Ecosystem-Scale Studies on the Role of Termites in Decomposition Processes of a Dry Evergreen Forest, Northeast Thailand

by

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Abstract

The importance of termites in decomposition processes is widely recognized, and is frequently emphasized especially in savannas. In tropical forests, there have been only a few studies that quantitatively demonstrated the roles of termites as a decomposer. We quantified the importance of termites in terms of carbon mineralization and nitrogen fixation on the basis of biomass data in a dry evergreen forest, northeast Thailand. By using observed respiration rates from termite individuals and fungus-combs with their biomasses, they were estimated to mineralize 11.2% of carbon (C) in the annual aboveground litterfall (AAL). Of these, fungus-combs were responsible for a major part (7.2% of the AAL) of the C mineralization mediated by termites. We measured nitrogen (N) fixation rates of termites and asymbiotic (free-living) bacteria in litter, dead wood and soil, and estimated the total N inputs from fixation to decomposing plant material on the forest floor. Annual mounts of N fixed by termites and asymbiotic bacteria were calculated to be 0.28 and 3.95 kg ha^{-1}, respectively, showing that termites are responsible for 6.6% of the total.

Key words: carbon mineralization, dry evergreen forest, ecosystem scale, fungus-combs, nitrogen fixation, respiration

Introduction

Termites are a major decomposer in tropical and subtropical regions (Lee & Wood 1971; Wood & Sands 1978), where net primary production is equivalent to 50-60% of that of all terrestrial ecosystems. Termites have been considered to be “ecosystem engineers”, which are large invertebrates ingesting a mixture of organic material and mineral debris, forming stable, long-lived faeces which are organo-mineral complexes (Lavelle et al. 1997). Examples are given by the well-known studies in savannas, which have demonstrated the ecosystem-scale impact of termites, especially fungus-growers (Macrotermitinae), as ecosystem engineers (Lee & Wood 1971; Wood & Sands 1978; Buxton 1981; Collins 1981; Schaefer 1990; Lavelle et al. 1997). At the same time, it is increasingly recognized that termites have potentially significant contributions to decomposition processes as mediators of carbon (C) mineralization and nitrogen (N) fixation (Holt 1987; Bignell et al. 1997; Eggleton et al. 1999; Nardi et al. 2002; Konaté et al. 2003). In the present paper, we present ecosystem-scale studies on C mineralization and N fixation carried out in the dry evergreen forest (DEF) at Sakaerat Environmental Research Station, northeast Thailand, where we previously observed the biomass of termites (Inoue et al. 2001; Yamada et al. 2003).

Carbon mineralization mediated by termites

Respiration rates of termite individuals have been employed to quantify the contribution of termites to decomposition processes mainly in tropical forests (Matsumoto 1976; Martius 1994; Bignell et al. 1997; Eggleton et al. 1999; Konaté et al. 2003), whereas studies conducting measurements of food consumption rates of termites have clearly demonstrated that the dominant fungus-growers consume the major part, up to 30% (Wood & Sands 1978), of annual aboveground litterfall (AAL) in savannas (Wood & Sands 1978; Buxton 1981; Collins 1981). This is partly because there are obvious difficulties in measuring consumption rates of abundant soil-feeders and wood-feeders in tropical forests (Abe & Matsumoto 1979; Eggleton et al. 1996; Bignell et al. 1997; Eggleton et al. 1999; Yamada et al. 2003). Most of the studies using respiration rates have shown that termites in tropical forests mineralize about 1% of C in AAL by respiration from their populations. A single study has demonstrated that a fungus-grower consume 22-32% of leaf litter (= 10-15% of the AAL) by a fungus-grower in a tropical forest (Matsumoto & Abe 1979). However, compared to the considerable consumption of leaf-litter by the termites, respiration from the termites has contributed to C mineralization on an unexpectedly small scale (Matsumoto 1976). This apparent anomaly has been mentioned by several authors (Bignell & Eggleton 2000; Sugimoto et al. 2000). Here, we give a possible explanation about it by observing respiration rates of termite individuals as well as fungus-combs.

Firstly, we investigated the biomass of fungus-combs in DEF, separately for subterranean and mound-building species. The biomass of fungus-combs of subterranean species was estimated by digging ten 2m x 2m x 30cm (in depth) quadrats, and that of mound-builders was calculated by using mean weights of fungus-combs in a mound, determined by excavating several mounds of each species, with the termite biomass (Yamada et al. 2003). The total biomass of fungus-combs in the DEF was 40.1 g fresh weight m^{-2}. Secondary, respiration rates were determined under the field conditions by using a CO_2 analyzer for major species of termite individuals and fungus-combs. With data of termite biomass (Yamada et al. 2003), we estimated an amount of respiratory C from termite population and fungus-combs to be 20.8 g C m^{-2} y^{-1}, which is equivalent to 11.2% of C in the AAL in the DEF (520 g C m^{-2} y^{-1}; Wachirinrat & Takeda 2003; Vogt et al. 1986).

