African Journal of Environmental Science and Technology Vol. 5(2), pp. 56-64, February 2011
Available online at http://www.academicjournals.org/AJEST
ISSN 1996-0786X ©2011 Academic Journals

Review

Green house gas emissions from termite ecosystem

Gomati Velu[1]*, Ramasamy K.[1], Kumar K.[1], Sivaramaiah Nallapeta[2] and Ramanjaneya V. R. Mula[3]

[1]Centre for Plant Molecular Biology, Tamilnadu Agricultural University, Coimbatore, 641003, India.
[2]ONAN Centre for Molecular Investigations, Secunderabad, 500047, India.
[3]Torrey Pines Institute for Molecular Studies, Port St Lucie, Florida, 34987, USA.

Accepted 9 August 2010

Methanogenic archaea **(methanogens) that inhabit the gut of termites generate enormous amount of methane that adds to the global atmospheric methane (CH_4). Methane is an important trace gas in the atmosphere, contributing significantly to long wave absorption and bringing in variations into the chemistries of both the troposphere and the stratosphere. In the troposphere, methane acts as a sink for hydroxide (OH) and as a source for carbon monoxide (CO). While in the stratosphere, methane is a sink for chlorine (Cl) molecules and a source of water vapor, which is a dominant greenhouse gas. Analysis has shown that atmospheric concentrations of methane have increased by about 30% over the last 40 years. Such an increase may greatly affect future levels of stratospheric ozone and hence, the climate of the earth. Recent estimates of the total annual source strength of CH_4 vary from 400 to 1200 Tg. Activities such as rice cultivation, cattle production, mining, use of fossil fuels and biomass burning is believed to be the cause of increasing methane levels in the atmosphere. To add to this list is the source from termites, which contributes measurable quantities of CH_4 ranging from 2 to 150 Tg per year. However, data indicate that while there are large variations in the amount of CH_4 produced by different species, the total methane addition due to termites is probably less than 15 Tg per year, thus making a contribution of less than 5% to global CH_4 emissions. Furthermore, the review addresses questions related to the biological aspects of termite harboring groups of bacteria that participate in methanogenesis and various other biotechnological potential of unique microbiota as well as possible strategies to mitigate methanogenesis by termite.**

Key words: Macrotermes, methane, carbondioxide, GHG, methanobacteria, methanosarcina.

INTRODUCTION

Termites are eusocial insects belonging to the order isoptera that play a major role in tropical ecosystem. One of the most fascinating nutritional symbioses exists between termites and their intestinal microflora: a symbiosis that permits termites to live by xylophagy (Breznak, 1982, 1984). For the microbial ecologist, termite gut represents an excellent model of highly structured micro environments (Cruden and Markovetz et al., 1984). Apart from its natural role of conversion of woody and cellulosic substances into useful products of termite gut, microbiota contributes significantly to greenhouse gas effect through methane generation.

However, the total annual source strength of CH_4 varies from 400 to 1200 Tg (Brockber 1996). In their report, Zimmerman et al. (1982) estimated the average CH_4 production rates of 0.425 μg CH_4/termite/day for the lower termite species and 0.397 μg CH_4/termite/day for the higher termite families. Though rough, estimates are suggesting an annual methane emission ranging from 2 to 150 Tg per year, in which the total methane source due to termites is probably less than 15 Tg per year, thus making a contribution of less than 5% to global CH_4 emissions. The recent reports confirm the figures above keeping the emission levels between 2 and 22 Tg per year (EPA, 2010). However, microbial ecology of the gut of termites has been well documented earlier (Brune and Friedrich, 2000; Erhart 1981; Schultz and Breznak, 1978; Bignell, 1984). In this review, the nature and role of gut

---

*Corresponding author. kvgmathi@yahoo.co.in.

