ISBN: 978-81-973427-0-7

15. Termites as GHG Contributors: A Potentially Large Source of Methane, CO_2, And Nitrous Oxide

Maharaj Satwika, Chava Asritha, Burjikindi Madhuri

Ph.D. Scholar, Department of Entomology,
Professor Jayashankar Telangana State Agricultural University,
Hyderabad, India

N. M. Ramesha

Ph.D. Scholar,
Division of Entomology,
Indian Agricultural Research Institute, New Delhi.

Abstract:

Termites are important contributors to global climate change, yet they are frequently ignored in debates on greenhouse gas emissions. Termites, especially those belonging to the Macrotermitinae subfamily, have a unique gut microbiome that enables them to break down diets rich in cellulose and release significant amounts of CH4 while they do so. Additionally, termite mounds serve as hotspots for CO2 emissions due to organic matter decomposition. Recent research highlights the production of N2O by termites as a result of microbial nitrogen transformations in their gut. These emissions are influenced by various factors including termite species, diet composition, and environmental conditions. Understanding the implications of termite-induced greenhouse gas emissions is crucial for climate change mitigation strategies.

Keywords:

Cellulose, Climate change, Methanogens, Symbiotic bacteria, Termite mounds.

15.1 Introduction:

Termites feed on wood, fungi, and soil and are recognized for having an intricate social system that includes workers, soldiers, and queens. They are often seen as pests that destroy wood in buildings, but they play a crucial role in natural ecosystems, especially in tropical regions. They aid in the process of decomposing dead wood from trees, which helps in recycling the nutrients back into the soil. There would be an imbalance in the ecosystem if there were no decomposers since the globe would be overrun with dead plants and animals. Termites, like small cows, generate two of the most significant greenhouse gases carbon dioxide and methane from the wood. Termites have long been of interest to scientists due to their unique biogeochemical properties. The majority of termites can digest lignocellulose, a recognized source of methane, because of symbiotic bacteria called methanogens archaea in their stomachs. It has been discovered that "hot spots" near mounds and nests are where most gas exchange with the atmosphere takes place, as determined by chamber and collar techniques. Due to the intensity of this source, termite CH_4 emissions have been evaluated from a global biogeochemical perspective in several studies. According to the Global Carbon Project's 2020 "Global Methane Budget," termites contributed 9 Tg of the 576 Tg of methane that was released globally annually between 2008 and 2017. One teragram, or 1012 g, is equivalent to 576 Tg. Up to 15 Tg of emissions are estimated annually by other sources. Therefore, with climate change and increased termite activity in the future, they could increasingly contribute to greenhouse gas emissions.

15.2 Types of Termites:

There are two categories of termites: lower termites and higher termites. While higher termites only consist of one family, lower termites consist of six distinct termite families, each with a unique microbial community in their stomachs that includes flagellated protists and prokaryotes (Ohkuma, 2007). It comprises around 85% of all termite species, and along with them is a densely distributed, diversified population of gut prokaryotes, which are generally devoid of eukaryotic flagellated protists. Higher termites are self-sufficient in their diet and secrete their digestive enzymes. Although they don't produce enough cellulolytic enzymes, the lower termites are still capable of doing this (Brune *et al.*, 1995, Brune, 2006). Therefore, the majority of lower termite’s food comes from the action of gut microbes, which are found in the hindgut (Figure 15.1).

