Fungal Ecology 60 (2022) 101178

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

Low temperature enhances the ability of the termite-egg-mimicking fungus *Athelia termitophila* to compete against wood-decaying fungi

Yasuyuki Komagata [a], Yu Fukasawa [b], Kenji Matsuura [a,*]

[a] Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwakecho, Kyoto, 606-8502, Japan
[b] Laboratory of Forest Ecology, Graduate School of Agricultural Science, Tohoku University, Naruko, Osaki, Miyagi, 989-6711, Japan

ARTICLE INFO

Corresponding Editor:Peter H.W. Biedermann

Keywords:
Insect–fungal interactions
Termite
Termite ball
Basidiomycota
Wood-decay fungi
Athelia termitophila
Mycelial interactions
Sclerotia

ABSTRACT

A unique symbiosis exists between subterranean termites and the sclerotium-forming fungus *Athelia termitophila*, which forms termite-egg-mimicking sclerotia called 'termite balls'. While the sclerotia gain a competitor-free habitat by being harboured by termite eggs, *A. termitophila* mycelia have to compete with wood-decay fungi in the life stage without termites. To understand its relationship with termites, the factors that affect the ability of *A. termitophila* to compete with other wood-decay fungi must be clarified. Here, we show that *A. termitophila* is competitive against other wood-decay fungi at low temperatures. In Petri dish experiments to evaluate the effects of the physicochemical conditions, that *A. termitophila* experiences in termite nests, on its competitive ability, *A. termitophila* overcame surrounding fungi in the winter, when termites are less active. Further studies quantifying the effects of *A. termitophila* on termites in winter will help us to understand this relationship.

1. Introduction

The relationships between insects and fungi range from mutualistic to antagonistic (Hajek and St. Leger, 1994; Vega and Blackwell, 2005). The degree of dependence on insects in the fungal life cycle also varies. *Athelia termitophila* (Atheliaceae, Agaricomycetes, Basidiomycota) forms a relationship with subterranean termites of the genera *Reticulitermes* and *Coptotermes* by mimicking termite eggs (Matsuura et al., 2000; Matsuura and Yashiro, 2010; Ye et al., 2019), while little is known of its life stage independent of termites. Understanding the termite-free life stages is essential for a proper understanding of the relationship between termites and this fungus.

Athelia termitophila is a wood-decaying fungus that forms sclerotia mimicking a termite egg called a 'termite ball' (TMB hereafter; Fig. 1A). These are frequently observed in egg piles in termite nests (Matsuura, 2005; Matsuura et al., 2000; Nagy et al., 2016; Yashiro and Matsuura, 2007). By mimicking termite eggs chemically and physically, this fungus successfully enters termite nests to the extent that, in some colonies, there are more sclerotia in the egg pile than termite eggs (Matsuura, 2006; Matsuura et al., 2000, 2009) (Fig. 1B). The TMBs within the egg piles are frequently groomed by workers, as are termite eggs, to protect them from dryness and pathogens (Matsuura, 2006; Matsuura et al., 2000). Once in a termite nest, *A. termitophila* achieves a competitor-free environment through egg mimicry, avoiding the substantial time and energetic costs of grooming (Matsuura, 2006). In addition, TMBs may germinate and absorb the surrounding eggs when the percentage of TMBs in the egg pile becomes too high to be groomed by workers (Matsuura, 2006). Therefore, in this relationship, *A. termitophila* is considered parasitic (Matsuura, 2006). While *A. termitophila* is frequently detected in mature termite colonies (Matsuura, 2005; Yashiro and Matsuura, 2007), its route to new termite colonies remains unknown. Although alates may carry spores (Matsuura et al., 2000), spore formation has rarely been confirmed (Maekawa et al., 2020) and no TMB has been observed in the egg piles of incipient termite colonies (Matsuura, 2005). Therefore, *A. termitophila* may have another life stage independent of termites (Maekawa et al., 2020; Matsuura, 2005). Indeed, *A. termitophila* has also been isolated from wood and locations unrelated to termites such as shiitake bedlog of *Quercus serrata* and dead wood of broad-leaved trees on Mt. Chokaisan, Akita Pref., which is too cold for termites to inhabit (Maekawa et al., 2020). Basidiomes of *A. termitophila* have been observed in the field in seasons with lower temperatures (3.9°C–17.5 °C), whereas sclerotia were produced at 15 °C-30 °C on MA media (Maekawa et al., 2020). This suggests that the temperatures suitable for sclerotium formation and basidiome formation of

* Corresponding author.
E-mail address: matsuura.kenji.6s@kyoto-u.ac.jp (K. Matsuura).

https://doi.org/10.1016/j.funeco.2022.101178
Received 13 January 2022; Received in revised form 8 June 2022; Accepted 12 June 2022
Available online 25 June 2022

A. termitophila are different. We consider that TMBs, i.e., sclerotia produced in termite nests, play an important role in the survival strategy of *A. termitophila* during summer when the fungus is not able to form basidiomes. Characterisation of this fungus under conditions without termites is important for estimating the degree of dependence of *A. termitophila* on termites.