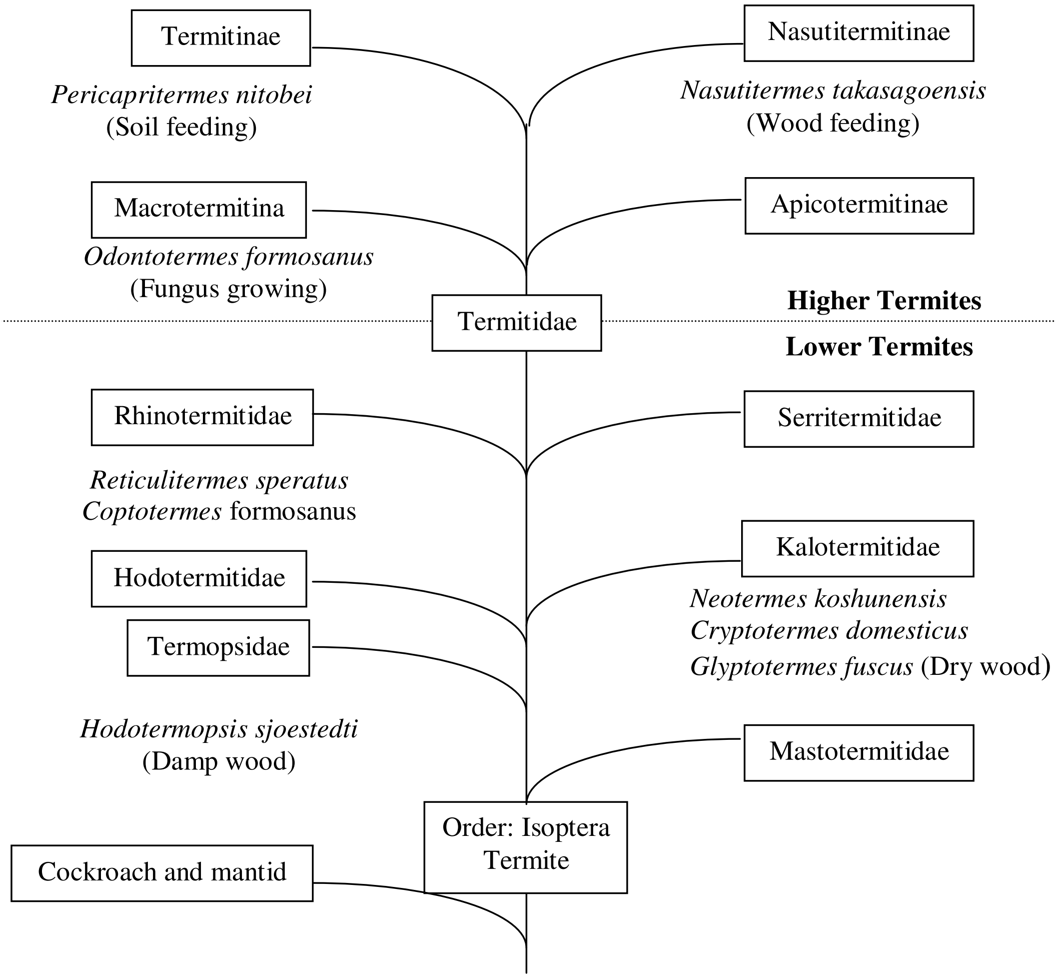

Figure 1. Flow diagram of phylogeny of termite family (Ohkuma et al., 2001).

microbiota of termites in the atmospheric methane contribution is analyzed in detail.

Higher and lower termites

Termites are divided into two groups, which are lower and higher termites. Lower termites is a group of six evolutionary distinct termite families (the microbial community in the gut of phylogenetically lower termites) comprising both flagellated protists and prokaryotes (Ohkuma, 2007); whereas higher termites comprise only one family. It includes approximately 85% of all termite species that also harbor a dense and diverse population of gut prokaryotes that typically lack eukaryotic flagellated protists. Higher termites secrete their own digestive enzymes and are independent of gut microorganisms in their nutrition. The lower termites also possess this ability, but their production of cellulolytic enzymes is apparently inadequate (Brune et al., 1995; Brune, 2006). Hence, lower termites mostly depend on the activity of gut microorganisms for their nutrition, which are present in the hind gut region (Figure 1).

Life cycle of termites

Termites' wings of isoptera are essentially similar in size, form (shape) and venation (Richards and Davies 1977), while the length and span of wings are different according to species. Other special characteristics that belong to this order are: social insect with caste differentiation, moniliform antennae, tarsi four segmented, the mouth-parts, which are formed for biting; moreover the metamorphosis is incomplete (Comstock and Comstock, 1890; Borror and White, 1998). The termites form colonies of a few hundred to a maximum of seven million individuals. The termites present in a colony consist of several castes, which are morphologically and functionally distinct (O'Brien and Slaytor, 1982). The caste may be divided into two broad groups, reproductive and sterile. Queen termite is the reproductive termite. However, most of the sterile castes are the soldiers and the workers. They subsist on a diet rich in cellulose, which may be in the form of living or dead wood, woody tissues of plants or dung. Some even feed on soil, whereas others have evolved the intriguing habit of cultivating fungus garden as a nutrient resource (Sands et al., 1970).

Gut microflora of termites

The termite gut consists of fore gut (which includes the crop and muscular gizzard), the tubular mid gut (which as in other insects is a key site for secretion of digestive enzymes and for absorption of soluble nutrients) and relatively, a voluminous hindgut (which is also a major site for digestion and for absorption of nutrients). The morphological diversity of the termite gut microbiota is remarkable and has been documented in recent years for both lower (Brian, 1978) and higher (Eutick et al., 1978) termites.

Although some bacteria colonize the foregut and midgut, bulk of intestinal microbiota is found in the hindgut, especially in the paunch, that is, the region immediately posterior to the enteric valve. Bignell (1984) reported that arthropod gut provided a suitable niche for microbial activity, but the nature of microflora and their distribution depended on the physicochemical conditions like pH, redox potential and temperature of that region. Brune (1995) reported that the presence of large number of aerobic, facultative and anaerobic microflora showed that hindguts are a purely anoxic environment together with steep axial pH gradients in higher termites. Among the different physiochemical conditions, pH and redox potential are the important factors which determine the type of microflora in the gut, while the pH of the foregut and midgut is around neutrality, whereas the paunch, colon and rectum appear to be slightly acidic. However, the foregut and midgut of termites were aerobic with E_0' in excess of +100 mv. The paunch and colon were anaerobic with E_0' at about –230 to 270 mv, whereas the hindgut of termites showed –120 to 270 mv, which proved the anaerobic conditions of the gut. In essence, termite gut harbors different kinds of bacteria, fungi and protozoa.

Termites are good sources of wood degrading enzymes such as cellulase-free xylanases (Faulet et al., 2006; Matoub and Rouland, 1995), laccases that are potentially involved in phenolic compounds degradation suitable for paper and pulp industry and glucosidases (Yavapa et al., 2005). The meatgenomic analysis of hindgut microbiota of higher termite showed the presence of diverse endoxylanases, endoglucanases, GH94 phosphorylases, glucosidases, nitrogenases, enzymes for carbon dioxide reduction and enzymes used in new ways for producing lignocelluloses based biofuels production (Warneck et al., 2007) and acetate production (Schmidt et al., 1999). Daily hydrogen turnover rates were 9 - 33 m^3 H_2 per m^3 hindgut volume, corresponding with the 22 - 26% respiratory activity of the termites. This makes H_2 the central free intermediate during lignocellulose degradation and the termite gut, with its high rates of reductive acetogenesis, the smallest and most efficient natural bioreactor currently known. The different groups of microorganisms present in the gut of termites are given in Table 1.

