarily of pest species of the genus *Coptotermes* (Kirton 2005; Kuswanto et al. 2015). Kuswanto et al. (2015) have concluded that there are five dominant termite species as pests, viz., *Coptotermes* sp., *Macrotermes* sp., S*chedorhinotermes* sp., *Odontotermes* sp., and *Nasutitermes* sp. In Malaysia and Singapore, 12 species of subterranean termites from 7 genera (*Coptotermes*, *Macrotermes*, *Microtermes*, *Globitermes*, *Odontotermes*, *Schedorhinotermes*, and *Microcerotermes*) can be readily found in and around buildings and trees, particularly in suburbia and rural settlements (Chow et al. 2007).

2.5.1 Coptotermes

Coptotermes is one genus closely related with pest (Fig. 2.9). It consists of major pest species causing damage to forest trees and also buildings (Anantharaju et al. 2014; Kuswanto et al. 2015). *Coptotermes* belongs to the family Rhinotermitidae and subfamily Coptotermitinae. There are 67 living and 4 fossil species of *Coptotermes* around the world (Krishna et al. 2013c).

This genus can be identified easily by the soldier head morphology and its behavior toward defense. The soldiers have a unique head shape with an opening (the fontanelle) on the head which looks like a volcano opening. In addition, the soldiers excrete a white fluid from the fontanelle when being disturbed, as a defense mechanism (Bong et al. 2012).

Two major destructive termite pest species in Asia are *Coptotermes gestroi* (Wasmann) known as Asian subterranean termite and *C. formosanus* Shiraki, known as Formosan subterranean termite. These species are native to Asia but have spread to other parts of the world. They look almost similar but can be differentiated under the microscope. The soldiers of *C. gestroi* have much larger head width compared to *C. formosanus* (Hapukotuwa and Grace 2012). The alates of *C. gestroi* have few hairs on the wing, while *C. formosanus* is covered with dense hair on the transparent wings (Li 2009). In the wild, these species can be differentiated by observing their tunnel systems (Hapukotuwa and Grace 2012). The tunnel of *C. gestroi* is much thinner and highly branched with more spatial dispersion, whereas that of *C. formosanus* is wider and less branched, with lesser spatial dispersion compared to *C. gestroi* (Hapukotuwa and Grace 2012).

Fig. 2.9 Soldiers of *Coptotermes curvignathus*

2.5.2 *Macrotermes*

The genus *Macrotermes* is classified in the family Termitidae and subfamily Macrotermitinae, comprising 59 living and 2 fossil species around the world (Krishna et al. 2013d). The unique characteristic of these species is their mounds. They are also known as fungus growers, due to the cultivation of fungi in their mound.

The species of this genus consist of dimorphic soldier and worker castes referred to as major and minor soldiers or workers. Major soldiers have relatively larger head, with well-developed mandibles compared to minor soldiers (Fig. 2.10). Morphologically, the most distinctive character of this genus is the presence of a hyaline tip at the end of the labrum of the soldier caste (Fig. 2.11).

2.5.3 *Schedorhinotermes*

Schedorhinotermes is classified in the family Rhinotermitidae and subfamily Rhinotermitinae. There are 34 living species of *Schedorhinotermes* in the world. This genus is widely distributed, being found in the Ethiopian, Papuan, Australian,

Fig. 2.10 Major (left) and minor (right) soldier of *Macrotermes*

Fig. 2.11 *Macrotermes gilvus* (major soldier)

and Indo-Malayan region (Tho 1992). It can be differentiated from other genera by their body color, smell of the colony, and presence of dimorphism among soldiers.

The *Schedorhinotermes* soldiers are usually yellowish in color when observed with naked eyes. They release their pigments when preserved in 80% ethanol, which tend to change the clear ethanol into yellowish color. Their colony also has a strong, pungent, and repulsive smell, unpleasant to the human nose. This species also consists of two types of soldier caste (dimorphic), which are the major and minor soldiers. According to Walker (2006), major soldiers have bulbous heads with 5–7 millimeter in size. Minor soldiers have relatively narrow heads and more slender mandibles, with 3–5 millimeter in size.

2.6 Conclusion

Correct identification is important to understand the role of any organism in nature, and this statement is valid for termites too. Morphological characteristics and behavior play a very important role in identifying a termite at the genus or species level. Most of the time, identification to species level can only be done by observing the termite's morphological characters under a microscope. Identification to the genus level can be achieved in the wild using the termite's behavioral characteristics, such as food and nesting habits, foraging, smell, and response toward disturbance (defense mechanisms). It is important to know that not all termites are destructive to human. About 90% of their species are beneficial to human and nature. Identification of termites as pest species will be helpful for management and control, either in urban or plantation areas.

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Chapter 3
Ecology of Termites

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Contents

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Abstract Termites show a structured social life, provisioned with work-based divisions, i.e., king, queen, workers, and soldiers. Ecologically, termites interact with living and nonliving surroundings and deliver a wide range of behaviors. They ensure the survival of colony members by harvesting food, constructing shelters, defending the external and internal threats, and nourishing the new borne progeny in a systematic manner. The termites are equipped with complex characteristics such as chemical communication, morphological and chemical defense, and brood care that enable their successful survival. Besides their usefulness, these tiny insects are a center of attraction because they damage the human economy as wood pests. In this chapter, the ecological role of termites is examined and explored.

Keywords Ecology • Behavior • Defense • Competition • Communication

3.1 Introduction

Termites are one of the most widespread eusocial isopterous insects, bearing complex division of labor within each colony (Roisin 2000; Eggleton 2001). They are a dominant group of invertebrate decomposers of dead organic matter, in tropical and subtropical terrestrial regions (Bignell and Eggleton 2000). Almost all species feed on a range of dead organic plant-derived matter (e.g., dead wood, leaf litter, dry grass, and soil substrates), grouped into five functional groups based on different stages of decay (humification) (Eggleton and Tayasu 2001; Inward et al. 2007; Dahlsjo et al. 2014). Termites spend their entire life in soil or within their food source and die once removed from their protected environment and favorable humidity (Edwards and Mill 1986).

Ecologically, the termites act as "ecosystem engineers" as they influence processes and properties of soil structure and hydrology, nutrient availability, and organic matter decomposition. They affect the productivity and composition of plant communities by tunneling, breakdown and deposition of organic matter (saliva and feces), and soil translocation (Wickings and Grandy 2011; Maynard et al. 2015). Many termite species produce methane and fix atmospheric carbon and nitrogen via symbiotic microorganisms in their hindgut, thus making them available to other soil organisms (Breznak et al. 1973; Brussaard 1997; Holt and Lepage 2000; Bignell 2006; Jouquet et al. 2006; Brune 2010). However, the amount of methane is negligible (between 0.02 and 0.09 Tg year^{-1}) as compared to other non-termite sources (over 600 Tg year^{-1}) (Fraser et al. 1986; Sanderson 1996; Sugimoto et al. 1998; Brune 2010; Maynard et al. 2015). They serve an important ecological role in the decomposition of cellulose materials that cannot be chemically broken down without the presence of the enzyme cellulase secreted by single-celled protozoans (Pearce 1997). Termite can produce up to 2 liters of hydrogen from digesting a single sheet of paper, making them one of the most efficient bioreactors on the planet (Ibrahim and Adebote 2012).

3.2 Termite Types

Primarily, the termites can be divided into three general categories based on their habitat: damp wood, dry wood, and subterranean (Paul and Rueben 2005). Based on microbial association, they have been classified into "lower" (all families except the Termitidae) and "higher" termites (Termitidae; constitute about 75% of all termite species) (Kambhampati and Eggleton 2000). The intestine of lower termites contains protozoa along with many species of bacteria, while higher termites have no protozoa and have a few species of bacteria only (Breznak and Brune 1993). However, on the basis of feeding behavior, the termites were grouped in different assemblies by different scientists. According to Abe (1987, 1990), they are (i) single-piece nesters (wood-feeding termites: feed and nest in the single discrete substrate), (ii) intermediate nesters (wood-feeding termites: nest in their feeding substrate but also forage out from the colony center to find other patches of feeding substrate nearby), and (iii) separate piece nesters that sometimes feed on the transformed fecal products used in nest building (usually woody carton) secondarily, but this material is completely transformed from the original feeding substrate (Eggleton and Tayasu 2001). Donovan et al. (2001) correlated gut content analysis with the morphology and anatomy of worker termites and grouped them as (i) group I, comprising wood-, litter-, and grass-feeding non-Termitidae; (ii) group II, comprising wood, litter, and grass feeders of Termitidae only; (iii) group III, comprising very decayed wood or high organic content soil feeders only of Termitidae; and (iv) group IV, including low organic content soil feeders ("true soil feeders") only of Termitidae (Eggleton and Tayasu 2001).

3.3 Ecology and Behavior

3.3.1 Food and Nutrition

Termites play a vital role in the ecosystem by recycling waste material such as dead wood, feces, plants, and dead tissues at every stage of decomposition (Freymann et al. 2008; De Souza and Brown 2009; Bignell et al. 2011). Many species consume cellulose with the help of protozoans in a specialized midgut (Tokuda et al. 1997). Approximately, 200 different species of microbes are known from their hindgut (Ibrahim and Adebote 2012). Termites are considered to be a major source of atmospheric methane (11%), one of the prime greenhouse gases, produced from the cellulose breakdown (Ritter 2006). To perform this task, they are dependent on symbiotic protozoa (metamonads) and other microbes (flagellate protists) (Slaytor 1992; Ikeda-Ohtsubo and Brune 2009). However, the protozoans (e.g., *Trichonympha*) utilize in turn symbiotic bacteria entrenched on their surfaces for necessary digestive enzymes. Although almost all the higher termites of the Termitidae family are capable of producing their own cellulase enzymes, they mainly bank upon the bacteria. However, according to Machida et al. (2001), the knowledge about the evolution of cellulose digestion by termites is still rudimentary, but it is presumed that the microbiota in termites and cockroaches got derived from their dictyopteran ancestors (Dietrich et al. 2014).

Some termite species feed seasonally, such as *Gnathamitermes tubiformans* that consumes *Aristida longiseta* (red three-awn) during the summer and *Bouteloua gracilis* (blue grama) during spring, autumn, and summer, with a lower consumption in spring as compared to autumn (Allen et al. 1980). The feeding is highly influenced by various atmospheric factors, such as the relative humidity, hardness, and resin and lignin content of the plant substrate. In one study, the dry-wood termite *Cryptotermes brevis* strongly preferred poplar and maple woods to other woods that were generally rejected by the colony. These preferences may in part have represented conditioned or learned behavior (McMahan 1966).

Termites are also well known for fungi cultivations inside their colonies (fungiculture). They garden specialized fungi (*Termitomyces* spp.) using the excrement of the colony members as a nourishment. Since the wood is not easily digested, the fungi cultivated inside these termite nests infect the wood before consumption, making it easier to digest. Additionally, these fungi provide a noble amount of protein. The spores of the consumed fungi pass undamaged via the termites' intestine and complete their life cycle by germinating on fresh excretions (Aanen et al. 2002; Mueller and Gerardo 2002). On the other hand, higher termites consume a wide range of food substrates such as humus, feces of other organisms, grass, leaves, and roots (Radek 1999).

3.3.2 Movement and Food Searching

Being eusocial insects, the food collection (foraging) remains an utmost need for the survival of other less or non-moving members. As workers and soldiers lack wings and the winged members use their wings for short time, the movement largely relies on legs (Bignell et al. 2011).

Termites exhibit two types of foraging behaviors: some species forage within the inhabited wood structures, while others harvest their surroundings (Traniello and Leuthold 2000). Usually, most of the workers avoid foraging in open and unprotected areas, as they congregate linear and make runways and sheetings, to escape predation (Bignell et al. 2011). Subterranean termites build tunnels and galleries to search and harvest food. In case of abundantly available food sources, workers recruit additional nest fellows by depositing a phagostimulant pheromone that acts as an attractant for other workers (Reinhard and Kaib 2001). During the course of foraging, workers use semiochemicals for communication (Costa-Leonardo and Haifig 2013), whereas workers outside of their nest release trail of pheromones (a secretion of sternal glands) to guide members between food and colonies (Costa-Leonardo 2006). In some species (e.g., *Nasutitermes costalis*), there is a highly specialized foraging, arranged in three phases. At first step, the soldiers detect an area with sufficient food, followed by informing the soldiers which results in the buildup of a small army. In a second step, the workers congregate in large proportions at the detected site. At the third and final step, the number of soldiers decreases from the site and that of workers increases, as they ultimately harvest the available food for the colony (Traniello and Busher 1985). The weak and mislead workers may use Levy flights (an improved strategy) for finding the foraging site and fellow members (Miramontes et al. 2014).

3.4 Habitation and Nesting

Generally, termite nesting is characterized by their social organization, diet, biology, and environmental factors. Being either wood dwellers or soil dwellers, the nests can be broadly classified in subterranean (belowground), epigeal (above and below the soil surface), and arboreal (aboveground) (Bignell et al. 2011). Earlier, Noirot (1970) classified the nesting in four categories, viz., within wood, underground, on the soil surface, and arboreal. The epigeal mounds are constructed by earth and mud (Noirot and Darlington 2000). Nesting (an organo-mineral structure) acts as shelter and protection against harsh environmental variability and predation risk. Underground colonies are more common, compared to mounds and multifunctional nests. In arboreal nesting, termite colonies are connected to the soil surface through covered galleries, facilitating hidden movement for workers and soldiers to and from foraging sites. The height above the ground is an important factor in nesting site selection (Merritt and Starr 2010).

Along with partly digested plant material and soil, termites use their own feces, having almost all properties of a construction material (Eggleton et al. 1996). Members of subfamily Apicotermitinae dwell only inside subterranean tunnels (Eggleton et al. 1996), while other termites make tunnels inside the wood in which they live and feed. The arboreal nests built from fecal elements and wood are usually weak; thus colony members always adorn counterattack strategies in case of invasion (DeVisse et al. 2008). Members of family Rhinotermitidae live and consume partially buried wood in an extensive gallery system and do not build mounds (Grace 1989). The nest construction is organized through a stepwise series of actions, beginning with material (different particles) collection, followed by mixing and cementing with the help of salivary secretions (Howse 1970; Lopez-Hernandez et al. 2006). The termite modifies the clay mineral composition of these soils and increases the soil organic matter content in order to build the nest (Jouquet et al. 2002). An architectural extension of the colony, known as polycalism, is also reported in subterranean termites (e.g., *Apicotermes* and *Trinervitermes*). It is a multiple nesting (polycalic nesting) connected by subterranean chambers (Choe and Crespi 1997). This nesting practice is apparently not common in mound-building species except in few species of *Nasutitermes* (Roisin and Pasteels 1986).

The nesting structures protruding above the earth ground are viewed as mounds (Eggleton et al. 1996), mainly constructed by the deposition of clay particles, organic carbon, and the saliva or secretions of the termites themselves and regarded as stronger as compared to nests (DeVisse et al. 2008; Sujada et al. 2014). The mounds made of clay are relatively more susceptible to continuous rainfall (may lead to erosion) than those made of fecal material along with partially digested plant material (arboreal) (Eggleton et al. 1996). Members of the genus *Macrotermes* are special mound builders, known to construct most complex and largest mounds (8–9m in height) with chimneys, pinnacles, and ridges. This capacity is followed by that of *Amitermes meridionalis* (3–4m in height) (Krishna 2016). The termites of genus *Cubitermes* construct tunnels narrow enough to be blocked by the soldiers in case of external invasion. These points are strong zones of the termite mound (Vane et al. 2013). The royal chambers of the queen and king are highly protected areas, which are the last line of defense (DeVisse et al. 2008).

Certain species of termites construct earthen tubes (shelter tubes) on erected structures and walls using soil and faeces during high relative humidity (Jacklyn and Munro 2002). These tubes aimed at safety against the predation risks and detected movement (Grigg 1973; Jacklyn and Munro 2002). The size of these long tubes is determined by the amount of food to be transported (Grigg 1973).

3.5 Defense

Communication is an essential tool for coordination and defense of a colony. Termites are primarily dependent on alarm pheromones to defend a colony (Costa-Leonardo and Haifig 2013). In a situation when the nest is breached or attacked by predators, the termite secretes the alarm pheromones. In case of fungal infection, the infected individuals release vibrational signals to save other nestmates (Rosengaus et al. 1999). Intense body jerking and secretion of fluids from the frontal gland and defecating feces containing alarm pheromones are additional means of termite defense (Wilson and Clark 1977; Costa-Leonardo and Haifig 2013).

The soldiers of some species create blockage at the opening point of the tunnels to prevent the entry of predators inside the colony and rupture themselves deliberately as an act of defense (Belbin 2013). If the size of intrusion from a breach is wider than the soldier's head, the soldiers form a structure similar to an "ancient army phalanx" and defend the colony from the intruders (Wilson 2014).

Any invasion or breach of colony or mound is a cause for alarm for the termites. During the emergency (at the time of breach), the soldier termites bang their heads apparently to create panic and to attract and recruit soldiers and additional workers to repair any breach. Furthermore, an alarmed soldier bumps into other unalarmed termites which is a signal for others to leave pheromone trails to the required area (Krishna 2016).

There is a specialized caste of soldiers in subfamily Nasutitermitinae (e.g., nasutes) which are able to ooze noxious liquids for defense through their hornlike frontal projection (Miura and Mutsumoto 2000). The liquid released is composed of a number of monoterpene hydrocarbon solvents (Miura and Matsumoto 2000). These nasutes are mandibular modifications, as the result of a long-term evolution that selected for dependence on other workers for feeding (Prestwich 1982).

Soldiers of the species *Globitermes sulphureus* commit suicide by autothysis – rupturing a large gland just beneath the surface of their cuticles. The thick, yellow fluid in the gland becomes very sticky on contact with the air, entangling ants or other insects which are trying to invade the nest (Prestwich and Chen 1981; Ross 2007). Another termite, *Neocapritermes taracua*, also engages in suicidal defense. Workers physically unable to use their mandibles while in a fight form a pouch full of chemicals and then deliberately rupture themselves, releasing toxic chemicals that paralyze and kill their enemies (Bordereau et al. 1997). The soldiers of the neotropical family Serritermitidae have a defense strategy which involves front gland autothysis, with the body rupturing between the head and abdomen. When soldiers guarding nest entrances are attacked by intruders, they engage in autothysis, creating a block that denies entry to any attacker (Sobotnik et al. 2012).

Workers use different strategies to deal with their dead, including burying, cannibalism, and avoiding a corpse altogether (Su 2005; Sobotnik et al. 2010; Ulyshen and Shelton 2011). To avoid pathogens, termites occasionally engage in necrophoresis, in which a nestmate will carry away a corpse from the colony to dispose of it elsewhere. The use of a particular strategy depends on the nature of the corpse a worker is dealing with (i.e., the age of the carcass) (Sun et al. 2013). Darlington (1982) opined that there may be "cemetery pits" for the burial of dead bodies.

3.6 Competition

Wherever two populations coexist, a competition always exists. These competitions result in fights causing mortality for both sides. These fights may be territorial, agonistic behavior, or food oriented (Polizzi and Forschler 1998; Jost et al. 2012). In case of fights for food, some of the termites deliberately block passages to prevent other termites from entering the site when they encounter the opponent (Cornelius and Osbrink 2010; Costa-Leonardo and Haifig 2013). In this event of passage blocking, some termites (e.g., *Coptotermes formosanus*) may confront physically. While other members of same species squeeze themselves very tightly in foraging tunnels to the extent they die. This phenomenon successfully blocks the passage and is called as "suicide cramming," known in *Coptotermes formosanus* (Messenger and Su 2005). The conclusion of such blockage is always not a confrontation. For example, the colonies of *Macrotermes bellicosus* and *Macrotermes subhyalinus* did not show violent behavior even after they blocked the passage for each other (Jmhasly and Leuthold 1999). Another competition is known among the reproductive termite castes (e.g., between queens). Here, a reproductive individual befalls to become the dominant queen in the absence of primary reproductives. This agonistic confrontation leads to the elimination of all other members including the other queen except the king. The proven dominant queen takes over the colony with the king (Korb et al. 2009). Sometimes termites and ants compete each other for nesting space (Mathew et al. 2005).

3.7 Communication

All population members always communicate to fulfill their needs, for example, foraging, competition, and fighting, locating mates for reproduction, building the nests, recognition of nestmates, nuptial flight, and defense (Costa-Leonardo and Haifig 2010). Being blind, most termites depend on chemical, mechanical, and pheromonal cues for communication (Table 3.1) (Costa-Leonardo and Haifig 2010). Attenuation (of signals) is the most common tool for interspecific communication in termites. The chemical communication involves a number of pheromones, such as contact pheromones, alarm pheromones, trail pheromones, and sex pheromones secreted from various glands (Costa-Leonardo and Haifig 2010). During the foraging, termites always move in columns and keep excreting the fecal pellets deliberately. These fecal pellets serve as recognition source for the following and returning workers. The pheromones on these fecal deposits left by the workers are perceived by other nestmates employing olfactory receptors (Krishna 2015). The mechanical communication in termites involves mechanical cues, vibrations, and physical contact (Costa-Leonardo and Haifig 2013; Krishna 2015). Primarily, these signals are meant to evaluate the food source or alarm the colony in state of emergency (Evans et al. 2007; Costa-Leonardo and Haifig 2013).

Termites also use chemical communication in recognizing their nest fellows from intruders. The chemicals released from the cuticle (composed of hydrocarbons) enable termite recognition (Richard and Hunt 2013). According to Dronnet et al. (2006), each colony can be differentiated based on their distinct odor that varies in accordance to their diet composition, colony bacteria, and environmental factors.

3.8 Relationship with Other Organisms

Termites are associated with several living beings in complex and interesting manners. For example, the workers of Japanese termite *Reticulitermes speratus* pile up the eggs laid by the colony reproductive as to take care of them. To avoid any danger of predation or theft, they harbor brown fungal balls (*Fibularhizoctonia* sp.) with their eggs (Matsuura et al. 2000). These small brown balls, often referred to as termite balls (Neoh et al. 2012), perfectly mimic the termite eggs by producing cellulose-digesting enzyme known as glucosidases (Matsuura 2006). The mimic similarity can also be seen between *Reticulitermes* and *Trichopsenius* beetles, sharing common cuticular hydrocarbons (Matsuura et al. 2009).

As a result of interaction with ants, termites become soft preys. For example, the ant subfamily Ponerinae (e.g., *Platythyrea conradti* and *Formica nigra*) captures termite workers and soldiers defending their nest entrances. The ant workers bent on their mid and hind legs and bring upper body forward and down to crouch and fold antennae of termites backward. The termites guarding at the entrance face the

Table 3.1 Pheromones in termites and associated gland

Pheromone	Secretion source	Genus	Family	References
Trail	Sternal glands	*Nasutitermes,* *Constrictotermes,* *Trinervitermes*	Termitidae	Costa-Leonardo et al. (2009), Sillam-Dusses et al. (2006)
	Sternal glands	*Prorhinotermes*	Rhinotermitidae	
	Sternal glands	*Kalotermes,* *Neotermes,* *Postelectrotermes*	Kalotermitidae	
	Sternal glands	*Hodotermes*	Hodotermitidae	
	Sternal glands	*Stolotermes*	Termopsidae	
	Sternal glands	*Mastotermes*	Mastotermitidae	
Sex	Sternal glands	*Pseudacanthotermes*	Termitidae	Costa-Leonardo et al. (2009)
	Posterior sternal glands	*Macrotermes*		
	Sternal glands/ posterior sternal glands	*Ancistrotermes*		
	Tergal glands	*Coptotermes*	Rhinotermitidae	
	Posterior sternal glands	*Reticulitermes*		
	Posterior sternal glands	*Prorhinotermes*		
	Sternal glands/ posterior sternal glands	*Kalotermes*	Kalotermitidae	
	Sternal glands	*Hodotermes*	Hodotermitidae	
	Sternal glands	*Zootermopsis*	Termopsidae	
	Posterior sternal glands	*Mastotermes*	Mastotermitidae	
Aggregation and phagostimulating pheromones	Salivary glands	*Coptotermes*	Rhinotermitidae	Costa-Leonardo et al. (2009)
Alarm and defense pheromones	Frontal glands	*Nasutitermes*	Termitidae	Costa-Leonardo et al. (2009), Prestwich (1984), Sobotnik et al. (2008)
		Armitermes		
	Frontal glands	*Prorhinotermes*	Rhinotermitidae	
Autothysis/suicidal altruism	Frontal glands	*Serritermes*	Serritermitidae	Costa-Leonardo et al. (2009)
	Dermal glands (located between the meta-thorax and first abdominal segment)	*Ruptitermes*	Termitidae	

crouching get folded to their backs and their legs batting the air. During the attack on termites, these ants release a volatile secretion from mandibular gland. Some species of ant are known to capture termites to use as a fresh food source later on, rather than killing them (Watson 1973; Dejean 2011). Some ant species are reported to steal the eggs or nymphs of termites (Korb et al. 2009). In addition, *Megaponera analis* and species of subfamily Dorylinae are some other termite-attacking ants (Forbes 1878; Korb et al. 2009). However, some ants share space with termites without any confrontation. Further, some ants (e.g., *Azteca*) and termites (e.g., *Nasutitermes corniger*) are known for joint defense against predators (Darlington 1985). This possible coexistence (termitophily) is due to the wide geographic occurrence of *Nasutitermes* and protection of ants from floods (Santos et al. 2010; Coty et al. 2014). Vice versa, some termite species are also reported to sustain with ants (Jaffe et al. 1995). Some species of beetles, caterpillars, and flies including millipedes are other termitophiles sharing the same hosts. Some birds, lizards, snakes, and scorpions prefer termite mound for their shelter and to avoid temperature fluctuation (Krishna 2016). Termites are also flower visitors and thus potential pollinators of many flowering plants (Trager 1991; Cingel 2001) such as *Rhizanthella gardneri* that only depends on termite workers for pollination (Trager 1991).

3.9 Natural Enemies

In an ecosystem, there always exists a food web mingled with hunters and prey. The termites are also subject to predation and parasitism or threatened by other natural enemies.

3.9.1 Predators

A wide range of predators is known to feed on termites. As much as 65 birds and 19 mammals are recorded predators on one termite species alone (e.g., *Hodotermes mossambicus*) (Kok and Hewitt 1990). Exploring the list of predators, we find frogs, toads, lizards, scorpions, spiders, centipedes, crickets, dragonflies, and cockroaches, including some bee species used to feed on termites (Dean and Milton 1995; Reagan and Waide 1996; Wade 2002). Among the listed predators, spiders of the family Ammoxenidae are specialists (Choe and Crespi 1997; Bignell et al. 2011; Bardgett et al. 2013). The ants are also one of the greatest natural enemies of termites (Holldobler and Wilson 1990; Culliney and Grace 2000). Ants of the genus *Megaponera* are strictly termitophagous (termite feeders) that invade the colonies and hunt them for several hours (Levieux 1966; Lepage 1981). Similarly, *Paltothyreus tarsatus* is another termite colony invader which stacks multiple termites in its mandibles and carries them to its niches (Holldobler and Wilson 1990). The ant species, *Tetramorium uelense*, is also a specialized predator that feeds on small termites in an unusual manner. They recruit a batch of up to 30 workers at site of termite congregation and kill them by immobilizing them with their stinger (Longhurst et al. 1979). Another ant, *Eurhopalothrix heliscata*, uses a unique technique to hunt the termites in rotting wood, housing colonies. They press themselves to get in constricted spaces and hunt their prey by beading them in their sharp mandibles (Holldobler and Wilson 1990). Some ant species (e.g., *Centromyrmex* and *Iridomyrmex*) are known to nest inside the termite colonies or mounds and gradually feed on the nestmate termites. Except predation, there is no apparent relationship between each other (Shattuck and Heterick 2011). Other termitophagous genera include *Leptogenys*, *Cylindromyrmex*, *Acanthostichus*, *Camponotus*, *Solenopsis*, *Crematogaster*, *Pachycondyla*, *Rhytidoponera*, *Wasmannia*, *Ophthalmopone*, and *Odontomachus* (Traniello 1981; Holldobler and Wilson 1990; Abe et al. 2000). In addition, a number of hymenopterous wasps (e.g., *Polybia lepeletier* and *Angiopolybia araujo*) are also known to invade mounds (Mill 1983).

Termites often overcome this predation. However, pangolins, foxes, anteaters, aardwolves, aardvarks, bears, bilbies, bats, many birds, echidnas, galagos, numbats, and mice are renowned threats for the whole colonies and mounds (Wilson and Clark 1977; Lavelle and Spain 2001; Bardgett et al. 2013; Abe et al. 2000). Bear breaks the mounds to consume the termites, while chimpanzees (e.g., *Paranthropus robustus*) insert wood sticks inside the colonies and mounds and utilize the defense aggression of termites to get them on the sticks to feed (Errico and Backwell 2009). The termites are the primary food for the aardwolves; it can consume thousands of termites at a time by using its long, sticky tongue. It locates its food by sound and also by detecting the scent secreted by the soldiers (Richardson and Bearder 1984; Mills and Harvey 2001).

3.9.2 Insect and Microbial Parasites

Parasitism in termites is a less recorded phenomenon as compared to predation (Schmid-Hempel 1998). However, some dipteran flies (e.g., *Diplonevra mortimeri* and *D. watsoni*) (Disney 2008), mites (e.g., *Pyemotes*), and nematodes (e.g., *Mermis*, *Diplogaster aerivora*, and *Harteria gallinarum*) infect termites. Parasitism often forces the whole colony to migrate to another location (Schmid-Hempel 1998). Some fungal pathogens, especially nonhost-specific (e.g., *Aspergillus nomius* and *Metarhizium anisopliae*), however, impose greater threats to the colonies, and their infection at a large scale may devastate the colony (Weiser and Hrdy 2009; Chouvenc et al. 2012). The source of infection is believed to be a direct physical contact (Schmid-Hempel 1998). The infection by *M. anisopliae* and *A. nomius* weakens the immune system of a termite colony under great stress (Chouvenc et al. 2012). Over 40 species of fungi have been found associated with a single termite species (Zoberi and Grace 1990). In addition, some pathogenic viruses, for example, *Entomopoxvirinae* and the nuclear polyhedrosis virus, are known to infect the colonies (Al-Fazairy and Hassan 2011; Chouvenc et al. 2013). Also, a total of 118 actinobacterial isolates were collected (Sujada et al. 2014) from the three types of nests (mound, carton, and subterranean nests).

3.10 Human Association

3.10.1 As Pests

In general, termites feed on dead or live plant materials like wood and leaf litter, soil or animal dung, and roots of healthy plants. Approximately, 10% of species are economically important as pests (Robert 1987). The dry-wood termites infect wooden structures such as windows, doors, furniture, etc., while the damp-wood species infest the material only exposed to rainfall, moisture, or soil, e.g., timber in tropical, subtropical, and other regions (Hadlington 1996). Considering protection from environmental risks, the concealed life of termites pays an additional benefit of being undetected until the substrate gets disturbed by external sources (Kahn and Easton 2010). The genus *Coptotermes* consists of a number of pest species known to cause severe damage (Hadlington 1996) (Table 3.2).

Table 3.2 Some termite species and their host plants

Species	Host	Reference
Hypotermes obscuriceps	Leaf litter	Chhillar et al. (2006)
Macrotermes convulsionarius	Leaf litter/soil	
Odontotermes anamallensis	Dead wood and leaf litter	
Odontotermes brunneus	Dead wood and leaf litter	
Odontotermes globicola	Dead wood and leaf litter	
Odontotermes obesus	Wheat, cotton, sugarcane, and castor plants	
Microtermes obesi	Wheat	
Microtermes obesi	Wood and litter feeder	
Microcerotermes fletcheri	Dead/live wood	
Trinervitermes biformis	Soil and grass	
Neotermes assmuthi	Dead wood	
Coptotermes formosanus	Neem tree	
Coptotermes heimi	Dead wood, wheat, and sugarcane	
Macrotermes gilvus, *Heterotermes philippinensis*, *Coptotermes formusanus*	Rice	Pathak and Khan (1994)
Microtermes thoracaJis	Groundnut	
Odontotermes obesus	Oil seeds	
Microtermes obesi, *Odontotermes obesus*	Maize	Reddy et al. (1994)
Macrotermes sibhyalinus	Cassava	Faye et al. (2014)
Reticulitermes flavipes	Sweet potato	Fleming (2009)
Macrotermes subhyalinus, *M. adschaggae*	Pepper	Ibrahim and Demisse (2013)
Odontotermes wallonensis, *O. obesus*, and *O. horni*	Neem, mango, eucalyptus, acacia, and tamarind	Veeresh et al. (1989)
Amitermes truncatidens, *Macrotermes falciger*	Mushroom	Sileshi et al. (2009)

Dry-wood termites are known to invade housing structures and thrive well in warm climates. The human commerce assists termites for movement to another place, even countries (Hadlington 1996). Some species (e.g., *Cryptotermes brevis*) are invasive in many countries (e.g., West Indies and Australia) and can survive in warm structures, though in cold regions (Heather 1971; Hadlington 1996; Su and Scheffrahn 2000). In addition to the attacks on buildings, termites also damage man-made fabrics (textile materials), plastics (polytene, polyvinyl chloride), and some metal foils (Howse 1970). In India, termites were reported to have consumed more than $220,000 worth of currency notes (Ibrahim and Adebote 2012).

The economic losses caused by termites for Malaysia, India, Australia, China, Japan, and the United States were 10, 35, 100, 375, 800, and 1000 million US dollars, respectively (Ghaly and Adwards 2011). According to Tsunoda (2005), more than 50% of Japanese housing is constructed of woods, vulnerable to termite damage. Grace et al. (1991) summarized various feasible control tactics. Ghaly and Adwards (2011) gave a detail account on preventive housing methods.

Termite mound materials, which are very fine, can be made hard and used in making roads, tennis courts, and bricks for building and also used as a source of pottery clay (Edwards and Mill 1986; Su and Scheffrahn 2000).

3.10.2 As Food

There are 43 termite species serving as food for mankind and livestock across the globe (Flores 2010). Termites are indeed consumed by people in many different cultures around the world. In Africa, the tribes harvest the alates, rich in fat and protein. The queens are regarded as highly delicious and hunted at first followed by the soldiers (Figueiredo et al. 2015). The cooked termites are famous for their pleasant taste (e.g., nuts-like flavor) (Su and Scheffrahn 1990). The less developed nations facing malnutrition are known to harvest the termites as food for the enrichment of their diets with protein. However, this termite food managed to attract the developed nations, recently (Flores 2010).

Along with Africa, Asia, Australia, and North and South America are the other termite-consuming countries (Nyakupfuka 2013). In Kenya, Tanzania, Zambia, Zimbabwe, and South Africa, the termites are harvested from large mounds (Knudsen 2002; Geissler 2011) (see Chap. 11 for more details). Nchito et al. (2004) opined that the termites are highly suitable as food in space farming (cultivation of crops for food and other materials in space or on off-Earth objects), suggesting they can be used in biological waste management for conversion into protein-rich consumable products for humans. The material of the termite mound is rich in mineral salts and thus eaten by the primitive tribes and also used as chicken feed (Howse 1970). Besides protein (36.0%), the presence of other nutrients such as ash (6.42%) and fat (44.40%) with 560 calories per 100 g caloric value of cooked flying termites enhances their nutritional importance (Harris 1970).

Certain species of termites (e.g., *Nasutitermes macrocephalus*) are traditional therapeutic resource to cure asthma, hoarseness, and sinusitis in Brazil. In Nigeria, *Macrotermes nigeriensis* is in use to treat wounds and sickness of pregnant women and as a charm for spiritual protection. Additionally, some peptides like espinigerine and termicine have been isolated from *Pseudocanthotermes spiniger*, exhibiting antifungal and antibacterial activities (Figueiredo et al. 2015).

3.10.3 In Agriculture

Termites are highly destructive and polyphagous pests of crop plants, which damage green foliage, seedlings, wood, fibers including household cellulose-based materials, and postharvest stored products (Upadhyay 2013). Most of the pest species are able to reduce yields significantly, and the crop losses may exceed over 100% in regions such as East Africa and North Asia (Saathoff et al. 2002). Usually they infest roots, woody tissue, and leaves of eucalyptus, upland rice, and sugarcane. Further, cassava, coffee, cotton, fruit trees, maize, peanuts, soybeans, and vegetables are other hosts of termites (Table 3.2). In African nations, the large mounds make farming activities cumbersome for the farmers (Capinera 2008). Termite-mediated decomposition of standing dead trees and stumps can influence the population dynamics and distribution of birds, bats, mammals, and arthropods including tree seedlings (Harmon et al. 1986; Evans 2011). On the positive side, termites improve the water infiltration by making speedy soaking of rainwater through tunnels in soil, reducing the risk of erosion. This phenomenon is called biological turbation (Katayama et al. 2008). Additionally, termites are beneficial to agriculture, as they are the main agents of decomposition of surface mulches into humus which plays an important role in soil aggregation, allowing aeration and water infiltration, boosting the crop yields, and enriching soil, indirectly (Nhamo 2007). Termites and ants can recolonize untilled land that contains crop stubble, which colonies use for nourishment when they establish their nests. The bioconversion of mulches after rainwater soaking increases the amount of nitrogen in soil, which is a major nutrient for crop production (Mitchell 2002).

3.11 Conclusion

As eusocial isopterous insects, the termites are delicate creatures that may get severely affected by a moisture loss. They build nests and mounds to avoid desiccation as well as the exposure against predation. Cultivation of fungi by termites suffices the additional nutrition along with moisture for the colony. Inside these confinements, they have social divisions, i.e., queen, workers, and soldiers. Termites basically feed on dead materials. The worker caste hunts for the food and harvests it to fulfill the need of colony. The soldiers are responsible to protect the colony members against any intrusion, most of the times at the cost of their lives. The colony royals are the only breeding individuals. The termites show a variety of behaviors like communication, defense, and competition and thus are an important component of the environment.

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Chapter 4
Termite Gut Microbiome

Navodita Maurice and László Erdei

Contents

Abstract Termites depend on their gut microbes for digestion of complex polysaccharides of wood into simpler molecules. Cellulose is a major polymeric carbohydrate present in the wood which is broken down to simpler byproducts through metabolic steps by the hindgut microbes. Termite gut microbes also produce gases during the cellulose degradation process, of which methane is the major product. Gut microbes belong to three major groups, namely, bacteria, archaea and protozoa. They show a mutualistic relationship and typically convert 95% of cellulose into simple sugars within 24 h. More than 200 species of microbes form this community,

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producing different types of wood-busting enzymes, mainly cellulases, cellubiases, hemicellulases, glucosidases and gluconases, during wood degradation. Studies suggest that lower termites utilize both endogenous and protozoal enzymes for cellulose digestion, while higher termites acquire enzymes from their diet instead of protozoal enzymes. Some termite species change their feeding habits with seasonal variations. These affect gut microbes population and therefore are responsible for enhancing their survival under changed environmental conditions.

Keywords Gut • Microbes • Cellulose • Enzymes

4.1 Introduction

Termites are among the most efficacious groups of insects on Earth that colonize most landmasses except Antarctica, with colonies assorting from a couple of hundred to several million individuals (Cranshaw 2013). Lower termites predominantly harbour species of oxymonads, trichomonads and hypermastigote flagellates as symbionts in the paunch of hindgut, that aid in wood ingestion. Higher termites (Termitidae) consist of about 75% of all termite species and show instead low protozoan populations (Sanderson 1996). The symbiotic associations in termites are crucial due to the presence of three groups of microorganisms. These are mainly bacteria, protozoa (inhabiting the hindgut) and fungi cultivated as ‘fungus gardens’ or ‘fungus combs’ in some species (Darlington 1994). Most termite species reside in the tropical, subtropical and warmer temperate zones of the world and subsist on a diet rich in cellulose either in the form of living or dead wood, woody tissue of plants, humus or dung (Higashi and Abe 1997). They, therefore, play an important role as terrestrial decomposers (Brune and Friedrich 2000).

4.2 Termite Gut

The digestive system of termites consists of three main parts: the foregut, midgut and hindgut (Ptacek et al. 2013; Noirot and Noirot-Timothee 1969). Foregut includes the crop and muscular gizzard and contributes in the secretion of digestive enzymes as well as absorption of soluble nutrients. Hindgut also aids in digestion and absorption of nutrients (Breznak 1994). It may be divided into five successive segments, namely: proctodeal segment, enteric valve, paunch (abundant in symbiotic microorganisms), colon and rectum. Enteric valve prevents return of paunch contents back into the midgut or foregut. Malpighian tubules enter the gut at the junction of the midgut and first proctodeal segment, just in front of the proctodeal valve. Some higher termites have an elongated midgut known as the 'mixed segment' or mesenteron, due to prolongation of one of the intestinal tube faces (Fig. 4.1).

The hindgut, being the largest part of the intestinal tract, is anaerobic. Here the symbiotic gut microbes depolymerize cellulose and hemicellulose and ferment resulting carbohydrates into short-chain fatty acids, which are later absorbed and oxidized by the host (Brune and Friedrich 2000) (Fig. 4.2). Guts of termites maintain anoxic conditions due to their steep oxygen gradients at the oxic-anoxic interface, which drives a continuous influx of O_2 into the gut. According to microsensor studies, O_2 can travel at a rate of 50–200 μm in the gut, therefore creating a microoxic periphery around an anoxic centre. In the lower termite *Reticulitermes flavipes,* radiotracer studies show an influx of O_2 through gut epithelium which gets reduced at the periphery of the hindgut (Boga and Brune 2003). The microbe-filled paunch region of lower and higher termites has a microoxic periphery where pH and redox potential undergo significant transitions along the guts anterior to posterior axis (Bignell 1994). However, the paunch region measurements are circumneutral and anoxic with a comparatively low redox potential of −150 to -250 mV. The pH values of hindguts also show neutrality from 6.2 to 7.6, but it can undergo alterations with environment changes (Abe et al. 2000).