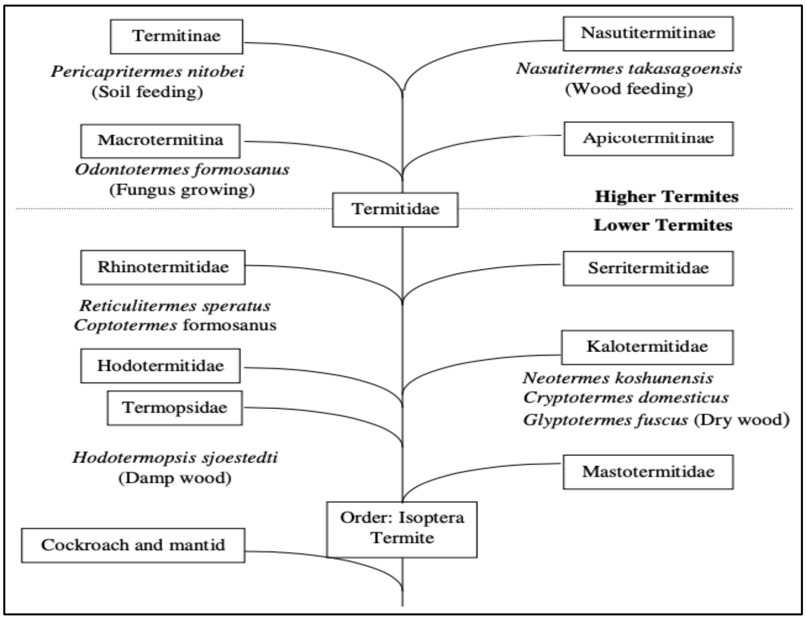


Figure 15.1: Types of Termites

15.3 Termite’s Life Cycle:

The size, form, and venation of termite wings are fundamentally identical among isoptera, although their length and span vary, as per Richards and Davies (1977). Additional unique features of this group include the following: Termites are a type of social insect that exhibit caste differentiation. They have moniliform antennae, four segmented tarsi, and mouthparts that are designed for biting. Their metamorphosis is imperfect (Borror and White, 1998). Interestingly, termite colonies can range in size from as little as one hundred individuals to as many as seven million. A colony of termites is made up of various castes that differ in both morphology and function (O'Brien and Slaytor, 1982). Reproductive and sterile are the two main categories into which the caste can be separated. The reproductive termite is called a queen termite. However, the workers and soldiers make up the majority of the sterile castes. They consume a diet high in cellulose, which can come from feces, woody plant tissues, dead or living wood. Some have even developed the interesting habit of growing fungal gardens as a source of nutrients, while others even feed on soil (Sands et al., 1970).

15.4 Greenhouse Gas Production in Termites:

15.4.1 Methane and Carbon Dioxide:

Cellulose is a complex carbohydrate found in plant cell walls. Not all the animals in the world can digest this cellulose. Ruminants such as cows, goats, and sheep can break down cellulose in the plant materials that they consume. As a result of this digestion, they release methane as a byproduct to the atmosphere. Except for these ruminants, termites are unique animals with that ability. Termites break down cellulose through symbiotic digestion, which involves a partnership between the termites and microorganisms in the gut. Termites consume cellulose-rich plant material, such as wood or grass, which enters their digestive systems. A complex array of microorganisms, including bacteria, fungi, and protozoa digest cellulose in the termite's hindgut and produce enzymes called cellulases, which can break down the complex cellulose molecules into simpler sugars, such as glucose. The termites absorb these simple sugars and other nutrients, released during cellulose digestion through their gut wall, to provide energy to the metabolism and growth. As a byproduct of microbial fermentation, termites produce and release methane gas through their excretory system.