Acid forming bacteria

Anaerobic bacteria present in the gut of termites arecellulolytic, CO_2 reducing acetogenic and methanogenic bacteria. Volatile fatty acids are present throughout the intestine and each segment contained a constant volatile fatty acid concentration. Organic acids are produced in the hindgut in the order of acetate > formate > propionate. Mannesmann (1972) reported that acetate is a dominant volatile fatty acid in the hindgut of *Reticulitermes flavipes*. The acetate, which occurs in the termite hindgut at a concentration of about 80 mm, which can constitute over 90-mol% of VFA, is taken up from the termite tissue for its nutrition (Ohkuma et al., 2001). It is also reported that acetate, propionate and other organic acids produced during microbial fermentation of carbohydrates in the hindgut are important oxidizable energy sources for termites. Schultz and Breznak (1978) reported that the *Bacterioides* in the guts are capable of fermenting lactate to propionate and acetate by interspecies lactate transfer that occur between *Streptococci* and *Bacterioides*. A classical model of the major metabolic reactions occurring in termite hindguts is presented in Figures 2, 2A and 2B.

Homoacetogenic bacteria

Homoacetogenic bacteria are present in the highly compartmentalized hindgut of soil feeding higher termites (Thayer et al., 1976). The homoacetogenic population is supported by either substrates other than H_2 or by a cross epithelial H_2 transfer from the anterior gut region, which may create micro niches favorable for H_2 dependent acetogenesis. Methanogenesis and homoacetogenesis occur simultaneously in the hindguts of almost all termites. Wagner and Brune (1999) reported that methanogenesis and reductive acetogenesis in the hindgut of the wood feeding termite, *Reticulitermes flavipes,* is based on the microbial population and relatively high hydrogen partial pressure in the gut lumen.

Cellulolytic bacteria

Cleveland (1924) was unsuccessful in isolating cellulolytic bacteria from the gut of termites, but Eutick

Table 1. Different groups of microorganisms present in the gut of termites.

Microorganisms	Insect	Reference
Aerobes		
Arthrobacter sp.	*Reticulitermes hesperus*	Paul et al. (1990)
Arthrobacter sp.	*M.darwiniensis*	Thayer (1976)
Bacillus cereus	*Reticulitermes virginicus*	Thayer (1976)
Bacillus sp.	*R. hesperus*	Eutick et al. (1978)
Citrobacter freundii	*M. darwiniensis*	Eutick et al. (1978)
Micrococcus sp.	*Odontotermes* sp.	Paul et al. (1986)
Serratia marcescens	*Coptotermes formosans*	Thayer (1976)
Streptomyces sp.	*Cubitermes severus*	Bignell et al. (1979)
Streptomyces sp.	*Soil feeding termites*	Pasti and Belli (1985)
Facultative anaerobes		
Bacteroides sp.	*R. flavipes*	Schultz and Breznak (1978)
Cellulomonas sp.	*Odontotermes* sp.	Paul et al. (1990)
Cellovibrio sp.	*Odontotermes* sp.	Paul et al. (1990)
Clostridium termitidis	*N. lujae*	Saxena et al. (1993)
Enterobacter sp.	*M. darwiniensis*	Eutick et al. (1978)
Staphylococcus sp.	*M. darwiniensis*	Eutick et al. (1978)
N_2 fixing bacteria		
Citrobacter freundii	*R. flavipes*	French et al. (1976)
E. agglomerans	*Kalotermes minor*	Bennemann (1973)
CO_2 acetogenic bacteria		
Acetonema longum	*Pterotermes accidensis*	Kane and Breznak (1991)
C. mayombei	*Cubitermes species*	Kane and Breznak (1991)
Sporomusa termitida	*N. nigriceps*	Breznak et al. (1988)
Methanogenic bacteria		
Methanobrevibacter sp.	*R. flavipes*	Lee et al. (1987)
M. curvatus	*R .flavipes*	Leadbetter and Breznak (1996)
M. cuticularis	*R. flavipes*	Leadbetter and Breznak (1996)
M. arboriphilicus	*N. nigriceps*	Yang et al. (1985)
M. bryantii	*N. nigriceps*	Yang et al. (1985)
Protozoa		
Trichomitopsis termosidis	*N. nigriceps*	Yamin (1978)
Trichonymphs sphareica	*N. nigriceps*	Yamin (1978)

(1978) and Schultz and Breznak (1978) were successful and reported the presence of cellulose degrading bacteria from termites. They further reported that cellulose digestion in the gut of termites was a slow process. Most of the energy available to termites from cellulose digestion appears to come from oxidation of the acetate derived cellulose. Many cellulolytic microbes like *Bacillus cereus*, *Serratia marcescens and Arthrobacter* sp., from *Reticulitermes* sp., *Staphylococcus* and *S. saprophyticus* from *Odontotermes obesus*, *Cellulomonas* and *Micrococcus* sp., which are also from the hindgut of *Odontotermes* sp were isolated (Hino 1958; Thayer, 1976; Paul et al., 1986; Saxena et al., 1991). Cellulolytic actinomycetes were isolated from the hindgut of four different termites *Macrotermes, Armitermes, Odontotermes* and *Microcerotermes* spp. The isolated actinomycetes (*Streptomyces* sp. and *Micromonospora* sp.) were grown on cellulosic substrates and their extracellular cellulase (C_l, C_x and cellobiase) activity were evaluated (Hydo et al., 2003, Korb and Aaanen, 2003); using filter paper as a substrate for C_l; carboxymethyl-cellulose (CMC) for C_x and d-cellobiose for cellobiase. All