Soil-feeding termites exhibit extreme pH changes along the gut axis with pH values as high as 11. This is an evolutionary adaptation to their diets, rich in tannins or other polyphenolic constituents as it prevents precipitation of digestive enzymes and enhances solubility of dietary proteins (Breznak 1994). The high gut alkalinity separates organic nutrients from the organo-mineral aggregates, as soil-feeding ter-

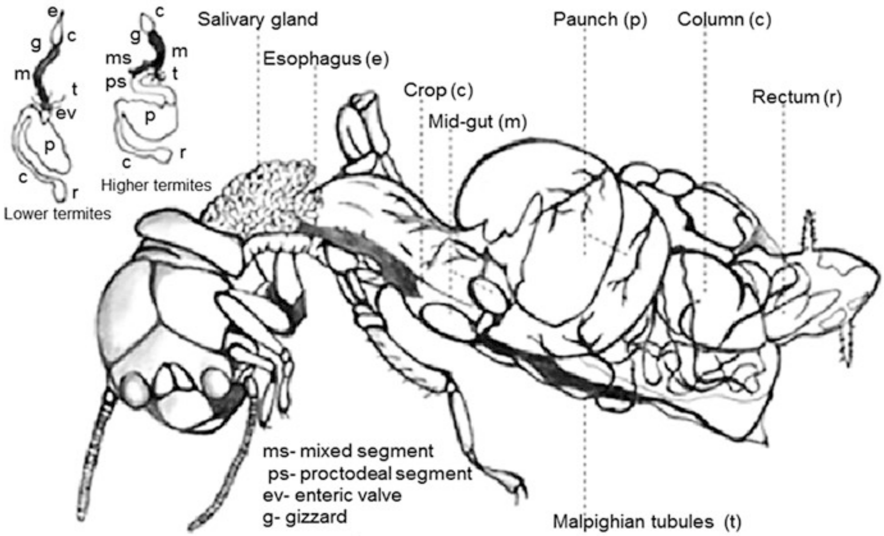

Fig. 4.1 Gut segments of a typical termite (worker) (Ptacek et al. 2013)

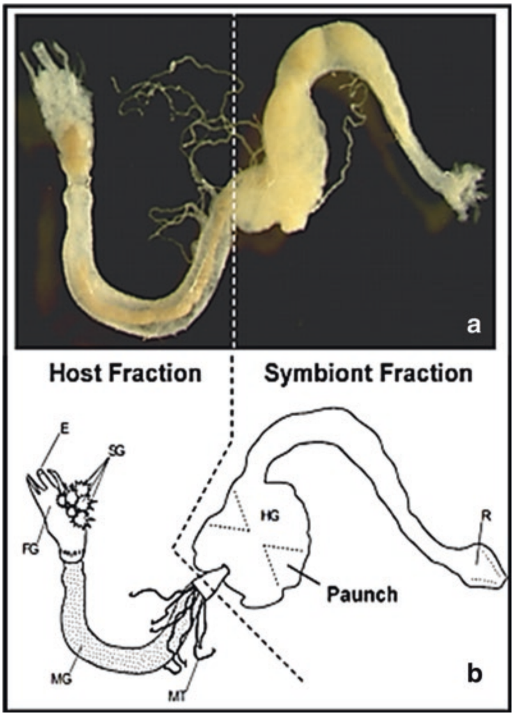

Fig. 4.2 Collaboration of the host and symbionts in lignocellulose digestion in *R. flavipes* (**a**) and different components of the digestive tract (**b**) showing the oesophagus (E), salivary glands (SG), foregut (FG), midgut (MG), Malpighian tubules, (MT) hindgut (HG) and rectum (R) (Scharf et al. 2011)

mite ingests organic matter from soil (Kappler 1999). The guts of the wood-feeding and soil-feeding termites are characterized by noticeable axial dynamics of O_2 and H_2 partial pressure followed by intestinal pH. These differences bring uneven distribution of H_2 production, methanogenesis and reductive acetogenesis by gut microbes (Brune and Friedrich 2000).

Numerous prokaryotes have been isolated in pure culture, and many of them are unique to the termite gut habitat (Graber et al. 2004), including oxygen reduction by anaerobic bacteria, such as lactic acid bacteria (Bauer et al. 2000), homoacetogenic bacteria (Boga and Brune 2003) and sulphate-reducing bacteria (Frohlich et al. 1999). Lower and higher termites differ in their gut microflora. Bacteria and archaea inhabit guts of both higher and lower termites. However, cellulolytic flagellates participating in wood digestion are present only in lower termites (Dietrich et al. 2014) that without them starve (Breznak and Brune 1994). Some higher termites exhibit symbiosis with the fungus *Termitomyces*, or *Bacteroidetes* and *Firmicutes*, while *Spirochaetes* and *Fibrobacteres* outnumber the guts of other higher termites with a cellulose-rich diet (He et al. 2013; Breznak 1994).

The 'mixed segment' present only in higher termites is composed of a mesenteric epithelium which occupies half of the gut wall, while the remaining area is covered by the proctodeal epithelium. The mixed segment has an elevated pH (Brune and Kuhl 1996) along with an alkaline fluid rich in potassium ions. Symbiotic bacteria occupy the mesenteric side of the mixed segment (Tokuda et al. 1997). A peritrophic membrane separates bacteria from wood particles present in the lumen as shown by in situ hybridization and electron microscopy studies. Due to their non-uniform distribution around the peritrophic membrane, the lumen is not a nutritional source for these bacteria. Electron microscopy indicates a close relationship between bacteria and mesenteric epithelium suggesting that symbiotic bacteria utilize some substances secreted by the mesenteric tissue of the mixed segment. Midgut cells are very quickly replaced in cockroaches (Dow 1986) and termites via endocytosis of the neighbouring epithelial cells, which are later digested by phagolysosomes (Yamaoka and Nagatani 1980). Similar phagosomes have been observed throughout the midgut columnar cells, including the mixed segment of *Nasutitermes takasagoensis* where the symbionts trapped among the microvilli of old cells can be endocytosed by young columnar cells and digested along with old cells. Since bacteria cannot pass through the peritrophic membrane, it is believed that they infect termites only when their peritrophic membrane is intact (Tellam et al. 1999). Phylogeny and distribution studies of the symbiotic bacteria dwelling in the mixed segment suggest that these bacteria have a significant role in the termites gut physiology. Microflora of the mixed segments of soil-feeding and wood-feeding termites are different; therefore, it is possible that these symbionts bear a close relationship with the feeding habits, gut physiology and phylogeny of their hosts (Tokuda et al. 2000).

The neutral pH value of the midgut of the wood-eating higher termite *N. nigriceps* increases in the mixed segment and reaches to 10.23 ± 0.46 in the first proctodeal segment, while a decrease in oxygen concentration in the mixed segment occurs, which ultimately becomes zero in the first proctodeal segment (Brune et al. 1995). The space between the gut wall and peritrophic membrane of the mixed segment is termed the ‘ectoperitrophic space’ and is the shelter home for the bacterial species. Cocci and rods have been identified in the wood-eating termite *N. exitiosus* (Czolij et al. 1985), while spirochaetes and actinomycete-like bacteria populate the guts of the soil-feeding termites *Cubitermes severus* and *Procubitermes aburiensis* (Bignell and Eggleton 2000). The symbiotic bacteria present in the mixed segment resemble the *Clostridium* group but differ from the bacteria of wood-eating lower termite *Reticulitermes speratus* (Ohkuma and Kudo 1996) as well as from the clostridia isolated from higher termites (Hethener et al. 1992). However, no low-GC-content Gram-positive bacteria have been yet discovered from the gut of the drywood-eating lower termite *Cryptotermes domesticus* (Kudo et al. 1998). *Clostridium* species are usually obligate anaerobes, while some are facultative anaerobes appearing as rods, short rods or cocci (Rieu-Lesme et al. 1996). Some of them are able to degrade polysaccharides by producing acetone, alcohol, acetate, lactate, CO_2 and hydrogen (Rainey et al. 1996), while others can ferment nitrogenous or lipidic compounds playing, therefore, an important role in the nutritional physiology of termites (Hethener et al. 1992).

4.3 Termite Gut Microbiome

Termite gut unveils one of the most complex microbial communities entailing diverse microbes from the three domains of life (Bacteria, Archaea and Eukarya) (Ohkuma and Kudo 1996). Detritivorous subsocial cockroaches believed as termite ancestors (Inward et al. 2007) can digest wood with the help of cellulolytic flagellates (Engel et al. 2009; Ohkuma et al. 2009). The evolution of termites coincides with three major events associated with dietary diversification and microbial symbiosis: (i) cellulolytic, flagellate protozoa inhabit the hindguts of all five lower termite families except Termitidae, (ii) an ectosymbiotic relationship with basidiomycete fungi in the litter-feeding Macrotermitinae and (iii) independent evolution of soil-feeding behaviour among the three higher termite subfamilies Nasutitermitinae, Apicotermitinae and Termitinae (Ohkuma and Brune 2011). The role of the cellulolytic flagellates in lower termites is well known, but the exact functions of uncultivated bacterial symbionts in digestion, especially in flagellate-lacking higher termites, need further research (Hongoh 2011). Subterranean termites primarily feed on woody tissue containing lignocellulose as their diets are deficient in vitamins and essential components for protein and fat synthesis. These termites produce their own cellulases (Inoue et al. 1997), but in order to meet their nutritional requisites, the association with symbionts becomes crucial and is achieved by coprophagy and trophallaxis (Grimaldi 2001). These symbionts display a mutualistic beneficial relationship by augmenting nutrients and energy to the termites and by gaining a stable food supply as well as protection under the constant gut environment (Nalepa et al. 2001). Each worker termite acquires an initial inoculum of symbionts from the parents or nest mates, right after hatching as well as after each moult (Thorne 1997).

The gut microbiota varies markedly among termite species comprising many unique phylogenetic clusters (Hongoh et al. 2006). The presence of microbes in the guts of cockroaches (Schauer et al. 2012) and termites (Noda et al. 2009) suggests that the bacterial microbiota of both originated from a common dictyopteran ancestor (Dietrich et al. 2014) (Table 4.1). Termites rely predominantly upon the symbiotic protozoa (metamonads) and flagellate protists for cellulose digestion as well as absorption of the end products (Ikeda-Ohtsubo and Brune 2009). Gut protozoa, such as *Trichonympha*, further rely on the symbiotic bacteria rooted on their body surfaces for the production of the necessary digestive enzymes. Termites of the family Termitidae, although able to produce their own cellulases, depend on bacteria as well (Li et al. 2013).

Table 4.1 Microbiota of termite gut

Domain	Genus, Species	Brief description/Function of microbes
Bacteria	*Treponema*	Swim freely in the gut or attached to the protest; acetogenic, carry out acetogenesis
	Bacteroides, *Bacteroides termitidis*	Fermentative, acidogenic; increase N source by recycling uric acid waste
	Desulfovibrio	Sulphate-reducing bacteria; transfer hydrogen as H_2 donor
	Citrobacter, *Citrobacter freundii*, *Enterobacter*, *Enterobacter agglomerans*	Nitrogen-fixing bacteria
	Enterococcus, *Lactococcus*	Lactic acid bacteria
Archaea	*Methanobrevibacter*	Methanogens, associated with protists as symbionts; carry out methanogenesis
Protists	*Trichonympha*, *Mixotricha*, *Dienympha*, *Eucononympha*	Degrade endocytosed cellulose and produce H_2 plus CO_2. Anaerobic, occur on mitochondria in the cells

4.3.1 Bacteria

Microscopic cell counts approximate presence of 10^6 to 10^7 bacteria in comparison with the protozoa ($4 \cdot 10^4$) in the gut of *R. flavipes* where the prokaryote groups principally consist of methanogens (Archaea), *Proteobacteria*, *Actinobacteria*, *Firmicutes*, *Bacteroidetes* and *Spirochaeta* (*Eubacteria*) (O'Brien and Slaytor 1982). Three species of methanogenic Archaea placed in the genus *Methanobrevibacter* have already been cultured from *R. flavipes* gut (Leadbetter et al. 1998). The culture-independent sequencing of archaeal 16S rRNA genes also indicates the presence of methanogens in the gut of *R. speratus* (Shinzato et al. 2001). Some methanogen species are both ecto- and endosymbionts of protozoa (Tokura et al. 2000). Methanogenesis is followed by acetogenesis in the wood-feeding termites and acetogenic bacteria compete with the methanogens for hydrogen (Brauman et al. 1992).

The hindgut of xylophagous lower termite harbours both protozoa and bacteria. However, due to their mutualistic relationship with termites and cellulose-degrading activity, more research has been done on protozoa, although prokaryotes are also important for the termites' survival (Mauldin 1977). The presence of bacteria is necessary for the persistence of protozoa as well as for normal termite nutrition (Breznak 1975). Nitrogen fixation by some bacteria shows a role in nitrogen utilization by termites, as many species exist in intimate physical association with the gut epithelium, thereby reflecting biochemical interactions (Thayer 1976). An anaerobic, cellulolytic actinomycete (*Micromonospora propionici*) from the guts of *Amitermes minimus* was isolated, but it turned out to be of limited importance in situ (Hungate 1946). *Anacanthotermes ahngerianus* and *A. turkestanicus* harbour $1.3 \cdot 10^6$–$4.3 \cdot 10^9$ viable bacterial cells per hindgut, depending on the developmental stage or caste of termite (Husseneder 2010; Krasil'nikov and Satdykov 1970).

The intestinal bacterial microflora of *R. speratus* contains taxa related to the enteric bacteria, such as *Enterobacter*, *Citrobacter*, *Desulfovibrio*, *Treponema*, *Bacteroides* and *Clostridium* which are either strict or facultative anaerobes and have been frequently isolated from animal intestines (Brauman et al. 1992). Apart from *Citrobacter freundii*, *Enterobacter agglomerans*, *Clostridium* and *Desulfovibrio* spp. also partake in nitrogen fixation in several termite species (Fuhrman et al. 1993). Species of *Sporomusa*, *Acetonema* and *Clostridium* act as CO_2-reducing acetogens within the termite guts (Kane and Breznak 1991). *Bacteroides* species (*Bacteroides termitidis*) participates in the uric acid metabolism (Potrikus and Breznak 1980). The termite *Desulfovibrio* cluster points out the presence of significant quantity of the sulphate-reducing bacteria in situ within gut, functioning in interspecies hydrogen (H_2) transfer as H_2 donors by utilizing small organic compounds. These include, for example, pyruvate, lactate and sugar monomers as oxidizable electron donors in comparison to the H_2 acceptors oxidizing sulphur compounds.

Streptococcus sp. occurs as the major bacterial species in several termites (Breznak and Brune 1994). The gut microbes enrich the termites with the required amount of carbon, nitrogen and energy to such an extent that survival of termites becomes almost impossible without them (Brune and Friedrich 2000). A predominance of five bacterial groups, viz., *Cytophaga-Flexibacter-Bacteroides* (CFB) group, low-G + C Gram-positive bacteria, *Proteobacteria*, *Spirochaeta* and the newly discovered ‘termite group I’ (TG I), has been found in many species (Hongoh et al. 2003). However, spirochaetes occur more in the gut of *R. speratus* as compared to the gut contents of *Nasutitermes lujae*, followed by the *Bacteroides*-related, clostridial and TG I clones which form the second most dominant group (Husseneder 2010; Paster et al. 1996).

Spirochaetes comprise a monophyletic group of motile bacteria with a characteristic spiral or wavy shape (Paster et al. 1991) and a coiled or undulate protoplasmic cylinder confined by a cell wall-cytoplasmic membrane complex, containing genomic DNA, ribosomes and other cytoplasmic constituents. An outer membranous sheath surrounds the protoplasmic cylinder. Between the outer sheath and the protoplasmic cylinder one or more periplasmic flagella are present (Canale-Parola 1984), functioning as organelles of motility (Charon et al. 1992). *Spirochaetes* are widely distributed in nature for example, as free-living forms in freshwater, marine and hypersaline waters or associated with invertebrate and vertebrate hosts, through commensalism, mutualism and parasitism. *Spirochaetes* were first documented by Joseph Leidy (1874–1881, 1877) in the hindgut of the eastern subterranean termite, *Termes* (now *Reticulitermes*) *flavipes*. *Spirochaetes* account for up to 50% of all prokaryotes in the hindgut of some termites and about a dozen of different morphological types can be identified on the basis of cell length, width, wavelength and amplitude or pitch (Paster et al. 1996; Leadbetter et al. 1999).

The nucleotide sequence of MDS1clone of the Australian termite, *Mastotermes darwiniensis* (family Mastotermitidae) (Berchtold et al. 1994), *R. speratus* (family Rhinotermitidae) (Ohkuma and Kudo 1996) and *Cryptotermes domesticus* (family Kalotermitidae) (Ohkuma 1998) indicates that the spirochaetes residing within the guts of these species are either anaerobes or microaerophiles (Breznak 1994). Termite gut spirochaetes are placed into two phylogenetic clusters namely *Treponema* clusters I and II. Cluster I contains diverse phylotypes of the gut spirochaetes containing the strains isolated from termite gut, while cluster II is smaller, belonging to the *Treponema bryantii* subgroup.

Spirochaetes can exist freely in the gut fluid or are attached as ectosymbionts on the cell surface of gut protists (Iida et al. 2000). They have specialized attachment sites on the protists as shown by ultrastructural observations (Bloodgood and Fitzharris 1976). *Treponema* strains ZAS-1 and ZAS-2 have been isolated from the dampwood termite *Zootermopsis angusticollis* (family Termopsidae) (Leadbetter et al. 1999; Breznak 2002). Recently, ectosymbiotic spirochaetes (*Treponema* sp. strains ZAS-1 and ZAS-2) associated with *Zootermopsis angusticollis* have been clustered with the major cluster I sequences, with function as H_2 and CO_2 consumers by environment absorbance from inside the protist. The other major ectosymbiotic spirochaetes (cluster II) placed in the *T. bryantii* subgroup can enhance the cellulolytic activity of other microbes (Ohkuma and Kudo 1996). Members of cluster II are ectosymbiotic spirochaetes of oxymonad protists as identified in the termite species *R. speratus*, *Hodotermopsis sjoestedti* and *Neotermes*. However, various species of devescovinid (*Devescovina* sp.), calonymphid and hypermastigote protists (*Holomastigotoides mirabile* in *Coptotermes formosanus*), in addition to the oxymonad protists, also harbour dense populations of ectosymbiotic spirochaetes (Iida et al. 2000).

The unique ultrastructure of spirochaete-protist attachment sites is known for several protists of termites and wood-feeding cockroaches, and two types of attachment structures have been identified in the symbiotic protists of *R. flavipes*, *R. tibialis* and *Cryptocercus punctulatus*. One structure is a narrow nose-like appendage making direct contact with the plasma membrane of the host cell, while the other is the flattened end of the spirochaete in contact with the protistan membrane, with a thick layer of electron dense material. The ectosymbiotic spirochaetes are involved in the maintenance of 'motility symbiosis' (Kitade et al. 1997). The termite gut bacteria are deliberated to be vertically transmitted from generation to generation via proctodeal trophallaxis known for the gut symbiotic protists in lower termites (Inoue et al. 2000). However, horizontal transfer among congeneric termites is also known for the bacterial community profiles of *Microcerotermes* species M1 and M2. Ambient temperature, food quality and humidity also affect variation in bacterial gut microbiota within congeneric termites (Donovan et al. 2004).

Gut epithelium is also an important habitat for the dense colonization of the symbionts. Methanogenic archaea utterly occupy the gut wall of *R. flavipes*, while in other termite species, they are located within some protist cells (Leadbetter and Breznak 1996). The methanogenic species present on the gut wall, as well as within the protists cells in *R. speratus* and *Hodotermopsis sjoestedti*, are phylogenetically different (Tokura et al. 2000). This is due to the radical changes in the physicochemical conditions, especially fluctuations of oxygen and hydrogen partial pressures, found inside the gut (Brune and Friedrich 2000).

Bacterial communities also diversify at the phylum or phylotype levels within the gut wall and gut luminal fractions, where bacteria residing on the gut wall are believed to be more dynamic than those populating the gut lumen (Noda et al. 2003). Divergence index, rarefaction curve and Chao1 richness estimators of biodiversity also confirm that a wide variety of bacteria are able to colonize the gut wall, directly or indirectly. However, the populations on the gut wall are five times lower in comparison to those on the gut luminal fraction (Iida et al. 2000).

Bacterial groups densely colonizing the gut wall fraction include species of *Actinobacteria*, *Bacteroidales*, *Clostridiales* and *Lactococcus.* Many of them are nonmotile species. However, gut lumen shows abundance of highly motile *Spirochaetes* and *Desulfovibrio* species (Wenzel et al. 2003). In order to resist fluid flow within the gut, bacterial symbionts also subordinate with the protists, for example, spirochaetes and TG1 bacteria that form associations with the gut protists. The central part of the gut is anoxic as oxygen penetrates the gut via its wall, thereby maintaining a steep oxygen gradient near the gut wall (Brune and Friedrich 2000). This affects the gut metabolism as already displayed by the isolated lactic acid (Tholen and Brune 1997) or sulphate-reducing bacterial strains (Kuhnigk et al. 1996) highlighting the presence of strict aerobic communities inside the gut (Moriya et al. 2003).

Bacteroidales endosymbionts dominate the gut bacterial community of *C. formosanus* and *Pseudotrichonympha* sp. by living intracellularly within eukaryotic cells, while few *Bacteroidetes* or the *Cytophaga-Flavobacterium-Bacteroides* (CFB) phylum bacteria occur as intracellular endosymbionts of eukaryotic cells (Bandi et al. 1995). Intracellular *Blattabacterium* sp. dwell within the bacteriocytes of fat bodies of cockroaches and *Mastotermes darwiniensis*. Intracellular acanthamoebae bacteria affiliated as *Flavobacterium* or '*Candidatus Amoebophilus asiaticus*' resemble with the endosymbionts of a tick and a whitefly through a novel phylogenetic lineage (Horn et al. 2001).

The ectosymbiotic *Bacteroidales* carry a typical Gram-negative cell wall along with inner and outer membranes. However, endosymbionts have lost the cell wall as they localize within the cytoplasm of the host protist. Ectosymbionts colonizing the protist cell surface are incorporated into vacuoles of the host cytoplasm, as structures required for attachment with the host cell membrane occur in the vacuoles (Stingl et al. 2004).

Endomicrobia (formerly termite group 1) represent a deep branching clade of the uncultivated bacteria of the phylum *Elusimicrobia* with single isolate, *Elusimicrobium minutum* which occurs as intracellular symbiont of termite gut flagellates and transferred vertically. Many genes of *E. proavitum* are highly similar to the closely related '*Candidatus Endomicrobium trichonymphae*' strain Rs-D17 (Brune 2014).

Bacteria of the *Cytophaga/Flexibacter/Bacteroides* (CFB) phylum predominate the guts of *Macrotermes michaelseni*, fungus-cultivating (*Macrotermes gilvus*) (Hongoh et al. 2006), wood-feeding (Ohkuma et al. 2004) and soil-feeding termites (Schmitt-Wagner et al. 2003). Many CFB phylum bacteria are capable of degrading plant fibres and proteins which form the ingredients of the termite diet (Shah 1992). *Proteobacteria*, *Desulfovibrio* sp., *Escherichia hermannii* and E. *senegalensis* also colonize the gut of *M. gilvus* instead of CFB phylum members (Hongoh et al. 2006). *Desulfovibrio* spp. are strict anaerobes partaking in sulphate reduction and nitrogen fixing. Clostridia are also present in the mixed segment of *Nasutitermes takasagoensis* (Shiraki) (Tokuda et al. 2000) and *M. gilvus* (Hongoh et al. 2006) where they degrade polysaccharides and produce acetone, alcohol, acetate, lactate, CO_2 and hydrogen (Chen 1995). However, *Clostridium mayombei* present in the mixed segment of *Cubitermes speciosus* brings about acetogenesis (Kane et al. 1991). The intestinal bacteria in termites aid in the production of short-chain fatty acids from carbohydrates or amino acid synthesis, just like they do in humans (Cummings and Macfarlane 1997).

The *Anaerobaculum-Thermoanarovibrio*, also denoted as the 'Synergistes group', shows coevolution with termites although the exact role of these members in the termite guts is unknown. It is believed that they are anaerobic amino acid degraders participating in the amino acid turnover in natural anaerobic ecosystems (Godon et al. 2005). The 'Synergistes' strains *Aminomonas paucivorans* (Baena et al. 1999a), *Thermoanaerovibrio acidaminovorans* (Baena et al. 1999b), *Dethiosulfovibrio* sp. (Surkov et al. 2001), *Aminobacterium mobile* (Baena et al. 2000) and *Aminobacterium colombiense* (Baena et al. 1998), for example, degrade amino acids, but some strains such as *Thermanaerovibrio velox* (Zavarzina et al. 2000) and *Anaerobaculum* sp. can utilize carbohydrates as well (Rees et al. 1997).

The population of spirochaete-like cells in the gut contents of fungus-cultivating termites is generally low, ranging 2–3% in *Pseudacanthotermes*, 6–10% in *Odontotermes* sp. (Liu et al. 2013), 11–19% in *Ancistrotermes* and 22–29% in *Microtermes* sp. (Makonde et al. 2013).

Firmicutes and *Bacteroidetes*, placed in the *Treponema* I lineage, form the major fraction of the bacterial community in the Macrotermitinae (Dietrich et al. 2014) although their actual is not clear, but several of them resemble isolates from the lower termite hindguts. These species either partake in fermentation of mono- and oligosaccharides by producing acetate and other products or are homoacetogenic (Droge et al. 2008). Uncultured *Treponema* lineages in higher termites can carry out reductive acetogenesis from $H_2 + CO_2$ (Warnecke et al. 2007). Methanogenesis dominates the reductive acetogenesis as hydrogen sink in Macrotermitinae. Therefore, *Treponema* shows a faint representation which is consistent with the reduced acetogenesis observed in the guts of *Macrotermes mulleri*, *Postelectrotermes militaris* and *Pseudacanthotermes spiniger* (Brauman et al. 1992). The reason behind this is, however, unknown (Hongoh 2011). Variation in the microbiotas of Macrotermitinae reflects their ecological differences which is governed by the plant diet and *Termitomyces* association.

Diet shapes the gut communities of wood-feeding termites (Huang et al. 2013), but such variation in the Macrotermitinae is generally not very clearly understood (Hongoh 2010). *Macrotermes* spp., with the exception of *Macrotermes malaccensis*, are primarily leaf litter feeders (Hyodo et al. 2000). *Odontotermes* and *Ancistrotermes* sp. predominantly feed on wood, and *P. militaris* feeds on both leaf litter and wood (Hyodo et al. 2003). The role of *Termitomyces* also varies among different termite hosts (Nobre et al. 2011). Although this needs more attention, some termite species mainly gain access to cellulose via the lignolytic activity of *Termitomyces* (Hyodo et al. 2000). Some species exploit *Termitomyces* as a protein-rich food source (Hyodo et al. 2003), while other species extract cellulases and xylanases from *Termitomyces* for the decomposition of plant substrate (Rouland et al. 1991). Therefore, differences in gut communities among the termite hosts may be the result of specific diets or symbiont functions.

The role of the bacterial community in lignocellulose breakdown in the Macrotermitinae is not fully elucidated. Metagenomic studies suggest their possible contributions in the cellulose digestion in the wood-feeding termites (He et al. 2013). Glycosyl hydrolases showing cellulase activity in the P3 lumen metagenome of the wood-feeding *Nasutitermes* sp. are now taxonomically confined to the phyla *Fibrobacteres* and *Spirochaetes (*Warnecke et al. 2007). These phyla, along with the TG3 phylum, show high abundance in wood-feeding termites of the subfamilies Nasutitermitinae (Mikaelyan et al. 2014) and Termitinae (Dietrich et al. 2014).

4.3.2 Protozoa

The symbiotic associations between termites and their gut microorganisms are continuously under study since the beginning of the century, when earlier work was centred on the intestinal protozoa of lower termites and their role in digestion. Currently more attention is given indeed to the bacterial and archaeal populations, their metabolic activities, structure and function.

Intestinal protozoa provide shelter to the prokaryotes in the hindgut of lower termites by forming intimate associations with them. Previously, it was difficult to obtain protozoan cultures in vitro and maintain pure cultures of prokaryotic symbionts, so only a morphological description of the different associations was known. With advanced molecular biology tools, informations regarding the symbiotic associations between prokaryotes and termite gut flagellates have now become clear.

Symbiotic flagellates exclusively inhabit the lower termites and closely related cockroaches (*Cryptocercus*), whereas higher termites largely harbour prokaryotic microbiota. Molecular phylogeny of termites and *Cryptocercus* clarified that gut protists share a common ancestor (Lo 2003). The beneficial nature of these peculiar symbionts came into light for the first time by the studies of Lespes in 1856 (Leidy 1874–1881), who classified them as parasites, while Cleveland (1926) pointed out that termites cannot live without the gut flagellates. The symbionts heavily populate the hindgut paunch, with a fresh weight that may account for more than 50% of the fresh termite weight (Katzin and Kirby 1939). Phylogenetically, gut flagellates are extremely diverse, and almost 450 distinct species, from about 200 termite species, are into account till date (Yamin 1979).

Termite gut flagellates were earlier considered as primitive, primarily amitochondriate eukaryotes. Recent molecular data indicated that they share two separate eukaryotic lineages and can be placed under three distinct taxa, namely, trichomonads, hypermastigids and oxymonads (Yamin 1979). Phylogenetic studies conducted by 18S rRNA gene sequence analysis confirmed that majority of termite gut flagellates fall within two classes of the phylum Parabasalia, i.e. Trichomonadea and Hypermastigea (Gerbod et al. 2004). On the other hand, the phylogeny of Oxymonadea was under dark for a long time, but comparative sequence analysis indicated that they are a sister taxon of unidentified protists which are now classified in the phylum Loukozoa (Stingl et al. 2005).

Hypermastigea are exclusive termite gut symbionts, while Oxymonadea and Trichomonadea inhabit other habitats as well, such as the intestinal tract or body cavities of other animals, including humans (Cavalier-Smith 2002). Out of the 440 species of amitochondriate protists belonging to *Trichomonadida*, *Hypermastigida* and *Oxymonadida* are exclusively gut symbionts of wood-eating termites (Mastotermitidae, Kalotermitidae, Hodotermitidae, Termopsidae, Rhinotermitidae and Serritermitidae) and the wood-eating roach, *Cryptocercus*.

Bacterial symbionts associate either on the cell surface or in specific cytoplasm regions of the protozoan, as confirmed by morphology-based descriptions. Trichomonads and other amitochondriate protist symbionts of wood-eating termites and *Cryptocercus* can be easily identified by the presence of their motility structures (mastigont) while in Parabasalia (trichomonads, hypermastigids) by the parabasal body (Golgi complex). The key characters include number and arrangement of flagella (undulipodia), presence and shape of accessory structures (e.g. costa and cresta) and arrangement of connected microtubular structures, axostyle and pelta. The parabasal body bears a distinct shape as well as size and can branch or spirally coiled around the axostyle. It is connected to the mastigont in the trichomonads and arranged in multiple copies in the hypermastigids. Every termite species inhabits a characteristic community of gut protists. Therefore, in general the protist species are not restricted to one termite species only (Simpson 2006).

The phylum Parabasalia has a monophyletic but complex assemblage of diverse species of flagellated protists characterized by a unique parabasal apparatus (Golgi complex associated with striated fibres), closed mitosis with an external spindle (cryptopleuromitosis) and anaerobic energy-generating organelles (hydrogenosomes) (Brugerolle 2005). On the basis of their morphological characters, more than 80 genera and 400 parabasalid species are now known (Yamin 1979). Most parabasalids occur in the digestive tract of animal hosts either as commensals, parasites or symbionts, whereas the symbiotic parabasalids present in the gut of termites and wood-eating cockroaches have a key role in cellulose digestion (Brune and Ohkuma 2011). This symbiotic relationship between termites and parabasalids also provides an evidence for the evolution of social behaviour in the hosts and also carries an ecological significance for plant litter decomposition in terrestrial ecosystems (Ohkuma 2003).

Mixotricha paradoxa, a protozoan species with multiple bacterial symbionts living in the gut of the Australian termite species, *Mastotermes darwiniensis*, was first described in 1933 by Australian biologist J.L. Sutherland (Cleveland and Grimstone 1964). *Mixotricha* bears four anterior flagella which are used for steering rather than for locomotion. Locomotion is performed by cilia-like movements of approximately 250,000 hairlike *Treponema* spirochaetes attached to the cell surface. *Mixotricha* also shows the presence of rod-shaped bacterial *Bacteroides*-like species, arranged in an ordered pattern on the cell surface. Both these bacterial types (*Spirochaetes* and *Bacteroides*) are ectosymbionts. Apart from the ectosymbionts, *Mixotricha* has spherical bacteria inside the cell (endosymbionts) functioning as mitochondria, which are absent in this protozoan. Just like in its relatives, including *Trichonympha*, these bacteria help in cellulose digestion, as without *Mixotricha* the host termites fail to survive (Radek and Nitsch 2007).

Pseudotrichonympha (class Hypermastigea and order Trichonymphida) carries *Hoplonympha*, *Barburanympha*, *Urinympha* and *Staurojoenina* as ectosymbionts that form a monophyletic lineage. The endosymbionts of *Pseudotrichonympha* are distinct (Ohkuma et al. 2005) as they closely resemble the ectosymbionts of *Devescovina* protists (order Cristamonadida; class Trichomonadea). Two other protist species, *Holomastigotoides mirabile* and *Spirotrichonympha leidyi* also dwell in the gut of *C. formosanus*. Endosymbionts rarely occur within the cells of *H. mirabile* as this protist carries attached spirochaetes (ectosymbionts) of the cluster I of termite treponemas (Noda et al. 2003). The concentration of ectosymbiotic spirochaetes is less than 200 cells per *H. mirabile* cell. However, cells of *Spirotrichonympha leidyi* have an endosymbiotic methanogen (*Methanobrevibacter*) and only 300 cells of the methanogen occur within a single cell (Shinzato et al. 2005).

4.3.3 Fungi

The nests of the fungus-growing macrotermitine termites can occupy high volumes and can persist for decades, with million sterile helper individuals produced by a single queen (Shellman-Reeve 1997). This agricultural symbiosis with fungi has enabled this termite species to occupy niches loaded with abundant resources that were previously inaccessible (Waller 1988).

The fungal symbionts of Macrotermitinae produce sexual fruiting bodies (Katoh et al. 2002). Symbiotic relationship has a significant role in termite evolution, as it involves a wide range of intestinal microorganisms (Bignell 2000). Macrotermitinae is the only example of a single Termitidae subfamily displaying a mutualistic ectosymbiosis with a white-rot fungi, *Termitomyces* [tribe Termitomyceteae (Julich) Singer, family Tricholomataceae Roze, Basidiomycotina]. The fungus is capable of digesting lignin and provides food, either directly, when termites consume fungal nodules containing asexual spores, or indirectly, when they ingest partially degraded fungal biomass (Bignell 2000). The fungus is cultivated on a specialized structure within the nest, known as the fungus comb, which is maintained via continuous addition of predigested plant substrate. However, the older comb material is also consumed (Rouland-Lefevre et al. 2002). Approximately 40 species of *Termitomyces* symbiont are known till date, in Macrotermitinae (Kirk et al. 2001).

Just like most *Basidiomycetes*, *Termitomyces* shows homokaryotic and heterokaryotic stages in the life cycle, with one and two genetically different types of haploid nuclei (De Fine Licht et al. 2005). The fungus mycelium is heterokaryotic in all natural colonies, which emphasizes that the incipient termite colonies must contain at least two compatible and genetically different sexual spores, with a relatively short-lived homokaryotic stage (Aanen et al. 2007). The cultivation is beneficial to both the termites and the fungus in a number of ways, for example, the fungus is able to chemically degrade complex substances (e.g. lignin) in an easily accessible form for the termites and also the fungal component increases the termite diet N/C ratio, enabling the use of more diverse cellulose sources. On the other hand, the fungus gains advantages by accessing plant material for easier penetration, along with an increased surface area, in a suitable microclimate optimal for establishment, and, last but not the least, termite secretions prevent spread of microbial infections (Darlington 1994).

The Macrotermitinae nests exhibit an expanded thermoregulation by maintaining constantly high temperatures along with high relative humidity (Korb and Linsenmair 2000a, b). This provides an optimal microclimate for fungal cultivation (Wood and Thomas 1989) as well as a platform for the synergistic interaction of the complementary enzyme systems (enzymes derived from the termite and fungus) for cellulose digestion (Veivers et al. 1991).

The morphospecies of *Termitomyces* and its fruiting bodies form a monophyletic group intimately associated with the termite nests (Rouland-Lefevre et al. 2002), suggesting a single evolutionary origin of mutualistic symbiosis with termites. Cospeciation and specificity patterns are, however, consistent with the fungal symbiont transmission from host to host, outside the vertical host lineage [horizontal transmission] (Frank 1996).

Horizontal fungal transmission occurs in most of the Macrotermitinae-*Termitomyces* associations where the fungus produces fruiting bodies (basidiocarps) bearing sexual spores which are carried towards the newly formed nests by the first workers of the new colony through their first foraging trips (Darlington 1994). Laboratory trials confirm that alates (winged sexuals) fail to establish a colony unless provided with external fungal spores (Sieber 1983) and also the fruiting bodies of the fungus are in synchronization with the emergence of first fully developed foraging workers (Johnson 1981). Few Macrotermitinae termites also show vertical, uniparental symbiont transmission, in which reproductive units of termite and fungus are aligned together. *Microtermes* sp. and *Macrotermes bellicosus* alates (either male or female) carry in their foregut a bolus of conidia (asexual spores) from the fungus combs of the parent colony for inoculation of first fungus combs in their newly formed colonies (Wood and Thomas 1989). In *M. bellicosus* males transmit the fungus, while females transmit the fungus in *Microtermes* sp. However, fungal fruiting bodies have never been identified in these termite species (Darlington 1994). Phylogenetic and molecular investigations have supported this difference in sex-specificity in fungus transmission, pointing out an independent origin of uniparental and vertical transmission in these termite species. Termites with vertical transmission do not form a monophyletic group but fall in two unrelated clades, suggesting horizontal transmission as ancestral mode of transmission of which uniparental transmission is a derived trait, having two independent origins (Aanen et al. 2002).

Like most basidiomycetes, *Termitomyces* also have a heterothallic (i.e. outcrossing) life cycle where germinating spores form a monokaryon, and all cells carry a single nucleus. Later, two monokaryons of same species with different mating types fuse to form a stable dikaryon, and all cells have two nuclei, one derived from each monokaryon. This dikaryon can form fruiting bodies by meiosis, finally forming a spore. Macrotermitinae fruiting symbionts showing horizontal transmission follow this pattern, while some fruiting *Termitomyces* fungi also have a homothallic (i.e. non-outcrossing) mating system, in which only a single fungal spore completes the life cycle.

Two main models have been proposed for the successive evolution of the fungus in social insects. The first model is the traditional 'consumption first' model where consumption is followed by cultivation and the transmission fungi become essential component of the insect's diet (vertical fungus transmission). The second model is the alternative 'transmission first' model, in which transmission is preceded by consumption, resulting in the cultivation of a specialized fungus which is dispersed by the insect. Insects cultivate the fungus by the addition of substrate (Mueller et al. 2001).

Xylaria (*Ascomycotina*, *Xylariales*) occupies a wide variety of habitats including dead or live plant material as endophytic in living plants (Davis et al. 2003) and also a vast number of fungus-growing termite nests, where the termites actively control species composition by continuous excretion of antimicrobial peptides (Fuller 2007). This active suppression of spore germination or mycelial growth by termites results in a patchy distribution of *Xylaria* across fungus combs. *Xylaria* species can degrade lignin. Therefore, they cause white rot in wood and plant debris (Osono and Takeda 1999). Termites bring the inocula of *Xylaria* into their nests by their foraging activities. Certain *Xylaria* species (*X. escharoidea*, *X. furcate* and *X. nigripes*) show coevolution with termites as they carry smaller spores (Rogers et al. 2005) that can be easily ingested or carried by insects, enhancing the chances of dispersal (Rogers 2000). Termite-associated *Xylaria* act like 'sit-and-wait saprotrophs', foliar endophytes latently present on the leaf and start degrading processes only when the leaf falls from the tree (Herre et al. 2007).

4.4 Physiological Roles of the Microorganisms

The termite gut symbionts carry out the following physiological roles:

4.4.1 Nitrogen Fixation

Nitrogen fixation is a fundamental aspect of symbiosis in termites and is controlled by the gut microbes due to low nitrogen content of the termite diet. The rate of nitrogen fixation greatly varies among and within the same termite species (Braun et al. 1999). A nitrogenase complex catalyses the biological nitrogen fixation (Dean and Jacobson 1992) with the help of a molybdenum (Mo)-containing nitrogenase enzyme, encoded by the *nif HDK* operon. The cofactors of Mo-independent nitrogenases coordinate either with vanadium or lack Mo/vanadium (alternative nitrogenase) which in turn is encoded by the *vnfH-vnf DGK* and *anfH DGK* operons. The *nifH*, *vnfH* and *anfH* genes bear a high degree of sequence conservation (Widmer et al. 1999). Although there is a simultaneous regulation of genes within the single operon, the three operons (*nif*, *vnf* and *anf*) are differentially regulated. Availability of fixed nitrogen strictly regulates transcription of all the three nitrogenase operons, while Mo availability differentially affects expression of nitrogenase genes during transcription (Ohkuma and Kudo 1996).

The *nif* operon is repressed in the absence of Mo, but *vnf* and *anf* operons are repressed in the presence of Mo. A high nitrogen fixation activity, where more than half of the fixed nitrogen comes from the atmospheric N_2, is known in the drywood termite, *Neotermes koshunensis* (Tayasu et al. 1994). A wide diversity of *nifH* genes has been documented in the gut of *N. koshunensis* and other termite species as well (Ohkuma et al. 1999). In the symbiotic microbial community of *N. koshunensis*, the *anf* gene, connected with termite *anf*-methano cluster I, is the most critical gene responsible for fixation. It is believed that inadequate amount of Mo in the diet of this termite species is responsible for the expression of *anf* genes as the ordinary Mo-dependent nitrogenases require Mo as a cofactor for nitrogen-fixing activity. Termite species lacking *anf* genes in the gut community are possibly able to obtain sufficient amounts of Mo from their food (Ohkuma et al. 1996).

Some methanogenic archaea have *nifH* genes associated with the *anf*-methano group of *nifH* genes, but their *nifD* genes are phylogenetically grouped with Mo-dependent nitrogenases (Kirshtein et al. 1991). Mo-independent regulation of *anf* gene expression suggests encoding of a Mo-dependent ordinary enzyme, just like in methanogens. The *anfH*, *anfD* and *anfG* in the *anf* gene cluster encode both Mo- and V-independent alternative nitrogenases.

Gene organization and sequence features of the termite *anf* gene distantly resemble with those of well-characterized organisms. For example, in the Archaea domain, a Mo-independent alternative nitrogenase and *anfD* and *anfG* orthologous genes have not been reported yet, but the *anfH* gene resembles bacterial *anfH* gene. The Archaea domain including all diazotrophic methanogenic archaea contains two ORFs between *nifH* and *nifD* genes. In *Clostridium cellobioparum*, a sequence homologous to ORF105 has been recently identified, but the nucleotide sequence of the DNA region corresponding to ORF122, or even existence of ORF122-like genes, has not been documented yet. Presence of ORF105 in the genome of the bacteria domain indicates that it is not a characteristic of the Archaea domain only. The two ORFs of the termite *anf* gene cluster closely resemble the methanogen, *Methanosarcina barkeri* (Chien and Zinder 1996).