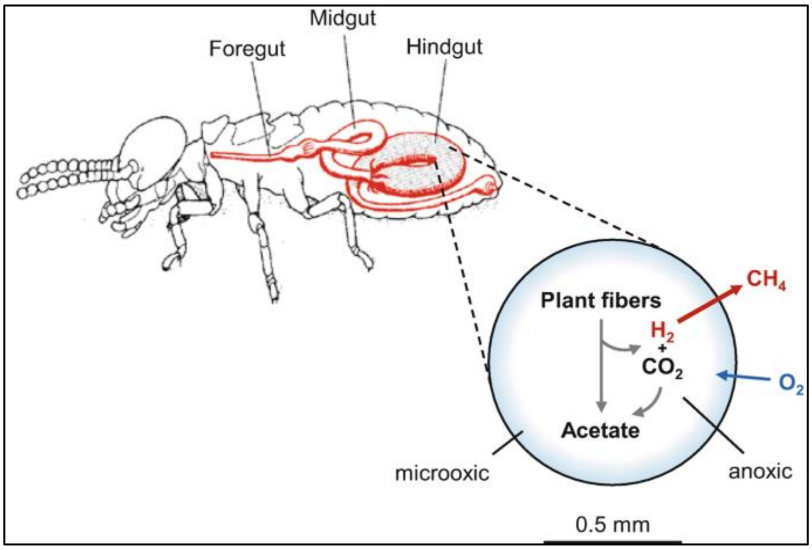


Figure 15.2: Methane and Carbon Dioxide

15.4.2 Nitrous Oxide:

In ecological processes like the mineralization of nitrogen and carbon, termites are essential (Bignell and Eggleton, 2000, Jouquet *et al.*, 2011). According to Bruce *et al*. (1995), the termite gut microbiota's metabolic activity keeps the gut lumen's steep oxygen gradients, which may facilitate the simultaneous occurrence of nitrification and denitrification processes. In tropical regions, termites have an impact on the amount of N_2O in the atmosphere. The primary sources of N_2O emissions are these two microbial processes, either as a denitrification intermediate or as a byproduct of nitrification (Conrad, 1996). Denitrifying gene abundance has recently been suggested by Morales *et al*. (2010) as a potential biomarker for greenhouse gas emissions from soils. Termites that feed on soil have been the primary subject of study on termite mineralization of soil nitrogen. In contrast to wood-feeding termite species, which can live on nutrient-poor material with as low as 0.05% N, soil-feeding termite species can feed on nitrogenous soil components (amino acids, peptides, and proteins) (Tayasu *et al*., 1994). Termite species that consume a diet high in nitrogen (N) release more N_2O into the atmosphere than those that consume a diet low in N. High levels of ammonia have been found throughout the termite gut, with the posterior hindgut accumulating significantly (Ji and Brune, 2006). Termites were found to induce denitrification in soil microcosms according to a study that used the 15N-tracer approach (Ngugi *et al*., 2011). In the gut of soil-feeding termites, nitrate was either converted to ammonia or denitrified to N_2 (Ngugi *et al*., 2011). Furthermore, Ngugi and Brune (2012) used the 15N-tracer method to study the fate of nitrate in the gut compartments of two *Cubitermes* species and *Ophiotermes* spp. Their study was the first to report on N_2O generation in living individuals of soil-feeding termite species and in their gut homogenates after it was shown that termite mounds were hotspots of N_2O emissions in the African savannah (Brummer *et al*., 2009). What happens to nitrogen in termite stomachs is determined by the feeding guild (Brune, 2014). Therefore, it is necessary to comprehend the relationship between feeding behavior and N_2O emissions to calculate the global termite contribution to the N_2O emission budget in tropical forests.