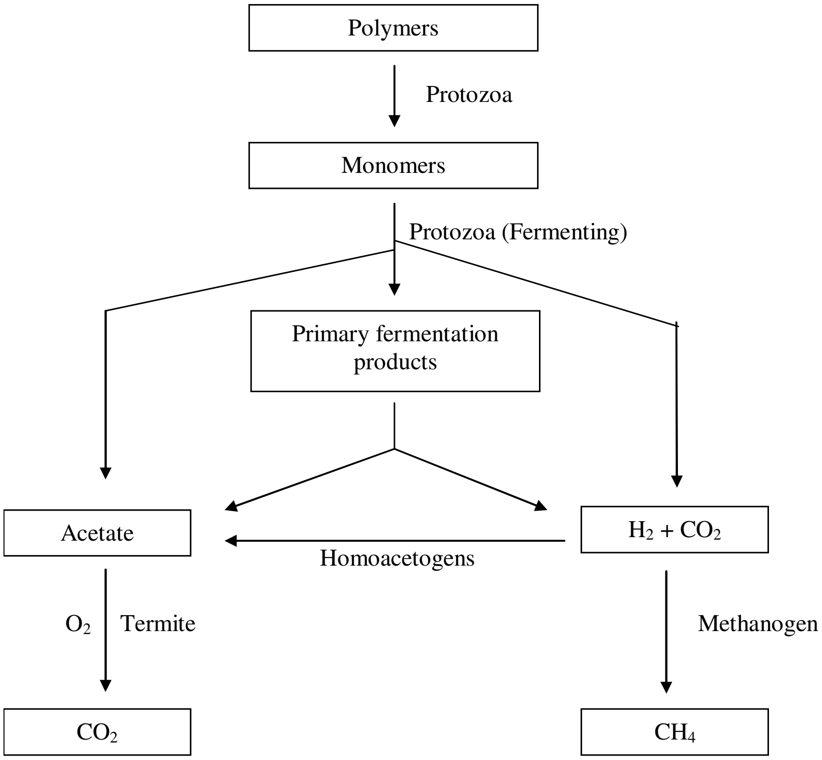

Figure 2. Fermentation of polymers in the termite guts (Tholen et al., 1997).

strains were shown to degrade soluble and insoluble cellulose, whereas optimum pH for growth was 6.2 – 6.7 at 28°C. However, the three strains could grow at 48°C on cellulosic substrates (Pasti and Belli, 1985).

CO_2 reducing acetogenic bacteria

Acetogenic bacteria capable of fermenting glucose and or cellobiose to acetate are present in the guts of higher and lower termites. These bacteria are capable of forming acetate by the reduction of CO_2. Acetate is not only an oxidizable energy source for termites, but an important precursor for synthesis of amino acids, cuticular hydrocarbons and terpenes. H_2 oxidizing CO_2, reducing *Sporomusa termitida* sp. nov. acetogenic bacteria, was isolated from the gut of *Nasutitermes nigriceps* (Breznak, 1984).

Methanogenic bacteria

Termites inhabit many different ecological regions, but they are concentrated primarily in tropical grasslands and forests. Symbiotic micro-organisms in the digestive tracts of termites (flagellate protozoa in lower termites and bacteria in higher termites) produce methane (CH_4). Methane has been considered to be an important greenhouse gas (GHG) contributing significantly to global warming (Thakur et al., 2003). Termites may emit large quantities of methane, carbon dioxide and molecular hydrogen into the atmosphere (Zimmerman et al., 1982), though considerable uncertainty exists regarding the true estimates of methane emission. Significant studies are available on diversity, social structure, physiology and ecology, still termites as source of methane contributing to the sources of atmospheric greenhouse gas is yet to be explored in India. An attempt has been made to focus on the importance of termites and their global contribution in GHG. There is need for a detailed study in India for abatement of termites to reduce the GHG emission from termite source, as termites also to some extent contribute to land degradation and have serious implications for desertification. Methane production by termites was first reported by Cook (1932) who observed the evolution of a gas from a species of termite. Studies during the following years indicated that methane is produced in a termite's digestive track during the breakdown of cellulose by symbiotic micro-organisms (Figure 3). Later, studies showed large variations in the amount of CH_4 produced by different species. More recent research by Zimmerman et al. (1982) found average CH_4 production rates of 0.425 µg CH_4/termite/day for the lower termite species and 0.397 µg CH_4/termite/day for the higher termite families. Environmental conditions such as light levels, humidity, temperature, and CO_2 and O_2 concentrations play a part in methane production. Termites prefer the absence of solar radiation, an immobile

