

Termites in a dry evergreen forest in Thailand: species diversity, abundance and ecosystem function.

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INTRODUCTION

Termites (Isoptera) are superabundant soil animals in tropical terrestrial ecosystems, and the biomass is high, for example approaching 10gm^{-2} in humid forests. They play an important role in decomposition processes through utilizing various stages of organic matter ranging from fresh plant materials to soils (Wood & Sands, 1978; Swift et al., 1979). For example, termites consume 24-32 % of the annual supply of fallen leaves in Malayan tropical forest (Matsumoto & Abe, 1979) and 63 % of grass litter in Nigerian savanna, as well as forming a food resource for various predatory animals (Wood & Sands, 1978). These abilities largely lies in the sociality and the symbiosis with microorganisms (Higashi & Abe, 1997).

Termites consists of about 2,600 species and 7 families, and can be divided into two groups (Kambhampati & Eggleton, 2000). The lower termites have a character that they harbor protozoa in their hind gut and mainly consume wood, while the higher termites are characterized by the absence of those protozoa and consume a various range of dead and decaying plant materials, and soil (Wood 1978). The higher termites, consisting of one family Termitidae, include about 70% of described species (Kambhampati & Eggleton 2000).

Termites are also known as one of the prominent “ecosystem engineers” (Jones *et al.* 1994), which modify the soil properties by constructing huge mounds and long subterranean galleries, and which provide many animals and plants with heterogenous habitats. The evolution, sociality, symbioses, and ecology of termites were recently reviewed in a textbook (Abe, Bignell, & Higashi, 2000)

Here, we report the results of our studies on the termites in a dry evergreen forest in Thailand. In this report, we firstly describe the termite fauna in the study site, and estimate the direct carbon mineralization by termites. Secondly, we investigate the effect of termites from various feeding habits on decomposition

processes. Thirdly, we present preliminary results on radioisotopes (^{14}C) together with C and N stable isotope ratios, in order to study feeding habits, trophic position, and turnover time of carbon in termites.

Study site

The study site is located in Sakaerat Environmental Research Station (14 ° 30' N, 101 ° 56' E), Nakhon Ratchasima province, northeast Thailand (Fig. 1), where is about 500m above sea level. The Station consists of 29.5 km² of seasonal evergreen forest (dry evergreen forest; DEF) and 12.2 km² of drought-deciduous forest (dry dipterocarp forest; DDF) (Wacharakitti *et al.* 1980). The most dominant species is *Hopea ferrea* and canopy trees attain 30 to 40 m (Kanzaki *et al.* 1995). The site is in the tropical



monsoon climate zone. Mean annual temperature is 26.2 °C, and annual rainfall is 1240mm. Monthly rainfall is less than 50mm during dry season, from December to February (Sakurai *et al.* 1998).

Species diversity and biomass of termites in the dry evergreen forest.

A total of 47 species of termites were collected, of which *Neotermes*, *Havilanditermes* and three genera of Termitinae are new record genera from Thailand. And *Euhamitermes*, *Speculitermes*, *Odontotermes*, *Hypotermes*, *Bulbitermes*, *Mirocapritermes* and *Pericapritermes* included new records to Thailand and some of them are probably new species (Table 1) (Takematsu *et al.*, unpublished data).

The termite species diversity in Southeast Asia has been studied in tropical rain forest of Brunei (Jones, 1996), Sabah of east Malaysia (Eggleton et al. 1997), Sarawak of east Malaysia (Collins, 1984) and west Malaysia (Abe, 1978; Jones & Brendell, 1998), dry deciduous forest of Thailand (Davies, 1997) and subtropical rain forest of Ryuku Islands (Ikehara, 1996). Compared with these studies, this study site can be characterized by the high species diversity of fungus growing termites (Macrotermitinae).

The biomass of termites has been assayed in several ecosystems from savanna to tropical rain forest. In DEF, Inoue et al. (2001) assayed the biomass of termites in soil and Yamada et al. (unpublished) studied termites in woods and mounds, and estimated the total biomass to be 17.1g/m² (Table 2). In order to evaluate the quantitative role of termites in decomposition process, Yamada et al. (unpublished) measured CO₂ emission rates of various species and

Table 1. Termites collected in dry evergreen forest of Sakaerat.

