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A Food Factory Strictly Managed by Fungus-growing Termites

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In this study, we analyzed fungus gardens of *Odontotermes feae* (Wasmann), which are associated with *Termitomyces eurhizus* (Berk.) R. Heim, and of *Ancistrotermes pakistanicus* Ahmad, which are associated with *T. striatus* (Beeli) R. Heim, to examine the ecological effects of termite use on primordium and fruiting-body formation. Our results indicate that the symbiotic termites strictly managed those fungus gardens that developed fruiting bodies. We also found that the termites prevented fruiting-body formation in fungus gardens of *O. feae* associated with *T. eurhizus* by eating the blackish tips of the primordia just prior to fruiting-body development. *Ancistrotermes pakistanicus*, however, did not eat the growing primordia of *T. striatus*. Instead, the primordia became fruiting bodies, the pseudorhizae of which were used along with the fungus garden as food for the termites. Moreover, our results revealed that *Termitomyces* developed fruiting bodies in the fungus gardens after the termites had deserted the nest. In conclusion, although the behavior between *O. feae* and *A. pakistanicus* toward fungus combs differs, their common goal is to maintain mycelial masses, including woody debris as a food resource.

INTRODUCTION

Many examples of mushroom cultivation by ants have been discovered (Weber, 1966; Abe, 1989; Moore-Landecker, 1990; Ridley *et al.*, 1996; Bass, 1997). In contrast, there are few reports on the ecological aspects of the symbiotic relationship between *Termitomyces* and termites. Termites eat dead and sometimes live plant tissues and pile their excrement in a porous structure (Abe, 1989; Murrin, 1996). They then make a fungus garden by cultivating *Termitomyces* hyphae on that structure. Finally, they eat the mature hyphae or fungus combs. Termites cannot live without a fungus garden, and *Termitomyces* has been observed only in termite nests (Abe, 1989; Darlington, 1994). Fruiting bodies of *Termitomyces* have been reported to develop in fungus gardens after termites desert the nest (Dixon, 1983). Fruiting-body formation is assumed to also occur in gardens being used by termites (Sagara, 2000). However, it is unknown whether some aspect of termite behavior prevents the formation of fruiting bodies of *Termitomyces* (Johnson *et al.*, 1981).

This study was conducted to clarify the symbiotic relationship between *Termitomyces* fruiting-body formation and termite behavior.

MATERIALS AND METHODS

Observation of fungus-growing termites associated with *Termitomyces* spp. was conducted in Bali, Indonesia, in January 2000 (rainy season: Nov.–Feb.). One species of *Termitomyces* was collected from two sites, located approximately 100 m from each other, in a community forest near a banana orchard. A second species of *Termitomyces* was collected from another two sites, located about 20 m apart, in a bamboo grove near an agricultural field. The termites were collected from their respective fungus gardens. The genera and species of the termites were determined from their morphological characteristics using systematic keys (Ahmad, 1965; Morimoto, 1973; Tho, 1992; Sornnuwat *et al.*, 2004). The fruiting bodies that developed in the fungus gardens were identified at the species level based on their macroscopic and microscopic characteristics (Imazeki and Hongo, 1995; Pegler and Vanhaecke, 1994). The sizes and shapes of the fungus combs and chambers were analyzed in detail. The specimens used in this study have been deposited in the herbarium of the Field Science Center for Northern Biosphere of Hokkaido University.

RESULTS AND DISCUSSION

We observed *T. eurhizus* associated with *O. feae* and *T. striatus* associated with *A. pakistanicus* (Ahmad, 1965; Morimoto, 1973; Pegler and Vanhaecke, 1994; Imazeki and Hongo, 1995; Sornnuwat *et al.*, 2004). Aanen *et al.* (2007) reported that the specificity of the interaction between fungus-growing termites and *Termitomyces* symbionts was high at the genus level but generally much lower at the species level. In particular, high mutual specificity was found for individual species of *Macrotermes* such as *M. natalensis*. In comparison, three species of the genus *Odontotermes* showed low symbiont specifi-

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city. Thus, there appears to be greater variation at the species level among termite and *Termitomyces* symbionts in nature.