N_2fixation by the gut microbes contributes to about 60% of the total nitrogen in some termite colonies (Breznak 2000). Several strains of spirochaetes residing in termite gut also fix N_2 (Tayasu et al. 1994), and recently ZAS strains, along with their two homologs of *nifH*, also exhibit nitrogenase activity, in which ZAS-9 shows greatest specific activity (100-fold greater) than ZAS-1 and ZAS-2 (Lilburn et al.

2001). ZAS-9 also fixes ^{15}N2. The NifH amino acid sequences of several spirochaetes along with the ZAS strains are identical or nearly identical to various NifHs observed in termite guts (Noda et al. 1999), indicating their spirochaete origin (Lilburn et al. 2001).

4.4.2 Acetogenesis

The symbiotic protozoa and bacteria present in the hindgut of *Reticulitermes flavipes* carry out homoacetic fermentation of cellulose. Cellulolytic protozoa first hydrolyse cellulose by fermenting every C (CO_2) and H_2 (Breznak 1984):

$$C_6H_{12}0_6 + 2\,H_2O \rightarrow 2\,CH_3COOH + 2\,CO_2 + 4H_2$$

CO_2-reducing acetogenic bacteria then convert H_2 and CO_2 to an additional acetate molecule (Breznak and Switzer 1986):

$$4\,H_2 + 2\,CO_2 \rightarrow CH_3COOH + 2\,H_2O$$

The three acetates formed per glucose monomer are absorbed and oxidized by the termite to supply 100% of the insect's respiratory requirement (Odelson and Breznak 1983):

$$3\,CH_3COOH + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O$$

H_2 and CH_4 (methane is formed by reduction of CO_2 by methanogenic bacteria) are also emitted by termites. The rate of CO_2 reduction to acetate in the wood- and grass-feeding termites is greater in comparison to the fungus-growing or soil-feeding termites, while the rate of CH_4 emission by soil-feeding and fungus-growing termites (lesser extent) is greater than wood-feeding termites. Three strains of CO_2-reducing acetogenic bacteria from the guts of a higher and a lower wood-feeding and a higher soil-feeding termite have been described (Kane and Breznak 1991). Each one was a novel and different bacterial species capable of fermenting a variety of organic substrates for energy, including methoxylated aromatics (components of lignin). One of these isolates, *Sporomusa termitida*, is mixotrophic deriving energy by simultaneous usage of organic and inorganic (H_2 + CO_2) substrate mixtures (Breznak and Blum 1991). Mixotrophy enhances the ability of acetogens to outcompete methanogens for CO_2 reduction in wood- and grass-feeding termites.

Termite emissions can be considered as a significant source of total annual global CH_4 production, ranging from <5% to >40%. The hydrogenotrophic activity of acetogenic hindgut bacteria of the wood- and grass-feeding termites produces <10% CH_4, while fungus-growing and soil-feeding termites do not have significant levels of bacterial acetogenesis from $H_2 + CO_2$ so are more potent sources of CH_4 emission (Khalil et al. 1990).

H_2/CO_2 acetogenesis by termite gut spirochaetes is already known (Breznak 1975). The spirochaetes in higher termites and protozoa in lower termites display the highest H_2 concentration (up to 50,000 ppmv) in the luminal region, as confirmed by microelectrode-determined radial profiles (Ebert and Brune 1997). H_2-consuming methanogens (nonspirochetal prokaryotes) in *R. flavipes* lie on or near the hindgut epithelium (Leadbetter and Breznak 1996) and maintain low H_2 concentrations (Tholen and Brune 2000). The attachment of spirochaetes on the surface of hindgut protozoa as well as their ability to grow by H_2/CO_2 acetogenesis is responsible for 'motility symbiosis' (Cleveland and Grimstone 1964) allowing access to major sites of H_2 production. Recently, fluorescent rRNA-targeted oligonucleotide probes showed that only few distinct phylogenetic types of spirochaetes attach to protozoa (Iida et al. 2000).

Treponema strains ZAS-1 and ZAS-2, although capable of H_2/CO_2 acetogenesis but not restricted to the substrate like many so-called homoacetogens (anaerobic microbes producing acetate as major fermentation product), also ferment various mono- or disaccharides either alone or by H_2 consumption. ZAS-2 also carries out homoacetogenesis by using methyl groups of methoxylated aromatic compounds (Graber and Breznak 2000). Therefore, spirochaetes contribute to demethoxylation of lignin (Esenther and Kirk 1974) as well as other methoxylated aromatic components of termite food, but all termite gut spirochaetes are not homoacetogens. The *Treponema* strain ZAS-9 ferments sugars and produces acetate and other products, including H_2, but cannot conduct H_2/CO_2 acetogenesis (Graber and Breznak 2000).

4.4.3 Lignin Degradation

Lignin degradation in the gut of insects is carried out by the diversified microbial community. Cellulose degradation in insect guts is very well known (Breznak and Brune 1994), but the fate of lignin needs further research (Brune 2007) as it is widely accepted that insect gut systems lack the capability to degrade lignin (Ohkuma 2003). Apart from this fact, many previous studies have indicated that several wood-feeding insects can overcome the lignin barrier either by feeding on pre-degraded wood (Kukor et al. 1988) or via exosymbiotic relationships with wood-degrading fungi (Johjima et al. 2006) and that a few insect species can feed on the inner wood of alive healthy trees (Taprab et al. 2005). The major products of undegraded wood are 3,4-dimethoxybenzaldehyde (G4) from guaiacyl (G) lignin and 3,4,5-trimethoxybenzaldehyde (S4) from syringyl (S) lignin. The fungal lignin degradation has three main reactions: (i) propyl side-chain oxidation/cleavage, (ii) ring hydroxylation and (iii) demethylation (Filley 2003). Side-chain oxidation is responsible for Cα–Cβ cleavage/depolymerization of lignin in the white-rot fungi. The oxidative alteration of lignin propyl side chain produces higher amounts of 3,4-dimethoxybenzoic acid (G6) and 3,4,5-trimethoxybenzoic acid (S6), increasing the G6/G4 and S6/S4 ratios (Filley et al. 2000). Ring hydroxylation of guaiacyl units brings hydroxylation of either intact or side-chain-oxidized lignin. The diastereomeric pair of the enantiomers 1-(3,4-dimethoxy)-1,2,3-trimethoxypropane represents integral lignin. Syringyl lignin can be more easily degraded and depolymerized (Chiang and Funaoka 1990).

The recent metagenome sequencing of the hindgut microbe community of the higher termite species *Nasutitermes corniger* strengthens the view that termites can degrade lignin although no genes encoding lignin-degrading enzymes are yet known (Warnecke et al. 2007). It is presumed that hindgut microbes are also anaerobic and can degrade lignin. The lignin modification by the lower termite *Cryptotermes brevis* showed only minor changes in the molecule, without modifying the side chains (Katsumata et al. 2007). Lignin biodegradation in *Zootermopsis angusticollis*, a lower termite feeding on coniferous trees, shows side-chain oxidation along with demethylation. All three reactions (side-chain oxidation, ring hydroxylation and demethylation) in this termite gut are possibly related to the brown-rot fungal decay, as brown and white fungi are already known to be associated with termite guts. Excluding the fungal components, aromatic degrading bacteria (actinomycetes) in termite guts are also known. However, they participate in evading lignin barrier although their actual biochemical abilities are not well defined (Delalibera et al. 2005). Actinomycetes plays similar aromatic degrading role in the gut of *Anoplophora glabripennis* (Schloss et al. 2006).

The well-coordinated cooperation between termites and fungi is responsible for the efficient utilization of lignocellulose. Old workers collect plant litter, while young workers masticate and ingest the collected plant litter which passes down the termite gut without digestion in the form of faecal pellets (primary faeces) used in the formation of fungus comb for the growth of the symbiotic fungi. The fungi form mycelia as well as fungus nodules, and lignin content progressively decreases, with the maturation of the fungus comb (Shary et al. 2007). The in vitro digestibility of cellulose in a matured fungus comb is approximately three times higher as compared to that in a newly formed one. Fungus nodules are consumed by young workers while old workers consume old combs for producing final faeces, but it is almost impossible to observe final faeces which suggest a highly efficient decomposition as well as complete biorecycling of plant litter. It is now very well known that symbiotic fungi degrade lignin bringing easy degradation of cellulose in comparison to the cellulase produced by the termites (Filley et al. 2006).

Lignocellulose digestion needs efficient cellulases along with glycoside hydrolases for the degradation of the cellulose and hemicellulose present in the plant cell wall, in addition to a mechanism for handling lignin barrier which is actually a combined effort of termite and symbionts (Brune 2014). Both higher and lower termites produce enzymes for the first stage of the tricarboxylic acid (TCA) cycle but lack an enzyme capable for the conversion of pyruvate to acetyl CoA or acetate (Breznak and Brune 1994).

Cellulose hydrolysis starts with endoglucanases released by the termites (salivary glands secrete endoglucanases in lower termites while they are secreted within the midgut epithelium in higher termites). Numerous exoglucanases, exoglucanases, β-glucosidases and numerous other glycoside hydrolases are produced by the gut flagellates in lower termites. Higher termites also produce many cellulases, xylanases and other glycoside hydrolases. Metaproteomic studies of the hindgut of *N. corniger* have shown the presence of almost a quarter of the 886 proteins identified as enzymes of which 36 are glycoside hydrolases (Burnum et al. 2011). These findings suggest that these enzymes are important for the symbiotic relationship of the hindgut microbes and termites. The metaproteomic and metatranscriptomic analysis carried out by He et al. (2013) on *N. corniger* and *Amitermes wheeleri* (both higher termites with different diets and habitats) displayed differences in the abundance of certain bacteria in the guts due to their varied diets, but both species contained many glycoside hydrolases for cellulose degradation. No lignin degradation genes were identified in hindguts of the two species (Fig. 4.3). (The details of the cellulose degradation will be discussed in another chapter.)

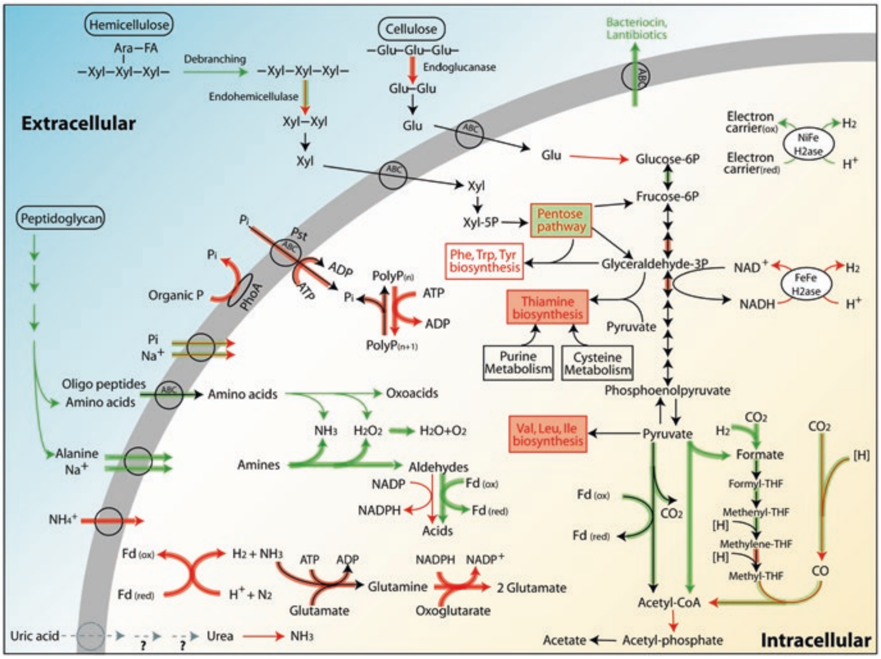

Fig. 4.3 Major metabolic differences between two higher termites from the metatranscriptomic study of He et al. (2013) (Green lines indicate the genes more abundant in *A. wheeleri* while red to *N. corniger*)

4.5 Conclusion

Termites play a vital role in recycling waste material important for the maintenance of the ecological balance. They produce about 11% of the atmospheric methane via cellulose breakdown. Symbiotic protozoa, as well as other flagellate protists residing in their guts, carry out the cellulose degradation. Gut protozoa (*Trichonympha*) are dependent on symbiotic bacteria for the production of necessary digestive enzymes. The higher termites (family Termitidae), however, produce their own cellulase enzymes. Some termite species practice fungiculture by maintaining 'fungal gardens' of specialized fungi *Termitomyces*, which are being nourished by their excrements. Researchers are trying to understand the details of the relationship between the termite digestive tract and the microbial endosymbionts.

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Chapter 5
Lignocellulose Degradation by Termites

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Abstract Host and symbiont enzymes are involved in lignocellulose processing by termites. A brief description of the structure of the main components of the plant cell wall and the most relevant degrading enzymes is presented. This chapter focuses on the dual cellulolytic system in lower and higher termites and provides an update on the current research strategies through culture-dependent and culture-independent "-omic" approaches. Significance for biofuel production and future perspectives are also discussed.

Keywords Lignocellulose digestion • Host and endosymbiont enzymes • Omics strategies • Biofuels

5.1 Introduction

During the last years, research on insect cellulolytic systems has gained attention because of their potential application in biofuel production. Among cellulose insect feeders, termites constitute one of the most promising sources of novel glycosyl hydrolase enzymes. Cellulose digestion in termites relies on both endogenous and exogenous enzymes. The implication of the former, long time disregarded, begun to emerge less than two decades ago. Even though, the digestive process cannot be accomplished without the action of exogenous enzymes, produced by a variety of endosymbiotic microorganisms hosted in the termite gut. In lower termites, the cellulolytic microbiota is composed mainly of protozoan flagellates. In contrast, higher termites lack such symbiotic protistan communities but have a huge diversity of intestinal bacteria. The increasing, available data provided by metagenomics and metatranscriptomics approaches will help to elucidate the insect's machinery for lignocellulose degradation. Understanding these mechanisms is a crucial step toward the establishment of efficient enzymatic processes for the bioethanol industry.

5.2 Cellulolytic Enzymes

5.2.1 Lignocellulose Structure

Lignocellulose is a heterogeneous matrix of three macromolecules: cellulose, hemicellulose, and lignin. This highly recalcitrant material makes up the cell wall in plants and therefore represents the most abundant biomass on earth (Isikgor and Becer 2015).

Cellulose, the principal component of lignocellulose, is a polysaccharide consisting of hundreds to thousands glucose monomers linked in linear chains of β-1,4 bonds. This polysaccharide is highly stable and very resistant to chemical attacks. Cellulose occurs in both crystalline and amorphous forms. The crystalline regions are packed very tightly, and consequently even very small active molecules have difficulty in breaking down this structure.

On the other hand, hemicellulose is a branched chain of polymers of structurally heterogeneous sugars: five-carbon sugars (such as D-xylose and L-arabinose), six-carbon sugars (frequently D-galactose, D-glucose, and D-mannose), and uronic acid. Because of its highly branched macromolecular structure, hemicellulose is relatively easy to hydrolyze to simple sugars (Bettiga et al. 2009).

Lignin is an amorphous aromatic polymer of phenolic compounds that are linked to each other and also covalently to hemicellulose by ester bonds. Lignin is usually more difficult to hydrolyze than cellulose and hemicellulose because of its cross-linked structure.

5.2.2 Main Lignocellulose-Degrading Enzymes

5.2.2.1 Cellulases

Cellulases are glycosyl hydrolases (GHs) that can cleave the glycosidic bonds present in cellulose. Indeed, the term "cellulase" encompasses all the cellulolytic enzymes, which include three main types: endoglucanases (1,4-β-D-glucan-4-glucanohydrolases, EC 3.2.1.4), exoglucanases (1,4-β-D-glucan cellobiohydrolases, EC 3.2.1.91 and 1,4-β-D-glucan cellobiohydrolases, EC 3.2.1.74), and β-glucosidases (EC 3.2.1.21).

Endoglucanases cleave amorphous sites in the cellulose chain at random, producing oligosaccharides of different lengths. Exoglucanases attack the ends of cellulose fibers to liberate cello-oligosaccharides (mainly cellobiose) or glucose. Finally, β-glucosidases hydrolyze cellobiose and other cello-oligomers to release glucose monomers from the nonreducing ends. The complete hydrolysis of cellulose usually requires the synergistic action of all these three types of cellulases and other accessory cellulolytic enzymes (Murashima et al. 2002; Tahir et al. 2005; Han and Chen 2010).

5.2.2.2 Hemicellulases

Hemicellulases are a diverse group of enzymes that catalyze the hydrolysis of hemicellulose. These enzymes are important in the digestion process because they expose cellulose to the action of cellulases, making it accessible for depolymerization. Because xylan is one of the main components of hemicellulose (Timell 1967), xylanases (EC 3.2.1.8) play a preponderant role in this respect. Other hemicellulolytic enzymes are also required to hydrolyze the hemicellulose in a synergistic way, including β-xylosidases (EC 3.2.1.37), β-mannanases (EC 3.2.1.78), α-L-arabinases (EC 3.2.1.99), α-L-arabinofuranosidases (EC 3.2.1.55), α-glucoronidases (EC 3.2.1.131), feruloyl esterases (EC 3.2.1.73), etc.

5.2.2.3 Ligninases

The major lignin-degrading enzymes are laccases (E.C. 1.10.3.2) and peroxidases: lignin peroxidase (E.C. 1.11.1.14) and manganese peroxidase (E.C. 1.11.1.13). A number of less significant oxidative ligninolytic enzymes include diaryl propane oxygenases, versatile peroxidases, and dye-decolorizing peroxidases. In addition, several accessory enzymes (oxidases and reductases) act as mediators favoring the ligninolytic activity of the principal enzymes. They participate in H_2O_2 production, needed by the peroxidases, or catalyze phenolic products reductions. Modification or cleavage of lignin improves the accessibility of cellulases and hemicellulases, thus increasing the efficiency of lignocellulose degradation (Plácido and Capareda 2015).

5.3 The Cellulolytic Systems of Termites

Lignocellulose degradation in termites depends on a dual system that includes activities of both the host and its intestinal symbionts. Mechanical digestion works together with the enzymatic action to maximize lignocellulose degradation (Fig. 5.1). For almost a century, the theory was accepted that cellulose digestion in termites was mediated only by the hindgut microbiota (Ohkuma 2003; Hongoh 2011; Ni and Tokuda 2013). The key role of a variety of enzyme-producing symbiotic microorganisms (including protistans, archaea, bacteria, and fungi) is well documented. Nevertheless, since the first description of an endogenous cellulase (an endoglucanase) in the lower termite *Reticulitermes speratus* (Watanabe et al. 1998), accumulated evidence proved that host hydrolytic enzymes contribute to lignocellulose processing in a non-negligible manner.

5.3.1 Lower Termites

In lower termites, which are generally xylophages, the cellulolytic process starts in the foregut; the wood fragments cut by the mandibles are further triturated by the muscular gizzard into smaller particles (10–20 μm in diameter). The endogenous enzymes secreted by the salivary glands into the foregut initiate cellulose hydrolysis. A number of papers and reviews have signaled the salivary glands as a source of endoglucanases, primarily (Watanabe et al. 1997; Zhou et al. 2007; Brune 2014). The production of β-glucosidases in this organ has also been established for several termite species (Tokuda et al. 2002; Zhang et al. 2012a; Shimada and Maekawa 2014). In the midgut, the high concentration of endoglucanases breaks down the amorphous regions of the cellulose fibers, and the synergistic action of β-glucosidases prevents product inhibition by reducing cellobiose accumulation (Watanabe and Tokuda 2010; Ni and Tokuda 2013; Brune 2014). Finally, the protistan flagellates housed in the hindgut produce the three principal types of cellulases (endoglucanases, exoglucanases, and β-glucosidases), as well as hemicellulases. Inside the

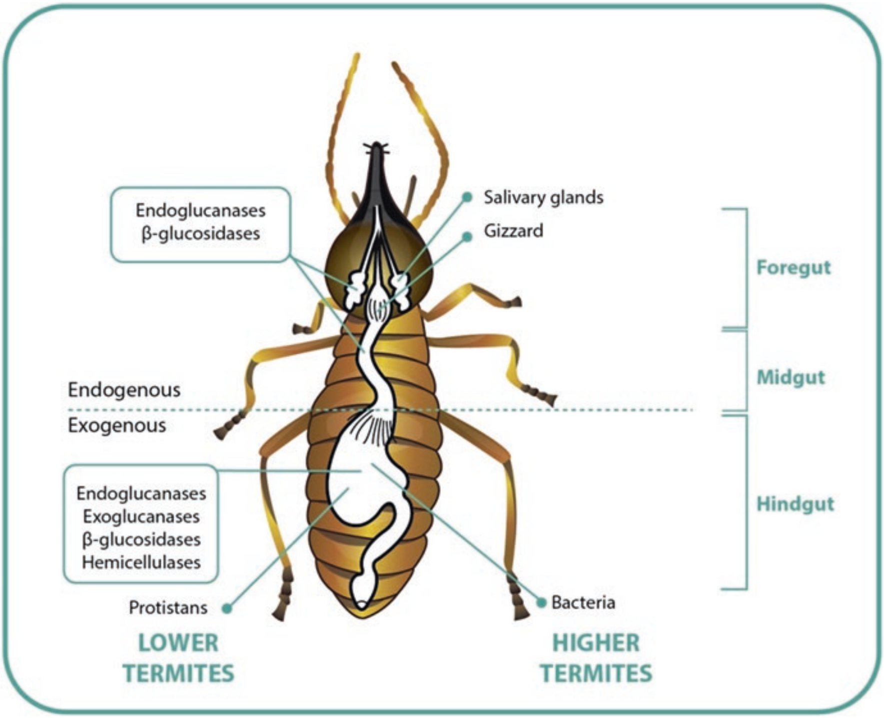

Fig. 5.1 The digestive process of lignocellulose in termites

protozoan digestive vacuoles, these enzymes cooperate in hydrolyzing hemicellulose, crystalline cellulose, and other remnants of ingestion.

The expression of cellulolytic enzymes in the termite gut varies according to the termite caste and developmental stages (Fujita et al. 2010; Shimada and Maekawa 2010). Regarding the classification, Henrissat and Bairoch (1993) demonstrated that, despite having different substrate specificities, members of the same GH family often have a common evolutionary origin, as revealed by their structural similarities. All the endogenous endoglucanases identified so far belong to the GH 9 family (Teather and Wood 1982; Watanabe and Tokuda 2010; Leonardo et al. 2011; Zhang et al. 2012b; Scharf 2015a). On the other hand, the protistan endoglucanases correspond to GHs 5, 7, and 45, which seem to belong to a core enzyme set conserved during symbiotic evolution (Ni and Tokuda 2013; Scharf 2015a). To date, host β-glucosidases were found to belong to GH 1 family (Slaytor 2000; Tokuda et al. 2002). Concerning hemicellulases, some works have reported xylanases from the host (GH 11) and protist symbionts (GH 45), which were recombinant expressed (Sasagawa et al. 2011; Sethi et al. 2013). Several ligninolytic enzymes, such as laccases, peroxidases, aldo-keto reductases, phenol oxidases, and esterases, have been also identified in termites (Coy et al. 2010; Chandrasekharaiah et al. 2011; Sethi et al. 2013).

In lower termites, the bacterial microbiota seems not to have a lead role in lignocellulose hydrolysis. It has been stated that when wood particles enter the hindgut, they are immediately arrested in the food vacuoles of the flagellate protists (Brune 2014). However, the recent discovery of a bacterial feruloyl esterase from *Coptotermes formosanus* (Rashamuse et al. 2014) opens new insights in this matter.

5.3.2 Higher Termites

During the Eocene period (around 60 Myrs ago), the higher termites lost the endosymbiont flagellates and, in consequence, diverged by evolving new strategies for cellulose hydrolysis (Lo and Eggleton 2011; Brune 2014). The higher termites have different feeding habits, including organic matter of soil, wood, herbivore dung, litter, lichen, and dry grass (Konig et al. 2013). Except for the fungi-associated termites (referred later), their hindguts evolved to increased length, compartmentalization, and alkalinity in order to partially palliate the absence of protozoans. Lignocellulose digestion in higher termites is poorly studied and needs further clarification. Endoglucanase secretion by the salivary glands seems to be the exception rather than the rule (Tokuda et al. 1997; Tokuda et al. 2004). Instead, there is a consensus about the enzymatic production in the midgut epithelium that is much more relevant to cellulose processing than in lower termites (Lo et al. 2011; Brune 2014). Thus, the cellulose hydrolysis is performed mainly by host and bacterial endosymbiont endoglucanases secreted by the midgut and the hindgut, respectively (Watanabe et al. 1998; Tokuda et al. 2004). Both host and bacterial GH 9 endoglucanases have been reported, while GH 5 and 45 are considered of bacterial origin only. Concerning the β-glucosidases (GH 1), the organs involved vary among termite species. In majority of *Nasutitermes* sp., β-glucosidases have been detected mainly in the salivary glands and midgut, whereas in other species, this activity occurs mostly in the hindgut (Slaytor 2000; Uchima and Arioka 2012; Wang et al. 2012; Ni and Tokuda 2013; Rashamuse et al. 2014). Also, two xylanases (GH 10 and 11) have been isolated and recombinant expressed from *Nasutitermes* sp. and *Globitermes brachycerastes* bacterial symbionts, respectively (Brennan et al. 2004; Han et al. 2013). A less frequent, but conspicuous association, can be found in the subfamily Macrotermitinae, in which a basidiomycete fungus, cultivated inside the nest, contributes to lignocellulose degradation (Johjima et al. 2006; Liu et al. 2013).

5.4 Omics Approaches Applied to the Discovery of Novel Cellulolytic Enzymes

Since the first genomic studies, the suffix "-omics" has been used to denote large-scale research in different fields, including metagenomics, transcriptomics, proteomics, and metabolomics. The term digestome was used to describe the ensemble of endogenous and symbiont genes that contribute to lignocellulose digestion in the digestive tract of animals, including termites (Scharf and Tartar 2008; Tartar et al. 2009).

A current scheme of the "-omics" approach to the cellulolytic systems in termites is illustrated in Fig. 5.2. There are two main ways to study the termite digestome. The first one explores genomic strategies through culture-dependent approaches, i.e., the isolation of microorganisms containing cellulolytic genes or the characterization of enzymatic extracts from cellulolytic enrichment cultures (Ben Guerrero et al. 2015; Butera et al. 2016). This method focuses on insect-associated microorganisms and therefore does not take into account the host genome. Its potential is further limited by the fact that it is widely accepted that only about 1% of the gut microbial diversity can be cultured through conventional techniques.

The second approach seeks to overcome these constraints applying strategies (which include metagenomics, metatranscriptomics, metaproteomics, and metabolomics) that do not require microorganism cultivation in artificial media and also considers the insect host. These studies can be performed independently or in combination. The main strategies dealing with metagenomics are (1) biodiversity analyses (symbionts); (2) functional metagenomics (through the construction of metagenomic libraries in fosmids or plasmids, functional screening, and selection of individual clones with cellulolytic activity); and (3) sequence-based analysis through next-generation sequencing (NGS) by Illumina, 454 pyrosequencing technologies, etc. To date, successful results in functional metagenomics and NGS allowed the identification of genes encoding lignocellulolytic enzymes or novel

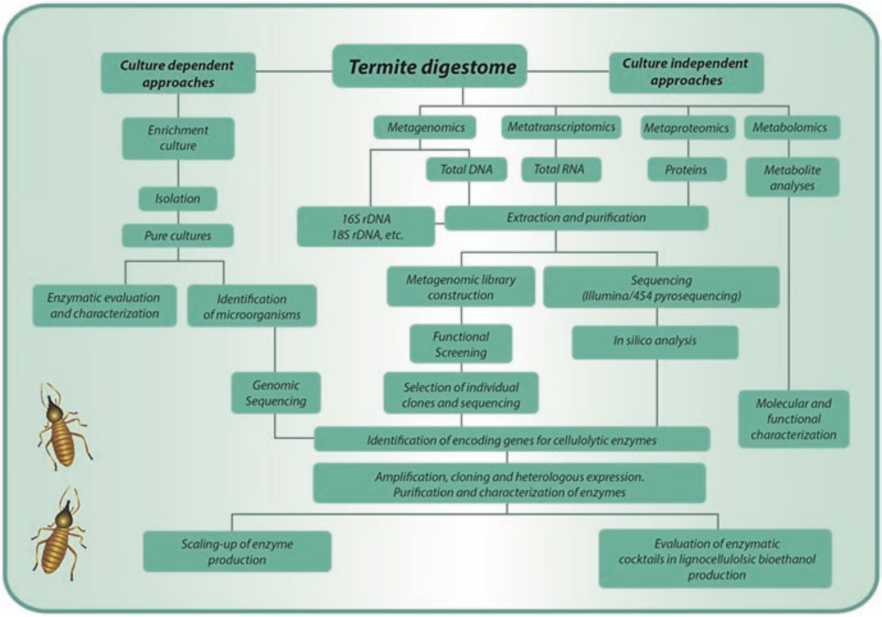

Fig. 5.2 Different approaches in termite digestome analysis for bioethanol production

protein families in both host and symbionts, as well as their heterologous expression, purification, and biochemical characterization (Fig. 5.2).

In termites, near 50 articles referring to "-omics" have been referenced in PubMed by June 2016, at least 25 concerned metagenomics (Warnecke et al. 2007; He et al. 2013; Liu et al. 2013; Do et al. 2014), around 18 metatranscriptomics (Huang et al. 2012; Sethi et al. 2013; Rajarapu et al. 2015), and 5 metaproteomics (Burnum et al. 2011; Sillam-Dusses et al. 2012; Bauwens et al. 2013). Several of them combined different approaches. Table 5.1 provides a summary of some relevant "-omics" studies concerning termites.

Most metagenomic studies have been based on the identification of lignocellulases from enriched lignocellulosic cultures of microorganisms (Liu et al. 2011; Matteotti et al. 2011; Matteotti et al. 2012; Nimchua et al. 2012; Wang et al. 2012; Rashamuse et al. 2014). Other studies have targeted total gut microbiota in termites with different feeding habits (Warnecke et al. 2007; He et al. 2013; Liu et al. 2013). Many transcriptomic studies have focused on host transcriptome by employing different techniques, such as subtractive hybridization or cDNA macroarrays, random or de novo cDNA library sequencing, and cDNA oligonucleotide microarrays, to reveal differentially expressed genes (Warnecke et al. 2007; Weil et al. 2009; Ishikawa et al. 2010; Hojo et al. 2012; Huang et al. 2012; Husseneder et al. 2012; Terrapon et al. 2014). Other studies have considered symbiont metatranscriptomic analyses by using traditional and NGS technologies (Scharf et al. 2005; Todaka et al. 2010; Rosenthal et al. 2011; Xie et al. 2012; Zhang et al. 2012b; He et al. 2013).

In higher termites, very few proteomic studies have been published. The results obtained were of limited resolution or just sufficient to corroborate the presence of some bacterial cellulases predicted by transcriptomic or metagenomic approaches (Warnecke et al. 2007; Burnum et al. 2011; Ben Guerrero et al. 2015). Proteomic studies in lower termites were more consistent and have allowed researchers to identify protist cellulases previously determined by metagenomic approaches (Todaka et al. 2007; Sethi et al. 2013) and describe symbiont diversity (Bauwens et al. 2013).

Several metabolomic studies have focused on lignocellulose digestion, paying special attention to lignin modifications. As mentioned earlier, termites are very efficient degraders of lignocellulose. However, lignin degradation constitutes one of the less-known aspects of the process and still needs to be clarified (Geib et al. 2008; Ke et al. 2011, 2013; Tokuda et al. 2014). The extent of lignin decomposition is actually a subject of controversy. Previous works identified gut bacteria able to degrade aromatic compounds, and peroxidase producers as well, suggesting that these bacteria could be involved in lignin modifications or degradation (Bugg et al. 2011; Ke et al. 2012). It is possible that termites are capable of degrading only some functional groups, monomers, or dimers but not large lignin molecules (Ke et al. 2011). However, no genes encoding ligninolytic enzymes have been identified in termite guts so far. Other metabolomic studies helped to understand the contribution of endogenous and symbiont microorganisms enzymes in the overall digestion process (Scharf et al. 2011; Tokuda et al. 2014).

Table 5.1 Some relevant -omics research in termites

Omic studies	Species name (termite group)	Endogenous or symbiont origin	Body section	Approach	References
Metagenomics	*Odontotermes yunnanensis* (higher)	Symbiont	Entire gut	454 pyrosequencing	Liu et al. (2013)
	Coptotermes gestroi (lower)	Symbiont	Entire gut	Illumina sequencing	Do et al. (2014)
	Pseudacanthotermes militaris (higher)	Symbiont	Entire gut	Fosmid metagenomic libraries and 454 pyrosequencing	Bastien et al. (2013)
	Amitermes wheeleri and *Nasutitermes corniger* (higher)	Symbiont	Hindgut	454 pyrosequencing (V8 region)	He et al. (2013)
	Microcerotermes sp. (higher)	Symbiont	Entire gut	Fosmid library	Nimchua et al. (2012)
	Reticulitermes santonensis (lower)	Symbiont	Entire gut	Genomic library (plasmid)	Mattéotti et al. (2012)
Metagenomics and proteomics	*Nasutitermes corniger* (higher)	Symbiont	Hindgut paunch (P3 luminal)	454 pyrosequencing and LC-MS proteomics	Warneke et al. (2007)
Metagenomics and metatranscriptomics	*Amitermes wheeleri* and *Nasutitermes corniger* (higher)	Symbiont	Hindgut	454 pyrosequencing (V8 region)	He et al. (2013)
Transcriptomics	*Odontotermes formosanus* (higher)	Endogenous	Head	Illumina Paired-end Sequencing	Huang et al. (2012)
	Reticulitermes flavipes (lower)	Symbiont	Entire gut	Illumina HiSeq 2500	Rajarapu et al. (2015)
Metatranscriptomics and proteomics	*Reticulitermes flavipes* (lower)	Symbiont	Entire gut	454 pyrosequencing and 2D-gel and LC-MS	Sethi et al. (2013)
Proteomics	*Nasutitermes corniger* (higher)	Symbiont	Hindgut paunch	LC-MS	Burnum et al. (2011)
	Reticulitermes santonensis (lower)	Symbiont	Hindgut	2D-gel and LC-MS/MS	Bauwens et al. (2013)
	Nasutitermes aquilinus (higher)	Symbiont-enrichment culture	Culture supernatant of gut endosymbionts	2D-gel and MS/MS	Ben Guerrero et al. (2015)

(continued)

Table 5.1 (continued)

Omic studies	Species name (termite group)	Endogenous or symbiont origin	Body section	Approach	References
Proteomics and metabolomics	15 termite species belonging to 6 families (lower)	Endogenous	Labial gland	N-terminal peptide sequencing MALDI-TOF and GC/TOF-MS	Silliam-Dussés et al. (2012)
Metabolomics	*Hodotermopsis sjostedti* (lower)	Endogenous and symbiont	Gut sections	Isotone-ratio mass spectrometry (IR-MS)	Tokuda et al. (2014)
	Zootermopsis angusticollis (lower)	Endogenous and symbiont	Entire gut	TMAH (thermochemolysis)-GC/MS	Geib et al. (2008)
	Coptotermes formosanus (lower)	Endogenous and symbiont	Entire gut	TMAH (thermochemolysis)-GC/MS	Ke et al. (2013)
	Coptotermes formosanus (lower)	Endogenous and symbiont	Entire gut	TMAH (thermochemolysis)-CP-MAS-NMRP and y-GC/MS	Ke et al. (2011)
Biodiversity analyses					
Enrichment culture	*Cortaritermes fulviceps* and *Nasutitermes aquilinus* (higher)	Symbiont	Entire gut	16S RNAr gene sequencing (clone sequencing)	Ben Guerrero et al. (2015)
Independent culture	*Coptotermes formosanus* (lower)	Symbiont	Bacteria on the cuticle and entire gut	16S RNAr gene sequencing (direct PCR sequencing)	Hussender et al. (2010a, b)
	Nasutitermes corniger (higher)	Symbiont	Hindgut	454 pyrosequencing (V3-V4 region)	KÖhler et al. (2012)
	Reticulitermes flavipes (lower)	Symbiont	Hindgut	Illumina MiSeq (V4 region)	Benjamino and Graft (2016)
Responses to different diets	*Reticulitermes flavipes* (lower)	Symbiont	Hindgut	454 pyrosequencing (V5-V6 region)	Boucias et al. (2013)
	7 families (higher)	Symbiont	Hindgut	Illumina MiSeq (V3-V4 region)	Mikaelyan et al. (2015)

Sequence surveys targeting 16S rRNA have been used in diversity analyses of bacteria and archaea (Wang and Qian 2009), whereas 18S rRNA screenings identified protist symbionts (Tai and Keeling 2013). Cloning-dependent and cloning-independent approaches were performed through low- and high-throughput analyses, focusing on both functional and taxonomic topics (Warnecke et al. 2007; He et al. 2013). In general, six major bacterial phyla are represented across higher and lower termites: Bacteroidetes, Firmicutes, Spirochaetes, Proteobacteria, Fibrobacteres, and Elusimicrobia (Brune 2014). Many hundreds to more than thousand species have been recorded in the different termite species investigated so far (Boucias et al. 2013). Interestingly, the 16S surveys revealed that lignocellulosic diet shifts have no short-term impacts on the microbiota composition of termites (Sanyika et al. 2012; Boucias et al. 2013). Otani et al. (2014) suggested a core microbiota of 42 genera shared among 9 termite species tested. Although less diverse than bacteria, the number of protist taxa revealed by 18S rRNA high throughput sequencing was found to be higher than estimated by morphology.

The advanced "-omics" research on termites has contributed to elucidate molecular and physiological issues of the host/symbiont relationships and the cellulolytic digestion processes mediated by the different actors involved. Further work is needed to better understand the functional significance of the data obtained by genome (and metagenome), transcriptome, and proteome sequencing.

5.5 Potential Industrial Applications and Future Perspectives

Termites are an interesting biotechnological model for various industrial applications, including fuels, food, breweries, pulp, and paper. The termite symbiotic system is a rich resource, promising the discovery of new genes and enzymes.

As lignocellulose is the main component of the plant cell wall, it is the most abundant, widespread, and renewable biofuel resource available on Earth. It is composed mainly of cellulose, hemicellulose, and lignin in different proportions, depending on the plant taxa. The conversion of the plant biomass into bioethanol can be divided into three main processes: pretreatment, hydrolysis, and fermentation (Merino and Cherry 2007). The major limitation in this process is the cost of the hydrolysis step and the inefficiency of industrial lignocellulose pretreatments (Scharf 2015b; Yang and Wyman 2008). Termites, and their associated microorganisms, contain enzymes that could be useful in order to remove or modify lignin and hemicellulose in the biomass pretreatment, then to hydrolyze cellulose into sugar monomers, and finally to ferment them into acetate. Thus, the study of the termite cellulolytic system could be a valuable tool for reducing the high costs experienced in the biofuel industry. Future research should increasingly focus on the characterization of these enzymes and on the genetic engineering work needed to make them more suitable for an industrial use.

5.6 Conclusion

The maintenance of a dual cellulolytic system across evolutionary time reveals that the combined action of both strategies is essential for termites' survival. More "-omics" efforts are needed to better understand the contribution of endogenous (host) and exogenous (symbionts) enzymes in the digestion of lignocellulose. The ability of termites to degrade recalcitrant plant biomasses and their ubiquitous distribution make them an ideal biological model for the industrial processing of cellulosic material. The discovery of novel enzymes, of either host or symbiont origin, is regarded as a major concern for biorefinery improvement.

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Chapter 6
Termite Biology and Social Behaviour

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Contents

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Abstract The present chapter focuses on the biology of termites, showing different life stages and caste systems. Mating, reproduction, parthenogenesis and factors affecting development are discussed. Termite life cycle comprises of eggs, immature forms or nymphs and mature forms or adults, which include sterile workers, soldiers, pseudergates and various fertile winged or wingless reproductive forms. Nymphs have a very intricate and active life and after a few moults get transformed into different adult forms. Reproductive caste of termites comprises of present and future kings and queens, whereas the nonreproductive caste is formed by sterile workers and soldiers. The castes are determined during post-embryonic development, and each larva, at the first or second instar stage, has the potential to become a soldier, a worker, a king or a queen. Termites can be grouped according to their habitats and feeding habits into, viz. dampwood, drywood and subterranean termites. They are herbivorous and feed on wood, vegetable, soil, organic and faecal matter. They exhibit a significant preference to a particular food and are primarily dependent on cellulose, which they obtain from both living and dead wood. For cellulose digestion, they are totally dependent on the microscopic intestinal fauna, as they cannot synthesize cellulase. Environmental factors affect termite colonies. Temperature has a positive correlation with the developmental rate. However, higher temperature may even increase the mortality rates.

Keywords Termite • Biology • Social behaviour

6.1 Introduction

Termites are terrestrial polymorphic eusocial insects originated from a common ancestor with the subsocial cryptocercid roaches, in the late Jurassic of Mesozoic Era (Engel et al. 2009). Members of family Termitidae are known as higher termites, while individuals of the families Mastotermitidae, Hodotermitidae, Termopsidae, Kalotermitidae, Rhinotermitidae and Serritermitidae are clubbed into lower termites. Termitidae is the most diverse family and has a wide range of social specifications (Kambhampati and Eggleton 2000). Termites have highly organized colonies and are characterized by overlapping generations. They are eurytopic and distributed throughout the temperate, tropical and subtropical regions of the world, with the highest diversity found in tropical forests (Eggleton 2000). Termites are good scavengers and decomposers, feeding on a wide range of living, faeces, dead or decaying plant material and soil rich in organic matter, and thereby help in recycling waste material (Freymann et al. 2008). They also alter soil composition and structure (Lee and Wood 1971), improve drainage and provide soil aeration (Donovan et al. 2001a) due to burrowing activities. They thus can be known as ecosystem engineers, enhancing soil fertility when the mounds, which are rich in minerals, are crushed down and incorporated into the soil. Over long periods of time, the termites can modify the physical properties of soil such as texture, water infiltration rates and nutrient content, at various spatial scales (Dangerfield et al. 1998).

However, they also negatively affect agriculture, forestry and housing and are a major factor of biodegradation (Tsai 2007). They are serious pests of fruit trees, rice, vegetables, sugar cane, tea, etc. (Yi 1954) and affect forestation (Yang et al. 2002). Certain household commodities and goods like window and door frames, furniture, wooden floors and ceilings are under constant threat of termites (Tsai and Chen 2000; Tsai 2007). Additionally, they have immense potential to destroy lead sheathing of electrical and telephone cables, resulting in short circuits (Tsai et al. 2004; Li et al. 2008).