Species
Kalotermitidae
1 <i>Glyptotermes brevicaudatus</i>
2 <i>Neotermes</i> sp.1
Rhinotermitidae
3 <i>Coptotermes curvignathus</i>
4 <i>Coptotermes havilandi</i>
5 <i>Schedorhinotermes medioobscurus</i>
6 <i>Schedorhinotermes rectangularis</i>
Termitidae
Apicotermitinae
7 <i>Euhamitermes</i> sp.1
8 <i>Euhamitermes</i> sp.2
9 <i>Euhamitermes</i> sp.3
10 <i>Speculitermes</i> sp.1
Macrotermitinae
11 <i>Ancistrotermes pakistanicus</i>
12 <i>Macrotermes annandalei</i>
13 <i>Macrotermes carbonarius</i>
14 <i>Macrotermes gilvus</i>
15 <i>Microtermes obesi</i>
16 <i>Odontotermes feae</i>
17 <i>Odontotermes formosanus</i>
18 <i>Odontotermes maesodensis</i>
19 <i>Odontotermes proformosanus</i>
20 <i>Odontotermes</i> sp.1
21 <i>Odontotermes</i> sp.2
22 <i>Hypotermes</i> sp.1
23 <i>Hypotermes makhamensis</i>
Nasutitermitinae
24 <i>Bulbitermes makhamensis</i>
25 <i>Bulbitermes prabhae</i>
26 <i>Bulbitermes</i> sp.1
27 <i>Nasutitermes matangensisiformis</i>
28 <i>Havilanditermes</i> sp.
29 <i>Hospitalitermes ataramensis</i>
30 <i>Hospitalitermes bicolor</i>
Termitinae
31 <i>Amitermes longignathus</i>
32 <i>Dicuspidermes garthwaitei</i>
33 <i>Dicuspidermes makhamensis</i>
34 <i>Globitermes sulphureus</i>
35 <i>Mirocerotermes crassus</i>
36 <i>Mirocapritermes concaveus</i>
37 <i>Mirocapritermes</i> sp.1
38 <i>Pericapritermes latignathus</i>
39 <i>Pericapritermes semarangi</i>
40 <i>Pericapritermes</i> sp.1
41 <i>Procapritermes parasilvaticus</i>
42 <i>Procapritermes prosetiger</i>
43 <i>Terms comis</i>
44 <i>Terms propinquus</i>
45 <i>n.gen.</i> sp.1
46 <i>n.gen.</i> sp.2
47 <i>n.gen.</i> sp.4

Table 2. The biomass of termites and its contribution to the decomposition of organic matter

Location	AP	Biomass of termites (g/m ²)				RT	RT / AP
		In soil	In wood	In mound	Total		
Thai, Sakaerat: Dry Evergreen forest	571	9.4	3.5	4.2	17.1	19.6	3.4%
Nigeria: Southern Guinea savanna	270	-	-	-	10.6	11.8	4.4%
Malaysia, Pasoh: Lowland rain forest	690	6.3	-	3.0	9.4	10.5	1.5%
Brazil, Amazonia: Terra firme forest	578	0.1	1.8	4.8	6.7	7.7	1.4%

AP= Annual litter and dead wood production (gC/m²/y)

RT= Respiration of termites (gC/m²/y)

- No information or not determined

estimated the total carbon emitted from termites to be 19.6 g(carbon)/m²/year, which accounts for 3.4% of the carbon content in annual litter and dead wood production in DEF. The values are comparable to those observed in savanna where it has been believed that termites contribute greatly on decomposition of organic matter (Table 2). These results suggest that the contribution of termites on the decomposition process in tropical forest could be emphasized more than before.

Role of the termites in Ecosystem

The most obvious role of termites in ecosystem is decomposition, and it determines specific pathways of subsequent humification and mineralization of residual materials. (Bignell & Eggleton, 2000). These functions are dependent on the species assemblages of the termite community (Lawton, et al. 1996). Therefore, ~~recently~~, many studies have been conducted on the termite assemblages in natural condition, and/or under disturbed conditions (e.g Eggleton, et al. 1997). In those studies, some categorization of feeding group has been made to separate functional roles of the termites in ecosystems; for example, wood-feeder, fungus-growing wood feeder, and soil-feeder (e.g. Davies, 1997).