Both *T. eurhizus* and *T. striatus* are widely distributed throughout Southeast Asia and Africa (Alasoadura, 1966; Bels and Pataragetvit, 1982; Dixon, 1983; Pearce, 1987; Van Der Westhuizen and Eicker, 1990; Sornnuwat *et al.*, 2004). *Odontotermes feae* associated with *T. eurhizus* constructed at least two and eight underground fungus chambers, respectively (Fig. 1 A, D). Four fungus chambers from one *T. striatus* fungus garden were observed, one of which consisted of five chambers (Fig. 1 G). The chambers were connected by underpasses, and most contained a fungus comb (Fig. 1 D, I).

The fungus chambers of *O. feae* associated with *T. eurhizus* were 10–17 cm tall and 15.5–29 cm wide, whereas those of *A. pakistanicus* associated with *T. striatus* were 2.5–5.5 cm tall and 2.8–9 cm wide. The largest fungus comb of *T. eurhizus* was 14 cm tall and 22 cm wide, whereas that of *T. striatus* was 3 cm tall and 5 cm wide. On the other hand, the smallest fungus combs contained a portion of what the termites had eaten in the fungus chambers of *T. eurhizus* and *T. striatus*.

The fungus combs of *T. eurhizus* associated with *O. feae* and *T. striatus* associated with *A. pakistanicus* were categorized into two types. The first was covered with whitish mycelia and formed primordia or a fruiting body, while the second was brown or greenish-brown with white to brown round structures, called fungus nodules, in the upper or entire comb (Fig. 1 B, H, J, and K). This second, novel type (Bels and Pataragetvit, 1982; Sagara, 2000) was characterized by a lack of primordia or fruiting bodies. In addition, the sizes of the fungus combs for both species were nearly equal to the sizes of the fungus chambers; thus, there were few openings between the fungus combs and chambers. In this study, the fungus combs that formed primordia or a fruiting body showed signs of being eaten by the termites, with remains of combs found at the bottom of the chamber (Fig. 1 C). Because of this, the gardens became smaller and showed evidence of eating, with a wide space at the top of the fungus chamber.

The maximum number of primordia formed from one *T. eurhizus* fungus comb was 65. The primordia were cylindrical to bulbous in shape (Fig. 1 E) and measured 1.3 cm tall and 0.6–1.7 cm in diameter at the widest part, with a 0.6 cm diameter at the base. The mature upper portions of the primordia were blackish and covered with a hard tissue composed of burnished and crustose mycelia; the tissue was destroyed and removed by the eating behavior of the termite workers. Such destructive behavior was observed two times on a single primordium (Fig. 1 F) and indicates that the eating behavior of the termites suppressed fruiting-body formation from the fungus combs. Similarly, leaf-cutting ants have been observed to actively suppress symbiont fruiting by eating the tops of young fruiting bodies in lab colonies (Muller, 2002). *Termitomyces eurhizus* is characterized by pseudorhizae, the surfaces of which are black and hard (Pegler and Vanhaecke, 1994) (Fig. 1 B, C).

Therefore, it is believed that pseudorhizae and fruiting bodies form outside of the chamber if a black-tipped primordium is placed on the fungus chamber. At the same time, the termites associated with *T. eurhizus* seem to control *T. eurhizus* fruiting-body growth by intentionally removing the black tips from the primordia so that they cannot become pseudorhizae, and thus suppress the formation of a fruiting body from the fungus combs. However, when the black tip of the primordium reaches the wall of the chamber, it cannot be destroyed by the workers and the primordium becomes a fruiting body on the ground.

On the other hand, Dixon (1983) reported that fungus combs of *T. striatus* bearing primordia were not actively torn down by termites during the dry season; however, after the fungus gardens were flushed with rain, the remaining aborted primordia and the mass of the fungus combs were actively reduced by the termites. In this study, mature primordia were observed in the fungus gardens of *A. pakistanicus* associated with *T. striatus*, but there was no sign that workers destroyed the tops of the primordia that were about to become fruiting bodies, as was observed for *T. eurhizus*. However, there were signs that the termites had aggressively eaten those parts of the pseudorhizae corresponding to the parts of the mature fruiting bodies that had leaked into the fungus chambers (Fig. 1 J, K).