6.2 Life Cycle

Primary and supplementary reproductive adults are present in termite colonies. The primary reproductives are king and queen, which are the founder of the nest and colony. They are pigmented adults with initial fully developed wings. Their role is reproduction and the initiation of the colony. King or male reproductive goes for nuptial flights, copulates with the queen and fertilizes her by insemination. Queen or female reproductive stores the sperm in the spermathecae after the copulation and uses them to sire the unfertilized eggs. These adults mate only once. The main role for a queen is to produce eggs as she lays more than 3000 eggs per day, gradually enlarging her body, especially the abdomen, to accommodate the eggs (Thompson 2000). These are yellowish-white in colour, and the incubation period may be prolonged to 50–60 days. After incubation, the nymphs hatch out in the form of neonates. They undergo a number of moultings before becoming adults.

The termites are hemimetabolous, undergoing an incomplete metamorphosis. Unlike most other insects, very little is known about moulting in termites, particularly in the subterranean group. Reasons for this lack of information include the absence of synchronization in the timing of moult, the cryptic nature of subterranean termites and their long life cycle. It takes about 4–5 years for a termite colony to reach its maximum size, with more than 60,000–200,000 workers. These further modify into sterile soldiers or remain as sterile workers during the course of time. Morphologically, the workers and soldiers are 6–8 mm in length and pale cream in colour. The soldiers have enlarged heads with black jaws. Both workers and soldiers are devoid of wings and usually lack eyes (Myles 2005).

The life cycle of termites starts with the dispersal of winged reproductives to colonize new resources. The mating pair sheds their wings and establishes a new nest. Then the queen oviposits, the eggs hatch and the nymphs develop into different forms (Fig. 6.1). The castes are determined during post-embryonic development, and each larva (first or second instar termite) can become a worker, soldier or reproductive (Laine and Wright 2003).

The reproductive caste can have multiple forms (reviewed by Thorne 1996). The primary reproductives are alate derived and are the king and queen in the colony. A neotenic reproductive is a reproductive that is not derived from an alate and still retains some juvenile characteristics. Secondary, or nymphoid, reproductives are

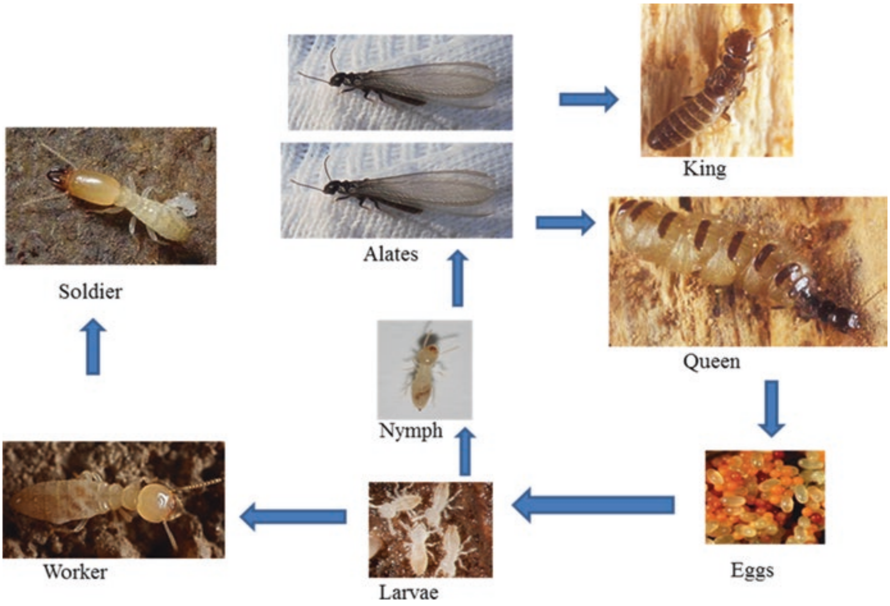


Fig. 6.1 Life stages and castes of *Reticulitermes* sp. (Photo courtesy: Lyle J. Buss, University of Florida)

neotenics derived from nymphs. They have wing pads, and their body pigmentation is generally of a yellow hue. Tertiary or ergatoid reproductives are those derived from false workers (pseudergates). These are generally smaller than nymphoid reproductives and are apterous with very light pigmentation.

6.3 Different Castes of Termites

Being eusocial insects, the termites have a caste system. The caste of each individual is determined during its post-embryonic development (Laine and Wright 2003), which is largely dependent on the pheromones present in the colony. Each caste can be visually differentiated by several key traits.

The division of labour in termite colonies is based on different castes. The caste system can vary according to termite species (Noirot and Pasteels 1987; Roisin 2000). In Termitidae, bifurcation occurs after the first stage of development. An apterous line gives rise to the worker caste, after one or two larval instars. Subsequently, the worker caste gives rise to soldiers. A nymph line, after five nymphal instars with wing buds, gives rise to alates (Roisin 1992, 1996; Moura et al. 2011).

Termites have four castes resulting from the expression of alternative post-embryonic developmental trajectories. The first two types of castes are those of worker castes, viz. (1) true workers and (2) pseudergates or false workers. True workers are the individuals diverging early and irreversibly from the imaginal development (Lima et al. 2013). The pseudergates are the individuals separating late from the imaginal line (Noirot and Pasteels 1987). The third caste is those of alates or imagoes, which develop normally as do the other hemimetabolous insects. The fourth caste is those of soldiers, which are formed from a pre-soldier or white soldier stage after the post-embryonic developmental pathway (Noirot and Pasteels 1987).

6.3.1 Workers

Workers of lower termites typically are unpigmented and white or black, lack eyes and show no signs of wing development. They are soft bodied but possess hard mouthparts, which are especially adapted for chewing wood. They are functionally sterile male and female individuals and are responsible for all the labour required in the nest.

Young workers execute domestic jobs like feeding, grooming and caring the young ones, while the older workers are recruited on the hazardous jobs of foraging and nest building. Hinze et al. (2002) reported that feeding habits in termite, *Macrotermes bellicosus* (Smeathman), differ in old and young workers, also referred to as major and minor workers, respectively. Major workers are foragers and the main food processors, while minor ones feed on fungus comb (have developed labial glands), and their main job is to feed the queen. It is also found in the same species that the age increase may result in a change of job in certain workers, from queen caring to external foraging activities (Hinze and Leuthold 1999). The authors inferred that age plays an important and decisive role in polyethism, which is the division of duties amongst the insect colony members.

Age polyethism also affects the longevity of workers, which take almost a year to mature with a mean longevity around 3–5 years (Myles 2005). Size polyethism is also evident amongst workers, as those with different body sizes have a different role in the construction of the nest (Jones 1980). Body size of workers has a crucial role in tunnelling galleries. Large workers make broad tunnel galleries with less segmentation, while small workers make narrow tunnels with more segmentation (Campora and Grace 2004). The medium head-sized workers in termite, *Odontotermes formosanus* (Shiraki), are foraging workers (Soleymaninejadian et al. 2014). Similarly, McMahan et al. (1984) attested that 96% of small workers attend queen chamber. On the contrary 99% of large workers take part in foraging, and 70% of them can be found around swarming sites or exit holes.

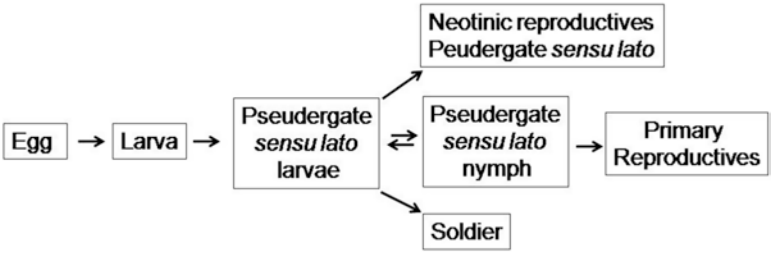
6.3.2 Pseudergates

Pseudergates are false workers, who do the job of workers like food collection, construction or brood care but still possess the capacity to become reproductives (Roisin and Korb 2011). Isopterans are eusocial due to the possession of a terminal sterile soldier caste. These sterile soldiers develop either from wing-budded/apterous instar through an intermediate unsclerotized pre-soldier instar. High juvenile hormone concentration has been reported as the reason for such development (Luscher 1969; Hrdy et al. 2006).

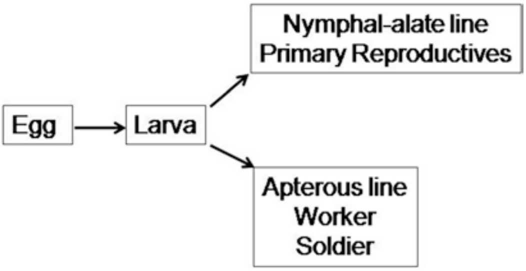
The use of terminologies in termite research has generated a considerable amount of confusion amongst the researchers all over the world. The presence and absence of wing rudiments during moult, and deviation of certain individuals to develop from the straight egg to alate pathway, generated considerable amount of confusion for use of terminologies in termite research. Grasse and Noirot (1947) coined the term pseudergate or false worker to designate the individuals who pass through regressive moults in *Kalotermes flavicollis* (Fab.). Generally the apterous line develops into workers and soldiers. Typically the termite caste patterns could be divided into two groups, one characterized by the development of pseudergates and the other by an early developmental fork, separating nymphal-alate line from the apterous line.

Kalotermes flavicollis is a wood-dwelling species (Korb 2007; Korb and Hartfelder 2008) with pseudergates that remain in a single piece of wood, serving as both food source and shelter [="one piece type" of Abe (1990), "single site nesters" of Shellman-Reeve (1997)]. Korb (2007) and Korb and Hartfelder (2008) proposed the existence of an alternative life type in foraging termites, where workers living in the nests are separated by their feeding sites, i.e. the "separate" and "intermediate" types of Abe (1990) or "central-site" and "multiple-site" nesters of Shellman-Reeve (1997). The workers have to move out for foraging to have an access to food. Species of Hodotermitidae, Termitidae, *Mastotermes* and several Rhinotermitidae belong to the multiple-site nester group.

The distinction between the nester groups is important because selective forces would fundamentally change, depending on whether individuals leave the protective piece of wood or not. They may develop from and into many different stages, including stages from the imaginal line. They have numerous developmental possibilities, and such species with pseudergates are very flexible in development. This could be an ancestral character consequently lost in some termite species or may be recently acquired (Noirot 1985; Watson and Sewell 1985). However, true workers show low developmental flexibility. Pseudergates can even indulge in attack and defence apart from doing other household jobs, as in those of *Hodotermopsis sjostedti* Holmgren (Ishikawa and Muira 2012). As per Roisin and Korb (2011), the linear pathway of termite development (wood-dwelling termites) is as follows:



The bifurcated pathway of termite development (foraging termites) is as follows:



6.3.3 *Soldiers*

Soldiers are responsible for defending the colony and are characterized by their distinct head capsules. Their powerful mandibles enable them to defend the colony against many predators. They cannot feed on their own and are dependent on fellow workers to be fed. They have an enlarged and sclerotized head capsule and mandibles as aid in colony defence. The soldier caste is considered ancestral in termites and is surmised to be evolved prior to that of the true workers. This caste is monophyletic and unlike the soldiers found in the other eusocial insects, viz. aphids, thrips and ants (Noirot and Pasteels 1987). Soldiers get matured in a year and may live up to 5 years (Myles 2005).

The intricate soldier lifestyle leads to evolutionary puzzling questions, such as: Why does one group of individuals like soldiers completely abstain from reproduction (Jeon and Choe 2003)? How soldiers have evolved? These questions are not fully addressed. However, few clues about the life of termite ancestors exist, which could be framed into three hypotheses. The first hypothesis on the evolution of soldiers considers a model based on increased relatedness systems, which was proposed by Yamamura (1993). The second hypothesis is based on the possibility that soldier traits originated amongst neotenics, as adaptations for fighting for the natal breeding position (Myles 1986, 1988). It was based on observations of secondary reproductives in *Zootermopsis* with soldier traits, known as soldier neotenics. The third hypothesis states that soldiers have evolved for their intrinsic benefit, which accentuates that soldiers get adequate indirect fitness benefits to counterbalance the trade-off due to the loss of their reproductive potential (Roisin 1999). Roux and Korb (2004) observed that the presence of soldiers was positively associated with the production of reproductives. This indicates that soldiers get indirect benefits by promoting the production of related reproductives.

Mostly, there exists a specific soldier proportion in termite species (Haverty and Howard 1981) which is also dependent on environmental factors (Liu et al. 2005a, b). This proportion might have two levels of internal regulation (Korb et al. 2003): first, the individual endocrinal regulation, where change in juvenile hormone titres activates the differentiation process (Mao et al. 2005; Park and Raina 2004) and, second, the social regulation, where the present soldier proportion becomes template for the production of new soldiers (Park and Raina 2005; Mao and Henderson 2010). The first soldiers produced are nanitic (Barsotti and Costa-Leonardo 2005), and in certain species, their primary role is to maintain a soldier proportion in the incipient colonies (Chouvenc and Su 2014). The soldier caste evolved in incipient colonies in termites could represent a survival strategy against an intense intraspecies competition (Thorne et al. 2003).

Size polyethism is also evident in the soldier caste. Small soldiers of termite *Nasutitermes exitiosus* (Hill) are better attackers against invaders than the large ones, as the latter are mostly non-fighters and may flee at the time of danger. These large soldiers may become messenger to prepare the nest mates by alerting through the danger signals (Kriston et al. 1977). Soldiers of *Nasutitermes costalis* (Holmgren) (Traniello 1981) and *Nasutitermes princeps* (Desneux) (Roisin et al. 1990) use chemical signals secreted from frontal glands to recruit other soldiers and workers to forage.

6.3.4 Reproductives

The primary reproductives (king and queen) are alates and hence show evidence of wings (i.e. wing scales). They have fully developed eyes and are fully pigmented. The termite queen shows the longest lifespan and lives up to 25 years (Myles 2005). Neotenic reproductives are often found in termite colonies, particularly those where the king and/or queen had died or is missing. They are non-alate derived and never have fully developed wings or eyes. They can be slightly or heavily pigmented. Nymphoid reproductives develop from the nymphal stage and have wing pads, but they do not show many of the mature characteristics of a primary reproductive.

Ergatoid reproductives are worker-derived neotenics that are smaller than nymphoid reproductives and lack wing buds (Thorne 1996). Winged reproductives go for mass nuptial flight in April and May, which are also an indication of termite infestations (Philip 2004). After nuptial flights, the queens instantly search for nesting sites while the kings follow them. When the search is complete, as they find a moist crevice with wooden material, a royal chamber in the form of nest is created, and the queen lays eggs (Su and Scheffrahn 2000). These are yellowish-white in colour and require 50 to 60 days of incubation. A queen may lay about 3000 eggs a day through its distended abdomen (Thompson 2000).

The reproductive caste has multiple forms (Thorne 1996), their exoskeleton being sclerotized to some extent. Reproductives indulge in parenting behaviour, as the king in Japanese dump wood termite, *Hodotermopsis japonica* Holmgren, grooms the queen during preoviposition period and feeds them by proctodeal stomodeal fluid. After oviposition and the hatching of eggs, the queen takes care of larvae and feeds them with trophallactic fluid (Machida et al. 2001). The king plays a more active role by moving around the nest and interacting with the queen and other nest mates (Maistrello and Sbrenna 1999). It may be inferred that the king has an important position in setting the social structure and dynamic development of the colony.

6.4 Types of Termites

Termites are categorized according to their distribution, feeding habit and moisture requirements. Lower termites are categorized as (1) drywood, (2) dampwood and (3) subterranean termites.

6.4.1 Drywood Termites

Drywood termites (Kalotermitidae) consume good drywood, which has very little moisture content and does not need an extra moisture source. They are well adapted to dry conditions and have more impermeable cuticle than other termites, in a bid to retain body moisture. They are highly efficient in reabsorbing water from their own excreta. In fact, these termites could be easily identified from their dry faecal pellets, known as frass. They get nutrition from the cellulose present in wood. Numerous symbiotic protozoans and bacteria inhabit the termite's gut which produce certain enzymes to digest cellulose (see Chap. 4 for more details). Some of the examples of drywood termites are *Incisitermes minor* (Hagen) and *Marginitermes hubbardi* (Banks).

6.4.2 Dampwood Termites

Dampwood termites (Termopsidae) infest damp and decaying wood. They do not need soil contact in order to sustain themselves but are commonly found in wood with ground contact. They are commonly found infesting damp or decaying wood, logs, stumps and dead trees but will commonly attack structures exposed to moist soil and high humidity. Although dampwood termites can cause significant damage, especially in association with decaying fungi, they are considered to be the least economically destructive pest.

6.4.3 Subterranean Termites

Subterranean termites inhabit within the soil. They attack moist wood and need a continuous supply of moisture for sustained feeding (Potter 2004). For this, subterranean termites require some kind of contact with the ground soil, or in the case of Formosan subterranean termites, ground contact can be cut off if the moisture source is available above ground (Henderson and Fei 2002). The detail of their foraging behaviour is discussed later in this chapter. Large subterranean termite colonies, for instance, those of *Reticulitermes flavipes* (Kollar), are often decentralized and later get divided into many nesting sites, which are interconnected by a web of underground tunnels (Miller 2010). Apart from foraging underground, these termites also forage above ground for food sources, like the structural wood in buildings.

Subterranean termites construct long tubes of mud and faecal matter, known as exploratory tubes, in a bid to save themselves from predatory ants and desiccation. These tubes are very conspicuous and help in the identification of a potential termite infestation. Foraging termites build labyrinth and highways of different permanent utility or working tubes after locating a wood source. These tubes may cover a long distance and connect the underground galleries to the food source. Termites may also build tubes that connect structural wood to the ground, which are referred to as drop or suspended tubes. These tubes have more wood fibre for the structure, which make them relatively lighter in colour than the utility tubes. Termites also build seasonal swarming tubes, which are just 4–8 inches above ground and are made purposefully to provide exit to the alate swarmers.

Despite of chewing mouthparts, these termites obtain nutrition only from cellulose. However, they fail to digest cellulose on their own and are fully dependent on several microorganisms living symbiotically in their gut, which convert the wood fibre into nutrients. Had there been no gut microorganisms, the termites would die by starvation. Workers feed directly on wood or other cellulose material and accumulate the food in their gut. Thereafter, they return to the other living stages and castes, such as immature termites, soldiers and reproductives, and feed them by sharing food mouth to mouth, which is known as trophallaxis.

Immature termites are unique in their nutritional needs because like all juvenile insects they must moult in order to grow (moulting). During moulting, they also shed the lining of their hindgut where the wood-digesting microorganisms live. After moulting, the termites no longer have their microorganisms and are unable to digest food. In order to replenish their microorganism supply, the young termites feed on fluids (which contain the microorganisms) excreted from the hindgut of older termites. This process of feeding from a nest mate's anus is called proctodeal feeding. Although it may sound disgusting, proctodeal feeding is essential for the survival of the termite colony.

6.5 Food and Feeding Habits

Termites are mostly herbivores and detritivores. They consume wide range of wood, living and dead plants, faeces, etc. They could be differentiated in accordance with their food sources into wood-feeding, grass-harvesting, fungus-growing, or soil-feeding termites. Lower termites consume wood and mostly preferentially consume fungus-infected wood as fungi are rich in protein. Higher termites, however, are euryphagous and have a wide range of food, including soil, humus, grass, leaves, roots and faeces (Radek 1999).

Termites largely feed on cellulose and lignocellulose, and they are known to process 50–100% of dead plant and decaying biomass in the tropical areas (Bignell and Eggleton 2000). Their diets may range from dead wood, grass, soil and forest litter to microepiphytes and cultivated fungi. These dietary habits tend to make termites important ecosystem engineers, which can alter the physico-chemical properties of soil (Dangerfield et al. 1998). Termites are fully dependent on gut symbionts such as protozoa, e.g. *Trichonympha*, flagellate protists, fungi and prokaryotes, to digest the cellulose and use the end products for their own nourishment (Ikeda-Ohtsubo and Brune 2009). Most species of higher termite family, Termitidae, despite producing their own cellulase enzymes, depend on bacteria to digest cellulose (Li et al. 2013). These species lack flagellates in their guts. However, the lower termite families (Engel et al. 2009) excluding grass-feeding Hodotermitidae and the inquiline Serritermitidae, which live in and consume the stored material of other termites, feed exclusively on wood, which they digest with the help of flagellated protistan symbionts (Vargo and Husseneder 2009). See Chap. 5 for more details.

Certain termites, like *Gnathamitermes tubiformans* (Buckley), feed on different food sources in different seasons. They feed on red three-awn in summer, buffalo grass during May to August and blue gram during spring and autumn (Allen et al. 1980). Additionally, their diet gets reduced a lot during spring compared to autumn. Preference to different kinds of wood is dependent on the habitat of termites along with hardness, moisture content, resin and lignin contents of the wood. Drywood termite *Cryptotermes brevis* (Walker) preferred poplar and maple woods (McMahan 1966) along with balsa and Western red cedar (Minnick et al. 1972) and rejected other woods, including pine (Minnick et al. 1972). Ravan et al. (2015) recorded that amongst 17 termite species inhabiting trees, 13 infested on *Populus alba* L. in Iran. This tree preferentially harboured the termite species, *Postelectrotermes pasniensis* Snyder. Similarly, two cogeneric species, i.e. *Anacanthotermes iranicus* Ravan & Akhtar and *A. vegans* (Hagen), were preferentially present on tree, *Tamarix gallica* L. (Ravan et al. 2015).

Soil-feeding termites comprise of 38.3% of Termitidae (Jones and Eggleton 2011), and their high diversity accentuates them to be the successful feeding guild of termites (Brauman et al. 2000). Gut content analysis revealed the presence of plant roots, arthropod body parts, fungal hyphae and plant tissues in their hindguts (Donovan et al. 2001b). Soil-feeding termites have less plant tissue content in the hindguts than wood feeders. However, arthropod body parts, fungal hyphae and plant roots are higher in hindgut contents of soil feeders than those of wood feeders (Donovan et al. 2001b).

Some species of termite are fungus growing and maintain a pool of specialized fungi, viz. *Termitomyces* sp., which are nourished by their excreta. These mycophagous termites complete the life cycle of the latter, as the fungal spores pass undamaged through termite intestines and germinate in fresh faecal pellets (Aanen et al. 2002).

Bignell and Eggleton (2000) categorized termites feeding groups based on the type of organic materials carried to the nest for storage and processing, location of foraging galleries and colony centres of non-mound building species and colour of the worker abdomen. They observed five major well-distinguished feeding groups. However, in some species, the feeding groups are overlapping. The five major groups are as follows:

- Soil feeders: Found only in the members of Apicotermitinae, Termitinae and Nasutitermitinae. They feed on mineral soils, rich in organic matter and silica and poor in recognizable plant tissue.
- Soil/wood interface feeders: Found only in the members of Apicotermitinae, Termitinae and Nasutitermitinae. They feed on strongly decomposed friable wood and soil under logs. The workers have dark-coloured body.
- Wood feeders: The most commonly found termites belong to this group. They mainly feed on wood and woody litter. Except members of subfamily Apicotermitinae, these species occur in all subfamilies of Termitinae.
- Litter foragers: Mainly litter feeders belong to Macrotermitinae, Apicotermitinae, Termitinae and Nasutitermitinae. They feed on leaves and small woody materials which are often transported to and stored in their nests.
- Grass feeders: Grass-feeder species are members of subfamilies Hodotermitinae, Macrotermitinae, Termitinae and Nasutitermitinae. They feed on standing dried dead grass and other low vegetation usually cutting and transporting to their nest.

There are also some further minor feeding groups which feed on algae, lichens, fungi, dung, vertebrate corpse and mounds built by other species (Black and Okwakol 1997; Bignell and Eggleton 2000).

6.6 Mating and Reproduction

Hartke and Baer (2011) gave a detailed review of the mating biology of termites. Mating in termites has been characterized by the pair formation and colony foundation during and after nuptial flights (Calleri et al. 2007; Husseneder and Simms

2008; Adam and Mitchell 2009). Termite kings can provide large numbers of viable sperm to the queen continuously for up to several decades. It is as remarkable as that of some social hymenopteran queens to store sperm of their deceased mates for similar amounts of time (Keller and Genoud 1997). Kings have paired testes and produce sperm as a product of spermatogenesis, which prematurely occur in the nymphal stage (Ye et al. 2009). Ejaculatory duct of fifth instar larva may contain sperm (Dean and Gold 2004). However, the testis may attain further sexual maturity as the male further develops into an adult. Sperm are absent in the accessory glands or seminal vesicles of lower termites, which have expedited growth as the termite colony is establishing. These glands also produce secretions that are vital to keep sperm alive and are transferred to the queen during ejaculation (King et al. 2011). These glands are, however, reduced or absent in higher termites (Grasse 1982), indicating the absence of postcopulatory sexual selection on seminal fluid components.

Sperm vary in morphology and motility in different species of termites. In *Mastotermes darwiniensis* Froggatt, the sperm is multiflagellated arrowhead-shaped (Baccetti and Dallai 1978), while *Zootermopsis nevadensis* (Hagen) has pin-shaped immotile sperm (Baccetti et al. 1981). Families, viz. Rhinotermitidae and Termitidae, have completely aflagellate spheroidal sperm (Baccetti et al. 1981). External sclerotized genitalia are absent in both kings and queens with the exception in *Stolotermes ruficeps* Brauer (Klass et al. 2001) and *M. darwiniensis* (Klass 2000). Males of these termites have small phallic lobes rather than the fully sclerotized genitalia, which also indicate the absence of sexual selection in certain species.

6.6.1 Termite Queen

Female reproductives or queens have a pair of ovaries that grow substantially in size after swarming (Dean and Gold 2004). There is an increased demand of egg production in termites, and hence the development of the ovaries of basal termite queens causes the abdomen to swell slightly so they become physogastric. Physogastry is extreme in most Termitidae such as in *Nasutitermes corniger* (Motschulsky), in which the mass of a mature physogastric queen can be 50–60 times larger than that of the initial dispersing female.

The queens are provided with a spermatheca, which is generally a recurved blind pouch meant to store sperm (injected by the kings). Spermathecal wall contains cells which seem to secrete mucopolysaccharides (Raina et al. 2007; Ye et al. 2009). The purpose of the spermathecae is to store sperm needed to fertilize eggs in a later phase of her life and also to ensure its viability. Immature females or swarming alates have spermathecae devoid of sperm, which is a strong evidence of no occurrence of mating in the parental nest before dispersal (Dean and Gold 2004; Ye et al. 2009). There is a sclerotized spermathecal duct, which connects the spermatheca with the bursa copulatrix.

6.6.2 *Nuptial Flight and Sexual Act*

Swarming is an integral phenomenon in termite life cycle. On attaining maturity, the reproductives develop wings and functioning eyes. They are known as alates and also become harder and darker to help swarming termites to withstand exposure to light and less humid air. Alates are the winged reproductives which can produce new kings and queens. A certain size of colony is needed before alates are produced; therefore it often takes several years before a colony reaches a size allowing production of alates. When the time has come, the alates leave the colony in a large swarm containing many thousands of termites. Rainfall may be the trigger for initial release. After attaining maturity, the unmated kings and queens participate in mass swarming events, which may last for a few days, once or twice per year. This nuptial flights has a (1) dispersing phase, which is characterized by both mating partners flying away from their nest, and a (2) pair formation phase, in which individuals may release pheromones to attract each other (Hanus et al. 2009). Even a prominent courtship occurs prior to mating, also known as "tandem running", as male follows the female and touches her abdomen with his antennae as she runs to find a nest (Kirton and Brown 2003; Husseneder and Simms 2008; Hartke 2010).

Mostly in lower termite families, only one king and queen inhabit the colony, and the sexual individuals who try to invade the nest for the mating purpose are attacked or killed (Nutting 1969). However, in certain higher termite families, multiple primary kings and queens are found in a single nest (Thorne 1985). Both monogamy and polygamy are featured in termite colonies. However, polygamy seemingly is facultative and not obligatory. It is also noticed that monogamous pairs are more potential mates in terms of quantitative progeny and survival rate than the polygamous ones (Hartke 2010).

Though mate selection and pair formation are a feature of the nuptial flight, it doesn't culminate in mating or copulation. A mating pair copulates only after attaining security in the form of founding a nest. In the nest, courtship act again gets started, including mutual antennation and grooming, and finally culminates in mating, when they face in opposite directions (Raina et al. 2003). Aflagellate sperm gets transferred during mating to the outer genital chamber and get stored in the spermathecae of the queen.

6.6.3 *Inbreeding Depression*

Neotenic or sexual reproduction within the parental nest occurs both in lower (62.7%) and higher (13.4%) termite families (Myles 1999). However, the percentage of reproducing neotenics in a colony and the proportion of new offspring produced by them show high variations both within and amongst species (Vargo and Husseneder 2009). Neotenic brothers may also compete to form mating pairs with the neotenic sisters. There is seemingly a possibility that termite colonies can achieve infinite lifespans through continuous rounds of inbreeding as the older kings and queens are dying and are replaced by the new ones.

In certain termite species, the neotenic queens are more fecund than the single primary one (Thorne and Haverty 2000; Brent et al. 2008). However, the limited size of the nest and food shortage may compel the newer, young kings and queens to move out of the nest and search for new ones (Vargo and Husseneder 2009). Kings of certain *Reticulitermes* species abstain themselves from inbreeding as the king copulates with the clones of his deceased queen, which are parthenogenetically produced, rather than mating with his daughters (Matsuura 2011). Termite colony is negatively affected with the deaths of primary king and queen, as then the colony is doomed to inbreeding depressions, resulting in weaker genotypes (Neoh et al. 2010).

6.6.4 Parthenogenesis

Parthenogenesis in termites was first reported by Light (1944) and reviewed by Matsuura (2011). In general, the percent of parthenogenesis is very low. It has been largely ignored in literature as it might be regarded as an unusual case with little adaptive significance in nature. Mostly, it was believed that the role of parthenogenesis in termites was no more than "the best of a bad job", that is, females resort to parthenogenesis only when they failed to mate with males (Matsuura and Nishida 2001; Matsuura et al. 2002). Nevertheless, in some termite species, it plays a much greater role than what has been previously understood.

Thelytoky is a kind of parthenogenesis in which females are produced from unfertilized eggs. There are two types of thelytokous parthenogenesis, viz. apomixis (i.e. ploidy stasis) and automixis (i.e. ploidy restoration). The frequency of thelytoky is very low in termites, and it has been reported in only seven species (Matsuura 2011). Mostly termites, such as *Reticulitermes speratus* and *R. virginicus* (Banks), largely resort to automixis thelytoky. Due to this, heterozygosity is highly reduced, and the original mother queen genome is restored in the daughters that are destined to become secondary/neotenic queens (Matsuura et al. 2004).

Queens of above-mentioned two species of termites exclusively go for parthenogenesis to produce secondary or neotenic queens. Such queens, if couldn't mate with males, are found to cooperate with female partner, or even alone, and reproduce by parthenogenesis (Matsuura and Nishida 2001; Matsuura et al. 2002). However, when they mate with the primary kings, they produce workers and alates (Matsuura et al. 2009). Normally, it is seen that if an alate's wings get broken after swarming, it runs on the ground and finds a partner. The couple then locates a suitable nest site with the male following the female. However, it is also noticed that two de-alated queens can also form a pair (Matsuura et al. 2002). This may be due to the fact that initiation of colony foundation can be delayed if only a single queen tries to make it as compared to that made by two queens or a heterosexual pair. Additionally, two queens can grow a colony faster than the heterosexual mating pair. Such paired queens then lay parthenogenetic eggs that are significantly larger than the sexual ones (Matsuura and Kobayashi 2007). Thus, in this scenario, parthenogenesis can be considered advantageous for faster development and sustenance of colony and species.

Laying larger eggs may also be considered adaptive as it is likely that larger eggs give rise to larger offspring that can survive better than small offspring in a stressful environment. Additionally, this type of asexual queen succession system restores the genome of the primary queen and avoids the loss due to an inbreeding depression. This kind of asexual queen succession system is highly advantageous. Primarily, it produces numerous secondary/neotenic queens, which cumulatively elevates the rate of increase of the individuals in the nest at a much faster rate (Grube and Forschler 2004). Secondly, it reduces inbreeding, and the secondary homozygous queens are always cared for and protected by the workers (Matsuura 2011). Thirdly, as secondary queens only inherit the queen's genes, the founder primary queen does not suffer any loss in her genetic contribution to future generations; thereby her genome is restored (Matsuura et al. 2009; Matsuura 2011). Fourth, the production of homozygous parthenogens may help in eliminating the recessive deleterious alleles, thus preventing their transmission to sexual offsprings in the next generation.

6.7 Factors Affecting Termite Biology

Both abiotic and biotic factors have a large effect on the biology of termites. Amongst abiotic factors, temperature, pH and rainfall have a significant effect on the survival, growth, development and reproduction, as they affect other insects (Omkar and Pervez 2002, 2004; Pervez and Omkar 2004). These abiotic factors are also responsible for their geographical distribution and local occurrence (Reddy and Sammaiah 1991).

6.7.1 Temperature

Temperature is a crucial factor for the survival, growth, development and reproductions of insects, including termites. Increase in temperature increases the development, growth and reproduction in termites. For instance, drywood termite, *Incisitermes minor* (Hagen), preferred 27 °C temperature to swarm and increase its fitness components (Harvey 1946). Subterranean termite, *Reticulitermes hesperus* Banks, prefers soil temperatures ranging from 29 to 32 °C (Smith and Rust 1994). Feeding rate (Nakayama et al. 2005) and survival rate (Fei and Henderson 2002) of *C. formosanus* were found to be highest at 30 °C. Highest wood-attacking activity was recorded by these termites at 36 °C (Imamura and Fujii 1995). Despite increased feeding propensity at higher temperatures, the survival rate is highly affected at temperature beyond 36 °C.

Quarles (2007) was worried about the fact that increase in global temperature is resulting in the outbreak of pests, especially termites. He expected a tremendous increase in the termite population with temperature. He noted that subterranean termites, *Reticulitermes* spp., have spread throughout the USA, but their numbers are highest in the Southeast and California, where climate is hot and the winters are warmest. Additionally, the gradual spread of Formosan subterranean termite, *C. formosanus*, towards cold, northern states of the USA, despite being a tropical species, is a clear indication of the effect of global warming in those regions (Potter 1997). Drywood termites are abundant in the southern part of the USA and are likely to expand their distributions northwards, with the increase in temperature (Potter 1997). Expansion of termite distribution could be a threat to the environment as they produce copious amounts of the greenhouse gas methane, which will further add to the problem of global warming (Thakur et al. 2003).

Termites inhabiting in temperate regions have lower temperature requirements, as reported in *R. hesperus*, whose feeding is optimum at 21 °C (Smith and Rust 1993). On increasing temperatures starting from 26 °C, high mortality was recorded. Similarly, termites living in higher temperature regimes require warmer temperatures for their sustenance, as in the case of desert subterranean termite, *Heterotermes aureus* (Snyder), whose feeding propensity was maximum at 36 °C (Haverty and Nutting 1974).

Temperature also influences foraging and seasonal activities (Potter 2004) albeit termites can ventilate and regulate temperature and relative humidity within their nests (Turner 1994). Foraging behaviour is seasonal in subterranean termites, and they refrain from foraging where soil surface temperatures are at both cold and hot extremes (Delaplane 1991; Smith and Rust 1994).

6.7.2 Moisture

Moisture and relative humidity (RH) are an important abiotic factor for the survival of termites. Certain termites, especially subterranean ones, have soft cuticle with poor water-retaining properties, resulting more susceptible to lose moisture through the integument and prone to desiccation. Termites are directly dependent on moisture either from environment or the food source. The nest material moisture requirements of subterranean termites range from 23% to 60% by weight (Sponsler and Appel 1990).

Heavy infestations of Formosan subterranean termites are more conspicuous on the water-bound trees, which indicate they forage better in high humid areas (Henderson 2008). This preference for high moisture content of wood could depend on the fact that moisture softens the wood fibre thereby easing its mastication (Delaplane and LaFage 1989). With the availability of moistened food, optimum RH for the activity of *C. formosanus* was greater than 70% at 28 °C (Yusuf et al. 2000). Similarly, 90% RH at 30 °C for *C. formosanus* was reported by Nakayama et al. (2004).

On the contrary, some termite species, such as *Reticulitermes* sp., have less water requirements and construct above-ground nests, sometimes in complete isolation, indicating their ability to forage in dry substrates (Forschler and Henderson 1995). The termite populations face a sharp declination due to heavy rainfall (Forschler and Henderson 1995). Termites such as *R. flavipes* and *Reticulitermes tibialis* Banks show a lesser moisture preference range than *R. virginicus* (Green et al. 2005).

6.8 Conclusion

From the above overview, it is clearly evident that termites, despite being serious pests, have many intricate properties, which make them so different from other eusocial insects. High longevity of the nest mates, especially queens, could explain why termites could be dangerous, as their numbers are increasing as they resort to both sexual and asexual reproduction. False workers or pseudergates again are intricate nest mates who perform all the foraging and household jobs but still have the potential to further develop into reproductives. Evolutionary aspects of early origin of workers or soldiers are still unclear and still need to be understood, by using both theoretical and pragmatic approaches.

Another interesting aspect in termites is polyethism, especially size-dependent polyethism in soldiers, as younger soldiers are better in recognizing, attacking and combating the potential raiders and invaders of the colony. Normally, in insects, the older individuals are more equipped for such mortal combats. Feeding behaviour further supports the intricacies of termites and accentuates why this group of insects is so unique. Wood-eating termites do not have enzymes to digest the wood, and gut symbionts are required. Certain species of higher termites (Termitidae) however do produce the enzyme cellulase, yet they are largely dependent on gut symbionts for the cellulose digestion. This successful symbiotic relationship with gut symbionts is a major reason why termites have such a vast potential to destroy any kind of wood and may be clubbed into one of the most notorious insect pests.

Termites are also very good architects and builders. Construction of different types of intricate galleries, tunnels and tubes provides impressive examples of their engineering skills. These nests are capable of giving shelter to several thousand individuals including numerous reproductives. Additionally, innate property of the alates to fly elsewhere and establish a new colony is another reason for the successful establishment of this group of insects. Overview from mating and reproduction revealed that display of parental care and role of kings are more conspicuous in termites as compared to other groups of eusocial insects. Thelytokous parthenogenesis, although not a regular feature in other insects, occurs in termites. However, its percentage is very low, but it is highly advantageous for the sustenance of species and for the restoration of the gene pool of the mother queen.

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Chapter 7
Trail Pheromones in Termites

Paulo F. Cristaldo

Contents

Abstract Termites use a range of semiochemicals to maintain the organization and integrity in their colonies. Among these semiochemicals, the trail pheromone is responsible for the orientation and recruitment of nestmates from the nest to the food sources. Trail pheromones in termites are secreted by a unique exocrine gland source, the sternal gland present in the abdominal sternites of all termite castes. In the majority of termite species, trail pheromone comprises a single compound. However, in the most advanced species, trail pheromone comprises two or, in one exception case, a blend of three compounds. In general, there is a clear difference between composition of trail pheromone in termite species from basal families and from those of more advanced families. Distinct responses of workers and soldiers to trail pheromone are observed as well as the response to trail pheromone from neighbouring colonies. The present chapter outlines the current states of knowledge of trail pheromones in termites.

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7.1 Introduction

Insect societies (termites, ants, some bees and wasps) have been calling attention over years due to their ecological role, social evolution, collective behaviour and the efficient and spectacular ways of communication. Most of the activities in social insects are chemically mediated, which allow to maintain the organization and integrity in their colonies. Chemical communication is even more evident in termite species since they are blind, and semiochemicals are involved in almost all activities of their life. Among these activities, it is the exploration of environment in search of food resources (e.g. foraging process). Such collective behaviour is coordinated by trail pheromones, and in some termite species, for example, *Constrictotermes cyphergaster* (Termitidae: Nasutitermitinae), it is responsible for the establishment of impressive columns with thousand individuals (Fig. 7.1). The ecology and behavioural aspects of foraging in termites have been reviewed by Traniello and Robson (1995) and Traniello and Leuthold (2000). Recently, Almeida et al. (2016) have showed a new behavioural repertoire of foraging in termites.

Trail pheromone is secreted by sternal glands and is deposited when a termite presses its abdomen against the substrate (Fig. 7.2). Such pheromone stimulates foragers to leave the nest and orient them to the food source (Stuart 1961, 1981). Foraging seems to begin with an explanatory phase of searching for food, proceed-

Fig. 7.1 Foraging in the open-air termite *Constrictotermes cyphergaster* (Termitidae, Nasutitermitinae). Sergipe, Brazil

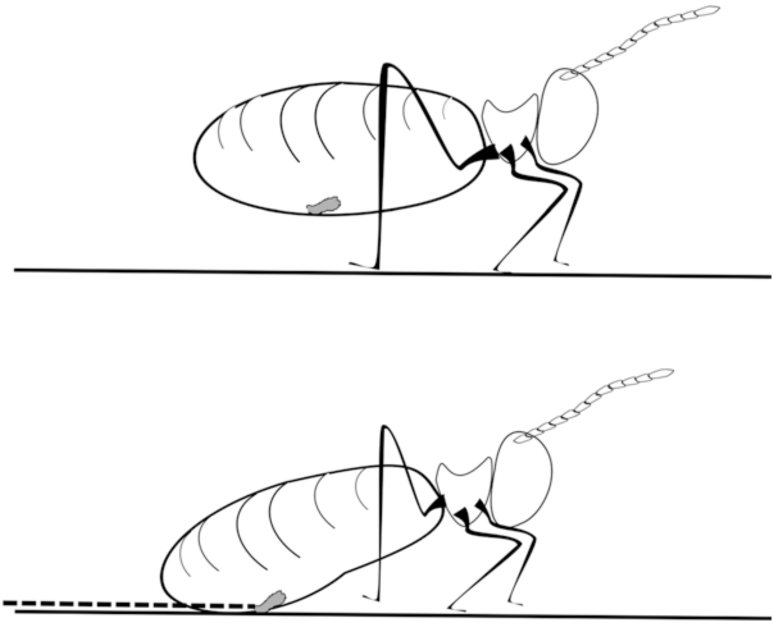


Fig. 7.2 A schematic drawing of termite worker depositing trail pheromone in the substrate

ing by the recruitment of the nestmate to the food source. In the explanatory phase, trail pheromone deposited appears less attractive than that deposited in the recruitment and foraging trails (Reinhard and Kaib 2001). Trail pheromone is responsible to trail-following behaviour. It is a decisive communication channel to those termite species that acquire their food resource outside of their nests (“separate” life type; Hodotermitidae, some Rhinotermitidae and almost all Termitidae) and also for species that consume a resource in which they nest or also those that move from one nesting site to another (“intermediate” life type; e.g. Mastotermitidae, Rhinotermitidae and some Termitidae). However, in “one-piece” termite species (e.g. Termopsidae and Kalotermitidae), trail pheromone is used to locate areas of disturbance and to colonize new food sources (Traniello and Leuthold 2000), because such species does not need orientation mechanisms to foraging.