15.4.3 Termite Gut Microbiota:

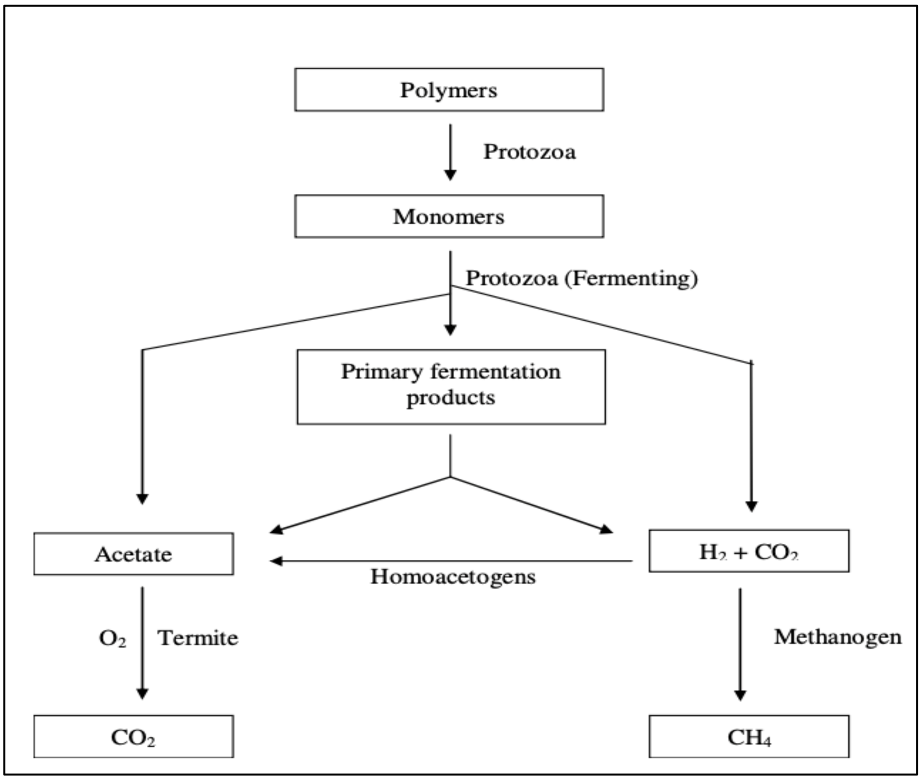
The tubular midgut of termites, like that of other insects, is an important location for the release of digestive juices, and the foregut houses the muscular gizzard and crop. and a comparatively large hindgut, which serves as a key location for both digestion and nutrient absorption. Recent research has shown the extraordinary morphological diversity of the gut microbiota of termites for both higher (Eutick *et al*., 1978) and lower (Brian, 1978) termites. The majority of the intestinal microbiota is found in the hindgut, namely in the paunch, which is close to the intestinal valve. As per Bignell (1984), the gut of arthropods provides a conducive environment for microbial activities. However, the kind of microflora found in the gut and their location are dependent on the physicochemical parameters of the area, such as temperature, redox potential, and pH. In a study by Brune *et al.* (1995), it was found that the hindguts of arthropods are exclusively in anoxic environments. Higher termites exhibit strong axial pH gradients and have abundant facultative, aerobic, and anaerobic microflora. The type of microflora found in the gut is mostly determined by various physiochemical factors, including pH and redox potential. The midgut and foregut of arthropods have pH values that are close to neutral, whereas the rectum, colon, and paunch have somewhat acidic pH values. Termites, however, have aerobic foreguts and midguts, with E_0 measuring more than +100 mv. Termites have anaerobic conditions in their colon and paunch, with E_0 measuring between -230 and 270 mv, and anaerobic conditions in their hindgut, which measures between -120 and 270 mv. Arthropod guts are essentially home to a variety of bacteria, fungi, and protozoa. Termites are found in environments with high concentrations of humidity and carbon dioxide where they construct tunnels and mounds. The type of termites and their habitats determine the humidity and CO_2 levels. Termites have a special kind of digestion called a mini bioreactor. Researchers think that the larger hindgut functions as an anaerobic digester, converting cellulose and hemicellulose into short-chain fatty acids through the fermentation of gut microorganisms. The termite's body then absorbs and oxidizes these fatty acids. Termite’s guts are home to bacteria and protozoa that break down carbohydrates and release a lot of volatile fatty acids. Additionally, the gut exhibits common anaerobic processes including methanogenesis and homoacetogenesis, which are akin to those observed in sheep and cow rumen. The majority of termites’ hindguts produce methane as a metabolic byproduct. Termites are thought to be responsible for between 2 and 4% of this significant greenhouse gas worldwide emissions.

Enzymes that degrade wood may be found in termites, including xylanases that are free of cellulases (Matoub and Rouland, 1995), laccases that are appropriate for the pulp and paper industry, and glucosidases that can degrade phenolic compounds. Several endoxylanases, endoglucanases, GH94 phosphorylases, glucosidases, nitrogenases, enzymes for carbon dioxide reduction, and enzymes used in novel ways for producing acetate and lignocellulose-based biofuels (Schmidt *et al*., 1999) were found by metagenomic analysis of the hindgut microbiota of higher termites (Warneck, 2007). The termite hindgut's daily hydrogen turnover rates vary from 9 to 33 m^3 H_2 per m3 of hindgut volume, or roughly 22-26% of the termite's respiratory activity. This suggests that the main free intermediate in the lignocellulose breakdown process is H_2. The termite gut is the tiniest and most efficient known natural bioreactor because of its high rates of reductive acetogenesis.

15.5 Different Groups of Bacteria in Termite Gut:

A. Acid-Forming Bacteria:

Termite’s anaerobic gut microorganisms are methanogenic, acetogenic, and cellulolytic bacteria that reduce CO_2. The intestine is filled with volatile fatty acids, and each section has a consistent amount of concentration of volatile fatty acids. The hindgut of termites produces organic acids in a specific order, which is acetate, followed by formate, and then propionate. Most volatile fatty acids are acetate which are found in the hindgut of *Reticulitermes flavipes,* according to Mannesmann's research in 1972. Termites absorb acetate from their tissues, which can make up more than 90 mol% of volatile fatty acid in hindgut at a concentration of 80 mm, as reported by Ohkuma *et al*. (2001). The hindgut's microbiological fermentation of carbohydrates generates acetate, propionate, and other organic acids, which are significant sources of oxidizable energy resources for termites. Schultz and Breznak found in 1978 that *Streptococci* and *Bacteroides* engage in interspecies lactate transfer, which allows the latter to digest lactate into propionate and acetate in the stomach. Figure 2 shows a traditional depiction of the main metabolic processes that take place in termite hindguts.