If *A. termitophila* had another life stage independent of termites, the fungus would have to compete with surrounding wood-decaying fungi for resources and space. Various environmental variables affect the competitive relationships among fungi (Boddy, 2000), so the specific environmental parameters that *A. termitophila* experiences in termite nests may affect its ability to compete with surrounding fungi. During the warm season, when termites are active, a specific physicochemical environment is created within termite-colonised deadwood. For example, the air in termite nests has less oxygen and more carbon dioxide than that in termite-free deadwood (Tasaki et al., 2020), and specific pheromones are released by the queen (Matsuura et al., 2010) and soldier caste (Mitaka et al., 2017). Queen and soldier pheromones affect the mycelial growth of *A. termitophila* (Matsuura and Matsunaga, 2015; Mitaka et al., 2017). During the cold season, termite activity declines and most termites burrow underground (Fig. 1C). During this period, there are no eggs in termite nests (Matsuura et al., 2007) and the TMBs are not groomed by workers. New TMBs form in termite-infested wood when the termites move underground in winter (Fig. 1C). If *A. termitophila* is highly cold-tolerant, it might be able to compete with surrounding wood-decaying fungi as mycelia to obtain resources in termite-colonised deadwood.

In this study, we performed a competition experiment to evaluate the effects of termite nest gas, termite queen and soldier pheromones, and low temperature on the ability of *A. termitophila* to compete with four wood-decaying fungi commonly found in *Pinus densiflora* deadwood.

2. Material and methods

2.1. Fungal strains

The ability of *A. termitophila* strains TMB-I (culture collection at Kyoto University: TK160513) and TMB-II (UR160523), collected from termite nests in rotten *P. densiflora* wood in Kyoto, Japan, to compete with other wood-decaying fungi was tested. Another strain TMB-III (culture collection at Kyoto University: MY211102) was collected from termite nests in rotten *P. densiflora* wood in Miyagi, Japan for hyphal growth experiment. The strains were isolated following the method of Mitaka et al. (2017): briefly, sclerotia collected from termite colonies were washed with sterile water and cultured on potato dextrose agar (PDA; Difco Laboratories) containing 4 ppm benzimidazole after field collection. The subterranean termite *Reticulitermes speratus* nesting in pine deadwood always harbour TMBs in egg piles (Matsuura et al., 2000). Therefore, four species of wood-decaying fungi isolated from *P. densiflora* deadwood (Fukasawa, 2018) were used as competitors: *Cryptoporus volvatus* (*C.v*; NBRC no. 110166), *Trichaptum abietinum* (*T.a*; NBRC no. 110190), *Fomitopsis pinicola* (*F.p*; NBRC no. 110169), and *Neolentinus suffrutescens* (*N.s*; NBRC no. 110181). All fungal cultures were maintained on PDA at 25 °C until they were used for the competition experiment.

2.2. Competition experiment

Five-mm-diameter mycelial discs were cut from the growing margin of 4-week-old cultures of *A. termitophila* and one of the four competing fungi on PDA using a sterilised cork borer, and inoculated upside-down onto the center of a newly prepared PDA plate (20 mm apart) (Fig. 2A). To test the effect of temperature on competition, the dishes were incubated at 5 °C and 25 °C in the dark for 6 weeks. To test the effect of atmosphere regimes, the dishes were incubated under conditions mimicking a termite nest (16.6% O_2 and 4.9% CO_2) and ambient air (20.5% O_2 and 0.04% CO_2) in a multi-gas incubator (9000EX; Waken B Tech) at 25 °C for 6 weeks (Tasaki et al., 2020). To test the effect of queen pheromone, a mixture of 5 μL of the pheromone component (2:1 nBnB:2M1B) and 15 μL of hexane was dropped on a 1 cm square of filter paper. For the soldier pheromone treatment, 20 μL of one individual equivalent of the soldier pheromone component, (−)-β-elemene (1 μg/μL) was dropped onto a 1 cm square of filter paper (Mitaka et al., 2017). The pheromone solutions were dropped onto the filter paper in glass Petri dishes on a clean bench. After 5 min (to allow the hexane to volatilise), the filter papers were placed on a 20 × 25 mm glass slide, in turn placed on PDA medium in the Petri dish (Fig. 2B). Control dishes were prepared without pheromones, but with hexane. The dishes were incubated for 6 weeks in the dark at 25 °C. Ten replicates were set up for each combination and treatment. The results of mycelial interactions were recorded as the replacement of one mycelium by another, or deadlock, where neither mycelium gained territory from the other, following (Boddy, 2000).

2.3. Effect of temperature on colony growth

To examine the effect of temperature on hyphal growth of *A. termitophila* in comparison with other wood-decaying fungi, the hyphal growth of TMB-III (MY211102) at different temperature conditions (5, 15, 25 and 35 °C) were measured following the method of Fukasawa (2018): 4 mm-diam hyphal plugs of TMB-III cultured in malt extract agar (MA) plate were cut using a sterilised cork borer and placed at the center of the MA plate in a 9 cm-diam Petri dish. The plates were incubated at either 5, 15, 25 or 35 °C under the dark. Five replicates were made for each temperature. After five days, the radial growth of each fungal colony was measured. The data of TMB-III was compared with that of *C.v*