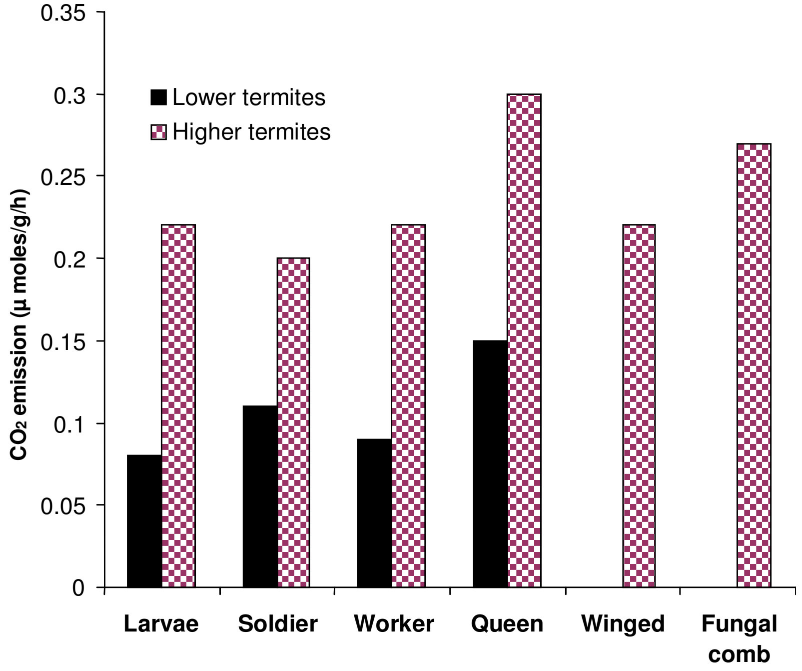

Figure 4. Carbondioxide emission *in situ* by different castes of termites.

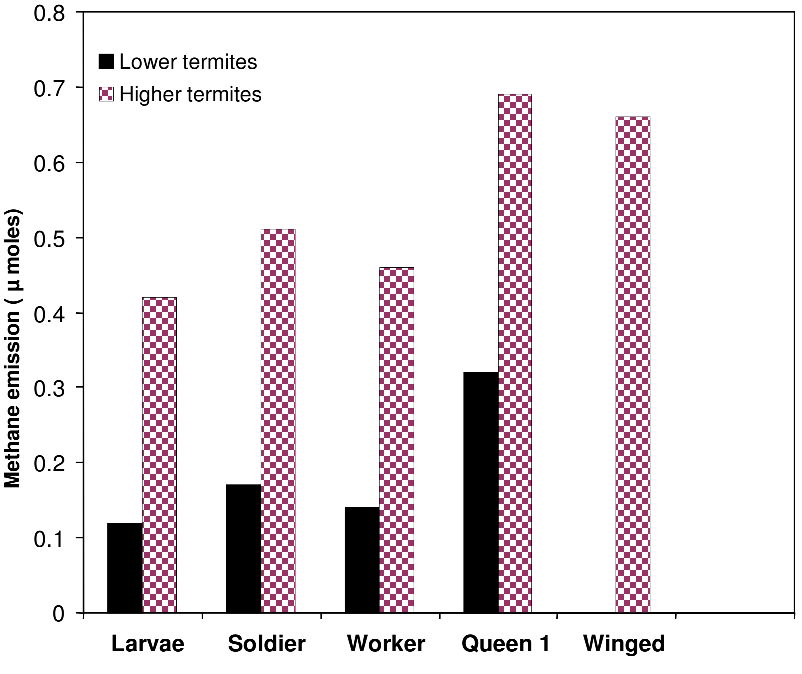

Figure 3. Emission of methane *in situ* by different castes of termites.

atmosphere, saturated or nearly saturated relative humidities, high and stable temperatures and even elevated levels of CO_2. Although termite populations are active in the middle latitude environments, the vast concentrations of mounds and nests are found in the lower latitude tropical forests, grasslands and savannahs of Africa, Asia, Australia and South America. It is estimated that these regions contribute approximately 80% of global termite emissions. Gomathi and Ramasamy (2001) reported maximum CO_2 emission from worker, larvae and queen of higher termite compared to lower termites (Figure 4). The results are in agreement with those reported in the literature (Zimmerman et al., 1982; Collin and Wood, 1984).

Fraser et al. (1986) performed an experiment using 6 different species of termites from the United States and Australia. Termite mounds under glass enclosures were studied in a laboratory setting, with diet and temperature allowed to vary, while all other variables were controlled. It was found that the capacity of termites to produce CH_4 varied from species to species, within groups from different mounds or nests of a particular species, and also with temperature. The 6 different species studied produced methane at rates that ranged over more than two orders of magnitude. Raising the temperature by 5°C within each species' preferred temperature range caused a 30 - 110% increase in the measured CH_4 emissions. Prior laboratory and field research seems to show that termites prefer temperatures in excess of 10°C above the ambient air temperatures determined by their geographical locations. A positive correlation between amounts of biomass consumed and CH_4 emitted was observed, with the average being 3.2 mg CH_4 per gm of wood. Seiler et al. (1983) performed a field research project near Pretoria, South Africa, to study termite methane production. His team placed aluminum framed boxes covered by plastic over termite mounds with the goal of separating the mounds from the ambient conditions while keeping the termite colonies in their natural environments. CH_4, CO_2 and temperature levels were monitored inside the mounds and flux rates of the carbon compounds were measured within the boxes by extracting air samples by means of syringes. Also monitored was the exchange of CH_4 and CO_2 at the soil surface within the vicinity of the nests. The calculated flux rates from termite mounds into the atmosphere showed significant variations which were related to the size of the mounds, the population density of the termites, termite activity and termite species. It was found that the flux rates exhibited diurnal variations, with maximum values during the late afternoon and minimum values during the early morning. The CH_4 flux rates from individual mounds were directly proportional to the corresponding CO_2 rates, with methane increasing linearly with increasing carbon dioxide. It was also shown that the ratios of CH_4 and CO_2 flux rates measured at different days, mounds and weather conditions were relatively constant for each species, but differed considerably from species to species. Most interestingly were measurements performed on the soil surface at distances of 1 to 20 m from the center of the termite nests, which generally showed a decrease in CH_4, indicating that CH_4 is decomposing in the soil. This observed destruction of atmospheric methane in the termite-free soil areas has led some researchers to suggest that such adjacent areas are a sink for CH_4, but it is agreed that much further tests and measurements are needed to fully more understand the effects of termites on atmospheric levels of methane. Methanogenic bacteria have been visualized in association with protozoa in termites. Though methanogens are generally strict anaerobes, their metabolic responses to the presence of oxygen and their sensitivity to it vary with the species. *Methanobacterium* sp. was isolated from the termite hindgut (Lee et al., 1987). Leadbetter and Breznak (1996) isolated *Methanobrevibacter cuticulam* and *M .curvatus* from the hindgut of the termite *Reticulitermes flaviceps*. The presence of *M. arboriphilicus* and *Methanobacterium bryantii* in the guts of wood eating higher termites has been reported also (Veivers et al., 1991). Termites are one of the contributors of methane to the atmosphere. They also produce more methane, carbon dioxide and molecular hydrogen (Darlington, 1994).