Source: (Tholen *et al.*, 1997).

Figure 15.2: Acid-Forming Bacteria

B. Homoacetogenic Bacteria:

Higher termites' hindguts, which feed on soil are extensively divided and contain homoacetogenic bacteria, as reported by Thayer *et al.* (1976). Either cross-epithelial H_2 transport from the anterior gut area sustains these bacteria or by substrates other than H_2, which could produce beneficial microniches for H_2-dependent acetogenesis. In almost all termites, both Hom acetogenesis and methanogenesis occur simultaneously in the hindgut. Wagner and Brune (1999) reported that the methanogenic and reductive acetogenesis processes in the hindgut of the wood-eating termite, *Reticulitermes flavipes*, are supported by the microbial community and the relatively high hydrogen partial pressure in the gut lumen.

C. Cellulolytic Bacteria:

Schultz and Breznak (1978) discovered termite-derived bacteria that break down cellulose. The energy that termites obtain from the digestion of cellulose seems to originate from the oxidation of the cellulose that is produced from acetate. Four distinct termite hindguts contained cellulolytic actinomycetes, including *Macrotermes, Armitermes, Microcerotermes,* and *Odontotermes* species.

The extracellular cellulase (Cl, Cx, and cellobiase) activity of the isolated actinomycetes (*Streptomyces* sp. and *Micromonospora* sp.) was assessed after the organisms were grown on cellulosic substrates (Hydo *et al*., 2003, Korb and Aaanen, 2003). For the substrates of Cl, Cx, and cellobiase, filter paper, carboxymethylcellulose (CMC), and d-cellobiose were utilized. All strains were shown to be capable of degrading soluble and insoluble cellulose, with 6.2–6.7 being the optimal pH range for growth at 28°C. However, the three strains were able to grow on cellulosic substrates at 48°C (Pasti and Belli, 1985).

D. Acetogenic Bacteria:

Both lower and higher termite gut include acetogenic bacteria that can ferment glucose and cellobiose to acetate by CO_2 reduction. Acetate is a crucial component in the production of many different molecules, including amino acids, cuticular hydrocarbons, and terpenes. It also serves as an energy source for termites. The acetogenic bacteria *Sporomusa termitida* sp. oxidizes H_2 and reduces CO_2. In 1984, Breznak identified this particular bacterium from the intestines of *Nasutitermes nigriceps*.

E. Methanogenic Bacteria:

Tropical grasslands and forests are the primary habitats for termites; however, they can be found in many different biological zones. In the digestive system, symbiotic microorganisms produce methane through the action of termite bacteria and flagellate protozoa. Methane is thought to be a significant greenhouse gas that contributes significantly to global warming, according to Thakur *et al.* (2003). Studies revealed that the amounts of CH4 that various species produced varied greatly. According to Zimmerman *et al.* (1982), the lower termite species release CH4 at a higher rate of 0.425 µg/day than the higher termite families, which emit 0.397 µg/day.

15.6 Environmental Conditions:

Several environmental factors, including temperature, humidity, light levels, and CO_2 and O_2 concentrations, influence the formation of methane. Termites favor high temperatures, excessive carbon dioxide levels, saturated relative humidities, and immobile environments devoid of sunshine. Although termite populations are active in medium-latitude settings, the majority of termite mounds and nests are located in lower-latitude tropical woodlands, grasslands, and savannahs in Africa, Asia, Australia, and South America. Approximately 80% of the termite emissions worldwide are thought to originate from these places. Considering their geographic regions, termites prefer temperatures more than 10°C above the surrounding air temperature.

A. Methane Production:

Cook (1932) was the first to report on termites producing methane. He noted that a particular type of termite evolved a gas. Research revealed that CH_4 is created in the digestive tract when symbiotic microorganisms break down cellulose (Figure 3). Termites of different species produce varying amounts of methane. According to a study conducted by Zimmerman *et al.* in 1982, lower termite species produce approximately 0.425 µg of CH_4

per termite per day, while higher termite families produce 0.397 µg of CH_4 per termite per day. Another study by Gomathi and Ramasamy in 2001 revealed that the maximum CO_2 emissions came from the workers, larvae, and queens of higher termites, in contrast to lower termites (see Figure 15.4).