The total AAL mineralization mediated by termites in the DEF (11.2%) is much larger than those previously estimated in tropical forests without considering fungus-combs (Matsumoto 1976; Martius 1994; Bignell et al. 1997; Eggleton et al. 1999). The large amount of C mineralized by fungus-combs would give an explanation to the above-mentioned disagreement between litter consumption by termites in tropical forests and respiration from them. In the DEF, against 11.2% of the AAL mineralized by termite population and fungus-combs, termites are estimated to consume 21-64%, though 30-40% would be conceivable, of the AAL by referring previous studies on their consumption rates (Wood & Sands 1978; Martius 1994). This value is fully comparable to those in savannas (Wood & Sands 1978).

An aspect of the fate of the AAL in the DEF is that a majority of the AAL is mineralized above the ground by respiration from wood/litter-feeders (2.8%), fungus-combs (7.2%) and microorganisms on the litter layer (70.4%), leaving a relatively small part of the AAL that subsequently enters the soil layer (belowground C pool) and might get partly mineralized by soil-feeders (1.2%) as illustrated in Fig.1. If termites consume 30-40% of the AAL as discussed above, the AAL appears to be completely removed from the forest floor before it enters the soil layer on the place. It is suggested that there are competitive relationships between termites and microorganisms in litter layers over the AAL.

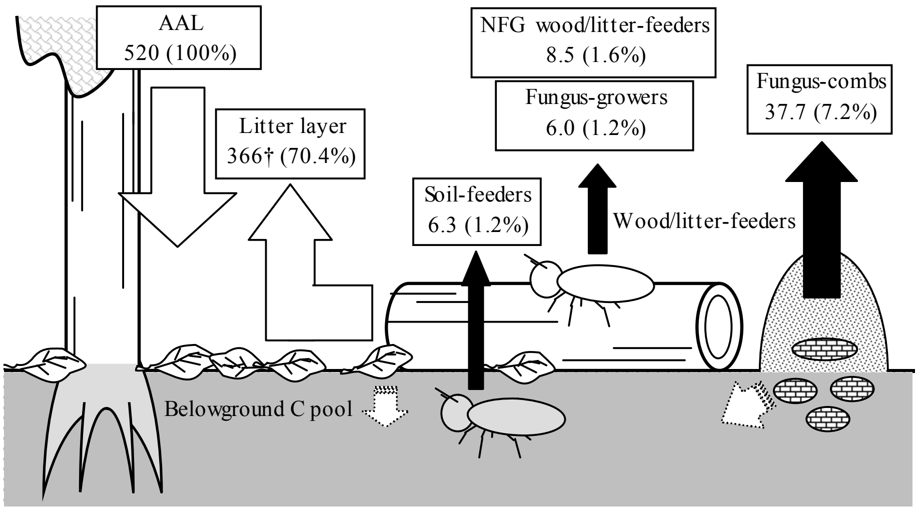

Fig.1. Fate of C in the annual aboveground litterfall (AAL; 520 g C m^{-2} y^{-1}; Wachirinrat & Takeda 2003; Vogt et al. 1986) in the dry evergreen forest at Sakaerat Environmental Research Station. The figures indicate the annual amounts of respiratory C (g C m^{-2} y^{-1}) with the percentages to the AAL in parenthesis. NFG: non-fungus-growing; †A season-weighted mean of respiration rates of the litter layer was calculated by using those measured in the DEF during dry and rainy seasons (Yoda & Nishioka 1982), with the assumption that the ratio of dry and rainy seasons is 5:7.

Nitrogen fixation by termites

N is one of the elements affecting decomposition of dead plant material (Vitousek et al 2002), as well as primary production (Vitousek & Howarth 1991; Vitousek et al. 2002). Biological N fixation is the primary process of N input to ecosystems, and generally occurs in bacterial symbionts in plant root nodules, asymbiotic (free-living) bacteria in surface soil layer, on the surfaces of dead plant material, and bacterial symbionts in xylophagous arthropod guts (Breznak 1975; Nardi et al 2002). N fixed in plant root nodules increases the plant growth (Vitousek & Howarth 1991), while asymbiotic bacteria and termites supply N to decomposing plant material. Many species in non-fungus-growing (NFG) wood/litter-feeders have been shown to fix N in order to compensate the N deficiency (Benemann 1973; Breznak et al. 1973; Prestwich & Bentley 1981; Tayasu et al. 1994). Although N fixation by termites has been studied by many researchers using acetylene reduction assay, only a few studies have quantified N fixed by specific termites on the scales covering their populations in the ecosystems (Schaefer & Whitford 1981; Pandey et al. 1992). Here, we present the first study that estimate N fixed by termites on the ecosystem scale and that evaluate the N amount in the context of N supply to decomposing plant material by considering asymbiotic N fixation.