Even though the information on the termite assemblage has been accumulated in many tropics, the

effect of each feeding group on the decomposition processes, remains unclear. We present our results on the effect of each feeding group,

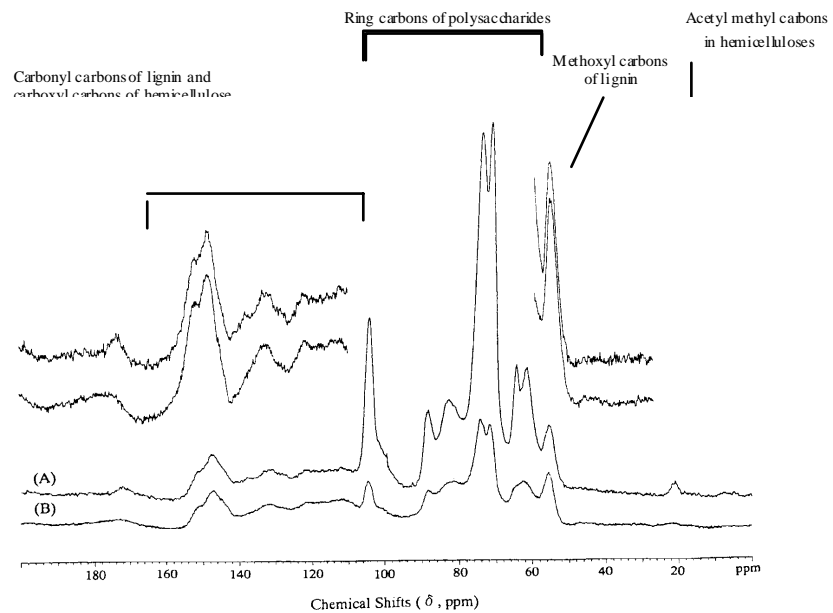


Fig. 2. CP/MAS ^{13}C NMR spectra of earlywood of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.): (A) sound control; (B) subjected to passage through the gut of *C. formosanus*. Insertions are expanded spectra at regions of 0 to 40ppm and 110 to 200ppm.

(wood-feeder,

fungus-growers,

and soil-feeders) on the decomposition process.

Effect of wood-feeding and soil-feeding termites on carbon structure

In order to assess the effect of passage through the gut of wood-feeding termites, Hyodo et al. (1999) fed a lower termite, *Coptotermes formosanus* Siraki, on Japanese red pine and compared food and fecal materials using solid-state CP/MAS ^{13}C NMR, which had been shown to be a powerful tool to characterize lignin degradation by some fungi (Gilardi et al., 1995; Martinez, et al., 1991). They showed that *C. formosanus*, and their gut symbionts can extensively utilize cellulose and hemicellulose, but had little or no ability to degrade lignin (Fig. 2), supporting the previous investigation using lignin labeled with radio isotope (Cookson 1987). This is very astonishing because it is well established that lignin must be disrupted for enhancement of enzyme accessibility toward the wood polysaccharides (Kirk & Chang 1981). The most

plausible reason for effective enzymatic digestion of wood polysaccharides by lower termites without lignin degradation is in an increase of surface area available for enzymatic attack through mechanical grinding of wood at molar region in the mandible (Lutz 1986) and gizzard in their foregut. Indeed, for effective *in vitro* enzymatic saccharification of wood, it must be physically ground into small fragments by milling (Matsumura *et al.* 1977; Ford 1983).

Hyodo *et al.* (2001) also applied the CP/MAS ^{13}C NMR technique to the effect the soil-feeding termite, *Dicuspiditermes makhamensis*, on carbon structure in soil organic matter by comparing the termite mound (egested soil) with the surrounding soil. In terms of CP/MAS ^{13}C NMR, they suggested that there is no clear difference between the carbon composition of the termite mound and that of the surface organic soil layer, suggesting that the effect of the soil-feeding termite is not so prominent on soil carbon structure (Fig.3).

What substances soil feeders really eat is unknown. Abe & Higashi (2000) proposed an interesting idea that soil feeders eat microorganisms such as bacteria and fungi in ingested soil, and therefore they are important members of microbial chain in the tropical forests, which appears to be supported by stable isotope analysis (Tayasu *et al.*, 1997, 1998). In fact, Ji & Brune (2001) provided an evidence that bacteria and microbial

biomass as well as structural

polysaccharides of plants are carbon

and energy sources for soil-feeding

termites, *Cubitermes orthognathus*,

based on radio isotope technique.

Furthermore, Fujita *et al.*

Fig. 3. CP/MAS ^{13}C spectra of the L, F, A1 and A2 layer and mound of *D. makhamensis*.

(unpublished data) supported the idea by demonstrating that lysozyme, decomposing cell wall of bacteria, is produced the salivary gland of a soil feeding termite, *Pericapritermes nitobei*.