According to Sillam-Dusses (2010), trail pheromone in “one-piece” termite species may be involved in the alarm communication, in which a trail laid by an alarmed termite from the point of disturbance leads the nestmates to defend and repair the disturbance point. Recently, Cristaldo et al. (2014) suggested that the obligatory inquiline *Inquilinitermes microcerus* (Termitidae, Termitinae) should use trail pheromone in similar way that in “one-piece” termite species, because such species seems not to forage outside from their host nest (Florencio et al. 2013; Barbosa-Silva et al. 2016). In this species, trail pheromone must be used to avoid contact with host colonies, inside the shared nest (Cristaldo et al. 2014).

In the last decades, numerous studies have shown the chemical nature of trail pheromones in different termites (see Costa-Leonardo et al. 2009; Sillam-Dusses 2010; Bordereau and Pasteels 2011). This chapter outlines the current status of knowledge of termite trail pheromones.

7.2 The Glandular Source of Trail Pheromone: The Sternal Gland

The sternal gland located in the abdominal sternites is the sole glandular source of trail pheromone in termites (Noirot 1969) (Fig. 7.2). The sternal gland has been observed in all castes and secretes not only the trail pheromone but also the sex pheromone (Noirot 1969; Bordereau and Pasteels 2011).

The number and position of sternal glands are variables across termite families (see Noirot 1995; Quennedey et al. 2008). In Mastotermitidae (*Mastotermes darwiniensis*), the most basal termite family, three separate sternal glands are present in the middle of the 3rd, 4th and 5th abdominal sternites. Although *M. darwiniensis* have three active sternal glands, their efficiency varies considerably. According to Sillam-Dusses et al. (2007), the trail pheromone secreted by the sternal gland present in the 4th abdominal sternites induces a higher activity, compared to that of the sternal gland present in the 3rd abdominal sternites. However, the trail pheromone produced by sternal glands from 5th abdominal sternites was almost inactive.

In other termite families, a single sternal gland is observed. In Termopsidae and Hodotermitidae species, the sternal gland is found in the margin of the 4th abdominal sternites. In Kalotermitidae, Rhinotermitidae, Serritermitidae and Termitidae, a single sternal gland is observed in the margin of the 5th abdominal sternite (Noirot 1995; Quennedey et al. 2008).

A decrease in the size of sternal glands is also observed among termite families, varying from the large one found in Mastotermitidae (200/300 μm × 450/800 μm × 15/25 μm) (length × width × height) to the very small sternal gland of Nasutitermitinae species (100 μm × 195 μm × 25 μm) (Quennedey et al. 2008).

Another interesting point is the presence of different cell classes in the sternal glands across termite families: class 1 and 2 cells are found in all termite species, while class 3 cells are found only in Termopsidae, Serritermitidae and Rhinotermitidae species (see details in Quennedey et al. 2008). The presence of different class cells can be related with semiochemicals secreted in the sternal glands that can have another role than the trail-following behaviour. In the dampwood termite *Zootermopsis angusticollis* (Archotermopsidae), for example, sternal gland secretions have been reported to have fungistatic properties (Rosengaus et al. 2004).

7.3 Chemistry of Trail Pheromones in Termites

7.3.1 Composition

The trail pheromones have been identified in 66 species across 7 termite families (Table 7.1). Their chemical diversity is very low, with only nine compounds identified (Fig. 7.3; Table 7.1), belonging to four chemical classes (alcohols, aldehydes,

Table 7.1 Chemical compounds acting as trail pheromones across termite families

Family/Subfamily	Genus	Trail pheromone	References
Mastotermitidae	*Mastotermes*	(*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
Archotermopsidae	*Hodotermopsis*	*syn* 4,6-dimethyldodecanal + traces of 4,6-dimethylundecan-1-ol	Lacey et al. (2011)
	Zootermopsis	*syn* 4,6-dimethyldodecanal	Bordereau et al. (2010)
Stolotermitidae	*Porotermes*	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
	Stolotermes	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
Kalotermitidae	*Cryptotermes*	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Incisitermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Kalotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Neotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Postelectrotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Procryptotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
Rhinotermitidae	*Coptotermes*	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Tokoro et al. (1989) and Sillam-Dussès et al. (2006)
	Heterotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Reticulitermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Matsumura et al. (1968), Tai et al. (1969), Tokoro et al. (1991), Laduguie et al. (1994) and Wobst et al. (1999)

(continued)

Table 7.1 (continued)

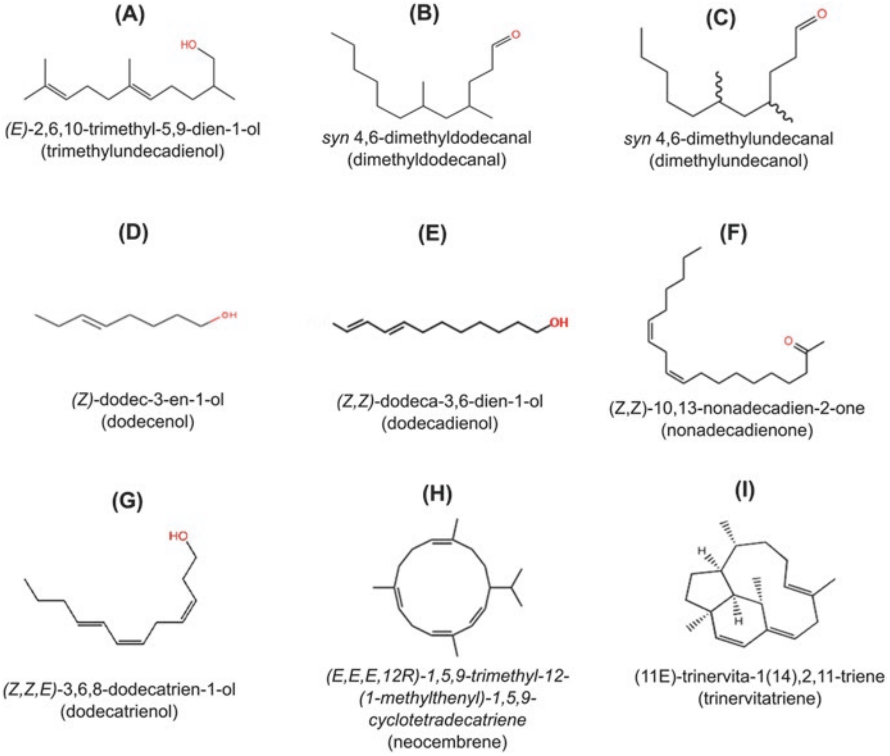
Family/Subfamily	Genus	Trail pheromone	References
	Prorhinotermes	Neocembrene	Sillam-Dussès et al. (2005)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2009a)
	Rhinotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Schedorhinotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
Serritermitidae			
	Glossotermes	(10Z,13Z)-nonadeca-10,13-dien-2-one	Hanus et al. (2012)
Termitidae			
Macrotermitinae	*Ancistrotermes*	(Z,Z)-dodeca-3,6-dien-1-ol	Robert et al. (2004)
	Macrotermes	(Z)-dodec-3-en-1-ol	Peppuy et al. (2001a)
	Odontotermes	(Z)-dodec-3-en-1-ol	Peppuy et al. (2001b)
		(Z,Z)-dodeca-3,6-dien-1-ol	Deng et al. (2002)
		(3Z)-dodec-3-en-1-ol + (3Z,6Z)-dodeca-3,6-dien-1-ol	Wen et al. (2014)
	Psammotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2011)
	Pseudacanthotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Bordereau et al. (1993)
Termitinae	*Amitermes*	Dodecatrienol + neocembrene	Kotoklo et al. (2010)
	Cubitermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Drepanotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Inquilinitermes	Dodecatrienol +neocembrene*	Cristaldo et al. (2014)
	Termes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
Syntermitinae	*Silvestritermes*	Dodecatrienol + neocembrene	Bordereau and Pasteels (2011)
	Cornitermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Embiratermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Bordereau and Pasteels (2011)
	Syntermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)

(continued)

Table 7.1 (continued)

Family/Subfamily	Genus	Trail pheromone	References
Nasutitermitinae	*Constrictotermes*	Dodecatrienol +neocembrene	Sillam-Dussès et al. (2010) and Cristaldo et al. (2014)
	Nasutitermes	Neocembrene	Moore (1966) and Birch et al. (1972)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2010)
	Nasutitermes	Dodecatrienol +neocembrene + trinervitatriene	Sillam-Dussès et al. (2010)
	Trinervitermes	Neocembrene	McDowell and Oloo (1984)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2010)

*Trail pheromone identity was inferred by results obtained by behavioural bioassays; no compounds were found in the sternal glands of workers (see more details in Cristaldo et al. 2014)



(A) *(E)*-2,6,10-trimethyl-5,9-dien-1-ol (trimethylundecadienol)

(B) *syn* 4,6-dimethyldodecanal (dimethyldodecanal)

(C) *syn* 4,6-dimethylundecanal (dimethylundecanol)

(D) *(Z)*-dodec-3-en-1-ol (dodecenol)

(E) *(Z,Z)*-dodeca-3,6-dien-1-ol (dodecadienol)

(F) (Z,Z)-10,13-nonadecadien-2-one (nonadecadienone)

(G) *(Z,Z,E)*-3,6,8-dodecatrien-1-ol (dodecatrienol)

(H) *(E,E,E,12R)-1,5,9-trimethyl-12-(1-methylthenyl)-1,5,9-cyclotetradecatriene* (neocembrene)

(I) (11E)-trinervita-1(14),2,11-triene (trinervitatriene)

Fig. 7.3 Compounds identified as trail pheromone in termite species hydrocarbons and ketones). In most of the termite species, the trail pheromone is made of a single compound while in others, particularly in Nasutitermitinae species, it is made of two compounds. The presence of three compounds acting as trail pheromone was described only in *Nasutitermes corniger* (see Sillam-Dusses et al. 2010).

The trail pheromone seems to be very conserved across termite families. The (*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol (trimethylundecadienol; Fig. 7.3a) is the compound acting as trail pheromone in *Mastotermes darwiniensis* (Mastotermitidae) and also in two species of Termopsidae, *Porotermes adamsoni* (Porotermitinae) and *Stolotermes victoriensis* (Stolotermitinae) (Sillam-Dusses et al. 2007). In the family Archotermopsidae, *syn* 4,6-dimethyldodecanal (dimethyldodecanal; Fig. 7.3b) is the trail pheromone in *Zootermopsis angusticollis* and *Z. nevadensis* (Bordereau et al. 2010). However, in *Hodotermopsis sjoestedti*, the trail pheromone is composed of *syn* 4,6-dimethylundecan-1-ol (dimethylundecanol; Fig. 7.3c) and traces of dimethyldodecanal (Lacey et al. 2011). In Kalotermitidae, all species studied so far have (Z)-dodec-3-en-1-ol (dodecenol; Fig. 7.3d) as trail pheromone (Sillam-Dusses et al. 2009b). The (3*Z,6Z,8E*)-dodeca-3,6,8-trien-1-ol (dodecatrienol; Fig. 7.3g) is the trail pheromone in almost all species from Rhinotermitidae family (see Table 7.1 for references). The exception is the *Prorhinotermes* sp. that has (1E,5E,9E,12R)-1,5,9-trimethyl-12-(1-methylethenyl)-1,5,9-cyclotetradecatriene (neocembrene; Fig. 7.3h) or the mixture of neocembrene and dodecatrienol as trail pheromone (Sillam-Dusses et al. 2005, 2009a). In Serritermitidae family, it has been identified the (10Z,13Z)-nonadeca-10,13-dien-2-one (nonadecadienone; Fig. 7.3f) as trail pheromone of *Glossotermes oculatus* (Hanus et al. 2012).

In the advanced termite species (Termitidae), trail pheromone differs among subfamilies. Dodecenol (Fig. 7.3d) was identified in Macrotermitinae as trail pheromone of *Macrotermes* sp., *Odontotermes hainanensis* and *O. maesodensis* (Peppuy et al. 2001a), while dodecadienol (Fig. 7.3e) was identified as trail pheromone of *Ancistrotermes pakistanicus* (Robert et al. 2004) and *O. formosanus* (Deng et al. 2002). Dodecatrienol was identified as trail pheromone for *Pseudacanthotermes militaris* and *P. spiniger* (Bordereau et al. 1993).

Among Termitinae sp., dodecatrienol was identified as trail pheromone in *Cubitermes* sp., *Drepanotermes perniger* and *Termes hispaniolae* (Sillam-Dusses et al. 2006). The mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Amitermes evuncifer* (Kotoklo et al. 2010) and *Inquilinitermes microcerus* (Cristaldo et al. 2014). Dodecatrienol is the trail pheromone in almost all species of Syntermitinae studied so far (Sillam-Dusses et al. 2006; Bordereau and Pasteels 2011). However, the mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Silvestritermes euamignatus* (Bordereau and Pasteels 2011). In Nasutitermitinae species, the mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Constrictotermes cyphergaster* (Sillam-Dusses et al. 2010; Cristaldo et al. 2014), some species of *Nasutitermes* genus and also in *Trinervitermes geminatus* and *T. trinervoides* (Sillam-Dusses et al. 2010). In *N. corniger*, the compound trinervitatriene (Fig. 7.3i) was also identified as trail pheromone, additionally to the mixture of dodecatrienol and neocembrene (Sillam-Dusses et al. 2010). Neocembrene was reported as single component of trail pheromones in

N. exitiosus, *N. graveolus*, *N. walker* (Moore 1966; Birch et al. 1972) and in *T. bettonianus* (McDowell and Oloo 1984). The trail pheromone of termites from Apicotermitonae subfamily remains unidentified.

In general, there is a clear difference between trail pheromone from species of basal termites (from Mastotermitidae to Stolotermitidae) and those from more advanced families (from Kalotermitidae to Termitidae): basal termite species have trail pheromone made of C14 alcohol or a C14 or C18 aldehyde, while advanced termite species have trail pheromones made of C12 alcohols or C20 diterpenes. Such distinction seems to be related to their ecology and life style (Sillam-Dusses 2010).

7.3.2 *Activity Threshold of Trail Pheromones*

The trail pheromone activity threshold varies from 1 ng/cm in the most basal termite *M. darwiniensis* (Sillam-Dusses et al. 2007) to 10^{-8} ng/cm in *Reticulitermes hesperus* (Saran et al. 2007). Optimal activity threshold ranges, in most species, between 10^{-2} and 1 ng of pheromone per cm of trail (Bordereau and Pasteels 2011). Above 1 ng of trail pheromone, trail-following behaviour is generally reduced once chemoreceptors are saturated and termite is unable to follow the trails.

7.4 Responses of Workers and Soldiers to Trail Pheromone Signals

Different responses of termite castes (workers and soldiers) to the trail pheromone have been reported in the literature. In almost all termite species studied, the trail pheromone seems to be deposited only by workers during the recruitment phase (Costa-Leonardo et al. 2009). However, soldiers have been shown to be responsible for the initial exploration of foraging area, proceeded by the recruitment of workers in some Rhinotermitidae (*R. santonensis* (Reinhard and Kaib 2001), *Heterotermes tenuis* (Casarin et al. 2008) and *Coptotermes intermedius* (Olugbemi 2011)) and also in Nasutitermitinae species (*N. corniger* (Traniello 1981; Traniello and Busher 1985), *Longipeditermes longipes* (Miura and Matsumoto 1998), *Constrictotermes cyphergaster* (Moura et al. 2006) and *N.* aff. *coxipoensis* (Almeida et al. 2016)). In *Coptotermes gestroi*, workers initiate the foraging, but soldiers are recruited after discovery of the food source (Arab et al. 2012). Workers and soldiers have been reported to initiate the exploration of new areas in *Velocitermes heteropterus* (Haifig et al. 2015). According to Almeida et al. (2016), the participation of soldiers in the initial exploration of areas, with continued participation in trail construction and escorting services during tunnel construction, must be common among the Nasutitermitinae species.

The precise role of emission of trail pheromone and responses to these signals by the termite soldiers are still poorly explored. However, in *Nasutitermes* species, soldiers have been shown to deposit trails more attractive than those deposited by workers (see Arab et al. 2006; Almeida et al. 2016). In *N. corniger*, trails laid by soldiers were observed to recruit only soldiers, but those laid by workers recruited both workers and soldiers (Traniello 1981). These observed differences in the responses of castes to trail pheromone must be related to qualitative or quantitative differences between workers and soldiers, as already hypothesized by Arab et al. (2006) and Almeida et al. (2016).

Different responses to pheromone trails was also observed among small workers in *M. bellicosus*, preferentially following trails established by small workers than those established by large ones (Gessner and Leuthold 2001).

7.5 Detection of Trail Pheromones by Neighbouring Colonies

Although the ecological success of any organism depends on the specificity of its communication channels, perception of heterospecific signals by other individuals is widely observed in nature (Danchin et al. 2004; Valone 2007; Evans et al. 2009; Cristaldo et al. 2016b). The ability to perceive and respond to trail pheromones from neighbouring colonies can benefit the exploiter about food source location.

In termites, perception and response to trail pheromone from neighbouring colonies have been observed among neighbouring colonies of the same as well as of different species. Oloo (1981) observed that workers of *Trinervitermes bettonianus* do not show a significant preference to trails from their own colony compared with those from neighbouring colonies of the same species. However, *T. bettonianus* as well as the sympatric species *M. michaelseni* and *Odontotermes* sp. was not able to follow trail from neighbouring colonies of sympatric species. In another study, allopatric populations of *T. bettonianus* were able to follow alien as well as their own trails (Oloo and McDowell 1982). Similar results were also reported for *R. grassei* and *R. santonensis* (Wobst et al. 1999) and in *P. spiniger* and *P. militaris* (Bordereau and Pasteels 2011). According to Peppuy et al. (2001b), specific signals of trail pheromone must be more marked among species from different genera than among species from the same ones.

Recently, Cristaldo et al. (2016a) have shown that resource availability can modulate the perception and response of neighbouring colonies in *Nasutitermes* aff. *coxipoensis*. Workers from colonies reared under low and intermediate resource availability followed the same distance on trails with extracts from their own colonies, compared to extracts from neighbouring colonies. However, workers from colonies reared with high resource availability avoided the following chemical cues from neighbouring colonies. Such results indicate that chemical cues from neighbouring colonies can be detected by termites and may influence colony foraging choice.

The perception and response of chemical cues from neighbouring colonies should have a strong impact on termite community structure, including the spatial distribution of foraging areas, species co-occurrence and species coexistence in a single nest (termite inquilinism) (see details in Cristaldo et al. 2016a; Araújo et al. 2017). In fact, the perception and avoidance of trail cues from host nest by inquilines seem to ease the cohabitation among different termite species, in a single nest (see Cristaldo et al. 2014).

7.6 Conclusion

The study of trail pheromone in termites has been increased in the last decades; however, its composition in species of Apicotermitinae subfamily has not been studied yet. In general, the termite trail pheromone seems to be very conserved among families, with only nine compounds identified as trail pheromone. There is a clear difference between trail pheromone from basal termite species and that from more advanced families. Such distinction seems to be related with their ecological life style. In Nasutitermitinae species, trail pheromone deposited by soldiers plays a key role in the recruitment of workers, from the nest to the food source. Although few studies have reported the ability of termites to follow chemical cues from neighbouring colonies, such behaviour possibly has a strong impact on termite community structure.

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Chapter 8
Cues Used by Subterranean Termites During Foraging and Food Assessment

Timothy M. Judd

Contents

Abstract Subterranean termites tunnel through soil to locate new food sources, an energetically expensive process. The use of efficient search patterns and food location cues reduce the cost of foraging. Once arriving at a potential food source, termites assess its quality using a different set of cues. These types of cues could affect recruitment and colony health and survival. This chapter reviews what is known about the foraging process of subterranean wood-feeding termites, a group that con-

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tains a number of economically important pests. It summarizes what is known about search patterns used by these termites and the role of food location cues to effectively reach a viable food source. This chapter also discusses what is known about wood preference and how different components of wood such as density, secondary metabolites, nutrients, and other factors affect food selection in subterranean wood-feeding termites.

Keywords Subterranean termite • Foraging • Food selection • Wood preference • Foraging cues

8.1 Introduction

Termites have been traditionally grouped according to their feeding ecology including one-piece termites (those that live in and feed on wood), arboreal termites, and subterranean termites (Abe 1987). Subterranean termites include soil feeders, litter feeders, and wood feeders (Abe 1987; Donovan et al. 2001; Eggleton and Tayasu 2001). There are several reviews of termite nutritional ecology and foraging behavior that include all feeding types of termites (Wood 1978; Waller and La Fage 1987; Traniello and Leuthold 2000). This chapter will instead focus on the location and selection of food in one feeding group, the subterranean, wood-feeding termites (hereafter just referred to as subterranean termites). Due to the economic importance of many of them, there have been a number of studies that have examined the types of cues used during foraging and selection of food. This review discusses what is known about the cues used by subterranean, wood-feeding termites during different stages of foraging, including search patterns, localization cues, and assessing food quality. Understanding the search patterns and cues used during the foraging process could improve methods for controlling termites and possibly lead to methods that prevent termite infestations.

8.1.1 Nutrition and the Role of Wood in the Termite Diet

Wood contains high levels of carbohydrates that are accessible by termites especially with the aid of symbionts (Brune 2014). The primary carbohydrates found in wood, cellulose and hemicelluloses, are broken down in the termite gut (Esenther and Kirk 1974; Inoue et al. 1997; Slaytor 2000). Starches may also be found in wood especially in the sapwood, and their amount in wood depends on the tree species (Buchanan 1963). The large amount of accessible polysaccharides means that wood provides an excellent energy source for termites (Traniello and Leuthold 2000). Nitrogen is very limiting in wood as are other nutrients (Waller and La Fage 1987). Ash makes up 0.2–0.9% of the total wood dry mass (Buchanan 1963), creating possible limitations in acquiring adequate amounts of vitamins and minerals.

The primary minerals that make up the ash are calcium, potassium, magnesium, and iron, with calcium and potassium making up the bulk of that minor mineral component (Buchanan 1963). Termites have other means of accessing limiting nutrients. It has been known for some time that termites have nitrogen-fixing bacteria in their gut (Breznak et al. 1973; Bentley 1984; Slaytor and Chappell 1994; Ohkuma et al. 1999; Yamada et al. 2006). Other symbionts help manufacture vitamins such as vitamin B_{12} (Wakayama et al. 1984). Recently, it has been found that *Reticulitermes flavipes* will acquire minerals directly from the soil (Janzow and Judd 2015). It is likely that other species of subterranean termites can obtain minerals from the soil as well. Although wood can supply some of the other nutrients termites need (La Fage and Nutting 1978), it may primarily represent an energy source for subterranean termite colonies.

8.2 Locating Food

Foraging can be described as a three-stage process: (1) search patterns, (2) response to food location cues, and (3) assessing a food source (Kennedy 1965; Bernays and Chapman 1994). The first stage occurs in the absence of cues that indicate the location of a food source. Central-place foragers, those animals foraging from a central nest, need to maximize the search area but minimize the energy expenditure in doing so (Bell 1990). At the second stage, the forager identifies a potential target. In general, cues will allow foragers to determine the location of a food source and potentially some indication of its quality. The final stage occurs at the food source itself. It is at this stage that phagostimulants and other cues allow the forager to determine the palatability of the food source. Subterranean termites are central-place foragers, and based on the research so far, it appears they apply strategies based on these three stages when foraging for food.

8.2.1 Search Patterns

Burrowing is an expensive endeavor, and measurements taken from burrowing arthropods have found their energetic costs to be similar to those of burrowing vertebrates (White 2001; Xu et al. 2014). The energetic cost of burrowing also depends on the composition and moisture level of the substrate (White 2001) and on the metabolic level of the organism (Xu et al. 2014). Given the energetic cost of burrowing, subterranean termites should use strategies and search patterns that minimize energetic costs (Su 2005). Several studies have shown that tunneling patterns are nonrandom and minimize overlap (Lee et al. 2007, 2009; Lee and Su 2010a, b). Although different species have different tunneling patterns (Puche and Su 2001; Grace et al. 2004), they all maximize the search area and minimize energetic costs (Lee et al. 2008; Hapukotuwa and Grace 2012). However, soil is not homogenous, and a number of soil characteristics will influence the termite tunneling behavior (Su and Puche 2003; Grace and Campora 2005). Moisture level (Su and Puche 2003; Green et al. 2005; Cornelius and Osbrink 2010, 2011b), gaps in the soil, structural guides (Lima and Costa-Leonardo 2012), and soil type (Haverty 1979; Houseman and Gold 2003; Su 2005; Hua and Kirton 2007) can all alter termite tunneling patterns. Gaps may reduce the energetic cost of tunneling, and moisture may increase the chance of encountering chemical cues. Substrates such as sand have larger particles which may reduce tunneling costs (Houseman and Gold 2003). However, the sand cannot retain water and other charged particles as well as other soil types (Brady and Weil 1996) which may reduce the availability of localization cues to foraging termites.

8.2.2 Localization Cues

An airborne forager can use a number of cues when searching for a food source. Color, visual patterns and chemical odor gradients provide cues to locations of food sources (Bernays and Chapman 1994). These types of cues are not mutually exclusive and would benefit a forager to be able to rely on several cues to locate a food source. Likewise, a subterranean forager would also have to rely on multiple cues to increase the likelihood of detecting suitable food sources. Subterranean termites are more likely to feed on food sources located at the surface than on those that are buried (Ettershank et al. 1980). Thus, it can be inferred that the termites are expecting cues from the surface to determine the location of a food source. The local cues discovered thus far include thermal shadows and chemical gradients.

8.2.2.1 Thermal Cues

Ettershank et al. (1980) measured the temperature of the soil under food sources and compared the measurements to those of exposed soil. They found that the soil temperature was lower under food sources and proposed that the food sources created thermal shadows, temperature gradients that could act like cues for the subterranean forager. In a laboratory study, Swoboda and Miller (2005) tested the hypothesis that *Reticulitermes* would respond to thermal shadows. They confirmed that termites were more likely to move under a food source if the temperature was cooler under the food than the surrounding soil. Furthermore, when they created a scenario in which the soil was warmer under the food source, the termites did not respond. Organic substrates contain more water and would be greater heat sinks than mineralized substrates such as rocks (Swoboda et al. 2004). Thus, it is possible for a subterranean forager to distinguish a potential food source from a non-food source item on the surface.

8.2.2.2 Chemical Cues

In the natural environment, wood will go through several stages of decomposition. During this process, chemicals from the wood leech into the soil (Fukasawa et al. 2014). It has been shown that termites prefer wood that is decomposing to wood that has been freshly cut (Su 2005; Gazal et al. 2012). Interestingly, termites have been found to be attracted to wood or sawdust that is being decomposed by certain fungi (Esenther et al. 1961; Cornelius et al. 2002, 2014). Even extracts from wood or sawdust will attract termites or increase tunneling behavior (Reinhard et al. 1997; Cornelius et al. 2014). The exact nature of the attractants was not examined by these studies. Su (2005) found that laboratory colonies of *Reticulitermes flavipes* and *Coptotermes formosanus* were attracted to decaying wood disks in a laboratory setting. He proposed that the termites were attracted to small particles that leeched from the wood into the soil. Several possible candidates that match the prediction made by Su (2005) have been found to attract termites.

One molecule in particular that is given off during decomposition is the gas carbon dioxide. It is used by other subterranean insects such as the corn rootworm to locate food sources (Bernklau and Bjostad 1998a, b). Damp wood gives off CO_2, and this gas is a metabolic by-product of some wood degraders. A number of termite species were found to be attracted to higher levels of CO_2 and followed CO_2 gradients to their source in the field and laboratory settings (Bernklau et al. 2005; Broadbent et al. 2006). Waller et al. (1999) simulated the by-products of wood degradation by fungi by drenching soil with sucrose and yeast or urea and tested the effects of these treatments on termite foraging behavior. Laboratory experiments showed that *Reticulitermes flavipes* and *R. virginicus* preferred soil drenched with sucrose plus yeast or soil drenched with a urea solution over soil drenched with water. Field trials showed weaker responses to both cues, but they were higher than the controls. It is possible that the yeast and sucrose combination was producing CO_2, but this was outside the scope of that study.

Ions represent another small chemical that could leech through the soil. Rotting logs release a number of ions into the soil (Fukasawa et al. 2014). Botch and Judd (2011) examined the levels of ions at different soil depths and found that potassium was the only ion examined that formed gradients under the soil. When tested in the lab, the presence of potassium caused *Reticulitermes flavipes* workers to tunnel more than in its absence. Thus, there are a number of small chemicals that could act as potential cues for subterranean termites that are near decomposing wood.

Based on the work so far, we can now conclude that subterranean termites are not digging blindly to locate food sources but that there are a number of cues available to them. Subterranean termites are searching for food that is at the surface, and the cues they are using, thermal shadows and chemical gradients, originate from the surface. Thermal shadows indicate to foraging termites that an object is above them. Organic materials will produce different thermal shadows than inorganic substrates (Fig. 8.1); however, termites may not be able to use thermal shadows to determine the state of wood decomposition. The decomposition process of wood releases many particles, some of which can readily travel through the soil and form gradients. CO_2, potassium

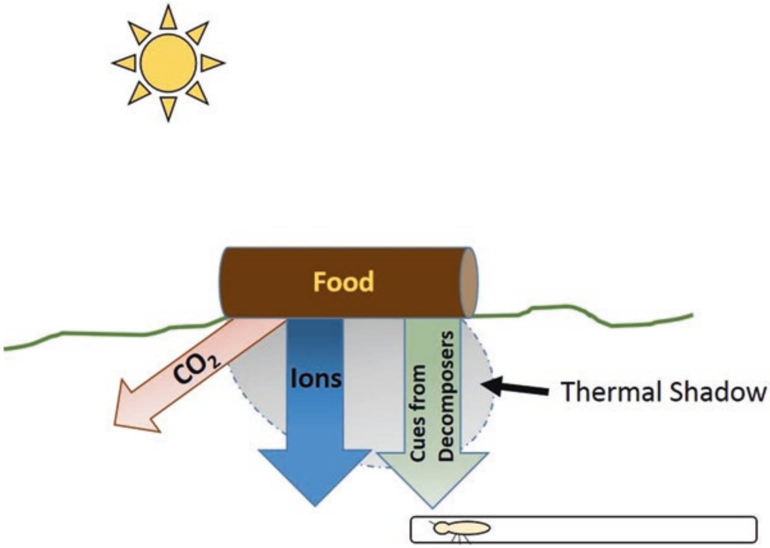

Fig. 8.1 Localization cues that can allow subterranean foragers to locate a food source include thermal shadows, CO_2, ions, and volatile produces from decomposers

ions, and urea fit this description (Fig. 8.1), and all three increase termite foraging behavior. Additional molecules released from the decomposers may play a role as well (Cornelius et al. 2002, 2014). Thus, termites would be able to detect a piece of wood on the surface and determine if it is in the correct stage of composition.

8.3 Cues Used at the Food Source

Once the forager reaches a food source, the individual must determine if the food item is palatable. These cues should indicate the level of decay, the nutrients available to the termites, and the presence of secondary metabolites that would affect survival.

8.3.1 Wood Preference

A number of studies have tested the preference of wood in subterranean termites. Many of those workers compared wood commonly used in construction, while others compared common wood to exotic ones that are not commonly used. A number of studies used wooden blocks in choice and no-choice tests to determine the relative palatability of wood from different tree species. Results from many of the laboratory assays are summarized in Table 8.1. Although differences in methodology can produce different results (Haverty and Nutting 1974; Su and La Fage 1984; Lee and Forschler 2016), overall some trends can be seen from comparing these studies.

Table 8.1 Results of several laboratory studies investigating the relative level of feeding on different wood species

Termite species	Order of wood preference (most eaten to less eaten)	Source
Coptotermes curvignathus	*Hevea brasiliensis* > *Alstonia angustifolia* > *Cinnamomum scortechinii* > *Khaya ivorensis* = *Dialium kunstleri trifoliolatum* > *Fagraea fragrans* = *Dipterocarpus grandiflorus* = *Pometia pinnata* > *Madhuca utilis* = *Neobalanocarpus heimii* = *Cotylelobium lanceolatum* = *Shorea curtisii*	Kadir and Hale (2012)
Coptotermes Formosanus	*Picea* sp. = *Pseudotsuga menziesii* > *Betula alleghaniensis* = *Quercus rubra* = *Juglans boliviana* > *Sequoia sempervirens* > *Hymenaea courbaril* > *Swietenia macrophylla* > *Chamaecyparis nootkatensis* > *Tectona grandis*	Cornelius and Osbrink (2015)
	Pseudotsuga menziesii > *Sequoia sempervirens* > *Chamaecyparis Nootkatensis*	Grace and Yamamoto (1994)
	Pinus sp. = *Pseudotsuga menziesii* = *Cardwellia sublimis* = *Eucalyptus deglupta* > *Eucalyptus robusta* = *Metrosideros polymorpha* = *Acacia koa* > *Pandanus tectorius* > *Thespesia populnea* = *Cryptomeria japonica* > *Cordia subcordata* > *Calophyllum inophyllum*	Grace et al. (1996)
	Albizia falcataria = *Acacia mangium* = *Pinus sylvestris* = *Pinus caribaea* = *Hevea brasiliensis* = *Araucaria cunninghamii* > *Azadirachta excelsa* = *Tectona grandis* (Malaysia) > *Koompassia malaccensis* = *Casuarina equisetifolia* = *Tectona grandis* (Burma)	Grace et al. (1998)
	Pseudotsuga menziesii > *Intsia palembanica*	Grace and Tome (2005)
	Pseudotsuga menziesii > *Shorea laevis*	Grace and Tome (2005)
	Pseudotsuga menziesii = *Pinus* sp. > *Sequoia sempervirens*	Hapukotuwa and Grace (2011)
	Pseudotsuga menziesii > *Pinus Palustris*	Hapukotuwa and Grace (2010)
	Betula alleghaniensis > *Liquidambar styraciflua* > *Araucaria angustifolia* > *Acer saccharum* > *Carya illinoensis* > *Quercus rubra* = *Liriodendron tulipifera* = *Fraxinus americana* = *Pseudotsuga menziesii* = *Pinus taeda* > *Pinus ponderosa* = *Thuja plicata* > *Taxodium distichum* > *Gleditsia triacanthos* = *Tilia americana* = *Sequoia sempervirens* = *Chamaecyparis nootkatensis* = *Prunus serotina* > *Juniperus virginiana* = *Juglans nigra* = *Sassafras albidum* = *Quercus alba* = *Maclura pomifera* = *Dalbergia latifolia* = *Dalbergia stevensonii* = *Machaerium* sp. = *Cedrela odorata* = *Swietenia macrophylla* = *Ochroma lagopus*	Morales-Ramos and Rojas (2001)

(continued)

Table 8.1 (continued)

Termite species	Order of wood preference (most eaten to less eaten)	Source
	Acer saccharum > *Pinus taeda* > *Pinus elliottii elliottii* > *Larix occidentalis* > *Pseudotsuga menziesii* > *Juglans nigra* > *Sequoia sempervirens* > *Quercus* sp. > *Pinus ponderosa* > *Taxodium distichum* > *Prunus serotine*	Smythe and Carter (1970a)
Coptotermes Gestroi	*Pseudotsuga menziesii* = *Pinus* sp. > *Sequoia sempervirens*	Hapukotuwa and Grace (2011)
	Pinus palustris > *Pseudotsuga menziesii*	Hapukotuwa and Grace (2010)
	Hevea brasiliensis > *Alstonia angustifolia* > *Diallium kunstleri trifoliolatum* > *Dipterocarpus grandiflorus* = *Khaya ivorensis* = *Cinnamomum scortechinii* > *Madhuca utilis* = *Pometia pinnata* = *Shorea curtisii* = *Fagraea fragrans* > *Neobalanocarpus heimii* = *Cotylelobium lanceolatum*	Kadir and Hale (2012)
	Pseudotsuga menziesii = *Pinus ponderosa* = *Picea engelmannii* = *Tsuga heterophylla* > *Thuja plicata* = *Sequoia sempervirens*	Su and Tamashiro (1986)
Coptotermes Heimi	*Populus deltoides* > *Mangifera indica* > *Erythrina suberosa* > *Betula utilis* > *Elaeis guineensis* > *Ficus religiosa* > *Heterophragma adenophyllum* > *Terminalia arjuna* > *Moringa oleifera* > *Putranjiva roxburghii* > *Syzygium cumini* > *Zizyphus jujube* > *Melia azedarach* > *Abies pindrow* > *Acacia arabica* > *Eucalyptus citriodora* > *Azadirachta indica* > *Alstonia scholaris* > *Cordia obliqua* > *Albizia lebbeck* > *Pinus roxburghii* > *Cedrus deodara* > *Pinus wallichiana* > *Dalbergia sissoo*	Manzoor et al. (2015)
Heterotermes Aureus	*Cercidium floridum* > *Opuntia fulgida* > *Prosopis juliflora velutina* > *Acacia greggii*	Haverty and Nutting (1974)
Heterotermes Indicola	*Populus deltoides* > *Mangifera indica* > *Betula utilis* > *Erythrina suberosa* > *Moringa oleifera* > *Eucalyptus citriodora* > *Syzygium cumini* > *Elaeis guineensis* > *Ficus religiosa* > *Zizyphus jujube* > *Abies pindrow* > *Melia azedarach* > *Heterophragma adenophyllum* > *Terminalia arjuna* > *Putranjiva roxburghii* > *Acacia arabica* > *Cordia obliqua* > *Pinus wallichiana* > *Albizia lebbeck* > *Alstonia scholaris* > Cedrus *deodara* > *Pinus roxburghii* > *Azadirachta indica* > *Dalbergia sissoo*	Manzoor et al. (2015)
Reticulitermes Flavipes	*Ochroma pyramidale* > *Pinus* sp. = *Ceiba pentandra* > *Pseudotsuga menziesii* = *Poulsenia armata* = *Tsuga heterophylla* = *Chamaecyparis nootkatensis* = *Qualea* sp. > *Juniperus* sp. = *Erisma* sp. = *Tabebuia* sp. = *Chamaecyparis thyoides*	Arango et al. (2006)

(continued)

Table 8.1 (continued)

Termite species	Order of wood preference (most eaten to less eaten)	Source
	Pinus elliottii elliottii > *Pinus taeda* > *Prunus sertina* > *Pinus ponderosa* > *Larix occidentalis* > *Acer saccharum* > *Pseudotsuga menziesii* > *Juglans nigra* > *Quercus* sp. > *Taxodium distichum* > *Sequoia sempervirens*	Smythe and Carter (1969)
	Pinus taeda > *Pinus elliottii elliottii* > *Acer saccharum* > *Larix occidentalis* > *Juglans nigra* > *Sequoia sempervirens* > *Quercus* sp. > *Prunus sertina* > *Taxodium distichum* > *Pinus ponderosa* > *Pseudotsuga menziesii*	Smythe and Carter (1970a)
Reticulitermes Virginicus	*Pinus elliottii elliottii* > *Pinus taeda* > *Larix occidentalis* > *Sequoia sempervirens* > *Acer saccharum* > *Juglans nigra* > *Pseudotsuga menziesii* > *Pinus ponderosa* > *Taxodium distichum* > *Quercus* sp. > *Prunus sertina*	Smythe and Carter (1970a)
	Pinus sp. > *Quercus* sp. > *Sequoia* sp. > *Populus* sp.	Lee and Forschler (2016)

Orders are list from highest to lowest preference from termites, according to the authors' results. Tree species separated by ">" indicates the species on the left has a higher level of palatability. Species separated by "=" indicates no difference in palatability

One general trend is that yellow pine (*Pinus*) and Douglas fir (*Pseudotsuga menziesii*) are generally among the more susceptible woods to attacks by most termite species tested. Many of the studies found that teak (*Tectona grandis*) and tropical species in the genus *Shorea* are resistant to attacks by termites of the genus *Coptotermes*. It also appears that exotic and tropical woods seem to resist to attacks by the commonly studied subterranean termites (Table 8.1). Smythe and Carter (1969) and Morales-Ramos and Rojas (2003) noted that there was a correlation between wood preference and survivorship. For this review, a combined analysis of the relationship between level of feeding and survivorship was examined across studies and found that the relationship between wood selection and survivorship seems to exist for many of the studies shown in Table 8.1. For those laboratory studies that reported mass of food consumed and percent mortality or survivorship, the mean weight loss was converted to milligrams of wood consumed per day, and percent mortality was converted to percent survivorship, based on the data provided in the published papers. When the date were combined, there was a significant positive correlation between the amount of wood consumed per day and the percent survivorship (arcsine transformed for the analysis) (regression $F = 48.8$, $p < 0.001$, Fig. 8.2). Thus, the general pattern is that termites are avoiding wood that reduces survivorship.

It should be noted that despite the general trends, it is also evident that different termite species have different preferences (Wood 1978; Ngee et al. 2004; Kadir and Hale 2012; Li et al. 2015; Manzoor et al. 2015) and that intraspecific variation also occurs (Ngee et al. 2004). Field studies on naturally occurring wood species also showed that different species of termites in the same habitat have different wood preferences (Haverty and Nutting 1975; Ravan et al. 2015).