The surface of the *T. striatus* pseudorhiza, which was extremely wide and bulky relative to the size of the fungus garden, was soft and white. The *T. striatus* primordium was conical in shape (0.5 cm tall and 0.7 cm in diameter at the bottom) when it swelled. The head of each primordium became the cap of the mature fruiting body (Fig. 1 J). One to ten primordia were observed in each fungus comb, but only one or two mature basidiomes were observed in each comb. These observations suggest that the termites associated with *T. striatus* use not only the fungus combs but also the fruiting bodies, including the pseudorhizae, as food. They likely prefer the mycelium, including the fruiting bodies, rather than the lignin produced by *T. striatus* from plant debris. There are several possible reasons for this. First, the tips of the primordia of *T. striatus* were not destroyed by the termites as was the case for *T. eurhizus*. Instead, the termites allowed the primordia to develop fruiting bodies for food. Second, the mature pseudorhizae of the fruiting bodies were aggressively eaten.

Without *Termitomyces*, termites cannot maintain their nests and they die (Dixon, 1983). Other reports have shown that termites eat their fungus gardens when they have difficulty finding food outside of the nest. Thus, fungus combs are an important food source for termites. On the other hand, the results of this study suggest that termites control or suppress the growth of fruiting bodies from *T. eurhizus* fungus combs. Previous studies have shown that a change in the nutrients, such as lignin or cellulose, contained in a *T. microcarps* fungus garden occurs before and after the growth of fruiting bodies in the fungus combs (Rohrman, 1987; Side Gowda and Rajagopal, 1990; Botha and Eicker, 1992). This loss