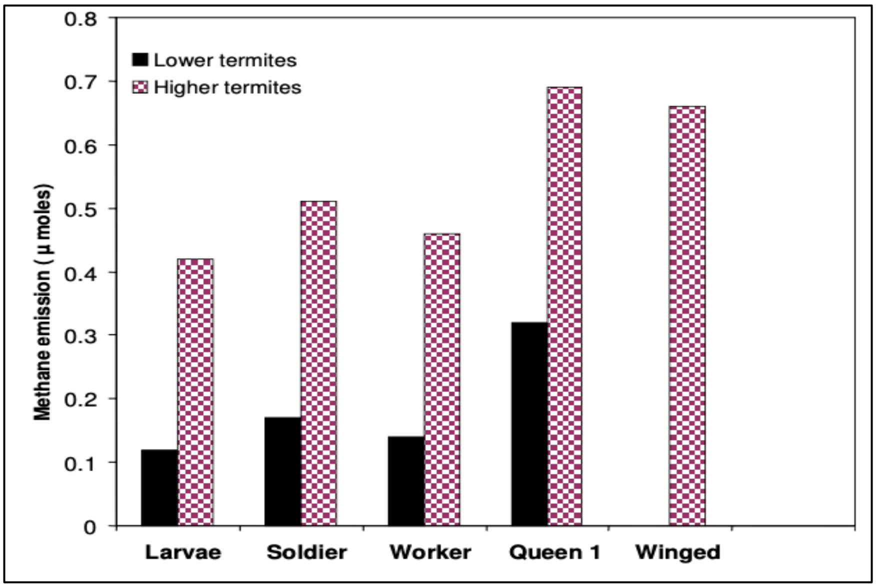


Figure 15.3: Emission of Methane in Situ by Different Castes of Termites

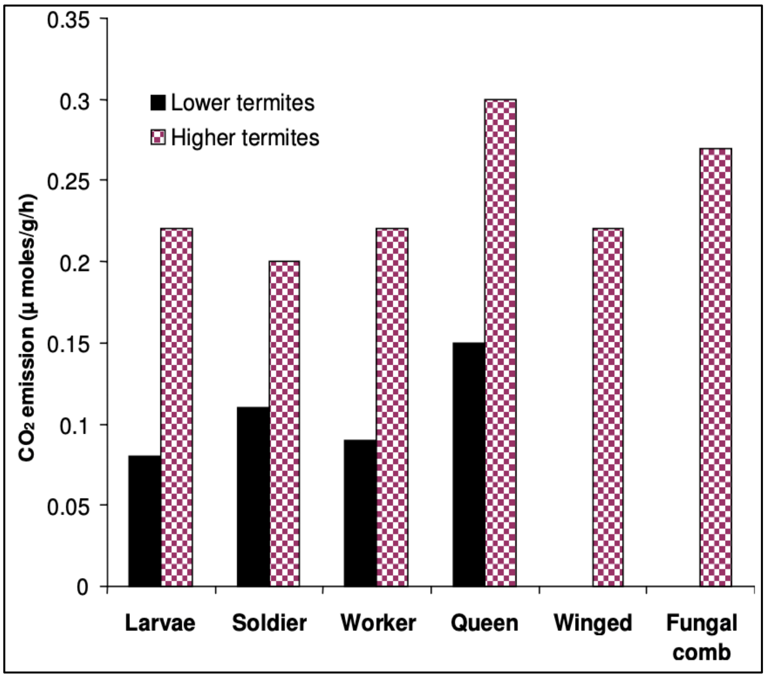


Figure 15.4: Carbon Dioxide Emission in Situ by Different Castes of Termites

Environmental factors like light, temperature, humidity, and gas concentrations (CO_2 and O_2) affect methane production. In addition to high and steady temperatures, termites may survive under conditions devoid of solar radiation, immobile atmospheres, saturated or nearly saturated relative humidities, and even increased CO_2 levels. Although there are termite populations in some middle-latitude areas, lower-latitude tropical forests, grasslands, and savannahs in Africa, Asia, Australia, and South America are home to the bulk of termite mounds and nests. Roughly 80% of the termite emissions worldwide are thought to originate from these places. Studies have shown that the ability of termites to produce methane varies depending on the species, as well as the particular mound or nest the termites belong to. In addition, the amount of CH_4 produced also changes with temperature. In a recent study, researchers found that six different termite species produce methane at varying rates. The observed CH_4 production rates differed significantly, extending more than two orders of magnitude. The study also discovered that there was a 30–100% increase in the recorded CH_4 emissions when the temperature was raised by 5°C within each species' optimum temperature range. Termites typically prefer temperatures that are at least 10°C higher than the local ambient air temperature, according to prior field and laboratory studies. Additionally, researchers have found that termites' consumption of biomass positively correlates with the quantity of methane they release, with an average of 3.2 mg of CH_4 per gram of wood (Fraser *et al.*, 1986). The methane and carbon dioxide exchange at the soil's surface near termite nests was observed in an experiment. The estimated flux rates from termite mounds into the atmosphere showed significant changes that were correlated with termite activity, species, mound size, and population density. The flux rates fluctuated throughout the day, reaching their maximum in the late afternoon and decreasing in the early morning. Furthermore, it was demonstrated that methane flux rates from individual mounds were linearly related to corresponding CO_2 rates, meaning that methane rose as CO_2 increased.

15.7 Conclusion:

Termites are crucial to the planet's cycles of nitrogen and carbon. They release methane, carbon dioxide, and nitrous oxide, which can collectively have a significant impact. Methane is produced during the digestive process of termites, particularly in their hindgut. Methane, a powerful greenhouse gas with a far greater potential for global warming than carbon dioxide, is released when cellulose-rich materials break down in the gut of some microbes. This process occurs primarily in the short term. Termites also produce carbon dioxide during the decomposition of plant materials. They break down cellulose and release carbon dioxide during respiration. Additionally, termites contribute to nitrous oxide emissions through their digestion processes. Although nitrous oxide is a potent greenhouse gas, it is not as common in the atmosphere as carbon dioxide or methane. It's crucial to comprehend the part termites play in releasing greenhouse gases to manage carbon and nitrogen cycles effectively, predict climate change effects and mitigate them.