We preliminary assayed a diverse group of termite species by acetylene reduction method, and only the wood/litter-feeding termites were found to fix N at significant levels. More intensive samplings of two abundant species, *Microcerotermes crassus* and *Globitermes sulphureus*, were done in the DEF across several seasons. Acetylene reduction method was modified, and the assays were carried out under field conditions in order to minimize an artifactual error. An N fixation rate of 0.28 kg N ha^{-1} y^{-1} was obtained by using mean rates of the two species and their biomasses (Yamada et al. 2003). An asymbiotic N fixation rate was estimated to be 3.95 kg ha^{-1} y^{-1}, by using observed fixation rates of litter and dead wood and the biomass (Yamada et al. 2003).

Termites is calculated to be responsible for 6.6% of N inputs from fixation to decomposing plant material in the DEF. N from precipitation (Jordan 1985; Edwards 1982; Strigel et al. 1994) and immobilization by fungal hyphae (Frey et al. 2000) is also given as potential sources of additional N Taking these potential N sources into consideration, the amounts of N fixed by termites might be of minor importance in decomposition processes. However, from the spatial and temporal point of view, N fixed by termites is expected to contribute significantly to decomposition processes in different ways from the other sources of additional N. Many species of NFG wood/litter-feeding termites, for example *M. crassus*, attack and break more or less freshly fallen branches and trunks, and feed on woody material in the centers of the woods (Abe 1980) by utilizing fixed N in their guts. In contrast, additional N from asymbiotic fixation, precipitation, and fungus-mediated immobilization is expected be supplied mainly to surfaces of fallen branches and trunks. Here, we suggest that N fixed by termites plays its role in the early decomposition processes and in the different part of dead wood from the part where the other additional N is supplied. With regard to the fate of N fixed by termites, it would be excreted as their feces out of their bodies. A stable isotope analysis has shown that feces of the termite *Neotermes koshunensis* contain atmospheric N (I. Tayasu, personal communication). It is most likely that at least a portion of feces containing fixed N is put into the centers of woods where termites are feeding and/or nesting. Therefore, the feces containing N fixed by termites would be an exclusive source of additional N to the centers of freshly dead wood, promoting further decomposition.

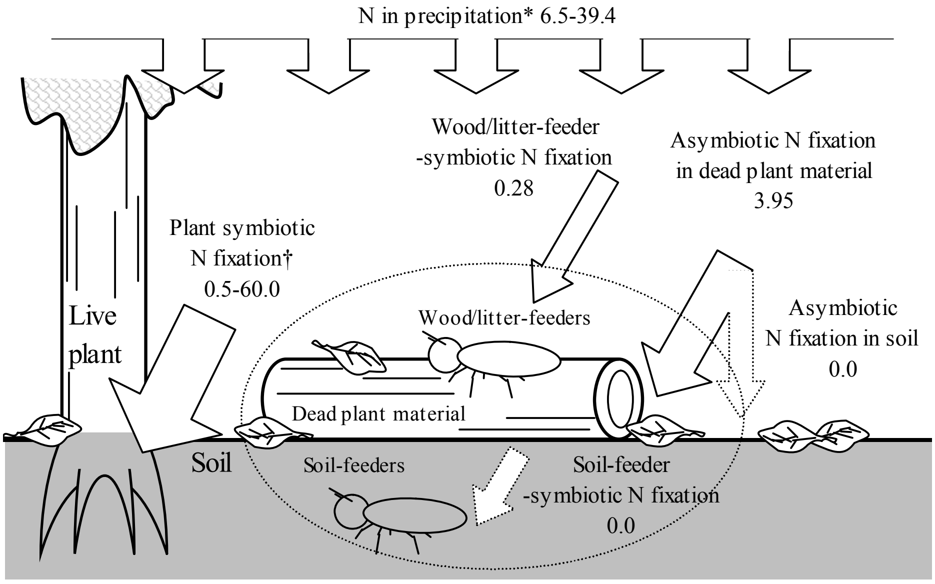

Fig. 2. Schematic figure on N inputs (kg N ha^{-1} y^{-1}) to the dry evergreen forest at Sakaerat Environmental Research Station. Only non-fungus-growing wood/litter-feeders of termites fixed N, and asymbiotic N fixation activity was detected from litter and dead wood but not from the soil. * data for tropical forests in Jordan (1985), Edwards (1982), and Strigel et al. (1994); † data for tropical evergreen and deciduous forests in Cleveland et al. (1999).

Conclusions

The role of termites in decomposition processes was quantitatively elucidated in a dry evergreen forest, northeast Thailand, in terms of C mineralization and N fixation. Termites mineralized 11.2% of C in an annual aboveground litterfall by respiration from their population (4.0%) and fungus-combs (7.2%) (Fig. 1). Despite lots of previous studies emphasizing the importance of fungus-growers in savannas, it is fully possible that fungus-growers are of great importance in tropical forests as well. In relation to N fixation, an amount of N fixed by termites, especially non-fungus-growing termites, was estimated to be 0.28 kg N ha^{-1} y^{-1} and was represented 6.6% of N inputs from fixation to decomposing plant material (Fig. 2).

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