Termite mounds and galleries in the natural environment contain high levels of CO_2 and humidity depending on the types of termites involved and their habitats. Termite guts are the world's smallest bioreactors. It was generally believed that the enlarged hindgut serves as an anaerobic digester where a symbiotic gut microflora ferments cellulose and hemicelluloses to short chain fatty acids, which are then absorbed and oxidized by the host (Breznak and Pankratz, 1977). The presence of carbohydrate–fermenting bacteria and protozoa, high levels of volatile fatty acids in the gut fluid and the occurrence of typical anaerobic activities such as homoacetogenesis and methanogenesis resemble the situation encountered in the rumen of sheep and cattle. Methane (CH_4) is a metabolic end product in the hindgut of most termites. It has been estimated that these insects contribute appro-ximately 2 to 4% to the global emissions of this important greenhouse gas. Methanogenic archaea, which are easily identified by their coenzyme F_{420} auto fluorescence, have been located in several microhabitats within the hindgut. Depending on the termite species, these organisms can be associated either with the hindgut wall or with filamentous prokaryotes attached to the latter, or they can occur as ectosymbionts or endosymbionts of certain intestinal flagellates. Methane emission from termites has often been debated to be a significant source of global atmospheric CH_4. Methanogens produce about one billion tons of methane every year. They thrive in oxygen-free environments like the guts of cows and sheep, humans and even termites (Zeikw et al., 1977). Methanogenic bacteria share physiological and biochemical characters such as the ability to anaerobically oxidize hydrogen (H_2) and reduce carbon dioxide (CO_2) to CH_4. Methane is formed in the rumen by methanogens (part of the domain Archaea), mainly from H_2 and CO_2. The methanogens from a wide range of habitats are being genome-sequenced to gain a better understanding of their biology and, in particular, to identify targets for inhibition technologies for gut-associated methanogens. Within the rumen microbial food web, methanogens perform the beneficial task of removing H_2, which allows reduced cofactors to be reoxidized and recycled, thereby enhancing the breakdown

Table 2. Enumeration of total anaerobes from the different gut regions of termite.

Organisms	Foregut (CFU ml^{-1})	Midgut (CFU ml^{-1})	Hindgut (CFU ml^{-1})
Total anaerobes 10^5	44.7	27.7	22.3
Celluloysers 10^3	14.0	16.3	21.0
Acid formers 10^4	40.3	30.3	20.4
Methanogens 10^4	10.3	15.6	28.0
Klebsiella 10^4	20.0	17.0	11.6
Clostridium 10^4	39.7	22.3	26.7
SD	0.92	0.81	0.81
CD (0.05)	1.62	1.70	1.77

and fermentation of plant material.

Methanogens occur on and within the cells of symbiotic protists. Okuma (2001) identified the endobiotic methanogens as novel phylotypes of the genus *Methanobrevibacter*, of which it utilizes H_2 plus CO_2, but use other substrates poorly. Brauman et al. (1992) studied the probes for methanogenic archaea which detected members of two families (*Methanobacteriaceae* and *Methanosarcinaceae*) in termite guts, and these accounted for 60% of all archaeal probe signals in methane emission. In four species of termites, *Methanosarcinaceae* were found to be dominant, a novel observation for animal gut microbial communities, but no clear relationship was apparent between methanogens family profiles and termite diet or taxonomy. Gomathi and Ramasamy (2001) reported that methanogens were predominantly present in the hind gut of fungus growing termites (Table 2).

Conclusion

Termites are a complex assemblage of species showing considerable variation in terms of social behavior and nutritional ecology. The digestive tract of termites normally paves a suitable niche for a variety of microorganisms to inhabit and multiply. The nutritive metabolism of termite is based on the exploitation of cellulosic materials by facultative anaerobes and obligate anaerobes, which are symbiotically associated with the termites and exist in the hindgut of the insect. Cellulolytic microorganisms are responsible for the digestion of cellulose and the nitrogen requirements are met out by the presence of nitrogen fixing aerobic and anaerobic microorganisms present in their gut.