Lignin degradation in termite-fungus symbiotic system.

Fungus growing termites are a distinct subfamily, which have evolved to cultivate the symbiotic fungi, the genus *Termitomyces*, grown on special medium, fungus comb, which is housed within their nests. Fungus comb is made from the termites' faecal pellets

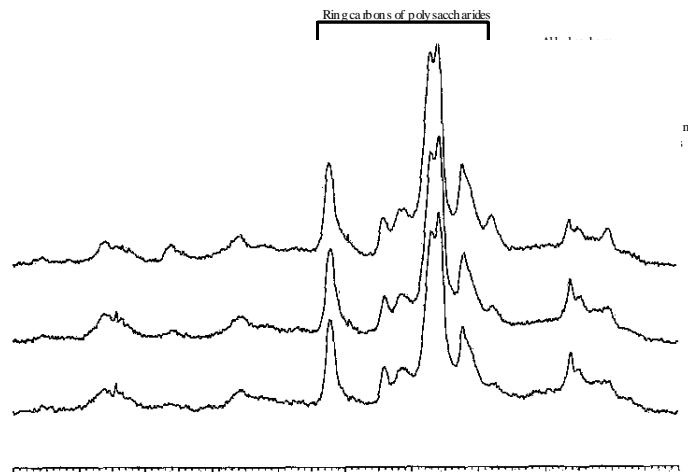
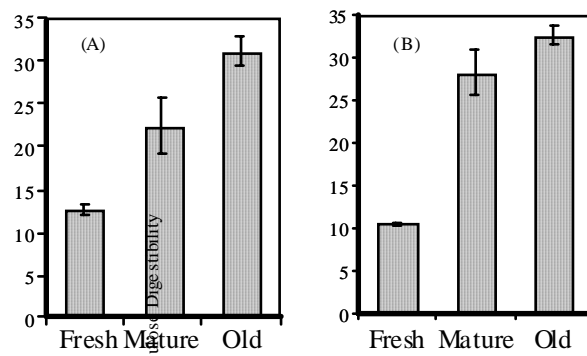


Fig. 4. CP/MAS ¹³C NMR spectra of three parts (Fresh

after partly digestion of plant debris and the old comb is consumed by the termites (Darlington 1994). As with the role of the symbiotic fungi in the termites, Grasse & Noirot (1958) proposed that the fungal partner degrades lignin in fungus comb, so that the termite can utilize cellulose more efficiently. Hyodo et al. (2000)

examined the “lignin degradation hypothesis” by using CP/MAS ¹³C NMR to characterize lignin, and estimated the *in vitro* digestibility of cellulose in fungus combs from a southeast Asian fungus-growing termite, *M. gilvus*. They



found evidence that lignin degradation took place progressively in the fungus comb (Fig.4). *In vitro* digestibility of cellulose in old fungus comb, on which the termites feed, was approximately three times higher than that in the fresh part (Fig.5). These results confirm the “lignin degradation hypothesis” that the role of the mutualistic fungi is to degrade lignin and enhance the digestibility of cellulose for the termites, suggesting the ability of the termite-fungus association to make extremely efficient use of plant material.

Functional group of termites based on the effect on organic carbon.

According to the effect on decomposition of organic matter, wood-feeders and fungus-growers can be classified into two functional groups; cellulose-feeders and cellulose-lignin feeders, respectively (Abe & Higashi, 2000).

Especially, the two functional groups, might have an opposite effect on humification processes. Lignin fraction of plant litter is assumed to become humus in many models of soil organic matter (e.g. Parton et al. 1987). Given this assumption, it is expected that cellulose feeders, which deposit the faeces with high concentration of lignin as their nests, may have significant role in humification in tropics, where the accumulation of humus is generally poor (Jordan, 1985). Inversely., the cellulose-lignin feeders may act to reduce the accumulation of humus.

In general, gradients from arid and semiarid ecosystems to tropical forests are characterized by a gradual shift of dominance from wood- and litter-feeding to soil-feeding (Bignell & Eggleton, 2000; Abe & Higashi, 2000). The species diversity of fungus growers is the highest in a little dry areas such as savannas and dry forests where microbes are poorer than moist forests. Abe & Higashi (2000) explained this change in relation to the activities of microbes. Assumed that soil feeders utilize microbes as their food source, soil

feeders are abundant and diversified in tropical rain forests, where fungi, in particular white rot, may be active and decompose lignocellulose efficiently, decreasing the litter accumulation on the ground. On the other hand, cellulose-lignin feeders (fungus growers) cultivating white rot of *Termitomyces* in the nest chambers with high humidity and temperature and dominant in dry areas where the low humidity may suppress the decomposition of lignocellulose by white rot. Cellulose feeders are widely distributed in the area where fungi may be inactive due to low temperature and/or inadequately humidity.