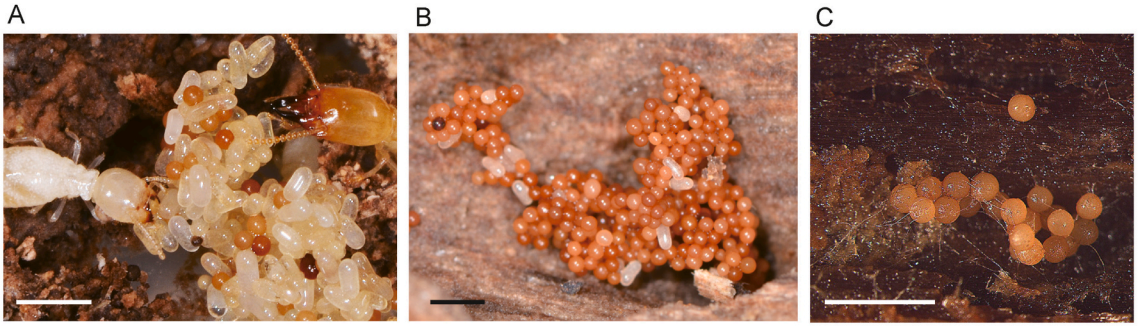

Fig. 1. Termite balls in the nest of a subterranean termite, *Reticulitermes speratus*. (A) Termite balls in an egg pile in July (summer). The termite eggs are transparent and oval, whereas termite balls are brown and spherical. (B) Termite balls in an egg pile in September (early autumn). The egg production season is over and most of the eggs have hatched, leaving only termite balls in the egg pile. (C) Termite balls formed in a *R. speratus* nest in February (winter). Most termites move from aboveground to underground in winter, and the termite balls left in the nest germinate and grow. The scale bars represent 2 mm.

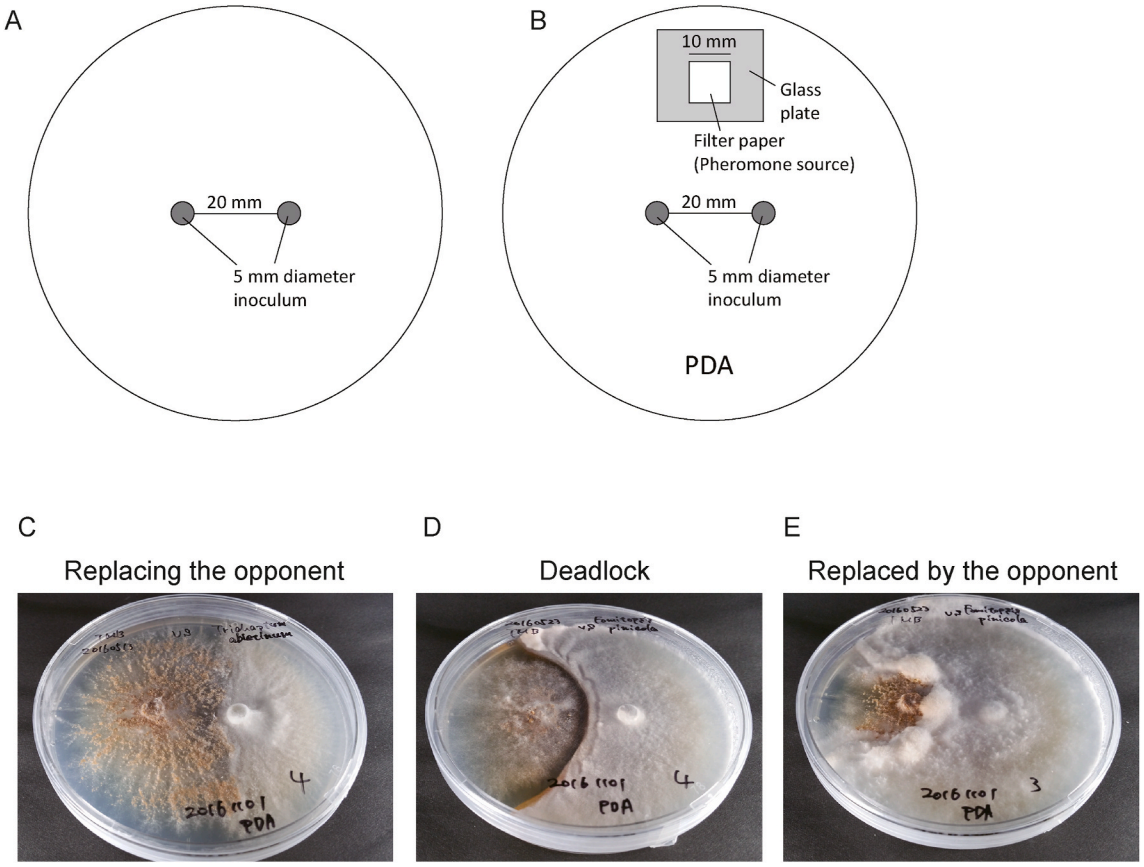

Fig. 2. Experimental set-up of the competition experiments. (A) One of the TMB strains and one of the four basidiomycete species were incubated at 5 °C or 25 °C, or under the gaseous conditions mimicking a termite nest, or (B) under termite queen pheromone, soldier pheromone, or hexane-only (control) conditions. The results of the mycelial competition were classified into three categories: (C) replaces the opponent, (D) deadlock, and (E) replaced by the opponent.