Therefore, rumen methane mitigation strategies need to consider alternative routes of H_2 utilizations in the absence (or decreased levels) of methanogenesis to maintain rumen function. Two main alternatives are possible: enhancing rumen microorganisms that carry out reductive acetogenesis (combining CO_2 and H_2 to form acetate) or promotion of organisms that consume reducing equivalents during the conversion of metabolic intermediates (malate, fumarate and crotonate) into propionate and butyrate. A better understanding of the role and scale of methane oxidation in the rumen may help to develop mitigation strategies. Reducing ruminant methane emissions is an important objective for ensuring the sustainability of ruminant-based agriculture. The authors' studies suggest that although overall methane fluxes from soil invertebrates under study cannot substantially influence a methane budget in most ecosystems, methane production is significant at least in some millipedes and therefore can impact meso and microenvironments inhabited by these invertebrates. This work also confirms that methane production is not only supported by tropic soil invertebrates, but also by temperate species.

REFERENCES

Bignell DE (1984). The arthropod gut as an environment for microorganisms, In: Symposium of the British Mycological Society and the British Ecological Society, Univ. Exeter., pp. 205-227.

Bignell DE, Eggleton P, Nunes L, Thomas KL (1979). Termites as mediators of carbon fluxes in tropical forests: budgets for carbon dioxide and methane emissions, In: Forests and insects (Watt, A. S. N. E. Stork, and MD Hunter eds., Chapman and Hall, London., pp. 103-134.

Boror DJ, White RE (1998). A Field Guide to Insects: America North of Mexico, HMCo Field Guides Publisher.

Brauman A, Kane MD, Labat M, Breznak JA (1992). Genesis of Acetate and Methane by Gut Bacteria of Nutritionally Diverse Termites. Sci., 257: 1384-1397.

Breznak JA (1982). Intestinal microbiota of termites and other xylophagous insects, Ann. Rev. Microbiol.. 36: 323-343.

Breznak JA (1984) Biochemical aspects of symbiosis between termites and their intestinal microbiota, In Invertebrate-Microbial Interactions, ed. JM Anderson. ADM Rayner. DWH Walton.

Breznak JA, Pankratz HS (1977). *In situ* morphology of the gut microbionts of wood eating termites (*R.flavipes* Kollar and *Coptotermes formosanis*), Appl. Environ. Microbiol., 33: 406-426.

Breznak JA, Switzer JM, Seitz HJ (1988). *Sporumusa termitida* sp. nov., an H_2 / CO_2 utilizing acetogen isolated from termites, Arch Microbial., 150: 282-88.

Brian MV (1978). Production Ecology of Ants and Termites, New York Cambridge Univ. Press.

Brien GW, Slaytor M (1982). Role of microorganisms in the metabolism of termites, Aust. J. Biol. Sci., 35: 239-262.

Brockber G (1996). Termites as a Source of Atmospheric Methane, web report. http://www.iitap.iastate. edu/gcp/studentpapers /1996/ atmo schem/brockberg.html).

Brune A (2006). Symbiotic associations between termites and prokaryotes. In: Dworkin M, Falkow S, Rosenberg E, Schleifer

K-H, Stackebrandt E (eds). The Prokaryotes. An Online Electronic Resource for the Microbiological Community, 3rd edn. Springer-SBM: New York.

Brune A, Friedrich M (2000). Microecology of the termite gut: structure and function or a microscale, Current Microbiol., 3: 262-269.

Brune AD, Emerson and Breznak JA (1995). The termite gut microflora as an oxygen sink: Microelectrode determination of oxygen and pH gradients in guts of lower and higher termites, Appl. Environ. Microbiol., 61: 2681-2687.

Cleveland LR (1924). The physiological and symbiotic relationship between the intestinal protozoa of termites and their host with special reference to Reticulitermes flavipes, Biol. Bull., 46: 1708-21.

Collins NM, Wood TG (1984). Termites and Atmospheric Gas Production, Sci., 6: 84-86.

Comstock JH, Comstock AB (1890). A manual for the study of Insects. Comstock Publishing Company.

Cruden DL, Markovetz A J (1984). Microbial aspects of the cockroach hindgut, Arch. Microbiol., 138: 131-139.

Darlington JE (1994). Nutrition and evolution in fungus- growing ants In: Nourishment and evolution in insect societies (Hunt J.H. and Nalepa eds.), West view press, Boulder, Colo., pp. 105-130.

EPA (2010).Methane and Nitrous Oxide Emissions from Natural Sources, April, 2010.

Erhart AJ(1981). The importance of biological phenomena in the formation of ferruginpus crusts in the tropics, C. R. Acad. Sci (Paris). 233: 804-806.

Eutick ML, Brien RW, Slaytor M (1978). Bacteria from the gut of Australian termites, Appl. Environ. Microbiol., 35: 823-828.

Eutick ML, Veivers P, Brien RWO, Slaytor M (1978). Dependence of the higher termite, Nasutitermes exitious and the lower termite, *Coptotermes lacteus* of their gut flora, J. Insect Physiol. 24: 363-68.

Fraser PJ, Rasmussen R, Creffield JW, French JR and Khalil MAK (1986). Termites and global methane: another assessment, J. Atmos. Chem., 4: 295-310.

Gomathi V and Ramasamy K (2001). Gut microflora of termite and associate with emission of green house gases (CO2 + CH4). Ph.D Thesis, Tamil Nadu Agricultural University, Coimbatore.

Gomathi V, Ramasamy K (1992). Characterization of *Azotobacter vinelandii.* Paper presented at 32nd Annual Conference of Association of Microbiologists of India, held at Madurai Kamaraj University, Madurai. p. 54.

Hino S, Wilson PW (1958). Nitrogen fixation by a facultative *Bacillus*, J. Bacteriol., 75: 126-138.