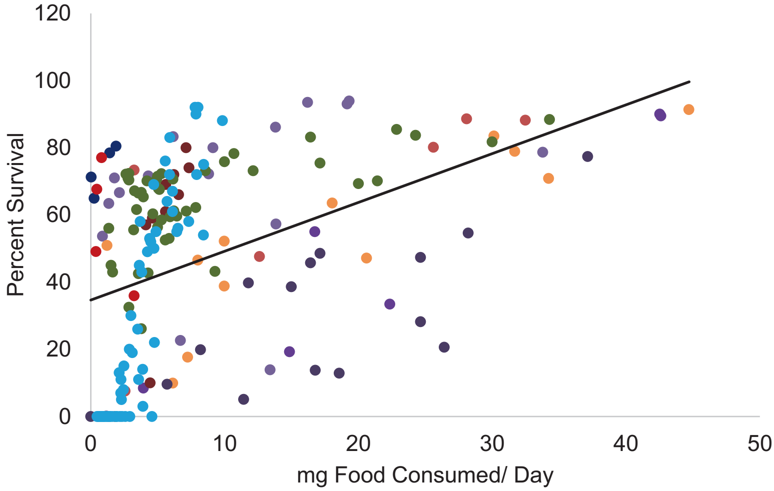

Fig. 8.2 Mean percent survival of termites vs. mean food consumed per day from laboratory studies which tested wood preference using wood blocks from several different tree species. Combined data show a significant positive correlation between the amount of food consumed and the percent survivorship in the colony (F = 46.5, $p < 0.001$). Different colored dots indicate data from different studies: orange (Cornelius and Osbrink 2015), yellow (Grace et al. 1996), dark blue (Grace and Tome 2005), green (Grace et al. 1998), purple (Grace and Yamamoto 1994), brown (Smythe and Carter 1969), light blue (Smythe and Carter 1970a), red (Hapukotuwa and Grace 2010), gray (Manzoor et al. 2015), red (Arango et al. 2006)

8.3.2 Properties of Wood Affecting Preference

There are a number of factors that could explain the differences in wood selectivity, including (1) secondary metabolites, (2) hardness (or density), (3) composition, and (4) nutritional value (Fig. 8.3). These properties are not mutually exclusive (Bultman and Southwell 1976; Shanbhag and Sundararaj 2013). Wood can change its properties depending on the soil it grows in (Buchanan 1963). For example, Grace et al. (1998) noted that teak (*Tectona grandis*) from Burma was more resistant to termite attack than the same species from Malaysia (Table 8.1).

8.3.2.1 Secondary Metabolites

One obvious difference between wood species is the secondary metabolites that are present. Several lines of evidence suggest that these are important factors. Earlier studies have shown that extracts taken from sawdust of wood that are not favored by termites will repel them as well and lower their survival in a laboratory setting (Smythe and Carter 1970b; Carter and Smythe 1974; Carter and de Camargo 1983; Grace et al. 1989; Sattar et al. 2015). If secondary metabolites are extracted from wood, it can become more palatable to termites (Kirker et al. 2013). Adding extracts

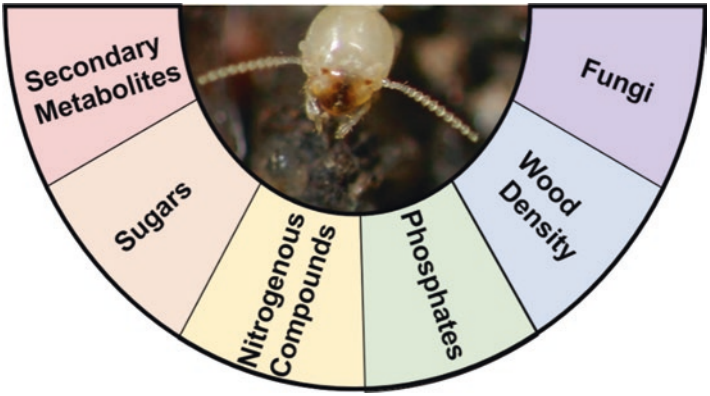

Fig. 8.3 Properties and components of wood that termites use to assess food quality

to normally favored food can also reduce palatability (Carter and de Camargo 1983; McDaniel 1992). In addition to other components mentioned above, Shanbhag and Sundararaj (2013) also found, in field studies, that wood with higher levels of phenols had lower levels of termite attacks. Thus, secondary metabolites effectively play an important role in termite food selection and survival.

8.3.2.2 Hardness or Density of Wood

A number of studies have examined the influence of density or hardness of wood on termite preference. Laboratory (Behr et al. 1972; Arango et al. 2006) and field studies (Bultman and Southwell 1976; Wood 1978; Souza et al. 2009; Owoyemi and Olaniran 2014) have found that harder wood is generally more resistant to termite attack than softer wood. However, this is not always the case (Mustafa 2011). Waller et al. (1990) compared the feeding levels of *Coptotermes formosanus* when given pine (*Pinus* sp.) or mahogany (*Swietenia macrophylla*) that were compressed or uncompressed. They found that the termites ate more of the uncompressed wood vs. the compressed one, for the same species. However, when the amount of biomass removed from each block was calculated, the biomass consumed from a compressed or uncompressed block of wood from the same species did not differ. Thus, in studies that use percent mass consumed as an indicator of preference, it may be considered that the same amount of biomass is consumed if one wood species is denser than another.

One aspect that relates to density is the concentration of cellulose and lignin in wood. *Reticulitermes flavipes* prefers artificial food sources that have higher concentrations of cellulose (Judd and Corbin 2009). Higher ratios of cellulose to lignin are also preferred. This preference has also been confirmed in the field. Shanbhag and Sundararaj (2013) found that wood preferred by subterranean termites had higher levels of cellulose and lower levels of lignin than non-preferred wood. One interesting question is how termites assess the amount of cellulose. One possible mechanism is that termites break down the cellulose into its components, then tasting the sugars. Subterranean termites have cellulase in their saliva (Inoue et al. 1997), thus higher concentrations of cellulose would produce higher concentrations of sugar in the mouth. Cypret and Judd (2015) tested this concept using starch and glucose. When *R. flavipes* was presented with a choice between food enriched with equal levels of glucose and starch, they found that there was no preference. When the same experiment was run with an amylase inhibitor in each food source, the termites preferred the food enriched with glucose. When given a choice between food enriched with xylose and xylan, *R. flavipes* preferred food with xylose. *Reticulitermes flavipes* lacks xylanase in its saliva (Inoue et al. 1997). Thus, termites are only capable of detecting polysaccharides when there is an enzyme in their saliva to break these molecules down.

8.3.2.3 Simple Sugars

A number of studies have examined the effect of sugars on the feeding preferences of termites. Glucose, xylose, sucrose, and fructose were the most common sugars examined across all studies. Results for trials testing the preference of food enriched with one of these four sugars, compared to an unenriched control, are summarized in Table 8.2. The results for each of these sugars were not consistent across termite species. The genera *Heterotermes* and *Coptotermes* seemed to have a low response to the four sugars compared. Castillo et al. (2013) found that *Coptotermes curvignathus* responded positively to disks soaked in 3% glucose, while *C. gestroi* only responded to xylose. However, Haifig et al. (2010) found that *C. gestroi* did not respond significantly more to food enriched with xylose than to unenriched food. Similarly, responses to different sugars were not consistent in the genus *Reticulitermes*. The two species found in the eastern United States, *R. flavipes* and *R. virginicus* [Swoboda et al. (2004) collected their termites in the Eastern United States], seemed to prefer food enriched with 1–3% glucose (0.1 M is about 1.8%) and 1–3% sucrose. *Reticulitermes hesperus* showed a positive response to 2% xylose and 2% fructose (Saran and Rust 2005). Wallace and Judd (2010) noted these discrepancies and proposed that there may be seasonal and population differences. They tested the sugar preferences of *R. flavipes* collected from four populations in the spring, summer, and fall and found that populations differed in their response to food enriched with glucose, xylose, and sucrose. There were also seasonal shifts in preferences for food enriched with xylose and sucrose within populations.

Other sugars were tested in some of the aforementioned studies as well, and they showed mixed results between species as well. Saran and Rust (2005) found that *R. hesperus* preferentially fed on filter paper enriched with 2% maltose or 2% arabinose. Arabinose is found in some hemicellulases in wood (Buchanan 1963). They also found that *R. hesperus* fed on filter paper enriched with 5%, but not 2%, ribose. Interestingly, *C. curvignathus* did not prefer food enriched with ribose at levels

Table 8.2 Summary of experiments that tested the potential preference between sugar-enriched substrate and a control substrate in single-choice tests

Species	Media	Glucose (%/ Y/N)	Xylose (%/ Y/N)	Sucrose (%/ Y/N)	Fructose (%/ Y/N)	Source
Coptotermes curvignathus	Filter paper	3%/Y	3%/N			Castillo et al. (2013)
	Filter paper	6,9,12,15%/N	6,9,12,15%/N			Castillo et al. (2013)
Coptotermes Gestroi	Filter paper	3%/N	3%/Y			Castillo et al. (2013)
	Filter paper	6,9,12,15%/N	6,9,12,15%/N			Castillo et al. (2013)
	Filter paper	3, 5%/N	3, 5%/N	3%/N	5%/ml/N	Haifig et al. (2010)
Heterotermes Tenuis	Filter paper	3, 5%/N	3, 5%/N	3%/N	5%/ml/N	Haifig et al. (2008)
Microtermes traegardhi	Millet stem disks	20%/Y		20%/Y	20%/Y	Abushama and Kamal (1977)
Microtermes obesi	Filter paper	0.1,1,2,3,4,5,6,7%/Y				Sattar et al. (2015)
Reticulitermes sp.	Brown paper towel	0.1 M/Y	0.1 M/N	0.1 M/Y	0.1 M/N	Swoboda et al. (2004)
	Brown paper towel	0.01 M/N	0.01 M/N	0.01 M/N	0.01 M/Y	Swoboda et al. (2004)
	Brown paper towel	0.001 M/N	0.001 M/N	0.001 M/N	0.001 M/N	Swoboda et al. (2004)
Reticulitermes flavipes and *R. virginicus*	Filter paper	1%/Y	1%/N	1%/Y		Waller and Curtis (2003)
	Filter paper	3%/Y	3%/Y	3%/Y		Waller and Curtis (2003)
Reticulitermes Flavipes	Cellulose agar	3.5%/Y^{P}	3.5%/Y^{P,S}	3.5%/Y^{P,S}		Wallace and Judd (2010)
Reticulitermes Hesperus	Paper disks	2%/N	3%/Y	2%/N	2%/Y	Saran and Rust (2005)

Only the results for glucose, xylose, sucrose, and fructose are shown. For each sugar “Y” indicates a significant preference for the enriched food, “N” indicates no significant preference as reported by the authors of the paper.^{P} indicates only certain populations showed a preference,^{S} indicates the preference varied between seasons equal or higher than 5%, when tested (Castillo et al. 2013). Galactose-enriched food was preferred over controls by *Reticulitermes* sp. (Swoboda et al. 2004), but this was not the case for *C. gestroi* (Haifig et al. 2010) or *Heterotermes tenuis* (Haifig et al. 2008). A similar result was found with raffinose at very low levels (Swoboda et al. 2004; Haifig et al. 2008, 2010). However, food enriched with trehalose was preferred by all of the termites tested (Swoboda et al. 2004; Haifig et al. 2008, 2010). The overall conclusion that can be drawn is that not all species respond to sugars in the same way, and population and seasonal differences should also be taken into account when performing these studies.

8.3.2.4 Nitrogenous Compounds

Due to the fact that the nitrogen content in wood is low, nitrogenous compounds seem like potential phagostimulants for termites. Unlike sugars, there has been less overlap among the nitrogenous compounds examined in different studies, but some comparisons can be made. Like sugars, studies using amino acids have also produced mixed results. Mauldin and Rich (1975) found that casein and egg albumin are toxic to *Reticulitermes flavipes* and *Coptotermes formosanus* at concentrations greater than 0.5%. In a choice test, Castillo et al. (2013) found that *C. curvignathus* and *C. gestroi* preferred filter disks soaked in 3% casein solution, compared to a control. Higher concentrations (6%, 9%, 12%, 15%) were not preferred. Survival was not affected by concentrations as high as 9% for *C. curvignathus* or 12% for *C. gestroi*. A few studies have tested the effect of food preference by individual amino acids. *Coptotermes formosanus* preferred filter paper enriched with either D-aspartic acid or L-glutamic acid, over controls (Chen and Henderson 1996). L-proline, L-lysine, and L-isoleucine increased feeding rates in no-choice tests (Henderson et al. 1994; Chen and Henderson 1996). Swoboda et al. (2004) tested the effectiveness of eight amino acids (L-arginine, L-aspartic acid, L-cysteine, L-isoleucine, L-lysine, L-methionine, L-phenylalanine, and L-proline) on influencing the feeding preference and feeding rates of *Reticulitermes* sp. None of the amino acids tested showed any positive effects, and several (L-arginine, L-aspartic acid, L-isoleucine, L-phenylalanine, and L-proline) actually reduced the feeding rates. L-alanine showed similar effects on the feeding behavior of *C. curvignathus* and *C. gestroi* (Castillo et al. 2013). The results from amino acids differed from species to species and in some cases caused a negative feeding response. Consistent patterns of selectivity, at the genus level, do not even seem to be present.

The effects of urea and uric acid on termite feeding behavior have also been tested. Urea was found to increase feeding rates in *C. formosanus* (Henderson et al. 1994), *Microtermes obesi* (Sattar et al. 2015), and *Heterotermes tenuis* (Haifig et al. 2008), but it did not appear to act as phagostimulant for *C. gestroi* (Haifig et al. 2010). Uric acid was only found to be attractive to *Reticulitermes* sp. at very low concentrations, while higher concentrations had no effect (Swoboda et al. 2004).

Coptotermes formosanus did not respond to uric acid differently than controls (Morales-Ramos et al. 2009). Morales-Ramos et al. (2009) also tested the effect of glucosamine and salicylic acid on termite feeding at concentrations of 50, 225, 450, and 675 ppm. They found that food enriched with 450 ppm of glucosamine and that food enriched with 50 ppm of salicylic acid were preferred over their controls. Other concentrations showed no effect.

One possible reason for the variation in response to nitrogenous compounds by termites is the changes in the need for nitrogen during the year. There is evidence that the need for dietary nitrogen fluctuates during the year. Curtis and Waller (1998) found that levels of nitrogen fixation fluctuated during the year in *R. flavipes* and *R. virginicus*, with rates that were not the same for all castes. Thus, the need for dietary nitrogen may also vary during the year and may affect the influence of nitrogenous compounds on feeding rates. This is a research area yet to be fully explored.

8.3.2.5 Phosphates

Phosphates represent another limiting nutrient in wood. Phosphates are important for the production of ATP and mRNA. Limitations in phosphates can reduce the production of protein even if nitrogen is readily available (Elser et al. 2000). Botch et al. (2010) examined the role of phosphates in food preference of *R. flavipes* and found that food enriched with phosphates was preferred over controls during the fall but not in the spring and summer.

8.4 Fungi and Other Decomposers

Termites have had a long association with fungi, and it is becoming increasingly clear that fungi can influence the foraging and food selection of subterranean termites. A number of species of fungi have been found to attract termites (Esenther et al. 1961) or make the wood more palatable (Waller et al. 1987; Getty and Haverty 1998; Little et al. 2012a, b; Cornelius et al. 2014). There are a number of reasons for these associations. Fungi offer a potential source of nitrogen and other nutrients if consumed (Sands 1969). Both *Reticulitermes flavipes* and *Coptotermes formosanus* will consume the fruiting bodies of white-rot fungi (Waller et al. 1987). As mentioned earlier, fungi can begin the decomposition process on wood and release some of the cues the termites need to locate a food source (Cornelius et al. 2002). Also, in the process fungi can potentially break down some of the secondary metabolites that might repel or harm termites (Waller et al. 1987). Thus, fungi may increase the palatability of the wood as they degrade it or act as phagostimulants themselves (Fig. 8.3).

8.5 Conclusion

The foraging process of subterranean termites is a three-step process. During the searching phase, the termites produce tunnel patterns that minimize overlap and energetic costs. Subterranean termites are expecting local cues that originate from the surface. Thermal shadows and chemical gradients of small particles such as CO_2, ions, and urea allow termites to locate a food source that is in the correct stage of decay. Finally, a number of cues will help determine palatability of wood including density, cellulose concentration, sugars, nitrogenous compounds, phosphates, secondary metabolites, and the presence of some fungi. There is a level of redundancy in the termite foraging system which is important, due to the energetic cost of burrowing and the fact that some types of wood can increase mortality.

One conclusion that can be reached by comparing multiple studies is that there is interspecific and even intraspecific variation on the types of cues used to determine palatability. There are a number of factors that could cause this variation, in addition to differences among species. The composition of wood from a tree species is not constant and can be influenced by soil, moisture levels, and other environmental factors (Buchanan 1963). In addition, feeding preferences change during the year, as the termite colony composition is not static. Colonies reproduce (produce winged alates) annually or biannually (Higa and Tamashiro 1983; Scheffrahn et al. 1988; Lax and Wiltz 2010; Mullins et al. 2015), and thus, they will show variations in their nutritional needs. In addition, termites in temperate climates or high altitudes may experience periods of time where foraging is not possible due to low temperatures. Termites in these climates need to prepare for winter. Seasonal changes in foraging activity have been observed in subterranean termites (Haverty et al. 1974; Cornelius and Osbrink 2011a), and studies have found seasonal effects in food preference (Botch et al. 2010; Wallace and Judd 2010) and nitrogen fixation (Curtis and Waller 1998). Understanding the nutritional changes in a termite colony throughout the season may help understand what might increase palatability of food sources.

Finally, termite food preference is affected by previous feeding experience (McMahan 1966). This was mentioned in a review by Waller and La Fage (1987) as an understudied topic and appears to remain so even today. Understanding the foraging behavior and food selectivity of a population of subterranean termites might require an understanding of the influence of soil on the wood, of the foraging cues used by that population, and of the seasonal patterns of termite nutritional needs.

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Chapter 9
Termite Preferences for Foraging Sites

Ibrahim G. Ali, Berhan M. (Shiday) Ahmed, Gary Sheridan, and John R.J. French

Contents

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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Chapter 10
Ecological Impacts of Termites

Md. Aslam Khan, Wasim Ahmad, and Bishwajeet Paul

Contents

Abstract Macroinvertebrates play an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats. Termites, as dominant invertebrates in tropical soils, have a major influence on soil chemical and physical structure. A diverse range of species processes a variety of plant organic matter at all stages of decomposition contributing to the efficient return of nutrients to the vegetation. Soil restoration and sustainable agricultural practices can be achieved through utilization of the ecosystem services of these organisms. The exploitation of termites for agroecosystem management and soil restoration remains, however, largely unexplored. Only few researches have been reported on the utilization of termite activity for the management of soil fertility or for the rehabilitation of degraded soils. The present chapter highlights the potentials of termites

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as detritivores, soil builders, restorers of degraded land, and producers of some greenhouse gases, in the light of available literature.

Keywords Termite • Detritivore • Soil • Mound • Degraded land

10.1 Introduction

Ecosystem engineers directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical changes in biotic or abiotic materials. In so doing, they modify, maintain, and/or build habitats (Jones et al. 1994). A wide range of different soil macrofauna provides several key ecosystem services. In the tropics, termites are arguably the most influential soil-dwelling ecosystem engineers (Bignell 2006) whose biogenic structures (nests, soil sheetings, foraging holes, etc.) modify the availability of resources for other organisms. Through bioturbation they incorporate plant litter and crop residues into the soil, thereby modifying biological, chemical, and physical soil processes that affect the flow of energy and material (Fig. 10.1). They hence modify the habitat of other soil biota (Jones et al. 1994; Lavelle et al. 1997b; Pulleman et al. 2012).

Termites form an essential component of soil ecology having successfully coevolved for millions of years (French 1988). They are dominant invertebrates in tropical soils (Bignell and Eggleton 2000) and represent as much as 10% of all animal biomass and up to 95% of soil insect biomass (Jones and Eggleton 2000). By

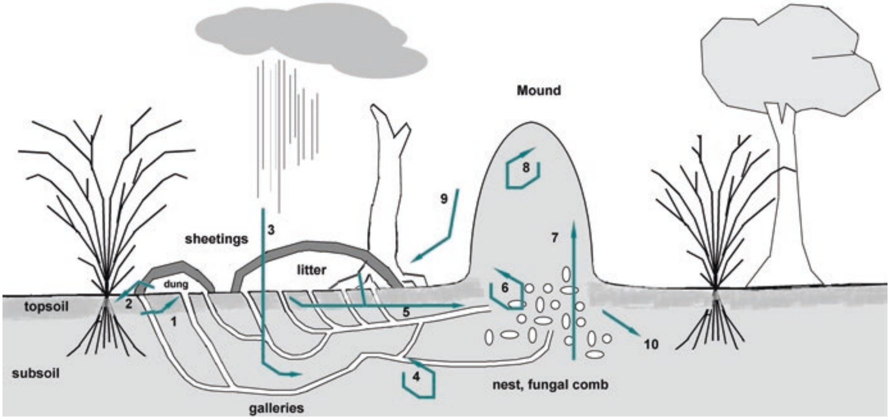

Fig. 10.1 Constructions built by *Macrotermes* spp. and mediated processes (arrows). (*1*) Soil turbation via construction of sheetings, (*2*) nutrient uptake from plant sheetings, (*3*) increased infiltration rates, (*4*) soil aeration, (*5*) organic matter relocation, (*6*) decomposition, (*7*) soil turbation via mound construction with subsoil, (*8*) mineralization and nutrient enrichment, (*9*) erosion and redistribution of mound material, (*10*) nutrient uptake from mound material by plants (Adapted and redrawn from Grohmann 2010)

virtue of microbial symbionts in their gut, they play a key role in processes such as carbon and nitrogen mineralization (Bignell and Eggleton 2000; Jouquet et al. 2011). Their role in ecosystems has been reviewed by several authors (e.g., Lobry de Bruyn and Conacher 1990; Bignell and Eggleton 2000; Jouquet et al. 2011).

Termites live in complex environments, and their functional domain (physical sphere of influence at the point scale) is designated as the termitosphere (Dangerfield et al. 1998; Lavelle 2002; Jouquet et al. 2006). They construct intricate networks of underground tunnels and soil-covered tubes to access resources as well as protect themselves from predators and harsh environmental conditions while foraging (Lee and Wood 1971; Lee and Su 2010). These soil insects also have the abilities to partially control their own living environments, where the humidity and temperature remain constant throughout all seasons. This gives them a striking ability to remain active during severe seasons, where most other soil macroinvertebrates are diminished or eliminated. Environmental factors along with availability of food and water resources, interactions with other predators and pathogens, and other genetic behaviors affect their population dynamics and behaviors of nesting and foraging, spatially or temporally, separately or in combination (Campora and Grace 2004; Cornelius and Osbrink 2010).

Being one of the most abundant biological compounds on the planet, cellulose is most commonly found in wood, providing an enormous resource for those organisms able to digest it (Norkrans 1963; Dixon et al. 1994). Termites are among the few organisms able to digest cellulose, contributing to their evolutionary and ecological success (Watanabe et al. 1998; Nakashima et al. 2002). Depending on the food source, the termites may be classified into three principal feeding guilds, mainly (1) wood feeders (xylophagous termites); (2) soil feeders, consuming organic residues in the soil (humivorous termites); and (3) termites feeding on both wood and organic residues (soil/wood-interface feeders Bignell and Eggleton (2000)). Besides, there are niche feeders like *Constrictotermes cavifrons*, which have been shown to feed on microepiphytes (Araujo 1970; Martius et al. 2000). They have considerable influence on soil organic matter turnover, nutrient cycling, and soil structure formation (Lavelle et al. 1997b; Brussaard 2012), strongly affecting animal and plant distribution (Holt and Lepage 2000).

Termites transport water from moist areas to relatively drier substrates and improve the microclimate by creating and maintaining a humid environment while softening their food material for easy consumption (Su and Puche 2003; Arab and Costa-Leonardo 2005; Wong and Lee 2010). Studies suggested that termites have a positive effect on soil structure and nutrient richness (Jouquet et al. 2011, 2014). Through their mound-building activities and impact on plant growth, termites enhance the heterogeneity of their ecosystems. Sileshi et al. (2010) reported that increased soil fertility and moisture found near termite mounds can have pronounced effects on vegetation communities and their productivity. Previous studies also found that woody vegetations growing on termite mounds were characterized by an increase of density (Moe et al. 2009), tree height (Levick et al. 2010), species richness (Traore et al. 2008), functional diversity (Joseph et al. 2014), and reproductive output (Brody et al. 2010).

Barrios (2007) concluded that soil organisms are essential for the functioning of natural and managed ecosystems and the productivity of land. Termites, by creating refugia for plants and nuclei for revegetation, can enhance dryland resistance to and recovery from drought (Bonachela et al. 2015). The exploitation of termites for agroecosystem management and soil restoration remains largely unexplored (Evans et al. 2011; Jouquet et al. 2014). This chapter reflects the present state of knowledge concerning ecological impacts of termites.

10.2 Detritivores

Termites are the dominant arthropod detritivores in many tropical soils, with highest diversity in lowland equatorial forests (Eggleton et al. 1996; Eggleton 2000). Their activities and interactions with soil result in significant temporal and spatial changes, through formations or modifications of soil, vegetation, and landscape (Ali et al. 2013). A diverse range of termite species processes a variety of plant organic matter at all stages of decomposition, from leaf litter to rotten wood and soil humus. Across all environments inhabited by termites, the litter feeders can be proposed as the most ecologically important, because of their consistent presence and their numerical preponderance in terms of both species and individuals (Jouquet et al. 2011). Overall, tropical termites may consume up to half of the annual litter production (Brauman 2000) and up to 90% of dead wood (Bezerra-Gusmão et al. 2011). Tropical rainforest is often associated with low-fertility soils (Jordan 1985), and termite cycling of organic matter efficiently contributes to the return of nutrients to the vegetation.

Termite associations with symbionts play 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 (Bignell et al. 1978; Holt and Coventry 1990). Via foraging activities, large amounts of organic matter are relocated and taken to the termite nest. The primary food source of *Macrotermes* species consists of dead wood, grass litter, and dung (Dangerfield and Schuurman 2000). This food rapidly passes through the gut of the termites, and the material is then expelled as so-called primary feces onto the fungus combs, which consist of more or less degraded plant material pervaded by the basidiomycete fungus of the genus *Termitomyces* (Westhuizen and Eicker 1991; Osiemo et al. 2010). Fungus combs degrade plant structural compounds. Further decomposition occurs as the termites ingest the old parts from the bottom of the fungus combs (Rouland-Lefèvre 2000).

Termites are also the main agents for primary breakdown of surface mulches under conservation agriculture. They also perforate soil surfaces resulting in increased water infiltration rates (Mando and Miedema 1997). Dung deposited on the soil surface by mammalian herbivores needs to be broken down and eventually incorporated into the soil layer, as part of the nutrient cycling. Freymann et al. (2008) reported a diversity of termite taxa feeding on a wide range of mammalian dung. They can quickly remove large amounts of mammalian dung, especially in the dry season, when on average about 1/3 of the dung deposited in a given habitat is removed by termites within 1 month (with the highest rates observed in savannas) (Freymann et al. 2008). These authors also address issues like to what extent and which species of termites consume mammalian dung and whether termites might fulfill a similar ecosystem role as dung beetles.

10.3 Soil-Building Properties

Macroinvertebrates have an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats. The potential beneficial effects of soil macrofauna on soil physical characteristics in general, and on soil aggregations in particular, are well recognized (Kooistra and van Noordwijk 1996; Mando and Miediema 1997). Termites, in particular, have a very strong impact on the soil environment and are therefore called "ecosystem engineers." It was suggested some time ago (e.g., Adamson 1943) that they have an important role in maintaining the fertility of tropical soils and the productivity of ecosystems. These insects are often overlooked as important drivers of habitat quality. Yet the effects of termites on soil character and quality may rival or exceed that of vertebrate herbivores, being one of the most important biological agents for reworking the soils. Their behavior in selecting, transporting, and manipulating soil particles and cementing them together with saliva brings some immediate changes in soil structure and properties (Lobry de Bruyn and Conacher 1990; Wood 1996; Mando 1997). During their feeding and nesting activities, termites improve soil aeration, enhance water absorption and storage in soils, and facilitate carbon fluxes and storage. These processes are crucial for long-term soil fertility, plant growth, and soil formation (Jouquet et al. 2014).

It has been shown that termite activity increases the content of organic matter in the soils that they use for the construction of nests and also modifies the clay mineral composition of these soil materials (Jouquet et al. 2002b; Roose-Amsaleg et al. 2004). Tunneling by termites creates channels in soil through which water preferentially flows (Leonard and Rajot 2001; Turner 2006). Also, their incorporation of feces and saliva is known to affect soil microorganisms (Jouquet et al. 2011), generating higher microbial abundances, activities, and diversity in nests, compared to surrounding soils (Gupta et al. 1981; Holt and Lepage 2000; Chouvenc et al. 2011). Abundant literature is also available in relation to the effects of termites on the mobility of a number of elements. Semhi et al. (2008) reported that termite activities increase the contents of most major and some trace elements in their mounds.

Soil restoration and sustainable agricultural practices can be achieved through utilization of their ecosystem service capability (Crain and Bertness 2006; Brussaard et al. 2007). Termites provide self-renewing services, which might be a relevant option for sustaining soil productivity and rehabilitating degraded soils in tropical agroecosystems (Jouquet et al. 2011). Kaiser et al. (2017) provided evidence about the effectiveness of some termite species in restoring barren soil and maintaining long-term soil productivity, thereby facilitating sustainable agriculture in sub-Saharan West Africa. They reported that the impact of termites is dependent on the particular species and their ecological requirements. Soil-feeding termites have a positive impact on the overall organic matter cycling in the tropics. This impact on the soil organic matter humification process is due to the most important feeding habit in terms of species diversity and soil-feeding species (Brauman 2000). Unlike other termites, their diet is not based on lignocellulosic plant degradation but on the consumption of the mineral-containing soil horizons, for acquisition of nutrients. During gut transit, the soil organic matter is then strongly modified, in terms of nature and organization.

Wood (1988) categorizes the main ways in which soil is modified by termites as physical disturbance of soil profiles, changes in texture, changes in nature and distribution of organic matter, changes in distribution of plant nutrients, and hence changes in soil fertility with, finally, construction of subterranean galleries. A number of studies focused on natural savanna ecosystems and reported beneficial effect of termites on soil porosity, water infiltration, nutrient uptake, and plant cover or biomass, demonstrating their capacity to rehabilitate degraded and crusted soils (Sarr et al. 2001; Dawes 2010).

Pedological influence of termites includes the production of biogenic aggregates, with physical and chemical properties different from the surrounding environment (Jouquet et al. 2016). Termites can mold up to 1300 kg ha^{-1} of soil annually (Kooyman and Onck 1987a), and it has been suggested that their biogenic structures constitute microsites that protect organic carbon against rapid mineralization (Mora et al. 2003). Sarcinelli et al. (2013) investigated the alterations in soil chemical and physical properties promoted by pedobioturbation, during mound building. These authors reported that the concentrations of nutrients, organic carbon, and clay-size particles were significantly higher in mounds than in surface soils. On a weight basis, termite mounds had up to 32 times more nutrients, 12 times more organic carbon, and 5 times more clay than surrounding soils. They mentioned that termites greatly improve soil properties, representing truly ecosystem engineers in sandy soils, with an average soil turnover by mound-building activity reaching 10.5 m^3 ha^{-1}. Studies have shown idiosyncratic effect of termites on pH, depending on the species and soil type. Nutting et al. (1987) found that subterranean termites in Sonoran Desert grassland, *Heterotermes aureus* and *Gnathamitermes perplexus*, slightly increased the soil pH by bringing clay-rich soil from deep layers to the surface.

There is strong evidence in the literature that ecosystem properties greatly depend on the diversity, distribution, and abundance of organisms (Hooper et al. 2005). The interactions among species, both above- and belowground, can have profound impacts on plant performance. In many arid ecosystems, however, termite nests impart substrate heterogeneity by altering soil properties, thereby enhancing plant growth (Bonachela et al. 2015). Jouquet et al. (2002a) showed that the sheetings of *Odontotermes* contain more nutrients, particularly carbon and exchangeable cations, than the underlying soil. Additionally, soil sheetings of *Macrotermes* and *Odontotermes* species contain large amounts of inorganic nitrogen (Ndiaye et al. 2004). Thus, sheetings might enhance the growth of plant root at sites with high termite activities. Termite interactions with soil depend 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 within a colony (Ali et al. 2013). It is well known that termite-induced changes in soil moisture, carbon availability, pH, and microbial biomass may have subsequent effects on soil carbon storage, plant community composition, and nutrient and water cycling. Yet it is virtually unknown as to how such changes in soil inputs and structure translate to changes in soil microbial biomass, carbon availability, pH, and moisture (Maynard et al. 2015).

10.4 Mound Properties

Several termite species build mounds or termitaria that provide a buffered environment against extreme temperature and humidity, as well as protection from predators. Termite mounds shape many environmental properties. Analogous structures built by ants and burrowing mammals are similarly influential worldwide (Alba-Lynn and Detling 2008). These mounds often differ from their parent soils in physical, chemical, and biological properties (Holt and Lepage 2000).

Termite mounds are often considered as “patches” or “hotspots” in ecosystems, which increase the spatial and temporal heterogeneity of ecological processes (Bottinelli et al. 2015). Thus termites are often referred to as “major bioturbators,” “soil engineers,” or even “master builders” (Lavelle et al. 1997a; Jouquet et al. 2006; Oberst et al. 2016). The materials needed for the construction of the nests are taken from the close environment, generally limited to a few meters surrounding the nested area. Termites mix soil materials with wood and excrements for the construction of their nests (Noirot 1970; Jungerius et al. 1999). The specific properties of mound soils are usually explained by the ability of termites to collect soil from deep layers. They specifically select fine-size particles such as clays and oxides (Watson 1962; Fall et al. 2001; Abe et al. 2009) and/or modify the mineralogical properties of clays while building their mounds (Jouquet et al. 2002b, 2007). Thus, termite mound soils are usually enriched in clay, compared to the surrounding soil environment.

These “biogenic” structures have a large impact on the regulation of major biogeochemical processes in most tropical ecosystems (Kaschuk et al. 2006; Robert et al. 2007). Normally a mound grows as the colony grows (Lee and Wood 1971), as a result of additions of soil particles to the mound structure. Termite mounds may persist in the landscape for more than two decades (Lobry de Bruyn and Conacher 1990). With time and abandonment, these mounds are eroded, and their material is redistributed on the soil surface, potentially creating a soil environment more favorable to plant establishment and development (Dangerfield et al. 1998; Konate et al. 1999).

Termite mounds form small islands of enhanced water and soil nutrient availability on otherwise dry and nutrient-poor hill crests, which can have important impacts on the community of plants (Davies et al. 2016). Rather, mound-field landscapes are more robust toward aridity, suggesting that termites may help stabilize ecosystems under global change (Bonachela et al. 2015).

Long-term enclosure of ungulate herbivores is known to decrease functional diversity of woody plant species, but this effect may be mitigated by termitaria. Joseph et al. (2015) reported that at regional scales, mounds can enhance functional diversity of woody plant despite the impacts of herbivory. Petipas and Brody (2014) tested how termites and vertebrate herbivores affect a common plant endosymbiont, arbuscular mycorrhizal fungi (AMF) and reported strong suppressive effect of termites on AMF communities. Mound soils provide a more hospitable environment for plant growth because of their higher levels of phosphorus, nitrogen, and micronutrients (Table 10.1) and enhanced water-holding capacities (Jouquet et al. 2011), thus reducing plant reliance on AMF for nutrient acquisition.

It is documented that termite mounds are rich in different plant nutrients (Semhi et al. 2008; Seymour et al. 2014) and can be safely used for different purposes like use in growing rice paddy cultivation, vegetable beds, and charcoal kilns (Miyagawa et al. 2011). Moreover, due to their higher density, mounds can be used as a bulking agent to speed up composting of agricultural waste as well as to enhance density of the matured compost. Karak et al. (2014) reported the suitability of termite mounds as a bulking agent for composting with crop residues and cow dung in pit method. These authors mentioned that use of 50 kg termite mound with the crop residues (stover of ground nut, 361.65 kg; soybean, 354.59 kg; potato, 357.67 kg; and mustard, 373.19 kg)

Table 10.1 Nutrient conditions from soils collected in fenced and open areas, on termite mounds, and in corresponding off-mound areas

	Fenced		Open		*F* value	*P* value
	Off	On	Off	On		
pH	6.17 (0.27)	7.36 (0.11)	6.31 (0.13)	7.50 (0.16)	135.11	<0.0001 ON
P	1.19 (0.08)	4.26 (2.61)	1.41 (0.15)	2.31 (0.20)	6.86	0.0307 ON
Mg	982.83 (53.08)	614.00 (10.33)	968.50 (19.87)	699.17 (224.16)	22.81	0.0014 OFF
Ca	4365.50 (554.32)	8256.67 (781.54)	4207.17 (236.08)	7860.0 (1798.77)	40.56	0.0002 ON
B	0.25 (0.04)	0.85 (0.19)	0.28 (0.03)	0.81 (0.17)	56.20	<0.0001 ON
Mn	73.28 (23.04)	45.83 (14.70)	70.75 (13.11)	34.93 (7.81)	12.25	0.0081OFF
ECEC	33.68 (3.02)	49.42 (4.48)	32.97 (0.85)	48.96 (5.43)	13.88	<0.0001 ON
NO^{-}_{3}	1.33 (0.59)	17.97 (4.18)	1.0 (0.06)	14.67 (19.76)	6.81	0.0311ON

Source: Petipas and Brody (2014)

Note: *ECEC* effective cation exchange capacity. Effective cation exchange capacity was estimated as the sum of exchangeable cations: Ca, K, Mg, and Na. Available phosphorus was extracted by Modified Morgan P (MM-P) method and measured colorimetrically. Means and standard deviations (±) are presented. *P* values are listed in the last column along with the higher main effect and cow dung (84.90 kg) formed a good-quality compost within 70 days of composting, having nitrogen, phosphorus, and potassium as 20.19, 3.78, and 32.77 g kg^{-1}, respectively, with a bulk density of 0.85 g cm^{-3}. Shanbhag et al. (2017) studied the abundance and properties of mounds built by *Odontotermes obesus* in relation to rainfall and parent soil properties in southern Indian forests. They analyzed carbon and clay contents in soil samples collected from mounds and the surrounding topsoil. These authors reported that mound numerical density was positively correlated with mound height and that rainfall had a negative relationship with the abundance. The carbon content in mound walls depends mainly on how much clay the termites used, and the amount of clay in the surrounding topsoil determines mound soil properties. Finally, the use of mound material may present an opportunity to resource-poor farmers, provided that the application of mound materials is optimized and that any adverse effect on soil physical properties can be mitigated (Adhikary et al. 2016).

10.5 Termite Diversity and Degraded Land

Soil feeders help create and maintain soil conditions favorable to plant growth. As many other organisms, also termite communities are affected by the degradation of the habitat. Termite diversity also decreases under long-term cultivation (Kooyman and Onck 1987b). Some studies focusing on termites in deforested/degraded landscapes showed that this group is a good bioindicator of perturbation and restoration processes (Attignon et al. 2005; e.g. Donovan et al. 2007; Vasconcellos et al. 2010; Bhavana et al. 2015). To promote macrofauna abundance and taxonomic richness in soils, integrated conservation soil management practices, with attention to the particular needs and preferences of termites and earthworms, are needed (Zida et al. 2011). According to de Paula et al. (2016), reforestation is a valuable strategy in restoring termite diversity, aiming at recovering the ecosystem services they provide. Only few researches have been reported on the utilization of termites for the management of soil fertility or for the rehabilitation of degraded soils. Jouquet et al. (2011) discussed the main obstacles hampering the development of such approaches. These authors suggested that the ecosystem services provided by termites are not sufficiently appreciated, especially in the context of long-term processes and of the possible biotechnologies derivable from a detailed knowledge of their biology.

10.6 Production of Gases

In the tropics, termites are major players in the mineralization of organic matter, leading to the production of greenhouse gases. They may emit large quantities of methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O) into the atmosphere. The emission rate of gases by termites is highly variable from species to species. Soil-feeding termites emit more methane than wood-feeding termites (Brauman et al. 1992; Bignell et al. 1997). Nitrous oxide production rates were higher in termites feeding on substrates with higher N content, such as soil and fungi, compared to those feeding on N-poor wood (Brauman et al. 2015).

Methane production by termites was first reported by Cook (1932) who observed the evolution of a gas from *Zootermopsis nevadensis* described as hydrogen and/or methane. Intensive studies during the following years have shown that methane is actually produced in the termite digestive tract by symbiotic microorganisms (Lee and Wood 1971). The flux of gases from termite nests into the atmosphere has been measured. The first quantitative figures for methane production by wood-feeding lower termites were reported by Breznak (1975). According to Zimmerman et al. (1982), global annual emissions calculated from laboratory measurements could reach 1.5×10^{14} g of CH_4 and 5×10^{16} g of CO_2. The largest emissions should occur in tropical areas disturbed by human activities. Rasmussen and Khalil (1983) verified the role of termites in the global methane cycle and reported that termites are indeed a potentially significant source of atmospheric CH_4 with an estimated global production of about 50×10^{12} g year^{-1}. Ho et al. (2013) reported that termites are a natural methane source contributing 3–4% to the total CH_4 budget, globally.

Termite production of gases is species specific and varies depending on the soil environment and their food quality (Brümmer et al. 2009; Jamali et al. 2013; Brauman et al. 2015). There are several important factors controlling the methane flux from a termite nest. The amount of CH_4 produced in a colony depends on the emission rate by termites and the population in the colony (Sugimoto and Inoue 1998). The mound material showed higher methanotrophic activity. Termites are not known to harbor methane-oxidizing microorganisms (methanotrophs). However, a considerable fraction of the methane produced can be consumed by methanotrophs that inhabit the mound material (Ho et al. 2013).

The contribution of termite mounds to the overall carbon balance has been shown to be negligible in tropical savannas (e.g., Jamali et al. 2013). However, De Gerenyu et al. (2015) estimated that CO_2 emissions from termite mounds constituted up to 10% of the total CO_2 emission in a tropical forest, in southern Vietnam. Ohashi et al. (2017) determined the carbon dioxide emission from nests of termites and ants in a tropical rainforest in Malaysia. They noticed that CO_2 emission from termite and ant nests was significantly higher than that from the bulk surrounding soils, suggesting that termite and ant nests are hotspots of CO_2 emission from soil.

10.7 Conclusion

Soil organisms are essential for the functioning of natural and managed ecosystems and the productivity of land. They maintain soil conditions favorable to plant growth. Termites, in particular, are ecosystem engineers, altering soil composition and hydrology. Their associations with symbionts play a significant role in the digestion and decomposition of organic matter. Overall, tropical termites may consume up to half of the annual litter production. A diversity of taxa also feed on a wide range of mammalian dung. Termite mounds are rich in different plant nutrients and shape many environmental properties. Rather, mound-field landscapes are more robust toward the impact of aridity, suggesting that termites may help stabilizing ecosystems, under global change.

Termites are a good bioindicator of perturbation and restoration processes. They can modify degraded environments and their biogenic structures, modifying the availability of resources for other organisms. During their feeding and nesting activities, termites improve soil aeration, enhance absorption and storage of water in soils, and facilitate carbon fluxes and storage. These processes are crucial for long-term soil fertility, plant growth, and soil formation. These insects may also emit large quantities of greenhouse gases like methane, carbon dioxide, and nitrous oxide into the atmosphere. Production of gases is, however, species specific and varies, depending on the soil environment and food quality.