(NBRC no. 110166), *T.a* (NBRC no. 110190), *F.p* (NBRC no. 110169), and *N.s* (NBRC no. 110181) reported in the previous study (Fukasawa, 2018).

2.4. Data analysis

The frequencies of the interaction outcomes between *A. termitophila* and wood-decaying fungi were compared between treatments using Fisher's exact probability test. The results for the two *A. termitophila* strains were analysed statistically.

The hyphal growth of TMB-III at each temperature was compared with the data of the other four wood decaying fungi collected by Fukasawa (2018). The generalized linear model (GLM) with Gaussian distribution was used to examine the effect of species, temperature and their interaction on hyphal growth. For each temperature condition, the significance of differences between the hyphal growth of the five species were determined by Tukey's Honestly Significant Difference (HSD) test at a significance level of $p < 0.05$. All analyses were performed in R version 4.1.3 (R Core Team, 2022).

3. Results

At low temperature (5 °C), the competitiveness of TMB against other fungi was significantly increased compared to the control condition (25 °C) (Fisher's exact test; TMB-I *vs. C.v*, $p = 0.003$; TMB-II *vs. C.v*, $p = 0.003$; TMB-I *vs. F.p*, $p < 0.001$; TMB-II *vs. F.p*, $p < 0.001$; TMB-I *vs. N.s*, $p < 0.001$; TMB-II *vs. N.s*, $p < 0.001$; Fig. 3), except against *T.a* (TMB-I *vs. T.a*, $p > 0.05$; TMB-II *vs. T.a*, $p = 0.474$). In the nest gas condition (O_2: 16.6% and CO_2: 4.9%), the competitiveness of TMB against *F.p* and *N.s* was significantly reduced (TMB-I *vs. F.p*, $p = 0.003$; TMB-II *vs. F.p*, $p = 0.011$; TMB-I *vs. N.s*, $p = 0.023$; Fig. 3).

Queen pheromone negatively affected the competitiveness of TMB-II against *F.p* (TMB-II *vs. F.p*, $p = 0.003$), but had no effect on TMB-I (TMB-I *vs. F.p*, $p > 0.05$; Fig. 4). Soldier pheromone also negatively affected the competitiveness of TMB-II against *F.p* (TMB-II *vs. F.p*, $p = 0.020$), but had no effect on TMB-I (TMB-I *vs. F.p*, $p > 0.05$; Fig. 4). Neither queen nor soldier pheromone had any effect on the competitiveness against *C. v*, *T.a*, or *N.s* (Fig. 4).

The effects of temperature, fungal species, and their interaction were significant for hyphal growth (likelihood ratio test, temperature: $\chi^2 = 29.36$, $p < 0.001$; species: $\chi^2 = 18.82$, $p < 0.001$; temperature × species: $\chi^2 = 17.55$, $p = 0.0015$). Under low temperature condition (5 °C), hyphal growth of TMB was significantly greater than that of other fungi ($p < 0.001$, Tukey's HSD, Fig. 5). At 25 °C, which is the optimum growth temperature for all fungi, hyphal growth of TMB was significantly less than that of other fungi ($p < 0.001$, Tukey's HSD). Under high temperature condition (35 °C), hyphal growth of TMB and *T. abietinum* were significantly less than that of *C. volvatus*, *F. pinicola*, and *N. suffrutescens* ($p < 0.001$, Tukey's HSD), while no significant difference between TMB and *T. abietinum* ($p = 0.974$, Tukey's HSD, Fig. 5).

4. Discussion

This study suggests that low temperatures have a strong positive effect on the competitive ability of *A. termitophila* against other wood-decaying fungi. In the competition experiment, *A. termitophila* invariably replaced the opponents at 5 °C (Fig. 3). This result is consistent with the results of the hyphal growth experiment, in which only *A. termitophila* was able to grow at 5 °C, while the other fungi were unable to grow at all (Fig. 5). *A. termitophila* tends to be superior to *C. volvatus* and *T.*