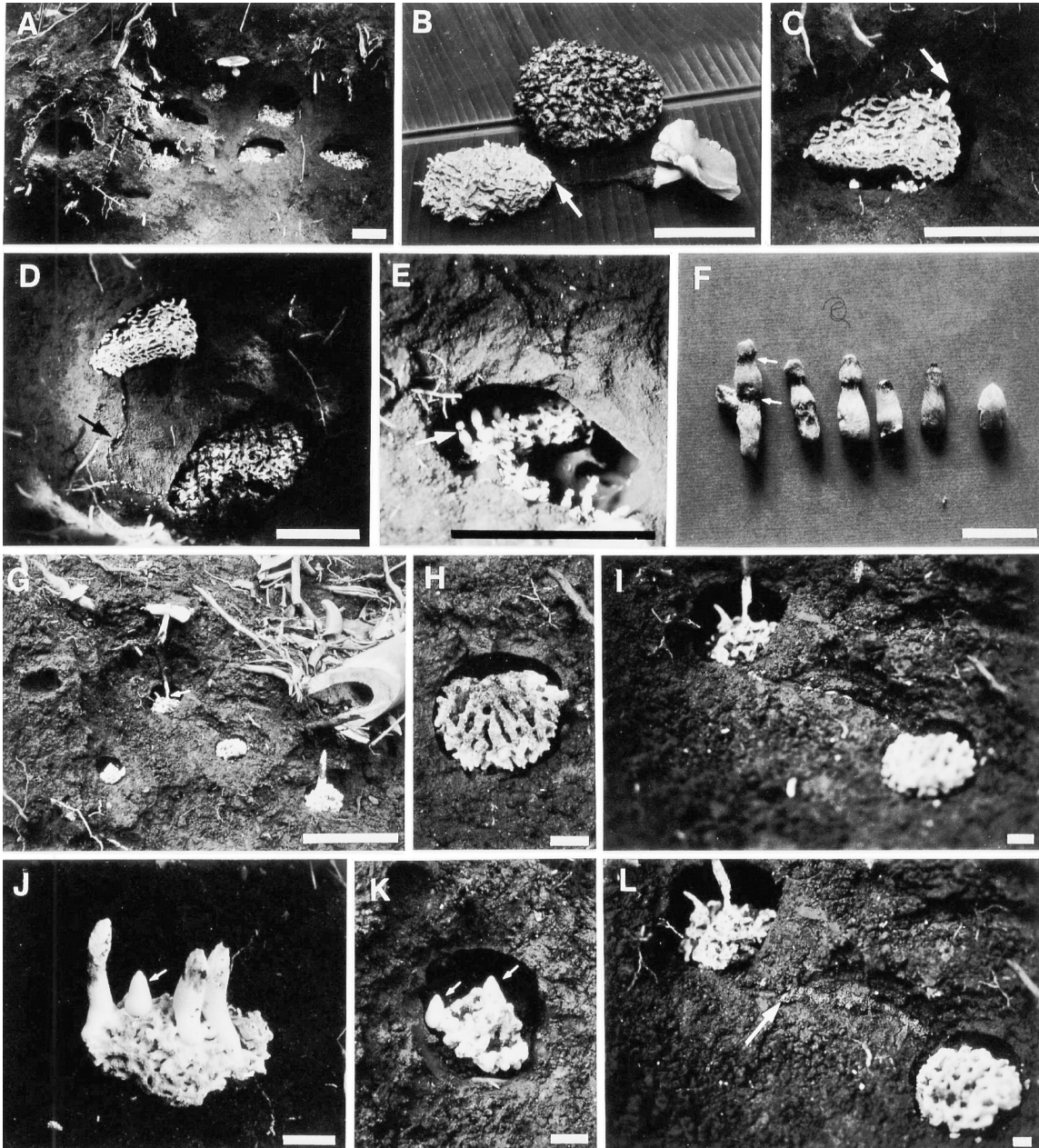


Fig. 1. *T. eurhizus* (A–F): A, A fruit body of *T. eurhizus* grown from a fungus comb; fungus combs in which primordia grew and did not grow (arrow). B, Fungus combs in which primordia and fruit body grow are grayish white (bottom, arrow: blackish tip of primordium with pseudorhiza), and those without primordia and fruit body formation are blackish brown or greenish brown and have brown projections, which are called nodules or termite excrement (above). C, A wide space at the bottom of chamber. A black and hard pseudorhiza that extends from a primordium (arrow). This black primordium tip reaches the wall of the nest. It seems that it was therefore not eaten by termites and grew to become a fruit body. D, Two-fungus chambers connected with underpass (arrow). Termites frequently commute through the underpass that connects fungus chambers. Shown are fungus combs that are actively being made by termites (bottom). E, Primordia formed in a fungus comb. F, Mature primordia have black tips and start to grow pseudorhiza, but they cannot become fruit bodies because the termites eat only black parts (arrow). They are sometimes eaten in two stages, resulting in the divergence of the primordia. No blackish primordia tip showed on the immature primordium (right). *Termitomyces striatus* (G–L): G, A fruit body of *T. striatus* formed in the fungus comb, and the base of the pseudorhiza of a mature fruit body made thin by eating (arrow). H, Without primordia or fruit bodies are blackish brown or greenish brown and have brown projections. J, K, Fungus combs in which fruit body or/and primordia growth are covered with whitish hypha. Pseudorhiza of *T. striatus* eaten by termites and a primordium that was not ate (arrow), the base of which is swollen due to growth. I, L, Destroyed underpass (I) being reconstructed by termites using surrounding soils (L, the arrow indicates the soldier of *A. pakistanicus*). Above fungus comb is production of fruit body. This behavior for termites shows that a fungus comb is a food factory and they protect it vigorously. Bar, 1 cm: F, H, I, J, K, L; 10 cm: A, B, C, D, E, G.

of nutrients during the growth of the fruiting bodies is believed to be damaging to termites. One reason for the absence of *Termitomyces* mushrooms on *M. natalensis* mounds may be that *M. natalensis* workers actively suppress the fruiting of their symbiont, which is a waste of resources for the termites (Aanen, 2006). On the other hand, in the case of *T. striatus*, the termites cultivated the fruiting bodies for use as part of their food supply. Although the behavior of *O. feae* and *A. pakistanicus* toward fungus combs is different, the goal of keeping and growing mycelial masses is the same. Hyodo *et al.* (2003) suggested that symbiotic fungi play different roles among fungus-growing termites. In *Macrotermes* spp., the main role of symbiotic fungi is to degrade lignin so that the termites can utilize cellulose more efficiently, whereas in *Odontotermes* spp., *Hypotermes makhamensis*, *A. pakistanicus*, and *Pseudacanthotermes militaris*, the main fungi role is to serve as a food source. Our results for *O. feae* and *A. pakistanicus* support the findings of previous studies.

Our results for *Termitomyces* indicate that termites strictly manage their fungus gardens as food factories. This finding contradicts Dixon's (1983) report on *T. striatus*, which showed that fruiting bodies grow from fungus combs after the termites desert their nests. This is supported by the fact that when an underpass connecting nests containing fungus combs of *T. striatus* was deliberately destroyed, the workers immediately reconstructed the pass within 10–20 min using soil (Fig. 1 I, L). Several termites were observed working in new fungus gardens with *T. eurhizus* and *T. striatus*, but there were only a few in fungus chambers containing combs in which primordia and fruiting bodies were growing. Thus, while most termites are dedicated to the construction of a new fungus garden, a few are engaged in managing the fungus garden as a food factory.

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