15.8 References:

1. Bignell DE. 1984. The arthropod gut as an environment for microorganisms. In *British Mycological Society Symposium Series [BR. MYCOL. SOC. SYMP. SER.]. 1984*.
2. Bignell DE and Eggleton P. 2000. *Termites in ecosystems* (pp. 363-387). Springer Netherlands.

3. Borer DJ and White RE. 1970. A field guide to insects: America north of Mexico. Peterson Field Guides.
4. Breznak JA. 1984. Biochemical aspects of symbiosis between termites and their intestinal microbiota. In *Symposium series-British Mycological Society*.
5. Brian MV. (Ed.). 1978. *Production ecology of ants and termites* (Vol. 13). Cambridge University Press.
6. Brummer C, Papen H, Wassmann R and Bruggemann N. 2009. Termite mounds as hot spots of nitrous oxide emissions in South-Sudanian savanna of Burkina Faso (West Africa). *Geophysical Research Letters*, *36*(9).
7. Brune A. 2014. Symbiotic digestion of lignocellulose in termite guts. *Nature Reviews Microbiology*, *12*(3), 168-180.
8. Brune ANDREAS. 2006. Symbiotic associations between termites and prokaryotes. *Prokaryotes*, *1*, 439-474.
9. Brune A, Emerson D 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. *Applied and environmental microbiology*, *61*(7), 2681-2687.
10. Conrad R. 1996. Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). *Microbiological reviews*, *60*(4), 609-640.
11. Eutick ML, O'brien RW and Slaytor M. 1978. Bacteria from the gut of Australian termites. *Applied and Environmental Microbiology*, *35*(5), 823-828.
12. Fraser PJ, Rasmussen RA, Creffield JW, French JR and Khalil MAK. 1986. Termites and global methane-another assessment. *Journal of Atmospheric Chemistry*, *4*, 295-310.
13. Gomathi V and Ramasamy K. 2001. *Gut microflora of termite and associate with emission of greenhouse gases (CO_2+ CH_4)* (Doctoral dissertation, Ph. D Thesis, Tamil Nadu Agricultural University, Coimbatore).
14. Hyodo F, Tayasu I, Inoue T, Azuma JI, Kudo T and Abe T. 2003. Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera). *Functional Ecology*, *17*(2), 186-193.
15. Ji R and Brune A. 2006. Nitrogen mineralization, ammonia accumulation, and emission of gaseous NH3 by soil-feeding termites. *Biogeochemistry*, *78*, 267-283.
16. Jouquet P, Traore S, Choosai C, Hartmann C and Bignell D. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, *47*(4), 215-222.
17. Korb J and Aanen DK. 2003. The evolution of uniparental transmission of fungal symbionts in fungus-growing termites (Macrotermitinae). *Behavioral Ecology and Sociobiology*, *53*, 65-71.
18. Mannesmann R. 1972. A comparison between cellulolytic bacteria of the termites *Coptotermes formosanus* Shiraki and *Reticulitermes virginicus* (Banks). *Int Biodeterior Bull*, *8*, 104-111.
19. Matoub M and Rouland C. 1995. Purification and properties of the xylanases from the termite *Macrotermes bellicosus* and its symbiotic fungus Termitomyces sp. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *112*(4), 629-635.
20. Morales SE, Cosart T and Holben WE. 2010. Bacterial gene abundances as indicators of greenhouse gas emission in soils. *The ISME Journal*, *4*(6), 799-808.