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Chapter 11
Termites as Food in Africa

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Abstract Apart from their important role in the breakdown of organic matter in tropical regions, termites are an important food source across sub-Saharan Africa, where they are consumed as delicacies both in rural and urban areas. This chapter reviews termite species as an edible insect and the overall role it plays in food and nutrition security in Africa. The study shows that *Macrotermes* is the most eaten genus with the species *M. bellicosus* taking the lead. The insects are always harvested from the wild during the rainy seasons, the months of March to June and November to December being the most important. Several methods of capture are employed using water in basins and lamps to attract them at night. Termites are highly nutritious with high levels of protein, fats, key vitamins, and minerals. With very little or no anti-nutrient, noxious chemicals and microbial concerns, they seem a great food source. Their inclusion in complementary food formulations has proved very satisfactory. However, climate change, seasonality, and overexploitation seem to be the current challenges to their full-scale use.

Keywords Termites • Edible insects • Entomophagy • Insects in Africa • Insects as foods

11.1 Introduction

The world population is continuously increasing with a growing requirement for food. Due to this growing population and changing eating habits, there is an increasing demand for sustainable alternative protein sources. While relatively new to the Western culture, the consumption of edible insects has been a common practice in many regions and cultures around the world, for hundreds of years. More than two billion people traditionally practice entomophagy worldwide (FAO 2012; van Huis 2013). Edible insects are rich in protein and fat and provide minerals and vitamins (Rumpold and Schlüter 2013; Nowak et al. 2016). In general, they meet amino acid requirements of humans and are high in unsaturated fatty acids (Rumpold and Schlüter 2013). Of the insect species consumed as food described in the literature (Jongema 2015), 31% are beetles (Coleoptera); 18% are caterpillars (Lepidoptera); 14% are bees, wasps, and ants (Hymenoptera); and 13% are grasshoppers, locusts, and crickets (Orthoptera) (van Huis 2013). Besides beetles and grasshoppers, termites rank highest among the most consumed insect species in the world (Chung and Yu 2010).

The importance of termites as an edible insect cannot be overemphasized. In a recent systematic review of nutrient composition for edible insects, the three most well-represented species were (1) termites (*Macrotermes* sp.) which are wild-harvested,

(2) palm weevil (*Rhynchophorus phoenicis*) which is semi-cultivated, and (3) black soldier fly (*Hermetia illucens*) which is intensively farmed (Payne et al. 2015).

Of the over 45 termite species eaten worldwide as food or feed, they are spread across just four families [Termitidae (39 spp., 87%), Rhinotermitidae (7 spp., 6%), Kalotermitidae (2 spp., 4%), and Hodotermitidae (2 spp., 4%)]. The most consumed are *Macrotermes bellicosus*, *M. subhyalinus*, *Nasutitermes macrocephalus*, and *Pseudacanthotermes spiniger*.

Large colonies of termites are found in arid and humid areas of Central and East Africa. In Africa, *Macrotermes* – otherwise referred to as "big termite" – is the most abundant genus and is among the favorite foods of humans and apes alike (de Figueirêdo et al. 2015). Though abundantly prevalent across Africa, termites are only available seasonally, particularly in the rainy or wet seasons. This coincides roughly with the months from April to July (Banjo et al. 2006; Ayieko et al. 2010a, 2011; Igwe et al. 2011; Aydoğan et al. 2016) and October to December (Ayieko et al. 2010a; Kinyuru et al. 2013).

Termites central role as an edible insect in Africa owes this prestigious status to its rich fat (44.82–47.31 g/100 g) and protein contents (33.51–39.74 g/100g) (Bukkens 1997; Ekpo et al. 2009; Igwe et al. 2011; Kinyuru et al. 2013; Adepoju and Omotayo 2014). The processing and preparation of the insects mostly included de-winging and then frying or toasting in its own oil, with salt occasionally added (Ayieko et al. 2010a; Kinyuru et al. 2010; Kinyuru et al. 2013). This minimal processing was usually adequate to ensure the consumption of safe products, however, with a decrease in digestibility and availability of some micronutrients (Kinyuru et al. 2010). The insects have also been converted into other unrecognizable forms in muffins and crackers (Ayieko et al. 2010b). Some instances of it being eaten raw were also encountered. However, reports of contamination, where five individuals in Kenya died of botulism following the consumption of termites, have been recorded (Nightingale and Ayim 1980).

The present chapter was undertaken to provide a concise review of the termite consumption in Africa with particular attention to their diversity and distribution, seasonality and harvesting methods, nutritional composition, safety concerns, and processing and preservation mechanisms, among others. The method to obtain data was collected from the systematic analysis of the literature available in online international databases.

11.2 Termites Used as Food in Africa

Several species of termites are eaten as food and feed in Africa. Table 11.1 lists the 48 species consumed, as found in the literature. It reveals *M. bellicosus* (13 countries) and *M. falciger* (12 countries) are the most widely eaten species across the continent. The genus *Macrotermes* (Termitidae) was the most prominent and widespread, while just one and three species, from families Rhinotermitidae and Hodotermitidae, respectively, were recorded. Not included in this table are the array of local names termites are referred to in various countries or by different tribes

Table 11.1 List of termite species by location, consumed across Africa

Species	Location (country)	Stage of consumption
Acanthothermes acanthothorax[8]	Tanzania; Uganda	–
Acanthothermes sp.[6,8]	Tanzania	–
Apicotermes sp.[4,6,8]	Central African Republic	–
Bellicositermes natalensis[6,8]	Central African Republic	–
Bellicositermes natalensis[4,6]	Central African Republic	Alates
Bellicositermes sp.[4,8]	Central African Republic; DR of Congo	Alates; soldiers
Bellicositermes sp.[4]	Ivory Coast	Alates
Coptotermes sp.[6] [R]	Kenya	Alates
Cubitermes[4,6]	Congo; Tanzania; Zimbabwe	–
Cubitermes[4,6]	South Africa	Alates
Hodotermes mossambicus[6,8] [H]	Botswana	Winged reproductive forms
Hodotermes sp.[6,8] [H]	South Africa	Alates
Macrotermes amplus[6]	DR of Congo	–
Macrotermes bellicosus[3,8]	Nigeria	Alates; queen
Macrotermes bellicosus[2,4,5,6,7,8]	Congo; CAR; DR of Congo; Nigeria; Kenya; Cameroon; Ivory Coast; Guinea; Togo; Liberia; G. Bissau; Burundi	All stages
Macrotermes falciger[6,7,8]	Zimbabwe; Congo; Benin; Zambia; South Africa; Burkina Faso; Burundi; Mali; Togo; Cameroon; Congo; Guinea	Alates; soldiers; queen
Macrotermes herus[8]	Tanzania	–
Macrotermes lilljeborgi[8]	Cameroon; Guinea	–
Macrotermes michaelseni[6]	Malawi	–
Macrotermes mossambicus[6,8]	East and Southern Africa	–
Macrotermes muelleri[6,8]	Congo; Cameroon; Guinea	Alates, soldiers
Macrotermes natalensis[6,7,8]	Central African Republic; Zimbabwe; Congo; Nigeria	–
Macrotermes nigeriensis[8]	Nigeria	Alates
Macrotermes nobilis[8]	Congo; Gabon; Cameroon	–
Macrotermes natalensis[3]	Nigeria; Zimbabwe; DR of Congo; Cameroon; Congo; CAR; Burundi; South Africa; Malawi	Alates; queen

(continued)

Table 11.1 (continued)

Species	Location (country)	Stage of consumption
Macrotermes renouxi[8]	Cameroon	–
Macrotermes sp.[4,6,7,8]	DR of Congo; Tanzania; Zimbabwe; Malawi; Zambia; Senegal; Uganda; Ivory Coast; Guinea; Ghana;Togo; Benin; Burundi	Alates, soldiers
Macrotermes subhyalinus[1,2,5,6,7,8]	Angola; Zambia; Kenya; Togo; Burundi; Senegal; Tanzania; Uganda	Alates
Macrotermes swaziae[6,8]	South Africa	Alates
Macrotermes vitrialatus[6,8]	Angola; Zambia	Alates
Megagnathotermes katangensis[8]	DR of Congo	–
Microhodotermes viator[6,8] [H]	South Africa	Alates
Microtermes sp.[8]	Kenya	Alates
Odontotermes badius[6,8]	South Africa; Zambia; Kenya	Alates
Odontotermes capensis[6,8]	South Africa	Alates
Odontotermes kibarensis[8]	Uganda	–
Odontotermes magdalense[8]	Cameroon	–
Odontotermes sp.[6,8]	DR of Congo; Kenya; Zimbabwe	Alates
Protermes sp.[4,6,8]	Central African Republic	–
Pseudacanthotermes militaris[5,6,8]	Kenya; Tanzania; Uganda; Angola; DR of Congo; Zambia	Alates
Pseudacanthotermes sp.[6,8]	Tanzania	alates; queens; soldiers
Pseudacanthotermes spiniger[5,8]	Kenya; Angola; Uganda; Zambia; DR of Congo	Alates
Termes fatale[8]	Africa (Southern Area); South Africa	Alates
Termes gabonensis[6,8]	DR of Congo	Alates; Soldiers
Termes sp.[2,6]	Tanzania	alates; queens; soldiers
Termitidae[2,6]	Mali	–
Trinervitermes sp.[8]	Central African Republic	Alates

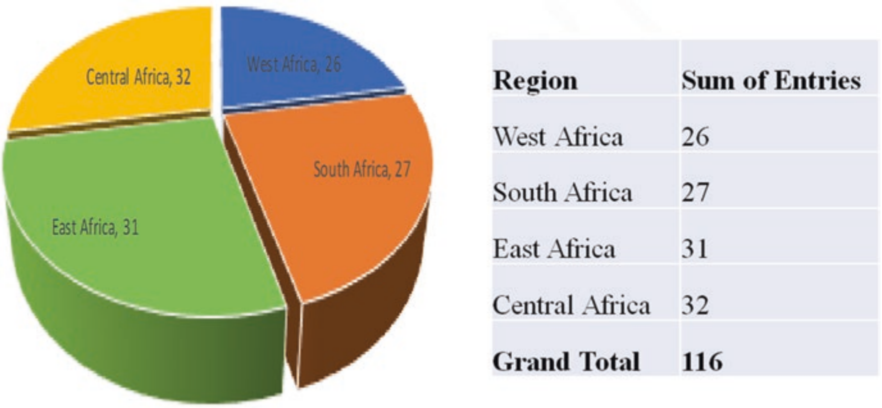
Sources: [1] Oliveira et al. (1976), [2] Bukkens (1997), [3] Banjo et al. (2006), [4] Hoare (2007), [5] Kinyuru et al. (2013), [6] Jongema (2015), [7] Kelemu et al. (2015), and [8] Mitsuhashi (2016)
[H] Hodotermitidae family; [R] Rhinotermitidae family
– not indicated

within the same nation. These vernacular names share no similarity with taxonomic classification as their nomenclature relates to the mound, use of the insect (food or medicine), swarming, and other termite behaviors (van Huis 2017).

11.2.1 Termite Diversity in Africa

South Africa, Tanzania, and the Central African Republic (CAR) topped the list of countries with the most records (*n* = 9). This was closely followed by Cameroon, DR of Congo, and Kenya, with eight termite species deemed edible. Figure 11.1 depicts the regional distribution of termite species as food in Africa. Of immediate attention is the complete absence of the North Africa region and countries, as also shown in Table 11.1. Though no reason was found for this gap in the literature, it was suggested that this may be due to the arid, sandy soils, coupled with the high ground temperatures encountered north of the Sahara. Thus, all reports examined thus far were of species in sub-Saharan Africa. Overall the records of termite consumption across this subregion were comparable. The Central (32) and East (31) African regions recorded the highest number of incidence of termites consumed as food, with the least entries in West Africa (n = 26).

Table 11.1 though complete may contain one or two duplicate entries. Species such as *Termes* sp., *Microtomes* sp., *Bellicositermes* sp., *Macrotermes* sp., and *Odontotermes* sp. were documented with question marks connoting doubts as to the validity of such names as pointed out by Jongema (2015) in his publication, the “World List of Edible Insects.”



Region	Sum of Entries
West Africa	26
South Africa	27
East Africa	31
Central Africa	32
Grand Total	**116**

Fig. 11.1 Regional distribution of edible termite by number in Africa (*Source*: Banjo et al. 2006; Hoare 2007; Kinyuru et al. 2013; Jongema 2015; Kelemu et al. 2015)

11.2.2 Termite Stages Consumed

Termite castes eaten have been differentiated into alate adults, soldiers, and queens (Table 11.1). The alates, also referred to as winged adults, are the most consumed stage of termites in Africa. This can be alluded to their swarming behavior during "nuptial flights" to establish new colonies, especially after rainfalls. They usually shed their wings after such flights making them available for harvest. The soldiers are also eaten, but they are mostly harvested from the mound itself by making holes and sending in twigs or sticks to get them out. It is not a surprise that the queen is the least eaten stage, since they are the most difficult to harvest as it would entail destroying an entire termite mound to locate them (van Huis 2017).

11.3 Termites Harvesting for Food

In African tropical countries, most insects are collected from the wild. Such is the case for termites. The tribes of Africa, especially those in Zambia, the Central African Republic, Angola, and the DR of Congo, collect winged sexual forms at the time of nuptial flights of species, such as *Macrotermes falciger* (Gerstacker) and *M. subhyalinus*, when adults emerge in large numbers from the termitaries subsequent to the maiden rains (Malaisse 2005).

Harvesting is mostly seasonal; for instance, in Ghana, *Macrotermes bellicosus* is available for harvesting only in June and July (Anankware et al. 2016). In East Cameroon, termites are only harvested in the rainy months of March, April, and May (Muafor et al. 2014). Termites were collected in Kenya during the short rain season from March to May and the long rain season from September to December. The termites are attracted by light from a lantern lamp causing them to fall in large swarms and are collected and put in a clean container (Kinyuru et al. 2010). Van Huis (2003) reviewed various methods of termite collection around Africa. The most popular and easy way used in the tropics is to collect them during the evening hours, by placing a basin of water right under the light source. As light is reflected on the water, termites are attracted and trapped on the water surface (Chung 2008).

In the DR of Congo, a basket is put upside down over an emergence hole of the mound. In alternative a dome-shaped framework of sticks is built up, or elephant grass is covered with banana leaves or a blanket, to cover part of the emergence hole near which a receptacle is placed to collect flying termites. Continuous beating and drumming on the ground around the hill trigger certain termite species to emerge to extract soldiers from the mound. Women and children push grass blades or parts of tree pods or the bark into the shafts of a termite mound or prepare smoke from charcoal from certain trees and blow it into the opening. Soldiers stripped into a container are then collected. Sometimes nests are dug up to collect queens (van Huis 2003).

In Benin, winged termites (*Macrotermes falciger*) are collected after the rain in a large pan containing water placed under an electric light. In the absence of grid-enabled light, lanterns are placed in large empty pans to trap the winged termites. The queen is captured after the termitarium has been completely evacuated. The most favorable season for gathering and collecting insects is the wet months of May, June, and July.

There is a considerable trade in termites in some areas, and sun-dried termites are found at the right season in the local markets in many East African towns and villages. They are sometimes transported long distances to markets. The Baganda, who live around the northern shore of Lake Victoria in Uganda, use termites and fried grasshoppers as snacks between the main meals. In many Bantu-speaking parts of the country, boiled and dried termites are on sale in the markets at some seasons of the year. R.J. Phelps, (personal communication, 1987), recorded that "Certainly dried caterpillars of saturniid moths are sold on the local market, and consumption of termites, locusts and tettigoniids by the clear majority of the population continues despite the presence of western cultures. In fact, many people of Europa background eat termites here, although not in the quantities that the local people do" (Fig. 11.2).

11.4 Nutritional Composition of Termites

Several papers have dealt with the nutritional composition of edible termites from Africa (Phelps et al. 1975; Oliveira et al. 1976; Finke et al. 1989; Banjo et al. 2006; Christensen et al. 2006; Ekpo et al. 2009; Kinyuru et al. 2010; Igwe et al. 2011; Ajai et al. 2013; Kinyuru et al. 2013; de Figueirêdo et al. 2015; Kinyuru et al. 2015). Table 11.2 is a summary compilation of the nutritional composition of species consumed in Africa, as recorded in the literature (based on dry matter).

Fig. 11.2 (**a, b**) Sale of harvested winged termites in the market (*Source*: Kinyuru et al. 2013)

Table 11.2 Proximate composition of edible winged insects (g/100g)

	Moisture	Protein	Fat	Ash	Fiber	Carbohydrate [NFE]	Energy content [Kcal/100g]
Macrotermes subylanus[1]	6.5	39.34	44.82	7.58	6.37	1.89	–
Pseudacanthotermes militaris[1]	5.04	33.51	46.59	4.58	6.59	8.73	–
Macrotermes bellicosus[1]	5.13	39.74	47.03	4.65	6.21	2.37	–
Pseudacanthotermes spiniger[1]	8.76	37.54	47.31	7.22	7.21	0.72	–
Macrotermes subylanus[2]	0.94	38.42	46.1	6.56	–	7.98	612
Macrotermes bellicosus[3]	6	34.8	46.1	10.2	–	–	–
Termes sp.[3]	40	28.8	32.2	0.9	–	–	414
Termes sp.[3]	1.7	35.7	54.3	4.8	–	–	656
Macrotermes bellicosus[4]	2.82	20.4	28.2	2.9	2.7	43.3	–
Macrotermes natalensis[4]	2.98	22.1	22.5	1.9	2.2	42.8	–
Macrotermes nigeriensis[5]	10.78	20.94	34.23	7.6	5.71	20.74	–
Macrotermes bellicosus[6]	12.6	38.36	36.12	11.26	–	14.25	–
Macrotermes falciger[7]	–	41.8	44.3	11.5	–	1.1	760.5
Average	**8.60**	**33.19**	**40.75**	**6.28**	**5.28**	**15.86**	**610.63**
% Total	**7.79**	**32.36**	**39.74**	**6.12**	**2.94**	**11.05**	–
% Total (dry basis)	–	**32.74**	**39.46**	**6.20**	**5.21**	**15.65**	–

Sources: [1] Kinyuru et al. (2013), [2] Oliveira et al. (1976), [3] Bukkens (1997), [4] Banjo et al. (2006), [5] Igwe et al. (2011), [6] Ekpo et al. (2009), and [7] Phelps et al. (1975)
– not indicated

11.4.1 *Proximate Composition*

Overall, termites were found to be good sources of fat, proteins, fiber, minerals (ash), and vitamins. Table 11.2 clearly reveals that, like most other edible insects, termites consist predominantly of fat (39.74%) and proteins (33.19%) on average (n = 13). These values agree strongly with those published in the literature on termites eaten in other continents (Oyarzun et al. 1996; Ramos-Elorduy et al. 1997). In a review on the nutrient composition of 236 edible insects, it was also shown that globally termites (n = 7) had mean fat and protein values of 32.74 and 35.34%, respectively (Rumpold and Schlüter 2013). Like the nutrient composition data of other edible insects, the nutritional values for termites are highly variable. For instance, fat contents range from 22.5% in *M. bellicosus* (Banjo et al. 2006) to 54.3% in *Termes* sp. (Bukkens 1997), while protein content varies from 20.4% (Banjo et al. 2006) to 39.74% in *M. subylanus* (Kinyuru et al. 2013). These huge variations have been attributed to the diversity in species, origin, insect food substrate, as well as measuring methods employed (van Huis 2013; Rumpold and Schlüter 2013). Moisture content was also variable and largely depended on the drying technique used. The mean moisture content was 8.86 g/100 g (7.79%), a value that agrees with moisture content range for termites of 6.50–8.76 g/100 g recorded (Kinyuru et al. 2013).

The next abundant solids were carbohydrates, also referred to as nonfat extract (NFE). This parameter was calculated as the difference of the sum of the others rather than by direct analyses. The mean NFE content of termites [15.86 g/100 g (15.65% dry matter)] was rather high compared to that of most edible insects. Average NFE for edible insect ranged between 4.63% and 22.84% (Rumpold and Schlüter 2013). Coincidently, this upper range was attributed to the order Isoptera to which termites belong. However, Banjo et al. (2006) recorded remarkably high values for NFE for termites (43.3% and 42.8%) in their study, with a corresponding lower protein and fat contents. The highest values of carbohydrates have been recorded in the ant *Myrmecocystus melliger* with 77–77.7% and the cricket *Brachytrupes* sp. with up to 85.3% (Rumpold and Schlüter 2013).

Ash is the residue obtained by burning all organic matter at very high temperatures above 500 °C after acid digestion. The average ash content was 6.1% (6.28 g/100 g), a value that falls nicely above the average range of edible insects of between 2.84% and 10.31%. The lowest value was 0.9 g/100 g in *Termes* sp. (Bukkens 1997) with the highest being *M. bellicosus* (11.26 g/100 g) from Nigeria (Ekpo et al. 2009). Similar numbers were recorded for termites in Kenya in the range of 6.21–7.21 g/100 g (Kinyuru et al. 2013). For ash contents in edible insects in general, maximum yields of 25.95% in Diptera have been highlighted, while on the other end of the spectrum, as low as 0.34% was noted for an orthopteran (Rumpold and Schlüter 2013).

The mean fiber content was 5.28 g/100 g. Except for Banjo et al. (2006), where values were below 3 g/100 g, all reported values were well above the average. Chitin makes up the most fiber content in termites and insects in general (Barker et al. 1998; Finke 2002). So, it is assumed the high fiber contents are due to chitin. Insects have been reported to serve as good source of fiber due to their high chitin content, accounting for about 10% of the whole dried insect. In another study, the average dietary fiber content of termites was 6.21–7.21 g/100 g (Gahukar 2011).

11.4.2 Energy Value

Mean energy content (n = 4) was 610 kcal/100 g which is reasonably high. This is attributed to the high value of the two major compositions of termites: fat and proteins. For example, the winged sexual forms of the African termite, *M. falciger*, have been estimated to have a calorific value of 761 kcal/100 g (dry, ash-free, weight basis), while the winged forms of another African species, *M. subhyalinus*, were found to contain 613 kcal/100 g (dry weight) (Oliveira et al. 1976). According to Rumpold and Schlüter (2013), the average energy content of edible insects ranges from 409.78 to 508.89 kcal/100 g.

11.4.3 Fatty Acid Composition

As earlier cited, fat is the most abundant constituent of termite body mass. Table 11.3 shows the spectra of the fatty acid profile of termite species as published in the literature. Overall, there was large variation of composition as well as quantity among the termite oils. Even within the same species (*M. bellicosus*, n = 3), differences were noted. For example, apart from palmitic acid, the amounts of the other fatty acids varied significantly. Ritter (1990) purported that the fatty acid composition of insects is dependent on the composition of their feed. Method of analyses can also result to such disparity on quantities measured. The most abundant mean fatty acids were oleic acid (35.06%) and palmitic acid (34.18%). Linoleic acid, the next abundant fatty acid, was about half that value (18.39%). These findings correlate well with results from other studies (Oyarzun et al. 1996; Kinyuru et al. 2013).

Short-chain fatty acids (C10:1, C10:0, C12:0) were considerably lower, probably due to the low data count (n = 2, caprylic acid, and n = 3, capric acid). Similarly, arachidonic acid (n = 2) had two extreme values, making comparisons difficult. Certain differences in fat and fatty acid composition do exist for different cases. For instance, lipid composition of the fat body of soldiers significantly differs from those of alates and queens. Looking further into the fatty acid profile, they consist predominantly of oleic, palmitic, and stearic acids, while in alates linoleic acids predominate (Cmelik 1969, 1971).

The average amount of saturated fatty acid (SFA) in termites was 40.32% (Table 11.3). This falls in line with values recorded for the overall average of the order Isoptera (41.97%) by Rumpold and Schlüter (2013). The two major components of the SFA were palmitic (C16:0) and stearic (C18:0) acids. Moreover, the three studies involved with *M. bellicosus* had similar values of SFA and unsaturated fatty acids (UFA). However, the total amounts of UFA were generally higher than the SFA. The average SFA/UFA ratio was 0.68, which is on the high end of the range for edible insects, between 0.43 and 0.79 (Rumpold and Schlüter 2013). This clearly shows that the fatty acid composition of termites was mostly made of UFA. This feature is deemed desirable as UFA have been advocated to show better health effects than SFA, especially for heart and cardiovascular diseases (Mann 1993). Within the UFA, the average amount of monounsaturated fatty acids (MUFA), chiefly oleic acid, was double that of the polyunsaturated fatty acids (PUFA), composed mostly of linoleic acid, a trend which is similar with other edible insects (Rumpold and Schlüter 2013). The average PUFA/SFA ratio (not shown) was 0.52, and only two species had such ratio below 0.2 according to Mann (1993). A PUFA/

Table 11.3 Fatty acid composition of termites (% of total lipids)

Species	Caprylic acid (C10:1)	Capric acid (C10:0)	Lauric acid (C12:0)	Myristic acid (C14:0)	Palmitic acid (C16:0)	Palmitoleic acid (C16:1)	Stearic acid (C18:0)	Oleic acid (C18:1)	Linoleic acid (C18:2)	Linolenic acid (C18:3)	Arachidonic acid (C20:4)	SFA	MUFA	PUFA	UFA	SFA/ UFA
Macrotermes bellicosus[2]	–	–	–	0,18	46,54	2,09	–	12,84	34,42	3,85	–	46,72	14,93	38,27	53,2	0.88
Macrotermes bellicosus[3]	–	–	1,5	2,17	42,45	2,1	2,86	15,8	24,2	3,90	4,94	48,98	17,9	33,04	50,94	0.96
Macrotermes nigeriensis[4]	–	–	0,2	0,62	31,39	0,62	7,14	52,45	7,57		–	39,35	53,07	7,57	60,64	0.65
Macrotermes subylanus[1]	–	–	–	1,06	27,65	4,17	6,34	48,6	10,75	1,43	–	35,05	52,77	12,18	64,95	0.54
Pseudacanthotermes militaris[1]		0,21	–	–	26,04	5,84	5,92	50,26	11,54	0,20	–	32,17	56,1	11,74	67,84	0.47
Macrotermes bellicosus[1]	0,42	0,24	0,18	1,16	38,35	0,63	9,53	41,74	5,03	0,87	–	49,46	42,79	5,9	48,69	1.02
Pseudacanthotermes spiniger[1]	0,38	0,31	0,22	0,76	28,04	3,24	6,12	49,27	10,48	0,78	–	35,45	52,89	11,26	64,15	0.55
Macrotermes subhyalinus[1]	–	–	0,1	0,9	33	33	1,4	9,5	43,1	3,00	0,4	35,4	42,5	46,5	89	0.40
Average	**0,40**	**0,25**	**0,44**	**0,98**	**34,18**	**6,46**	**5,62**	**35,06**	**18,39**	**2,00**	**2,67**	**40,32**	**41,62**	**20,81**	**62,43**	**0,68**

Source: [1] Kinyuru et al. (2013), [2] Bukkens (1997), [3] Ekpo et al. (2009), and [4] Igwe et al. (2011)
SFA saturated fatty acid $\sum$ (C10:0, C12:0, C14:0, C16:0, C18:0)
MUFA monounsaturated fatty acid = $\sum$ (C10:1, C16:1, C18:1)
PUFA polyunsaturated fatty acid = $\sum$ (C18:2, C18:3, C20:4)
UFA unsaturated fatty acid (MUFA+PUFA)
– not indicated

SFA ratio below 0.2 correlates positively with high risks of coronary heart disorders and high cholesterol levels. It can therefore be suggested that termites of African origin are associated with lower risks for coronary heart diseases.

11.4.4 Amino Acid Composition

Quality of proteins destined for human consumption is assessed by the amino acid profile and their digestibility (van Huis 2013). Due to the very low data volume of amino acid profile for termites ($n = 3$), only the essential amino acids were considered in this review. Table 11.4 shows the essential amino acid spectra of three termites. Histidine, which is the first limiting amino acid in cereal-based diets, was markedly present and thus could supplement such diets (van Huis 2013).

Insect proteins are reported to be low in the amino acids methionine and cysteine and high in lysine and threonine (DeFoliart 1992). The mean values shown in Table 11.4 agree strongly to this fact, with low values of methionine (7.93) and cysteine (6.53) and elevated amounts of lysine (40.58) and threonine (23.23 mg/g protein). Further insights into the contribution termites can provide to daily diets, in comparison with the Food and Agriculture Organization (FAO) recommended values of beef, are shown in Figure 11.3.

Apart from histidine, termite proteins were considerably lower in all the other essential amino acids. Given the low number of records here, no definitive conclusion can be drawn at this regard. It was observed that the termite essential amino acids met the daily requirements for FAO recommended values for adult (FAO 2007). However, for infant's needs, it felt short of the average requirements, except histidine. In comparison to beef protein, the termite amino acid spectra performed poorly, surpassing the former only in histidine.

Table 11.4 Amino acid composition (mg/g protein)

Termite specie	His	Ile	Leu	Lys	Met+Cys	Phe+Try	Thr	Trp	Val	Total
Macrotermes falciger[1]¥	29	38.5	–	64	15	106.5	38	–	–	291
Macrotermes bellicosus[2]	51.4	51.1	78.3	54.2	26.2	74	27.5	14.3	73.3	450.3
Macrotermes subhyalinus[3]	–	3.71	7.97	3.54	2.19	7.99	4.19	0.77	5.14	35.5
FAO/WHO (adults)[4]	16	13	19	16	17	19	9	5	13	127
FAO/WHO (infants)[4]	26	46	93	66	42	72	43	17	55	460
Termite average*	**40**	**31**	**43**	**41**	**14**	**63**	**23**	**8**	**39**	**259**
Beef	34	48	81	89	40	80	46	12	50	479

Source: [1] Phelps et al. (1975), [2] Bukkens (1997), [3] Oliveira et al. (1976), and [4] FAO (2007)
¥ = in g/16gN [At the reference level, amino acids are usually expressed as mg per g of nitrogen or as g per 16 g of nitrogen (approximately 100 g protein)]
– not indicated
* Average of[1,2,3]

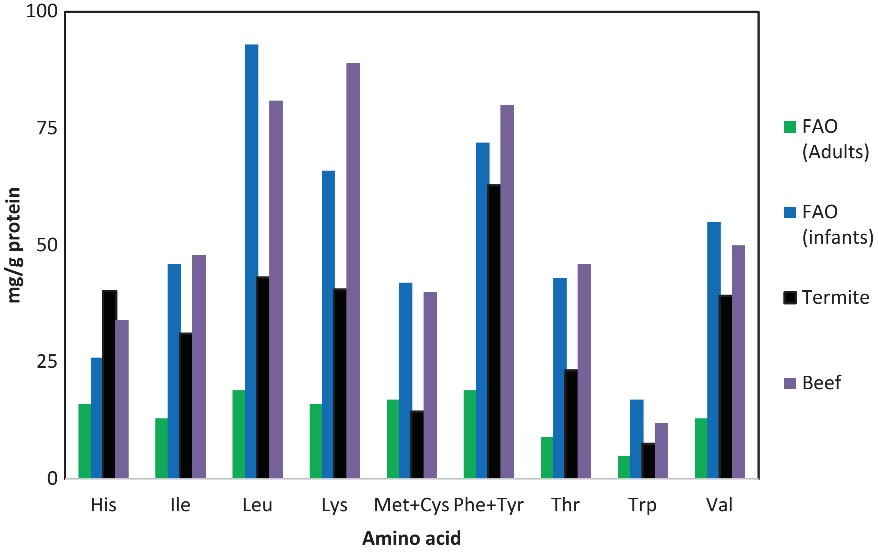


Fig. 11.3 Comparing termite average amino acid content to known standard (FAO and beef) values (*Source*: Phelps et al. 1975; Bukkens 1997; Oliveira et al. 1976; FAO 2007)

As has been observed with other edible insects, termite proteins were limiting in methionine and cysteine and could not meet the minimum daily requirement for adults. In general, studies on amino acid composition for edible insects are severely lacking, given the expensive nature of such analyses. Nonetheless, more studies must be carried out to properly ascertain the amino acid profile of edible termites, for their inclusion in food composition databases.

11.4.5 Mineral Content

Table 11.5 reveals mean values of some mineral elements. Calcium, iron, and zinc contents were the minerals of interest, as *M. bellicosus* had the highest calcium and iron content, while *Pseudacanthotermes militaris* had the highest zinc content. The levels of calcium, iron, and zinc of African termites agree with similar studies in other parts of the globe (Oyarzun et al. 1996; Ramos-Elorduy et al. 1997). However, there was wide variability in iron content between *M. bellicosus* (115.97 mg/100 g) and other species recorded such as *M. nigeriensis* (0.96 mg/100 g) (Igwe et al. 2011; Kinyuru et al. 2013).

In particular, termites contain high quantities of iron (12.3 mg/100 g) and could, therefore, be recommended as a food resource to combat iron deficiency, this micronutrient deficiency being the greatest health burden in developing countries (Meerman et al. 2012).

Table 11.5 Mineral content of selected termite species (mg/100g)

Species	Ca	K	Mg	P	Na	Fe	Zn	Mn	Cu
Macrotermes subylanus[1]	58.72	–	–	–	–	53.33	8.1	–	–
Pseudacanthotermes militaris[1]	48.21	–	–	–	–	60.29	12.86	–	–
Macrotermes bellicosus[1]	63.6	–	–	–	–	115.97	10.76	–	–
Pseudacanthotermes spiniger[1]	42.89	–	–	–	–	64.77	7.1	–	–
Macrotermes nigeriensis[2]	0.1	336	6.96	1.49	112	0.96	0.1	0.08	0.07
Macrotermes bellicosus[3]	21	–	0.15	136	–	27	–	–	–
Macrotermes natalensis[3]	18	–	0.26	114	–	29	–	–	–
Mean value	**36.07**	**336.00**	**2.46**	**83.83**	**112.00**	**50.19**	**7.78**	**0.08**	**0.07**

Source: [1] Kinyuru et al. (2013), [2] Igwe et al. (2011), and [3] Banjo et al. (2006)
– not indicated

Table 11.6 Vitamin composition of selected termites eaten in Africa (mg/100g)

Species	Vitamin A[ug] (retinol)	Vitamin C (ascorbic acid)	Vitamin B1 (thiamine)	Vitamin B2 (riboflavin)	Vitamin B3 (niacin)
Macrotermes nigeriensis[1]	350.00	17.76	0.67	1.56	2.74
Macrotermes bellicosus[2]	2.89	3.41	–	1.98	–
Macrotermes natalensis[2]	2.56	3.01	–	1.54	–
Macrotermes subhyalinus[3]	–	–	0.131	1.14	4.59
Mean Value	**118.48**	**8.06**	**0.40**	**1.56**	**3.67**

Sources: [1] Igwe et al. (2011), [2] Banjo et al. (2006), and [3] Oliveira et al. (1976)
– not indicated

11.4.6 Vitamin Content

As seen from Table 11.6, vitamin data for termites are very scarce (n = 3), and apart from riboflavin where the values are quite similar (mean = 1.56 mg/100 g), there are huge variations in the data for the detected vitamins. Vitamin contents depicted here were generally low; for instance, FAO recommends, for adults, 45 mg of vitamin C daily, but the mean vitamin C content was 8.06 mg. However, due to the huge dearth in data on termite vitamins, no meaningful conclusions could be drawn yet.

11.4.7 Anti-nutrients

The presence of anti-nutrients has also already been demonstrated in some insect species. This is of major concern among people whose diets are low or deficient in vitamins or any other important micronutrient (Belluco et al. 2013a, Belluco et al. 2013b).

The major anti-nutritional factors identified among insects include phytic acid, which decreases the bioavailability of phosphorus by complexing it into phytate. Oxalates, when absorbed in large quantities, cause irritation of the digestive tract. Hydrocyanic acid is highly toxic because it causes anoxia. Tannins also are toxic at high doses as they precipitate proteins. Thiaminase causes a deficiency in vitamin B1.

Generally, edible insects are low in anti-nutrients, with the values reported being dependent on the anti-nutrients in their diet basically from the plants (Omotoso 2006). In a study carried out on the anti-nutrient composition of roasted *M. bellicosus* from Nigeria (Adepoju and Omotayo 2014), it was shown that the insect was very low of anti-nutritional factors. The phytate, oxalate, saponin, and tannin levels were unsurprisingly very negligible since these compounds are mostly found in foods of plant origin. In Kenya, the winged termites consumed do not feed at their adult stage, thus eliminating the chances of edible insect containing anti-nutrients (Kinyuru et al. 2015). Besides anti-nutritional factors, the major safety concerns in termite consumption are with their microbial, chemical, or physical hazards.

11.5 Safety Aspects Involved in Termite Consumption

Being nutrient-rich, insects provide a suitable milieu for the growth of microbes, and an array of pathogens has been reported (Vega et al. 2009). Pathogenic bacteria *Staphylococcus aureus*, *Pseudomonas aeruginosa*, and *Bacillus cereus* (Banjo et al. 2006) have been reported in the West African rhinoceros beetle. Fungi belonging to the genera *Aspergillus*, *Penicillium*, and *Fusarium* have been associated with mopane worms in Botswana (Mpuchane et al. 1996). *Iridovirus* infections were observed in two species of fatally diseased crickets, *Gryllus campestris* L. and *Acheta domesticus* L. (Kleespies et al. 1999). These pathogens present a serious health risk to consumers. Moreover, food safety risk assessments of processed termites *Macrotermes* sp., sold on the roadside in Kenya, revealed lethal doses of *Streptococcus aureus* and *Staphylococcus aeruginosa* in the products, emphasizing the need for food safety assessments. Apart from microbial hazards, chemical, physical, and allergies are also of concern.

11.5.1 Allergies with Eating Termites

To our knowledge, few studies have been published on allergic reactions due to insect ingestion. Differences in geographical food traditions can result in differences in food allergy risk. Caterpillars, as well as termites, are commonly eaten insects in Africa where they provide an important amount of protein in the daily diet.

11.5.2 Microbial Hazards

Studies on the microbiological safety of insects as food, in general, are rare, so is the case of termites. Contamination of insects and products thereof can also occur after farming and before consumption, as happened when five individuals in Kenya died of botulism, following the consumption of termites (Nightingale and Ayim 1980). In this case, the insects had been stored in plastic bags, in anaerobic conditions during 4 days of transportation.

11.5.3 Parasitical Hazards

Among potential foodborne and waterborne pathogens, also protozoa, such as *Entamoeba histolytica* and *Giardia lamblia*, have been isolated in cockroaches. These insects can also harbor *Toxoplasma* sp. and *Sarcocystis* sp., but only for a limited time, as demonstrated for *Toxoplasma* sp. in *Periplaneta americana* and *Blattella germanica* (Graczyk et al. 2005). Also in flies, a variety of protozoan parasites of importance for human health have been isolated (*Sarcocystis*, *Giardia*, *Toxoplasma gondii*, *Isospora*, *Cryptosporidium*). Particular attention should be paid to *Cryptosporidium parvum*, which is an important lethal agent for immunocompromised individuals (Graczyk et al. 2005). These parasites could be present also in edible insects and should be considered in the case of insect consumption as food. Parasitic protozoa have also been described in termites in India (Kalavati and Narasimhamurti 1978); however, there are little or no such studies on their African counterparts.

11.5.4 Chemical Hazards

Chemical hazards in insects depend, in most cases, on habitat and plant feed contamination and can be controlled by selected farming and dietary conditions (Belluco et al. 2013a, b). Termites have been reported to be sensitive to harmful chemicals in the ground and burrow low in the grounds to form their nests. Mounds treated by insecticides may not realize the sexual winged termites that are harvested for human consumption. Through experience, villagers have learned that virgin land mounds yield more termites than others (Ayieko et al. 2011). Also, heavy metals are not a negligible problem, as they can be bioaccumulated in insect bodies. Crickets, as other soil-dwelling insects such as termites, are also able to introduce contaminants from solid waste into the food web, by preying on discarded consumer products (Gaylor et al. 2012). One of the most efficient ways to eliminate such health hazards and make the insects safer to consume is by subjecting them to one or more processing steps, especially those involving heat treatments.

11.6 Termite Processing and Preservation

Processing is an important part of food preservation, and one aim of processing insects is to reduce health risks. It is a common practice in the food industry to apply heat and pressure to whole insects, which reduce the risk of viable pathogens entering the food chain and improve palatability.

11.6.1 Human Consumption

In Africa, termites are eaten raw soon after catching or fried lightly or gently roasted to make them slightly crispy, or smoked/steamed in banana leaves, or simply sun-dried. Oil is not used as termites have a high content of oil in their body. In the DR of Congo and the Central African Republic, insects are squeezed or pressed into a tube to form a colorless oil for frying. In Botswana, winged reproductive forms of the harvester termite *Hodotermes mossambicus* (Hagen) are roasted in hot ash and sand before being consumed (Nonaka 2009). *Macrotermes nigeriensis*, the most widely eaten termite in Nigeria, is prepared by washing, salting to taste, and mild frying or roasting (in its own oil), giving rise to a nutty flavor. Raw ingesting of the insect is also practiced (Igwe et al. 2011).

In Benin, termite wings are removed and then fried in palm oil. In other instances, they are grilled whole to ease removal of the wings and thereafter grilled with some salt seasoning. A slightly different approach is employed with the queen, which is grilled intact (later the skin is taken off) or, sometimes, directly sucked out of her enveloped skin. Termite processing in Kenya involved either roasting or sun-drying, after which they are ground and mixed with other ingredients. Conventional cooking methods such as baking, boiling, and pressure cooking were employed to add value to the preprocessed termites. End products like termite crackers and muffins were obtained with very satisfactory organoleptic properties, as determined by participants (Ayieko et al. 2010b).

However, traditional processing at the villages mostly consisted of de-winging and then toasting the insects around 150 °C in their own oil in a cooking pan, over an open flame for about 5 min (Kinyuru et al. 2010). Despite the majority of consumers undertaking some kind of processing before eating, accounts of termites being eaten raw are not uncommon (Christensen et al. 2006; Ayieko et al. 2010a). Kinyuru et al. (2010) demonstrated that processing termites via toasting and sun-drying resulted in the slight decrease in protein digestibility, with a concomitant significant reduction in their vitamin content. They, therefore, suggested that processing methods that will retain nutrients, especially vitamins and other essential micronutrients, be explored.

11.6.2 Termites as Feed (For Animals)

Insects are natural feed sources for poultry and to a certain extent, also, for pigs. Feeding studies have been carried out in different animal species. Insects and processed insects are used as complementary feed sources for poultry in developing countries (Ravindran 2013). Termites (*Kalotermes flavicollis*) have reportedly been used as feed for chickens and guinea fowl in some African countries (Farina et al. 1991).