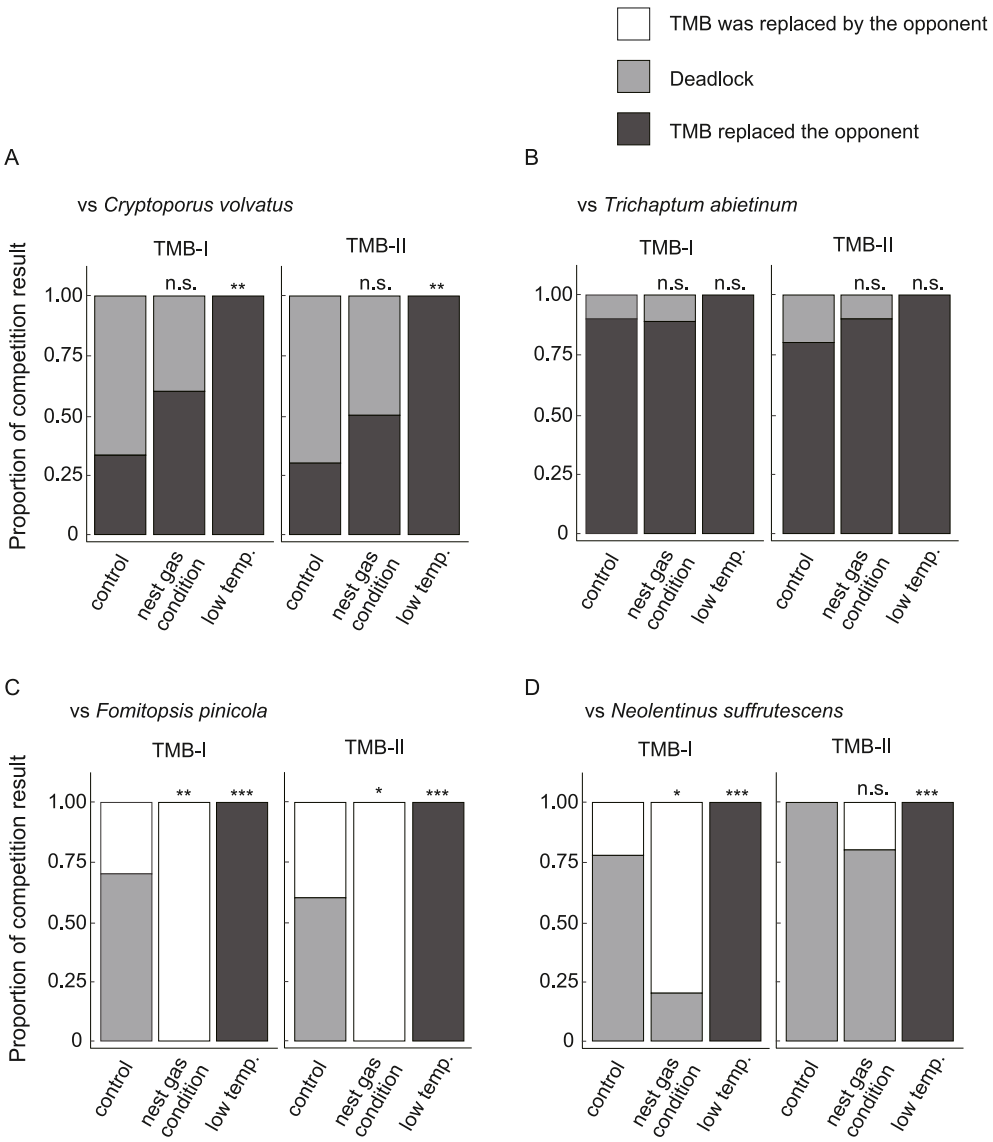

Fig. 3. Effects of gas and temperature conditions on the competitiveness of TMB. The four basidiomycetes are used as competitors of *Athelia termitophila* strains (TMB-I and II): (A) *Cryptoporus volvatus*; (B) *Trichaptum abietinum*; (C) *Fomitopsis pinicola*; and (D) *Neolentinus suffrutescens*. Control: incubated at 25 °C under ambient gaseous condition (20.5% O_2 and 0.04% CO_2). Nestgas condition: incubated at 25 °C under gaseous conditions mimicking termite nests (16.6% O_2 and 4.9% CO_2). Low temp.: incubated at 5 °C under ambient gaseous conditions. Ten replications were made for each treatment. Asterisks indicate that the mycelial interaction was significantly different from the control (Fisher's exact test, n.s. $p > 0.05$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

abietinum at 25 °C, which suggests that *A. termitophila* outcompetes some wood-decaying fungi for habitat and resources during the warm season. However, deadlock was observed in all combinations, and *A. termitophila* tended to be inferior to *N. suffrutescens* and *F. pinicola* at 25 °C (Fig. 3). In the hyphal growth experiment, the growth of *A. termitophila* was inferior to that of any other fungus at 25 °C (Fig. 5). Therefore, *A. termitophila* is highly dependent on termites for avoiding unfavourable competition during the warm season. The benefits obtained during this period may be so great that they are frequently detected in termite nests.

In *Reticulitermes speratus* nests, no eggs were observed in winter (Matsuura et al., 2007), so *A. termitophila* sclerotia were inevitably left behind. In such situations, *A. termitophila* cannot obtain habitat and resources without defeating other wood-decaying fungi. The strong cold tolerance of *A. termitophila* should facilitate the capture of organic resources, resulting in the high observation rate in mature termite nests (Matsuura, 2005). *A. termitophila* is often found in termite nests in temperate regions, but not in subtropical regions (Yashiro and Matsuura, 2007). This might be because *A. termitophila* cannot overcome other fungal species inside the termite nests in winter due to the relatively high temperatures in subtropical regions. A related species, *Athelia arachnoidea*, is a phytopathogen that becomes aggressive at low temperatures (Yurchenko and Golubkov, 2003), and the ancestral *A. termitophila* strain may also have been very cold-tolerant. Cold tolerance likely functioned as a pre-adaptive trait, and some of the sclerotia that formed from the resources acquired during the cold season were selected for termite egg recognition, resulting in strains with smooth structures that closely resemble termite eggs (Matsuura, 2006). *A. termitophila* may also have a competitive advantage due to its high relative abundance in the termite colony when the termites become inactive. At this time many TMBs are present in the nest and can germinate in order to colonize part of the nest wood before other fungi enter the nest.