21. Ngugi DK and Brune A. 2012. Nitrate reduction, nitrous oxide formation, and anaerobic ammonia oxidation to nitrite in the gut of soil-feeding termites (Cubitermes and Ophiotermes spp.). *Environmental Microbiology*, *14*(4), 860-871.
22. Ngugi DK, Ji R and Brune A. 2001. Nitrogen mineralization, denitrification, and nitrate ammonification by soil feeding termites: a 15N based approach. *Biogeochemistry*, 103, 355-369.
23. O'Brien RW and Slaytor M. 1982. Role of microorganisms in the metabolism of termites. *Australian Journal of Biological Sciences*, *35*(3), 239-262.
24. Ohkuma M. 2008. Symbioses of flagellates and prokaryotes in the gut of lower termites. *Trends in microbiology*, *16*(7), 345-352.
25. Ohkuma M, Noda S, Hongoh Y and Kudo T. 2001. Coevolution of symbiotic systems of termites and their gut microorganisms. *Riken review*, 73-74.
26. Richards OW and Davies RG. 1977. Imms' General Textbook of Entomology; Classification Andd Biology. Jonh Wiley & Sons.
27. Sands WA. 1970. Biology of termites, Academic Press. New York, 2: 495-524.
28. Schmidt JR, Graber TM and Breznak JA. 1999. Acetogenesis from H2 plus CO2 by Spirochetes from Termite Guts, Science *283*(5402), 686-689.
29. Schmitt-Wagner D and Brune A. 1999. Hydrogen profiles and localization of methanogenic activities in the highly compartmentalized hindgut of soil-feeding higher termites (Cubitermes spp.). *Applied and Environmental Microbiology*, *65*(10), 4490-4496.
30. Schultz JE and Breznak JA. 1978. Heterotrophic bacteria present in hindguts of wood-eating termites [*Reticulitermes flavipes* (Kollar)]. *Applied and Environmental Microbiology, 35*(5), 930-936.
31. Tayasu I, Sugimoto A, Wada E and Abe T. 1994. Xylophagous termites depending on atmospheric nitrogen. *Naturwissenschaften, 81*, 229-231.
32. Thakur RKB and Jeeva V. 2003. Termites and global warming - a review, Indian forester, 7 (129), 923-930.
33. Thayer DW. 1976. Facultative wood-digesting bacteria from the hind-gut of the termite Reticulitermes hesperus. *Microbiology*, *95*(2), 287-296.
34. Tholen A and Brune A. 1999. Localization and in situ activities of homoacetogenic bacteria in the highly compartmentalized hindgut of soil-feeding higher termites (Cubitermes spp.). *Applied and environmental microbiology, 65*(10), 4497-4505.
35. Warnecke F, Luginbühl P, Ivanova N, Ghassemian M, Richardson TH, Stege JT and Leadbetter JR. 2007. Metagenomic and functional analysis of hindgut microbiota of a wood-feeding higher termite. *Nature*, *450*(7169), 560-565.
36. Zimmerman PR, Greenberg JP, Wandiga SO and Crutzen PJ. 1982. Termites: a potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen. *Science, 218*(4572), 563-565.