Of the several studies that evaluate the value of insects when used to feed livestock, only three of such had focused on non-poultry animals (Finke et al. 1989). The very first of such studies evaluated the quality of protein from *M. falciger* on mice, in comparison to casein. The low value for termite protein was attributed to its low digestibility (51%) relative to that of casein (84%). The high temperatures the termites were subjected to during processing possibly altered its protein quality, by decreasing amino acid availability (Phelps et al. 1975).

The application of edible insects in complementary food formulations is yet to receive its deserved attention in Africa. However, in Kenya, a *WinFood* complementary food product based on edible termites to combat child malnutrition was successfully implemented. The composition yielded food that was nutritious (it met the recommended limits for energy, macronutrients, iron, and zinc for complementary foods), safe, and with a stable shelf life. Most importantly, it was of low cost and had potential to retail at prices lower than most commercially processed foods for young children produced in Kenya. This was the result of incorporating cheap, local traditional ingredients like *Dagaa* in addition to the termites (Kinyuru et al. 2015). Though successful, the researchers suggested further exploration of the bioavailability mechanisms of nutrients from edible termites. Apart from being processed into food and food products, the use of termites as traditional medicine has also received attention.

11.7 Medicinal Value of Termites

Termite products also have long-standing status as part of traditional medicinal systems. In several traditional African medicinal systems, the paste of termite and mound is boiled and topically applied to prevent infection of external wounds and ingested to treat internal hemorrhages (Hoare 2007). As medical devices, termites can be used to insert a drug substance subcutaneously, by biting into the area of the patient's skin coated with the substance, thereby injecting it under the skin (de Figueirêdo et al. 2015). Some termite species are used as an alternative treatment for physiological and spiritual problems. For instance, *M. nigeriensis* is used in Nigeria in the treatment of wounds and sickness of pregnant women and as a charm for spiritual protection problems (de Figueirêdo et al. 2015). Also, *M. bellicosus* is used in Somalia to suture wounds. Despite all these medicinal claims, there is a real need for more pharmacological investigations in order to scientifically verify such claims.

11.8 Economic Significance

Termites in Africa increase local plant species diversity because some plants can only grow on termite mounds (DeFoliart 1997). The edible mushroom, *Termitomyces*, emanates from termite mounds and is a delicacy in countries such as the Ivory Coast, Congo, Nigeria, and Cameroon (van Huis 2017). The same author also mentions the use of termite mounds as a long-term storage facility for nuts from the kola tree by certain tribes of Cameroon.

11.8.1 Industrial Potential

Well-known wood-degrading insects include species of Isoptera (termites), Coleoptera (beetles), and Blattodea (cockroaches). Termites belong to the most important lignocellulose-digesting insects (Rumpold et al. 2016). Termites not only degrade wood much more efficiently than fungi, but they are also superior to biogas plants, if retention times of energy plants are considered (Koenig et al. 2013). Due to their high efficiency, termites represent a promising alternative for the industrial conversion of lignocellulose and lignin to produce biofuels. In addition to the industrial fermentation of lignified plant fibers to biofuels, their enzymatic systems open opportunities for biotechnological applications and the production of novel enzymes (Brune 2014).

In 2009, villagers in western Kenya experienced a heavy emergence of alate termites which was distinct from the normal swarming. A surprising abundance of edible insects in the region was collected, contrary to the normal period the insects would be collected (from the onset of rains in March till early May only). Several pointers confirm the increased emergence of alate termites among other insects of economic importance in the countryside. They attributed this change to higher temperatures and moist mounds, favoring high reproduction rate (Ayieko et al. 2010a). Pickford (2006) reminded us that the harvest of alate termites flourished in the Namibian savannah and coastal regions, as evidenced by the presence of numerous termite mounds. But when a massive climate change occurred, millions of years ago, sand dunes buried all the mounds.

Contrary to the popular “green” notion pushed forward by proponents of entomophagy, studies have shown that representative termites produce methane. The researchers attributed this to bacterial fermentation by *Methanobacteriaceae* in their hindgut (Oonincx et al. 2010). This observation connotes that their future wide and large-scale rearing could represent a climate change concern.

11.9 Challenges of Termite Consumption

Generally, there is a dearth of research into how insect farming can be carried out on a large scale. If the practice is to improve food security significantly, safety and hygiene regulations will need to be introduced, as currently there are none. This process has fortunately already begun in Kenya with Kenyan universities like JKUAT, the government, and foreign donor agencies (DANIDA, VLIR-OUS), which are sponsoring projects to introduce standards in insect farming, which will be based on international food standards. However, disadvantageous for a technical application is the rather difficult breeding of termites, them being social insects in comparison to solitarily living species.

Also, not much is known about the effect of overharvesting on the supply and distribution of target species and on the ecosystems. More research is needed on this front, along with the development of sustainable harvesting practices. The biology, ecology, and population dynamics of edible insect species and their dependence on the habitat during the year also need to be studied further. Could climate change affect the supply and distribution of edible insect populations? Might habitat be manipulated to enhance the abundance of edible insect populations? Such, and many other research questions, need to be answered. More so, there are far more edible species of termites in Africa than are currently on record as edible. There is, therefore, the need to investigate, document, and explore the nutritional profile of other species, with little or no noxious chemicals that can be included in the edible database.

11.10 Conclusion

Termites have been around us for as long as mankind can remember; their devastating effects on wood and other valuable materials have had far negative impacts. However, we are now in the era where such vulnerabilities can be turned into useful opportunities and potential. The variability of nutritional data (even within same species, as in *M. bellicosus*) among research studies needs to be further considered to enable their flawless inclusion into the food composition database. Also, further analyses need to be done on the amino acid, mineral, and vitamin contents to enable reasonable comparisons with other food types and standard recommendations. As safe as termites may be after processing, there is still the need to elucidate the different spoilage and pathogenic microfauna that inhabit their gut, hemolymph, and exoskeleton. Though of necessity because of their seasonal appearance, the rearing of termites for food in Africa may prove a daunting task, given their intricate social behavioral patterns. With the heightened attention to using of termites and other insects as feed and medicine for humans, the impetus to overcome the obstacle of their periodic availability may sooner than later be surmounted.

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Chapter 12
Economic Importance of Termites and Termitaria in Mineral Exploration

Emmanuel Arhin, Millicent Captain-Esoah, and Belinda S. Berdie

Contents

Abstract Shelter comes to mind for staying alive. However the well-decorated buildings lose their beauty when termites feed on the wood members of the house. While they destroy the wood members of our shelters, they contribute also to human developments. Termites while transporting the inorganic and organic matters into their shelter, the nest in the termitaria, enriched the surrounding soils. Furthermore, the burrowing activities into the subsoils contribute to the development of soil profiles which help in agricultural production. The economic importance of termites extends to mineral exploration, particularly in regolith-dominated terrain, where mineral deposit haloes have been masked by exotic and redistributed weathered materials. Termitaria formed from deep-seated burrowed subsoil materials were able to show the real geochemical anomalies in such complex terrains. Termite mounds sampled and analysed for their element contents using XRF technique for

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multi-elements and fire assay (FA-AAS) for gold portrayed another economic significance of termites in the delineation of hidden mineral deposits. The case study revealed that the mounds are made up of several size fractions in which gold (Au) is enriched in a particular fraction. Additional economic advantage of termites realised from the study was that the complex regolith rendering determination of pathfinder elements from surface soils was possible from mounds formed from subsurface soils, brought to surface by them. Considering the declining trends especially in gold discoveries, often attributed to the complex regolith, pathfinder elements and gold anomalies concealed by the regolith can be determined and defined by sampling termitaria. It also concludes the suitability of termitaria as a sample medium, to support soil samples typically in areas under cover. It is further recognised that the <125 μm size portions of the termitaria are the most appropriate fraction that host gold signatures in the study area. We finally realised that the hidden gold anomalies in the thick complex regolith overburden were detectable using As and Zn identified as pathfinder elements in the termitaria samples.

Keywords Termites • Termitaria • Gold • Regolith • Exploration • Shelter • Burrowed

12.1 Introduction

Termites are social insects widespread in tropical and subtropical regions, with the highest diversity found in tropical forests (Eggleton 2000). In some cultures, they are used as food by various animals including man and have been identified to have a highly nutritious value (Harris 1970). Katayama et al. (2008) reported 43 termite species as food by humans or fed to livestock in less developed countries, where malnutrition is common, as proteins from termites are considered to improve the diet. They are also used in some cultures in many traditional medicines. Termites are able to act as herbivores as well as decomposers, feeding on a wide range of living, dead or decaying plant materials (Bignell and Eggleton 2000; Traniello and Leuthold 2000) including the consumption and turnover of large volumes of soil rich in organic matter and fungi. These feeding habits make them important ecosystem engineers, resulting in the long-term modification of physical soil properties. Subterranean termites construct tunnels and galleries in the ground to look for food, affecting soil properties such as texture, water infiltration rates and nutrient contents, at various spatial scales (Dangerfield et al. 1998; Freymann et al. 2008).

In agriculture, termites contribute to soil fertility and thus enhance the productivity of ecosystems. Their burrowing mechanism greatly improves water infiltration where termite tunnels and galleries in soils allow rainwater to soak in deeply, which helps to reduce runoff and consequently soil erosion through bioturbation. Besides promoting aeration, drainage and penetration of roots, they contribute to soil formation processes via their epigeal lifestyle. Tan and Wong (2013) recognised efficiency of termites in bioreactors. Culturally, particularly in Africa, termites are used as totems and are forbidden by some tribe members to eat the reproductive casts.

However, they are widely used in traditional medicines to treat asthma, bronchitis, influenza and whooping cough (Katayama et al. 2008). Termite mound materials, which are very fine, can also be made hard and used in making roads and tennis courts, be moulded into bricks for buildings and likewise be used as a source of pottery clay (Su and Scheffrahn 2000; Edwards and Mill 1986).

Despite their beneficial activities and uses, the destructive activities of termites as a result of their feeding habits cannot be overemphasised. This includes the damages to agricultural crops such as cash and food crops (Harris 1961; Abe et al. 2000) and timbers in buildings and fences and damages to clothes, books, underground cables and airfields, earth dams and irrigation canals.

Though the benefits from termites are enormous, there is one use of the insect and its mound that has been overlooked. The discovery rate of world-class mineral deposits continues to decline because the regolith and landforms, in which the minerals occur, have continued to evolve under climates ranging from humid rainforests and savannah to semiarid and hence are an expression of the cumulative effects of this long weathering history. Common in these areas is deep weathering, modified to varying degrees by weathering, erosion and depositional processes. The subsequent landforms, formed from the agents that shape the surface of the Earth, are broadly similar. The surface processes controlling the landscape evolution hinging on different climatic conditions can produce conspicuous changes along the pre-existing oxidising profiles, giving rise to new geochemical parameters. These will affect general procedures for geochemical exploration in different climatic zones. In terrains like these, termites could become the mining industry's best asset, bringing soil samples from far below the Earth's surface without the need for expensive drilling. This will minimise the environmental and cultural impacts of mineral exploration.

The capabilities of termites to burrow tens of metres below the Earth's surface and travel up in search of water and soil from which they build their nest make them the natural drillers, and samples from the mounds can support surface geochemical sampling in mineral exploration. So, by simply taking a sample of a termite mound, geologists obtain a good idea as to what minerals and metals can be found in the ground beneath it – making it a much cheaper way to undertake preliminary soil testing for mineral exploration.

The main objective of this chapter is to highlight another significance of termite as they are able to bring up hidden mineralisation in areas under cover, due to weathering history complexities and rapid geomorphic changes from changing climates. The successful demonstration of termites in gold exploration in Australia and in Ghana provides a new, cost-effective and environmentally friendly way of exploring for new mineral deposits.

12.2 Termite Mound Building

In tropical and subtropical regions, termites become more familiar and visible through their spectacular mound building. In mound building several million individuals of termites are involved. Generally, a new mound is founded by a male and female following nuptial flight of alates or swarmers (winged reproductive termites). A small cavity is excavated into which the pair (king and queen) seals themselves. Copulation takes place in a royal cell and egg laying starts. The colony then continues to grow with increasing numbers of termites being produced each year. Some of the mound-building termite species are *Macrotermes* and *Odontotermes* species (Pomeroy 2005). The parental king and queen have the longest life span in the colony. They often survive for a decade or longer and can produce huge colonies with thousand offsprings (Gullan and Cranston 1994; Miller 2010).

Workers are the first offsprings produced which are fed on regurgitated wood or other plant matter and minerals in the soil, primed with gut symbionts, until they are old enough to enlarge the mound. As the colony grows through production of workers, the mound is enlarged by layers of soil and termite faecal matter, until mounds attain massive dimension. The later production results in the soldiers which are armed with powerful mandibles to defend the mound (Gullan and Cranston 1994; Pearce et al. 1996).

Diverse mound architecture characterises different termite species. Mound architecture is an adaptation to long-term ambient temperature conditions (Korb and Linsenmair 1999). Mounds in the gallery forest have higher heat capacities, and therefore higher thermal inertia, than mounds in the savannah (Korb and Linsenmair 1998). Mounds vary in height from less than a foot to an incredible height of about 30 feet (9 metres), depending on the species. The giant mounds of tropical termites mostly belong to species in Termitidae. The biggest and tallest mounds are found in Africa, where they are constructed mainly by *Macrotermes* species, notably *M. bellicosus*, *M. natalensis*, *M. michaelseni* and *M. subhyalinus*. *Macrotermes natalensis* mostly build huge mounds with small tunnels on top. They are usually fungus-growing termites, whereas *M. bellicosus* build their mounds near trees, with the tree sometimes intruding the mound. They are fungus-growing species which eat large amounts of leaves (Mackean 2016). It is also believed that the height of the mound is related to the depth of the subsurface soil. Thus, the higher the mound, the deeper the source of the material burrowed for its construction (Butt and Zeegers 1992). Termite mound orientation relates to thermoregulation; the broad face of the mound receives maximum exposure to the warming of the early and late sun, while the narrowest face is presented to the high and hot midday sun. Also, complex internal design, especially in fungus-farming *Macrotermes* species, allows circulation of air to give microclimatic control of temperature and carbon dioxide (Gullan and Cranston 1994). Excavation of the passage ways revealed that termites from neighbouring colonies avoid one another by passage blocking.

Termites mostly have mandibulate mouthparts with an apical cutting edge and a basal molar that grinds the food. Their mandibles can be extremely hard with an indentation hardness of about 30 kg/mm^2 or approximately 3 on Mohs scale of mineral hardness. Hence they have no difficulty in boring through foils made from common metals such as copper, lead, tin and zinc (Gullan and Cranston 1994). This maximises the deposition of these minerals as well as gold in mounds. In addition, termites are able to use cellulose-rich food sources, from grasses and fungi to living and dead trees above and below the ground. These activities in turn fertilise the soils. Workers mostly radiate from the mound, often in subterranean tunnels and sometimes from galleries. The building of galleries and nests has different effects on physical soil properties and on metal upward transport. In general, galleries and foraging holes enhance the porosity of the soil (Elkins et al. 1986; Basappa and Rajagopal 1990; Mando et al. 1996) and create pathways for metal transport.

12.3 Locomotion and Foraging Mechanism for Food and Water

Termite foraging is a social process in which groups of individuals search in organised patterns for new food sources and communicate their location by the use of sternal gland pheromones to other colony members (Traniello and Leuthold 2000). Different phases occur during termite foraging. The first phase corresponds to exploration of the foraging area, and the second phase is characterised by the recruitment of other individuals. The exploration phase involves few termites (workers or soldiers) that act as scouts (Reinhard et al. 1997). The recruitment of other individuals starts when the first scout returns to the nest after discovering a new food source, and the second phase involves larger numbers of termites (Schedel et al. 1987).

Foraging activities help to detect division of labour between soldiers and workers. Soldier termite primarily functions as a nest defence (Noirot 1990; Traniello and Leuthold 2000). Nevertheless, in some species, soldier species of Rhinotermitidae as well as in some Nasutitermitinae and Termitinae are reported to play additional roles as scouts by exploring new food sources and recruit workers to newly discovered resources (Omo Malaka and Leuthold 1986; Wolfrum and Kaib 1988; Miura and Matsumoto 1995; Reinhard et al. 1997). Workers collect and process food, but may also defend foraging territory (Traniello 1981; Kaib 1985; Traniello and Leuthold 2000). According to Casarin et al. (2008), both workers and soldiers initiate the search for food.

Termites may vary their foraging activities throughout the day and from season to season in response to sun exposure and heating of the soil surface. Studies have shown that subterranean termites will not forage in areas where upper level soil temperatures are either too hot or too cold; rather they will like to operate within optimum temperature range from 75 °F to 95 °F (24 °C–35 °C) (Potter 2013). At temperatures above 100 °F or below 25 °F, termites may die in a matter of minutes. Through their movements (locomotion), termites are able to avoid such temperature extremes and exploit areas where temperatures are more suitable. According to Potter (2013), subterranean termites ingest and store soil moisture in water sacs (salivary reservoirs) in their bodies for transport to their above-ground feeding sites. Moist soil and faecal material deposited by termites aid in tunnel construction and help maintain high moisture content throughout the gallery system.

Termites construct shelter tubes or mud tubes from the ground as they forage. These shelter tubes can be found on walls and other structures and are usually made from soil and faeces. The size of these shelter tubes depends on the amount of food sources available (Hadlington 1996). These tubes provide protection to termites from potential predators, especially ants (Kahn and Easton 2010). Shelter tubes also provide high humidity and darkness and allow workers to collect food resources that cannot be accessed in any other way (Hadlington 1996). Foraging termites maintain their connection to the soil so that the workers and soldiers can return periodically to replenish their body moisture. Soil has the capacity to hold water for a long period of time and keep the colony moist and prevent termites from drying out (Miller 2010).

Most termites usually locate food sources by dividing up the territory around the nest or mound and start digging a network of tunnels. As they dig, they come into contact with buried wood, soil minerals and other materials in the process. Their activities help to transport organic and inorganic materials to the soil surface thereby enriching the soil. Small termite colonies may forage over only a few yards if food is plentiful. Some larger colonies may forage over areas the size of a football field (Miller 2010). The loosening of the soil by termites and the building of foraging holes enhance soil porosity (Elkins et al. 1986; Mando et al. 1996) and reduce the bulk density.

Some termites during foraging can burrow deep into the subsoil and contribute to the development of soil profiles (Debruyn and Conacher 1995; Watson 1970; Sako et al. 2009). Termite foraging behaviour results in the transportation and deposition of ore or mineral elements into the surface soil or termite nest structures. These have long been used as geochemical and mineralogical sample media for the discovery of ore deposits buried beneath weathered cover and shallow sediments (Prasad and Saradhi 1984; Prasad et al. 1987; Gleeson and Poulin 1989; Fassil 2005; Arhin et al. 2015).

Foraging termites produce a variety of chemicals called pheromones that influence their behaviour. These are basically odours that send messages to other termites in the colony. While tunnelling underground, the foraging termites lay down a trail of pheromone which they secrete from glands on their abdomen. When a food source is located, the odour trail is intensified to recruit other termites to the feeding site. However, the intensity of the recruitment effort (odour trail) is influenced by soil temperature, moisture and compaction as well as the size and quality of the food source (Miller 2010).

12.4 Landscape Modifications and Termitaria as a Tool for Mineral Exploration

Deep weathering landscapes consist of ferruginous duricrust and lateritic residuum towards the surface, which in places are buried by transported overburden and are characterised by complex weathering and geomorphic histories. They adversely impact gold discoveries particularly in regolith-dominated terrains as pertains in north-western Ghana. The gold discovery failures are the result of the exhaustion of the easy-to-find gold anomalies by traditional exploration methods that hitherto were able to detect gold anomalies from surface samples, in simple weathering history terrains. The thickness of regolith in the Birimian suites of rocks that host gold deposits in Ghana varies from a few metres to over 50 m, depending on the age of the land surface, tectonic activity, climatic history and the nature of the bedrock.

The problem that the mineral exploration faces in complicated regolith terrains is that a layer of eroded and depositional materials covers the gold anomalies or mineralised deposits in the underlying bedrocks. The mechanism of termite mound building, as previously described, suggests that the mineral exploration for gold in complex regolith terrains can rely on termites as miniature prospectors. The nests of the insects apparently can hold gold dust, revealing hints of treasures hidden deep underground. The habit of termites building nests relative to the local climate suggests burrowed materials might come from different depths in the weathered materials, collected in their search for food and water (Fig. 12.1).

The gold concentrations recorded in termite mound samples are just a fortunate consequence of their tradition of building nests and in part from material sourced a few metres below the surface from the underlying mineralisation. The termites, indeed, do not specifically select gold to bring into their nests.

12.5 Ecological and Economic Significance of Termites

The destructive effects of termites to man whenever they interact with each other are huge. It embraces damages done to timbers used in buildings and for other purposes (Su and Scheffrahn 2000; Sornnuwat 1996). The Building Research Institute (BRI)

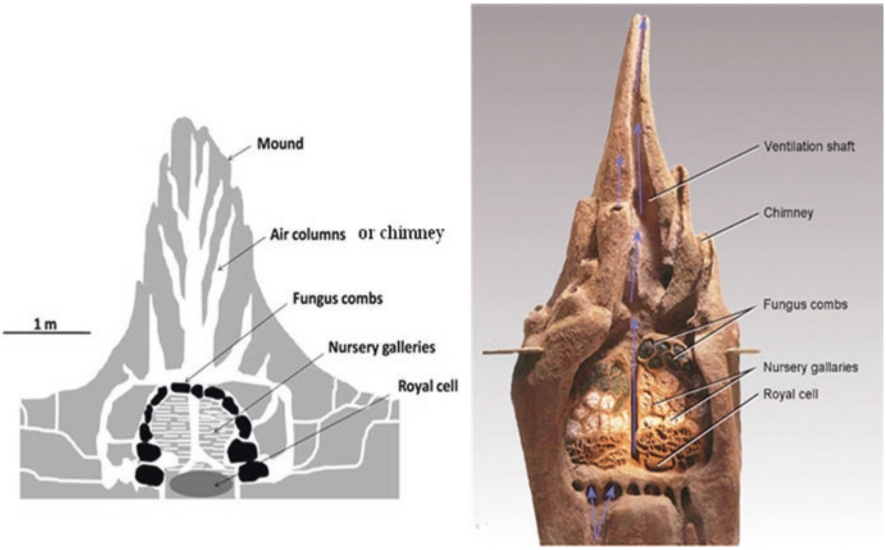

Fig. 12.1 Pathways created by termites during mound building

in Accra reports the annual cost of repairing buildings damaged by termite in West Africa to be in the range of 10% of their capital cost (Harris 1961). In addition to the attacks on buildings, termites also damage man-made fabrics (textile materials), plastics (polythene, polyvinyl chloride) and some metal foils (Howse 1970). Though this might seem insignificant, termites promote loss of soil by erosion, by removing the plant cover, thus exposing the soil surface to erosive forces (Harris 1970; Cowie et al. 1989). Accounts of termites damaging earth dams and irrigation channels have been documented (Harris 1971).

In spite of the destructive activities of termites, they too have their place and uses within their environment (Abe et al. 2000). Termites contribute to decomposition of dead wood in the forest, which would have piled up and subdued young plants from germinating and thus affected plant growth for human use. Some other positive significance is that the wood decomposed by termites can increase soil mineral nutrients. Traditionally, there have been so many beneficial ecological and economic significances of termites, including the use of termite mounds in making bricks and pottery and plastering walls and for surfacing roads and pavements (Harris 1961).

Ibrahim and Adebote (2012) suggested that termites can be considered as a source of energy because they can produce up to two litres of hydrogen from digesting a single sheet of paper, making them one of the planet's most efficient bioreactors. Additionally, they serve as source of income, being sold generally in tropical African markets and pressed for oil and cooking (Ene 1963). In rural communities termite nests are collected by inhabitants and used as poultry feeds, especially for domestic fowls, thereby making their flesh more delicious (Harris 1961; Marthur 1960).

The difficulty to detect gold anomalies in complex weathering history environments, characterised by complex regolith, has adversely influenced the detections of new gold discoveries in the world. This has been exacerbated particularly when the identification and naming of regolith units are misleading. Placing the surface geochemical signatures in correct perspective with the regolith tends to be a problem, due to the inherent errors associated in establishing the broad characteristics and distribution of the principal regolith types. The interpreted regolith surface mapped by Arhin et al. (2015) in the Lawra Birimian Belt of Ghana and summarised in Fig. 12.2 suggests great textural and spatial variability of surface materials. These are not expressly distinguished into the principal regolith types, leading to challenging geochemical interpretations. Similar conclusions were established by other researchers attempting to unravel gold mineralisation in other world prospective geological provinces (Fig. 12.3). As observed by many regolith science researchers, laterite caps and depositional overburdens are 1–5 m in thickness and form laterally extensive undulating sheets in deeply weathered terrains in some parts of the world (Butt and Zeegers 1992; Porto and Hale 1996; Anand et al. 2001; Arhin and Nude 2010). Their true extent, however, is uncertain due to erosion in dry savannahs and semiarid areas.

The theoretical foundation was based on the fact that bioturbation is capable of moving large amounts of soil material and thereby bringing up to the surface anomalous material from deeper layers. Termites are among the main bioturbators in

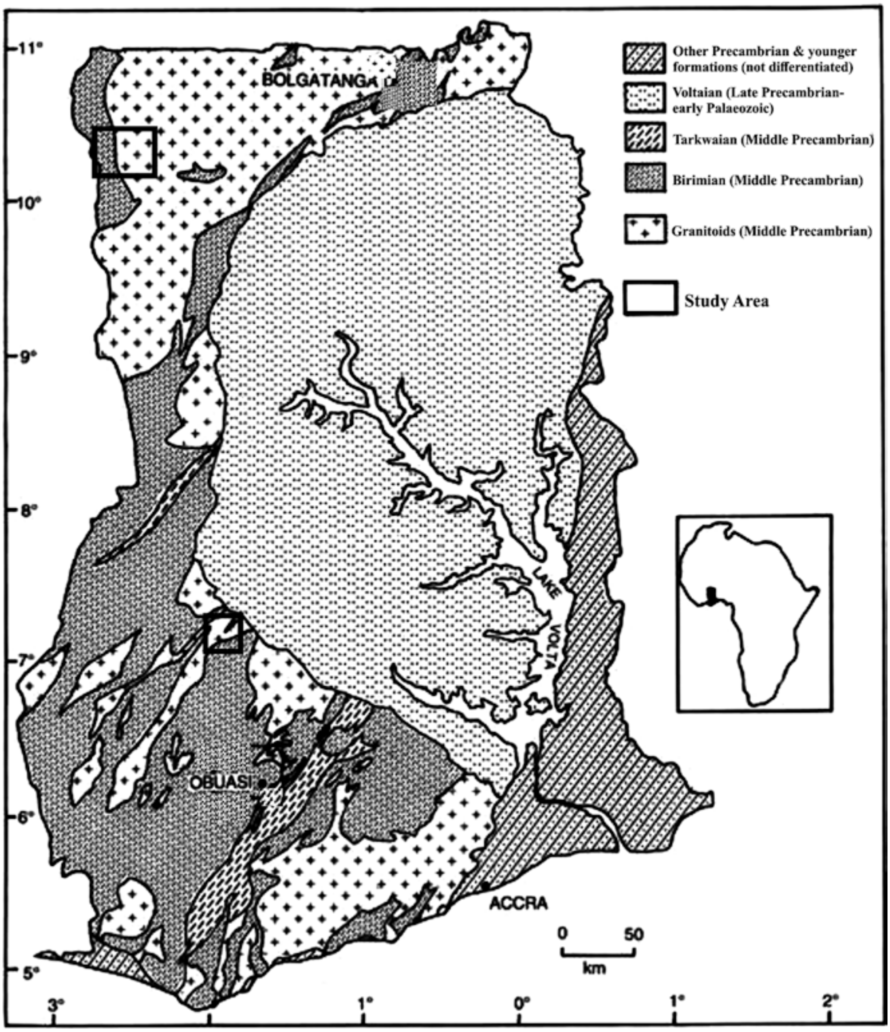

Fig. 12.2 Regional Geology of Ghana and locations of termites in gold exploration (Modified after Ghana Geological Survey 1988)

regolith environments and have the potential to provide a useful guide for mapping the subsurface materials and to bring the hidden anomaly out. Over the years, it has been shown that vertical transport of Au and pathfinder elements can occur through transported cover in above-ground nests of the grass-feeding termites. However, the depth to which termites can penetrate is unknown, although the depths of source materials are speculated to be proportional to the heights of the termitaria. This may not be completely true, because of climate variations, but will represent a more residual sample medium compared with surface sample materials that evolved, and is still evolving, due to regolith-landform evolutions.

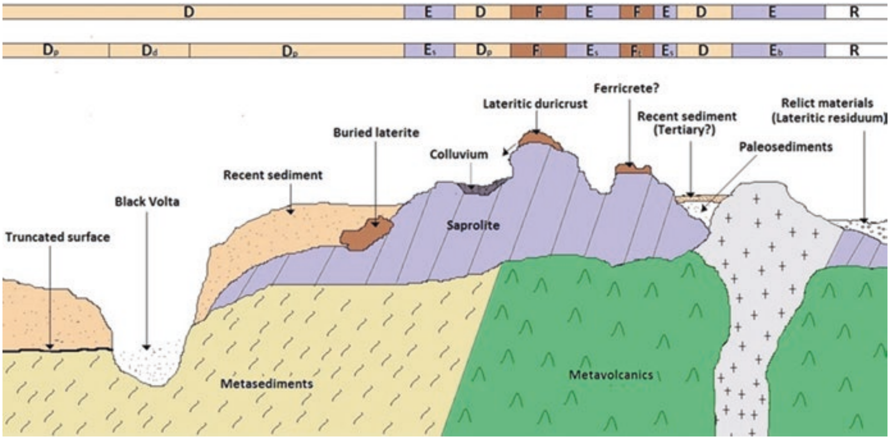

Fig. 12.3 Interpreted regolith-landform surface at the savannah regions of northwest Ghana (*F* ferruginous surface, *R* relict regolith, *E* erosional surfaces and *D*, D_p, D_d, D_o depositional areas)

The principal objective of this chapter is to highlight another significance of termite as they are able to bring up hidden mineralisation in areas under cover, due to weathering history complexities and rapid geomorphic changes from changing climates. Therefore, to obtain residual weathered materials to host residual mineral anomalies representing the sample environments, termite mound samples were collected in two gold prospective terrains in Ghana (Fig. 12.2), where surface gold anomaly definitions were difficult to interpret.

12.6 Termite Mound: An Effective Medium to Surface Geochemical Exploration

Gold exploration in known gold occurrence terrains in Ghana, West Africa (Fig. 12.2), tends to be fraught with gold anomaly detection problems from surface geochemical samples, particularly in areas characterised by extensive lateritisation and exotic sediments. This situation was, however, recognised to be a characteristic phenomenon in arid and semiarid regions (Anand 2001; Arhin et al. 2015). Testimonies indicating the use of termite mound as a supplement to support soil samples to detect hidden gold deposits in terrains with complex weathering histories had been proven by Affam and Arhin (2005), Arhin and Nude (2009) and Arhin et al. (2015). They expanded the economic significance of termites to include the mound as a sample medium in mineral exploration, especially in complex regolith terrains. Of great interest to the mineral industry is the over-exploration in most simple weathering history environments. They seem to be over-explored resulting in companies moving exploration to much complex weathering environments, where termites are unearthing gold and reveal where miners might strike it rich. Most mineral exploration surveys in the West African sub region currently have now moved into regions dominated by complex regolith comprising laterite caps and transported covers (Fig. 12.3).

The need to use termite mounds as geochemical sample media relies on the premise that soil burrowing by termites, bringing materials upwards from the deep-seated environments, induces higher infiltration rates (Elkins et al. 1986; Mando et al. 1996; Leonard and Rajot 2001) and creates pathways of mineral transport upwards (Fig. 12.1). Other motivations are based on the assumption that the mound-building activity results in an upward transfer of clay, silt, sand and fine metal grain particles to the surface. This process is opposite to leaching, which often results in significant mobilisation and dispersion of trace elements (Roquin et al. 1991; Chatuta and Direng 2000). Further indications from Lee and Wood (1971) suggest termites bring materials at depths of 8.5 m, 23 m and sometimes up to 70 m. The habits of termites during locomotion and foraging are able to transfer the geochemistry of the underlying rocks and mineralisation to the termitaria. D'Orey (1975) and Kebede (2004) have found anomalies expressed by sampling termite mounds, to represent site-specific or in situ mineralisation, as the materials sampled are usually from the subsurface and generally unaffected by superficial processes. The usefulness of the termite mound sampling technique has been confirmed by Gleeson and Poulin (1989) and Kebede (2004) as a supplementary geochemical method to support soils as geochemical sample medium. It has validated the direct linkage between the concentrations of metals, including gold, in termite mounds and the underlying rocks and mineralisation. Affam and Arhin (2005), after identifying the presence of concretions and iron oxide dominance within the laterite profile, checked concretions and lateritisation to weaken the gold signatures in the complex regolith. They preliminary sampled termite mounds (Fig. 12.4) as a supplementary technique to the classical soil sampling, in areas of transported overburden and lateritic cap.

Affam and Arhin (2005) work has been shown to be a successful way of locating hidden orebodies. Particle size variations in the termite mounds from deep-seated weathered environments ranging from clay, silt and sand and fine metal grain particles concentrate well in a particular textural size. This notion supports Arhin and Nude (2010) investigations to establish the particle size fraction that possibly hosts significant gold in the termitaria. Their investigations revealed the best size fraction hosting the best gold expressions, by analysing gold contents in the following size fractions: <125 μm, +125–250 μm, +250–500 μm and +500 μm using fire assay analytical technique (Fig. 12.5). The gold contents show relatively insignificant changes in concentration in the different size fractions, but the sample reanalysis returned quite different results in all the size fractions, except the <125 μm which returned precise results. The analytical quality of results using the fire assay method was consistent with <125 μm, as revealed in the repeated analyses, and showed relatively precise and near-accurate results in the fine size fractions (<125 μm) with

Fig. 12.4 Termite sampling processes in the savannah region of Ghana (Arhin et al. 2015)

decreasing gold geochemical signatures in the coarser size fractions. A recent study by Arhin et al. (2015) reconfirmed Affam and Arhin's (2005) work that termite mounds can be used as a geochemical sample medium to support conventional soil surveys, especially in areas with thick laterite cap and transported cover, and that <125 µm size fraction appears to host gold in termitaria in the savannah regions of Ghana.

Using termite mounds as geochemical sample medium and in identifying pathfinder elements for mineral exploration in complex regolith terrains was demonstrated by Arhin et al. (2015), where anomaly gold detection had been very difficult. In their study to identify pathfinder elements from termite mounds in northwest Ghana of the Birimian rocks of the Lawra Belt (Fig. 12.2), the geochemical data from termite mound samples were analysed using bivariate and multivariate analysis which showed that Au, As and Zn have moderate to strong correlations (Fig. 12.6).

Their study identified that As and Zn are associated with Au and therefore suitable as pathfinder elements. It supports termite samples to provide specifically residual anomaly which are real and better than those obtained from soils influenced by weathering and landscape processes. It also provides pathfinder elements for gold in complex regolith environments. Arhin et al. (2015) found that the mineralised termite mounds contained high concentrations of gold, with levels five to six times higher than those found in soils from the mound environments.

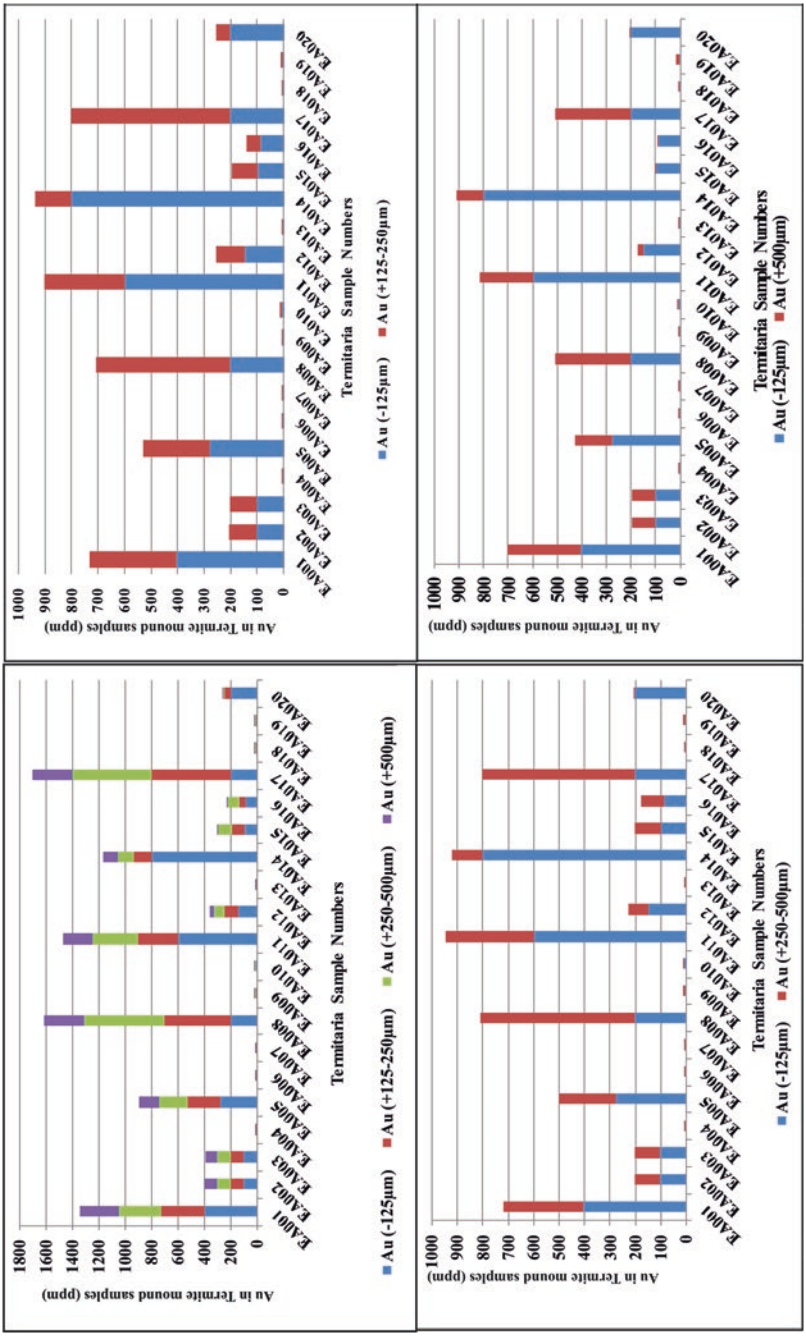

Fig. 12.5 Geochemical gold expressions in termitaria in samples collected from mounds in savannah region of northern Ghana and gold results per particle sizes

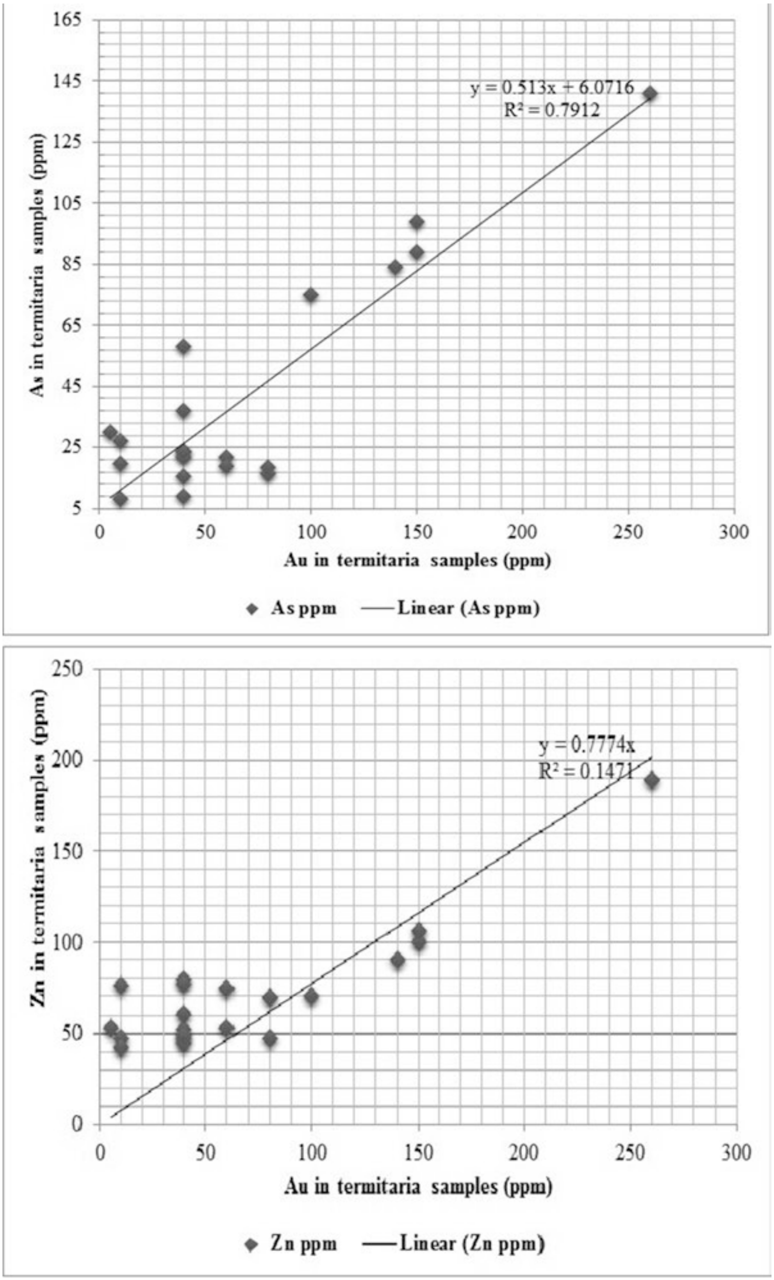

Fig. 12.6 As and Zn defined as pathfinder elements for Au in termitaria samples (Modified after Arhin et al. 2015)

12.7 Conclusion

Investigations by Arhin and team suggest that termites are able to transport gold and other minerals upwards and that the subterranean mounds are suitable for use in geochemical exploration. Their analyses of mounds located at mineralised terrains covered by thick laterite caps and extensive exotic sediments showed that hidden anomalies (that the surface soil samples failed to detect in the same area) can be detected by the mound samples. These samples can hence be considered as suitable and potentially useful media in surface geochemical exploration. It is therefore being recommended, for regional geochemical gold and other mineral exploration, to analyse the fine grain fractions of the termite mounds, as it may host gold and pathfinder elements.

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