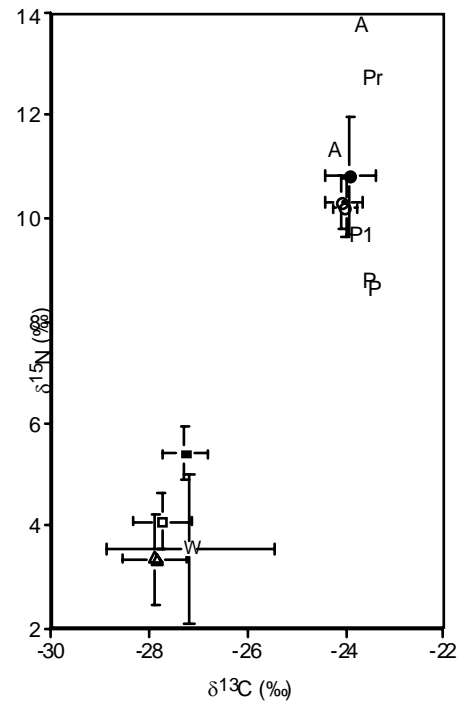
Application of radio carbon into feeding habit and carbon turnover in termites

^{14}C is a naturally occurring, cosmogenic isotope that is normally used for carbon dating of materials up to 45,000 years (half-life = 5730 years; Stuiver & Polach 1977). It has been also used to study retention time of carbon in the biosphere using “bomb carbon” that has been dispersed by thermonuclear tests that maximized atmospheric values of ^{14}C in 1962/63. Since the ending of atmospheric test, bomb-induced ^{14}C concentrations in the atmosphere declined with an e-folding time of (16.3 ± 0.2) year, which has been estimated from long-term $^{14}\text{CO}_2$ observations in Germany (Levin & Kromer 1997), mainly due to anthropogenic CO_2 emissions from fossil fuels and mixing between atmosphere and ocean. This trend can be used to study turnover of soil organic matter (O'Brien & Stout 1978), and to trace “bomb” ^{14}C incorporation in animals in the forested and grassland ecosystems (Rafter & Stout 1969; Stout & O'Brien 1972; Beavan & Sparks 1998). To be noted, ^{14}C technique is useful in the forested ecosystems or natural grassland, where changes in $\delta^{13}\text{C}$ signals between C3 and C4 plants are not available.

Tayasu et al. (2002) determined carbon and nitrogen stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and radio-carbon (^{14}C) for termites in Sakaerat. A wood-feeding termite, *Microcerotermes crassus*, was separated from soil-feeders: *Termes propinquus*, *T. comis* and *Dicupiditermes makhamensis* by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig.6), which was consistent with a species assemblage in Cameroon (Tayasu et al. 1997). *Termes* group in Thailand had less diverse values in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than those in Australia, where the feeding habits of “*Termes*” group are more diverse (Tayasu et al. 1998).

A wood-feeder (*M. crassus*) had higher ^{14}C -pMC values than soil-feeders (*A. longignathus*, *D. makhamensis* and *T. propinquus*). The differences in ^{14}C -pMC values between the soil-feeders and the wood-feeder were 2.6 to 3.0% (Fig.7). The fact that wood-feeding termites had higher ^{14}C -pMC values than soil-feeders suggests an interesting interpretation.

The ^{14}C activity in termites can be assumed as the sum of the two components: (1) “old” decayed carbon (before 1950) with a ^{14}C activity less than that of the 0.95 NBS oxalic acid standard (^{14}C -pMC < 100) (2) “modern” and “bomb” carbon with a ^{14}C activity significantly greater than the 0.95 NBS oxalic acid standard (^{14}C -pMC > 100) (Goh 1991). There is little possibility that such “old” decayed carbon contributes much to detritivores