The queen and soldier pheromones had a negative effect on *A. termitophila* in competition with *F. pinicola*. Queen pheromones inhibit *A. termitophila* mycelial growth (Matsuura and Matsunaga, 2015), and this might also have a negative effect on competitive abilities. Although the soldier pheromone promoted *A. termitophila* growth in monoculture (Mitaka et al., 2017), it did not enhance its competitiveness against other fungi in this study. It may be that, when competing with certain unfavourable fungi, *A. termitophila* shifts from active growth tactics to endurance tactics in termite nests.

The gas composition mimicking termite nests had a negative effect on *A. termitophila* in competition with *F. pinicola* and *N. suffrutescens*. Gas composition influences interspecific competition between wood-decaying fungi (Chapela et al., 1988). In deadwood, it is assumed that gas composition is not identical between sapwood and heartwood, where the heartwood, with its dense tissues, becomes more hypoxic

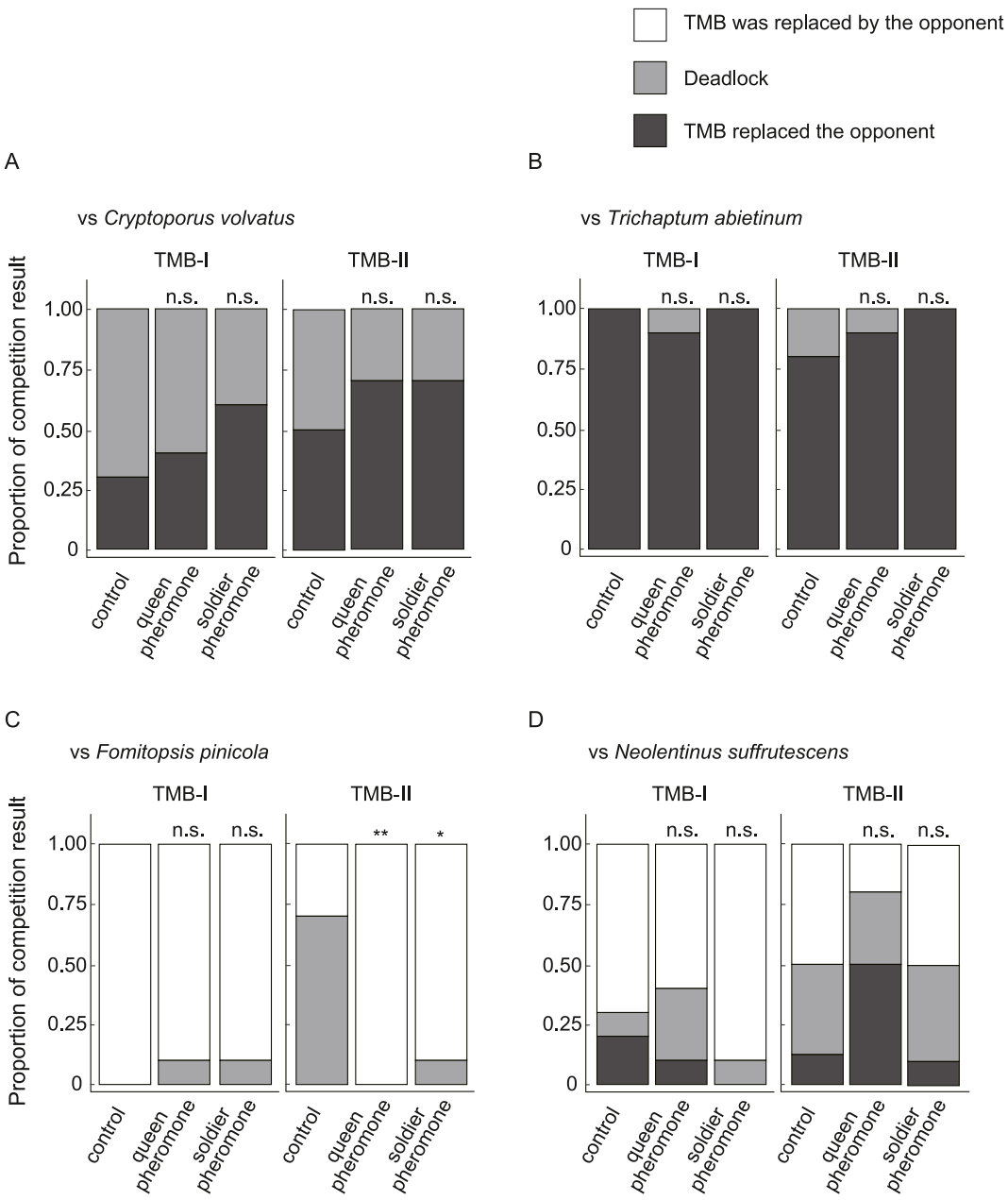

Fig. 4. Effects of termite pheromones on the competitiveness of TMB. Four basidiomycetes were used as competitors of *Athelia termitophila* strains (TMB-I and II): (A) *Cryptoporus volvatus*; (B) *Trichaptum abietinum*; (C) *Fomitopsis pinicola*; and (D) *Neolentinus suffrutescens*. Control: incubated with hexane only at 25 °C under the ambient gas condition. Queen pheromone: incubated with termite queen pheromone compounds (2:1 nBnB:2M1B) at 25 °C under the ambient gas condition. Soldier pheromone: incubated with the termite soldier pheromone compound (−)-β-elemene at 25 °C under the ambient gas condition. Ten replications were made for each treatment. Asterisks indicate that the result of mycelial interaction differed significantly from the control (Fisher's exact test, n.s. $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

because gas exchange is less likely. Both *F. pinicola* and *N. suffrutescens* are heartwood-decaying fungi (Table 1), so they may have become competitive against *A. termitophila* under hypoxic conditions.