Hyodo F, Tayasu I, Azuma T, Kudo T (2003). Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera), Funct. Ecol., 17: 186-193.

Kane MD, Breznak JA (1991). Acetonema longum gen. Nov. sp. nov., an H2 / CO2 acetogenic bacterium from the termite, Pterotermes occidentalis, Arch. Microbiol., 156: 91-98.

Korb J, Aaanen DK (2003). The evolution of uniparental transmission of fungal symbionts in fungus- growing termites (Macrotermitidae), Behav. Ecol. Social., 53: 65-71.

Leadbetter JR, Breznak JA (1996). Physiological ecology of *Methanobrevibacter cuticularis* sp. nov. and *Methanobrevibacter curvatus* sp. nov., isolated from the hind gut of the termite Reticulitermes flavipes, Appl. Environ. Microbiol., 62: 3620 – 3631.

Lee JM, Schreurs PJ, Messer AC, Zinder SH (1987). Association of methanogenic bacteria with flagellated protozoa from a termite hind gut, Curr. Microbiol., 15: 337-341.

Mannessmann R (1972). A comparison between cellulolytic bacteria of termites *Coptotermes formosanus* and *Reticulitermes virginicus*, Int. Biodeterior. Bull. 8: 104-111.

Mark D, Ashok R, Alan L, Raj B (2008). Presence of nitrogen fixing *Klebsiella pneumoniae* in the gut of the Formosan subterranean termite Bioresour. Technol., 99: 3297-3300.

Matoub M, Rouland C (1995). Purification and properties of the xylanases from the termite *Macrotermes bellicosus* and its symbiotic fungus Termitomyces sp. Comparative Biochem. Physiol., 112: 629-35.

Ohkuma M (2007). Symbioses of flagellates and prokaryotes in the gut of lower termites, Trends Microbiol., 16(7): 345-352.

Ohkuma MS, Noda Y, Kudo T (2001). Coevolution of symbiotic systems of termites and their gut microorganisms, RIKEN Review. 41: 73-74.

Ohkuma MY, Maeda M, Khjima T, Kudo T (2001). Lignin degradation and roles of white rot fungi: study on an efficient symbiotic system in fungus – growing termites and its application to bioremediation, RIKEN Rev., 42: 39- 44.

Paul J, Sarkar A, Varma A (1986). In vivo studies of cellulose digesting properties of *Staphylococcus* and *Saprophyticus* isolates from termite gut, Curr. Sci. 55: 710-714.

Paul B, Nancy AM (1990). Non-cultivable microorganisms from symbiotic associations of insects and other hotst, Antonie van leeuwenhoek, 72: 39-48.

Richards OW, Davies RG (1977). IMMs' general textbook of entomology, 10th ed. Chapman and Hall, London.

Sands WA (1970). Biology of termites, Academic Press. New York, 2: 495-524.

Saxena S, Bahadur J, Varma A (1991). Production and localization of carboxymethyl cellulase, xylanase, and glucosidase from *Cellulomonas* and *Micrococcus* sp, Appl. Microbiol. Biotechnol., 34: 668-670.

Saxena S, Bahadur J, Varma A (1993). Cellulose and hemicellulose degrading bacteria from termite gut and mound soils of India. Indian J. Microbiol., 33: 55–60.

Schmidt JR, Graber TM, Breznak JA (1999). Acetogenesis from H2 plus CO2 by Spirochetes from Termite Guts, Science 283: 686-690.

Schultz JE, Breznak A (1978). Heterotrophic bacteria present in the hind gut of wood eating termites (*Reticulitermes flavipes*) Kollar, Appl. Environ. Microbiol., 35: 930-936.

Seiler W, Conrad R, Scharffe D (1983). Field studies of methane emission from termite nests into the atmosphere and measurement of methane uptake by tropical soils, J. Atmos. Chem., 1: 171-186.

Thakur RKB, Jeeva V (2003). Termites and global warming - a review, Indian forester: 129: (7)923-930.

Thayer DW (1976). Facultative wood digesting bacteria from the hind gut of the termite Reticulitermes Hesperus, J. Gen. Microbiol., 95:287-296.

Tholen A, Brune A (1997). Location and in situ activities of homoacetogenic bacteria in the highly compartmentalized hindgut of soil feeding higher termites (*Cubitermes* spp), Appl. Environ. Microbiol., 65: 4497-5405.

Veivers PC, Muhlemann R, Slaytor M, Leuthold RH, Bignell DE (1991). Digestion, diet and polyethism in two fungus-growing termites: Macrotermes subhyalinus- Rambur and M. michaelseni sjostedt, J. Insect Physiol., 37: 675 – 682.

Wagner DS, Brune A (1999). Hydrogen profiles and localization of methanogenic activities in the highly compartmentalized hindgut of soil feeding higher termites Cubitermes sp, Appl. Environ. Microbiol., 65: 4490 –4496.

Warneck F (2007). Metagenomic and functional analysis of hindgut microbiota of a wood-feeding higher termite, Nature. 450: 560-571.

Yamin MA (1978). Cellulose Metabolism by the Termite Flagellate Trichomitopsis termopsidis, Appl. Environ. Microbiol. 39: 859-863.

Yang J, Bordeaux FM, Smith PH (1985). Isolation of methanogenic bacteria from termites, Abstr. In: Abstract of the 85th Annual Meeting of the American Society for Microbiology. Wash., D.C.1-83 p. 160.

Zimmerman PR, Greenberg JP, Wandiga SO, Crutzen P (1982). Termites: A potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen, Sci., 218:563–565.