(Scharpenseel *et al.* 1989), and turnover of litter (Aerts 1997) and soil organic matter (Trumbore 1993) in the tropics has been estimated to be very fast. Assuming that “old” decayed carbon was scarcely used by termites, and considering that ^{14}C concentration in the atmosphere has decreased 0.061yr^{-1} (Levin & Kromer 1997: in $\Delta^{14}\text{C}$ scale, followed by Stuiver & Polach 1977), lower ^{14}C activity (but $^{14}\text{C}\text{-pMC} > 100$) indicates the use of younger carbon. Therefore, the results suggest that the soil-feeding termites have used younger carbon than the wood-feeding termites. Using the exponential function of $^{14}\text{CO}_2$ fitted by Levin & Kromer (1997), the differences in ^{14}C between the soil-feeders and the wood-feeders were about 2.7 to 3.2 years. It is probable that carbon retention (calculated from the time when the CO_2 was fixed) in wood-feeding termites is longer than that in soil-feeding termites, because the latter consumes organic matter in soils originated from leaves and branches, or young carbon from the rhizosphere (roots or via root exudates). Further study is required to test under what condition this estimation is valid. For example,

comparison between the termites that subsist on fresh litter, e.g. grass harvesting species, and the “damp wood termites” that subsist on large wood tissues is a test for the extreme ends.

Although the assumptions and the calculations are so much simplified, the results propose an utility of “bomb carbon” in the study of detritivorous animals. It seems reasonable to

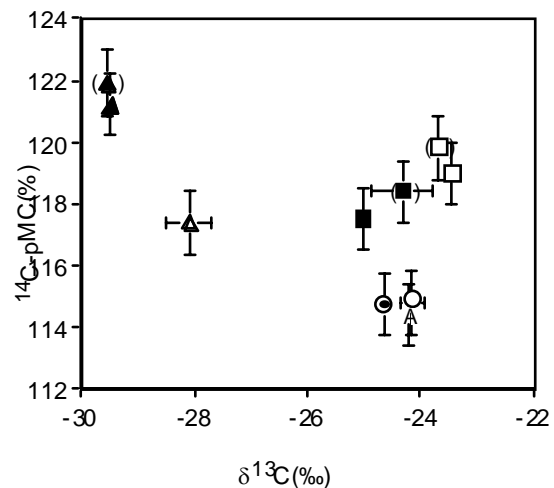


Figure 7 $\delta^{13}\text{C}$ and $^{14}\text{C}\text{-pMC}$ plot of termites from Thailand: *M. crassus* (), *T. propinquus* (), *D. makhamensis* (⊙) and *A. longignathus* (A), and from Cameroon: *M. parvus* (), *Th. macrothorax* (), *C. heghi* (). Termites from Cameroon are expressed in whole body (without parenthesis) or exoskeleton (within parenthesis). Data are expressed in means \pm SD for $\delta^{13}\text{C}$ and in ^{14}C activity \pm analytical error for ^{14}C .

adopt these assumptions in the sites where the accumulation of organic layer (L-, F- and H-layers) is small and the first-year decomposition rate is high (e.g. in the tropics, see Aerts 1997). It should be tested whether it can be applied to the area where the decomposition rate is low (mainly in high latitudes).

CONCLUSION

We investigated the species diversity, abundance and ecosystem functioning in a dry evergreen forest in Thailand. In the study site, a total of 43 species of termites was collected and termite biomass was estimated to be 17.1 g(w.w.)/m². Combined the biomass data and the respiration rates (CO₂ emission rates) of termites, direct carbon mineralization of organic matter (respiration) by total termites was estimated to be 19.6 gC/m²/year. Those values are comparable to those observed in savanna, where it has been believed that the contribution of termites on decomposition of organic matter is greater than in tropical forests, suggesting that it is needed to reevaluate the contribution of termites on the decomposition process in tropical forest.

Based on the studies on the effect of wood-feeding, fungus-growing, soil-feeding termites on organic matter, wood-feeding termites and fungus-growing termites can be considered as cellulose-degrading termites and cellulose-lignin-degrading termites, respectively. The food source of soil-feeding termites remains unknown, but it seems that the soil-feeding termites feeds on microbes, such as bacteria in the soil.

The results of our radio and stable isotope techniques suggested further applications. The proportion of carbon reservoirs in litter, soils and wood tissues changes between sites, and the decomposition rate depends on climate (*sensu* Aerts 1997). Different feeding groups in termites, and other detritivores as well (Beavan & Sparks 1998), subsist on different carbon reservoirs which have different turnover times. Thus, ¹⁴C, ^δ¹³C and ^δ¹⁵N may be useful in analyzing soil food webs.

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