The competitive relationships among fungal species observed in media tend to represent fungal community succession during wood decomposition (Boddy, 2000). Since *C. volvatus* and *T. abietinum* are found in the early to middle decay stages, while *F. pinicola* and *N. suffrutescens* are found in the middle to late decay stages (Table 1), *A. termitophila* might be found in deadwood classified as early to middle decay classes, even without termites. The results of the competition experiment suggest that *A. termitophila* adapts not to the physicochemical characteristics of termite nests, but rather to the low temperature when termites become inactive. Therefore, *A. termitophila* may have a life stage in which it actively competes with other wood-decaying fungi to obtain resources in deadwood during the cold season, and escapes competition with other fungi by mimicking eggs during the warm season, when termites begin to lay eggs.

Curiously, termite colonies invaded by *A. termitophila* are common, despite the substantial time and energetic costs (Matsuura, 2006). We speculate that *A. termitophila* conquers not only wood-decaying fungi, but also entomopathogenic fungi during the cold season. If the ability of *A. termitophila* to conquer entomopathogens at low temperature is verified, it would suggest a seasonal benefit for termites. That is, during the warm season, termites protect *A. termitophila* from competition with surrounding wood-decaying fungi, while during the cold season, when termites burrow underground, *A. termitophila* excludes termite

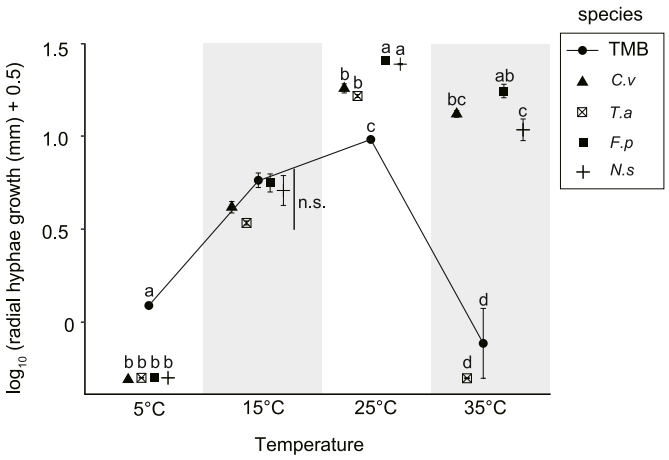

Fig. 5. Comparison of hyphal growth of TMB and other wood-decaying fungi under different temperature conditions. The growth data of *Athelia termitophila* (TMB-III) was compared to the data of other wood-decaying fungi (*C.v*: *Cryptoporus volvatus*; *T.a*: *Trichaptum abietinum*; *F.p*: *Fomitopsis pinicola*; *N.s*: *Neolentinus suffrutescens*) from the previous study Fukasawa (2018). All fungal strains were isolated from rotten *P. densiflora* wood. A base-10 log scale was used for the Y-axis, facilitating the visualization of the difference at low temperature. Different letters denote significant difference at each temperature (Tukey HSD test, $p < 0.05$). Error bar indicate the log (mean + 0.5) ± standard error (TMB, n = 5; *C.v*, *T.a*, *F.p*, and *N.s*, n = 3).

Table 1
Fungal species used in the competition experiment with *A. termitophila*. Decay class indicates the decay stage of logs when the fungi were observed in a five-decay class system (I, least decayed; V, most decayed). Position indicates the dominant wood, either sapwood (Sap) or heartwood (Heart).

Fungal species	Decay class	Position	Reference
Cryptoporus volvatus	I	Sap	Fukasawa et al. (2015)
Fomitopsis pinicola	II, III	Heart	Deflorio et al. (2008), Ovaskainen et al. (2013)
Neolentinus suffrutescens	III, IV	Heart	Fukasawa et al. (2015)
Trichaptum abietinum	I, II, III	Sap	Fukasawa et al. (2015)

pathogens from the nest due to its strong cold tolerance. Further studies of the dynamics of the microbial community in termite nests throughout the year will help us to better understand the relationship between termites and *A. termitophila*.

Declaration of competing interest

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

Acknowledgement

We thank S. Dobata, N. Mizumoto, T. Inagaki, M. Takata, and other members of the Laboratory of Insect Ecology, Kyoto University for helpful discussions and technical advice. This work was supported by the Japan Society for the Promotion of Science (JSPS) KAKENHI grants (Kiban Kenkyu S: No.18H05268 and Challenging Research (Pioneering): 18H05372) to KM.

References

Boddy, L., 2000. Interspecific combative interactions between wood-decaying basidiomycetes. FEMS Microbiol. Ecol. 31, 185–194.
Chapela, I.H., Boddy, L., Rayner, A.D.M., 1988. Structure and development of fungal communities in beech logs four and a half years after felling. FEMS Microbiol. Ecol. 4, 59–69.
Deflorio, G., Johnson, C., Fink, S., Schwarze, F.W.M.R., 2008. Decay development in living sapwood of coniferous and deciduous trees inoculated with six wood decay fungi. For. Ecol. Manag. 255, 2373–2383.
Fukasawa, Y., 2018. Temperature effects on hyphal growth of wood-decay basidiomycetes isolated from *Pinus densiflora* deadwood. Mycoscience 59, 259–262.
Fukasawa, Y., Takahashi, K., Arikawa, T., Hattori, T., Maekawa, N., 2015. Fungal wood decomposer activities influence community structures of myxomycetes and bryophytes on coarse woody debris. Fungal Ecol. 14, 44–52.
Hajek, A.E., St Leger, R.J., 1994. Interactions between fungal pathogens and insect hosts. Annu. Rev. Entomol. 39, 293–322.
Maekawa, N., Yokoi, H., Sotome, K., Matsuura, K., Tanaka, C., Endo, N., Nakagiri, A., Ushijima, S., 2020. *Athelia termitophila* sp. nov. is the teleomorph of the termite ball fungus *Fibularhizoctonia* sp. Mycoscience 61, 323–330.
Matsuura, K., 2006. Termite-egg mimicry by a sclerotium-forming fungus. Proc. Biol. Sci. 273, 1203–1209.
Matsuura, K., 2005. Distribution of termite egg-mimicking fungi ("termite balls") in *Reticulitermes* spp. (Isoptera : Rhinotermitidae) nests in Japan and the United States. Appl. Entomol. Zool. 40, 53–61.
Matsuura, K., Himuro, C., Yokoi, T., Yamamoto, Y., Vargo, E.L., Keller, L., 2010. Identification of a pheromone regulating caste differentiation in termites. Proc. Natl. Acad. Sci. U.S.A. 107, 12963–12968.
Matsuura, K., Kobayashi, N., Yashiro, T., 2007. Seasonal patterns of egg production in field colonies of the termite *Reticulitermes speratus* (Isoptera : Rhinotermitidae). Popul. Ecol. 49, 179–183.
Matsuura, K., Matsunaga, T., 2015. Antifungal activity of a termite queen pheromone against egg-mimicking termite ball fungi. Ecol. Res. 30, 93–100.
Matsuura, K., Tanaka, C., Nishida, T., 2000. Symbiosis of a termite and a sclerotium-forming fungus: sclerotia mimic termite eggs. Ecol. Res. 15, 405–414.
Matsuura, K., Yashiro, T., 2010. Parallel evolution of termite-egg mimicry by sclerotium-forming fungi in distant termite groups. Biol. J. Linn. Soc. Lond. 100, 531–537.
Matsuura, K., Yashiro, T., Shimizu, K., Tatsumi, S., Tamura, T., 2009. Cuckoo fungus mimics termite eggs by producing the cellulose-digesting enzyme beta-glucosidase. Curr. Biol. 19, 30–36.
Mitaka, Y., Mori, N., Matsuura, K., 2017. Multi-functional roles of a soldier-specific volatile as a worker arrestant, primer pheromone and an antimicrobial agent in a termite. Proc. R. Soc. B 284, 20171134.
Nagy, L.G., Riley, R., Tritt, A., Adam, C., Daum, C., Floudas, D., Sun, H., Yadav, J.S., Pangilinan, J., Larsson, K.-H., Matsuura, K., Barry, K., Labutti, K., Kuo, R., Ohm, R. A., Bhattacharya, S.S., Shirouzu, T., Yoshinaga, Y., Martin, F.M., Grigoriev, I.V., Hibbett, D.S., 2016. Comparative genomics of early-diverging mushroom-forming fungi provides insights into the origins of lignocellulose decay capabilities. Mol. Biol. Evol. https://doi.org/10.1093/molbev/msv337.
Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., Nordén, J., 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. ISME J. 7, 1696–1709.
R Foundation for Statistical Computing. version 4.1.3, 2022. https://www.r-project.org/.
Tasaki, E., Komagata, Y., Inagaki, T., Matsuura, K., 2020. Reproduction deep inside wood: a low O2 and high CO2 environment promotes egg production by termite queens. Biol. Lett. 16, 20200049.
Vega, F.E., Blackwell, M., 2005. Insect-fungal Associations: Ecology and Evolution. Oxford University Press, Oxford, UK.
Yashiro, T., Matsuura, K., 2007. Distribution and phylogenetic analysis of termite egg-mimicking fungi "termite balls" in *Reticulitermes* termites. Ann. Entomol. Soc. Am. 100, 532–538.
Ye, C., Li, J., Ran, Y., Rasheed, H., Xing, L., Su, X., 2019. The nest fungus of the lower termite Reticulitermes labralis. Sci. Rep. 9, 3384.
Yurchenko, E.O., Golubkov, V.V., 2003. The morphology, biology, and geography of a necrotrophic basidiomycete *Athelia arachnoidea* in Belarus. Mycol. Prog. 2, 275–284.