Sociobiology 65(1): 59-66 (March, 2018) Special Issue DOI: 10.13102/sociobiology.v65i1.1838

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - TERMITES

Changes in the Contribution of Termites to Mass Loss of Dead Wood among Three Tree Species during 23 Months in a Lowland Tropical Rainforest

Y Roh[1], S Lee[1], G Li[1], S Kim[1], J Lee[1], SH Han[1], H Chang[1], KA Salim[2], Y Son[1]

1 - Department of Environmental Science and Ecological Engineering, Graduate School, Korea University, Seoul, Republic of Korea

2 - Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam

Article History

Edited by
Og DeSouza, UFV, Brazil
Received 01 July 2017
Initial acceptance 14 August 2017
Final acceptance 02 October 2017
Publication date 30 March 2017

Keywords
Dillenia beccariana, *Elateriospermum tapos*, invertebrate, *Macaranga bancana*, mesh bag method.

Corresponding author
Yowhan Son
Department of Environmental Science and Ecological Engineering
Graduate School, Korea University
Seoul 02841, Republic of Korea.
E-Mail: yson@korea.ac.kr

Abstract

This study investigated the contribution of termites to mass loss of dead wood (*Macaranga bancana*, *Elateriospermum tapos*, and *Dillenia beccariana*) in a lowland tropical rainforest, Brunei Darussalam. Mesh bag method was used to exclude termites, and the mass remaining was monitored after 3, 7, 13, and 23 months. C/N ratio of the samples was analyzed after 13 and 23 months. Initial wood density was 0.63, 0.92, and 1.02 g/cm^3 for *M. bancana*, *E. tapos*, and *D. beccariana*, respectively, and the termite contribution to mass loss (%) was an average (range) of 13.05±5.68 (4.17-29.59), 3.48±1.13 (2.20-6.49), and 3.40±1.92 (0.74-10.78), respectively. Until 7 months, termites contributed highly to mass loss, given the low initial wood density, and interaction effect of species and treatment was significant. After 7 months, the contribution decreased in *M. bancana* and *E. tapos*, whereas it increased consistently in *D. beccariana*. The interaction effect was not significant, whereas differences in C/N ratio among the species were significant, with a lower C/N ratio in *M. bancana* and *E. tapos* than in *D. beccariana*. After 23 months, the differences in C/N ratio were not significant, and ants were present at 40% of control samples in *M. bancana* and *E. tapos*. Our results suggest that the contribution of termites to mass loss varies by dead wood species and is temporally variable. Initial wood traits could affect the termite feeding in the beginning, however, termites thereafter could forage in response to the varying C/N ratio among species and predators.

Introduction

Dead wood has a critical impact on the carbon and nutrient cycles in terrestrial ecosystems with slow decomposition rates, owing to its large size, limited nitrogen content, decay-resistant structure, and recalcitrant compounds (Cornwell et al., 2009; Kim et al., 2015). Dead wood is mostly decomposed by fungi and invertebrates, and invertebrates contribute to approximately 10-20% loss of dead wood in terrestrial ecosystems (Ulyshen, 2016). Especially in tropical rainforests, termites are abundant and diverse (Eggleton, 2000), and the activities of termites control the turnover of dead wood (Bradford et al., 2014).

Although termites decompose large amounts of dead wood, they can feed on only the accessible and digestible lingo-cellulose part of dead wood, which vary across species (Bultman & Southwell, 1976). When termites feed on dead wood, the mass loss of dead wood is accelerated (Stoklosa et al., 2016). Termites prefer certain tropical tree species, thereby, accelerating more rapid mass loss in these species (Gentry & Whitford, 1982). However, termite preference on major tree species of lowland tropical rainforests in Southeast Asia has rarely been investigated.

The contribution of termites to the mass loss of dead wood could vary over time, because of changes in termite activities in response to wood traits and predators. In the beginning, dead wood has certain specific traits. As termites mechanically attack dead wood with their mandibles, their feeding could be affected by dead wood traits such as density, which disturbs action of mandible (Gentry & Whitford, 1982).

ISSN: 0361-6525

Also, as termites prefer the relatively labile and nutritious parts of woods (e.g. nitrogen-rich cambium, or the softest rings of spring wood), they can selectively forage for new dead wood after consuming the parts (Shellman-Reeve, 1994; Stoklosa et al., 2016; Traniello & Leuthod, 2000; Ulyshen et al., 2014). Finally, as dead wood loses its specific traits during the decomposition, the termite activity could be suppressed because of the invasion of non-tree specific termite predators on dead wood. Besides, tunnels made on dead wood by termite mechanical attack also facilitate the invasion (Cornwell et al., 2009). Nevertheless, quantification on the changes in the termite contribution to dead wood decomposition has rarely been identified, and the contribution was considered as constant over time (Ulyshen et al., 2016).

The aim of this study was to investigate the changes in the contribution of termites to mass loss among major tropical tree species over time in a lowland tropical rainforest of Southeast Asia. The following hypotheses were examined: (i) termites would accelerate the mass loss of dead wood, (ii) termite contribution to the mass loss of dead wood would differ by species, and (iii) the contribution would change over time.

Materials and Methods

The study site was located in a lowland tropical rainforest, at the Kuala Belalong Field Studies Centre, Brunei Darussalam (04°63′50.3″N, 115°22′79.1″E). The forest is classified as an old-growth mixed dipterocarp forest, with a mean annual temperate of 26.5 °C, and a mean annual precipitation of approximately 5203 mm, without a distinct dry season. The topology consists of ridges with steep slope on Ultisol soils (Anderson-Teixeira et al., 2015; Ashton & Hall, 1992; Small et al., 2004).

Three species were selected for the study: *Macaranga bancana* (Euphorbiaceae), *Elateriospermum tapos* (Euphorbiaceae), and *Dillenia beccariana* (Dilleniaceae). They are common in the lowland tropical rainforest at Kuala Belalong, and have distinct traits. *M. bancana* is a myrmecophytic tree species, which has an obligate mutualism with ants via development of a hollow stem (domatia) and food body (Heil et al., 2004). *E. tapos* is a non-myrmecophytic tree species; however, it has a facultative mutualism with various invertebrates. This species not only has extrafloral nectaries to attract invertebrates but also produces soft resin to defend the stem from the invertebrates. The pith of this species is soft (Fiala & Maschwitz, 1992). *D. beccariana* is a non-myrmecophytic tree species without mutualism, and has a solid stem.

Trees with similar diameter were selected and logged, and the logs were cut into 10-cm pieces. The mean diameter (± SD) of the samples was 6.96 (0.77), 6.88 (0.40), and 6.98 (0.59) cm for *M. bancana*, *E. tapos*, and *D. beccariana*, respectively, and the mean initial air-dried density (± SD) of the samples was 0.63 (0.05), 0.92 (0.05), and 1.02 (0.07) g/cm^3, respectively. The mesh bag method was used to physically block the termite access. A nylon mesh with 1.4 mm openings was used, and each sample of dead wood was tightly wrapped with the mesh twice (Fig 1a). Control (without mesh) samples were also prepared to measure the mass remaining of dead wood without blocking the termite access (Fig 1b).

A 20 m × 20 m plot was established on a slope. The plot was subdivided into three 4 m × 13 m subplots. The samples were laid on the soil at the distance of 1 m, along three transects (Figs 1c & 1d). In Jan., 2015, a total of 108 samples (3 subplots × 3 species × 2 treatments (mesh bag & control) × 6 samples) were laid in the site. The samples were retrieved after 3 (108 samples), 7 (101 samples), 13 (97

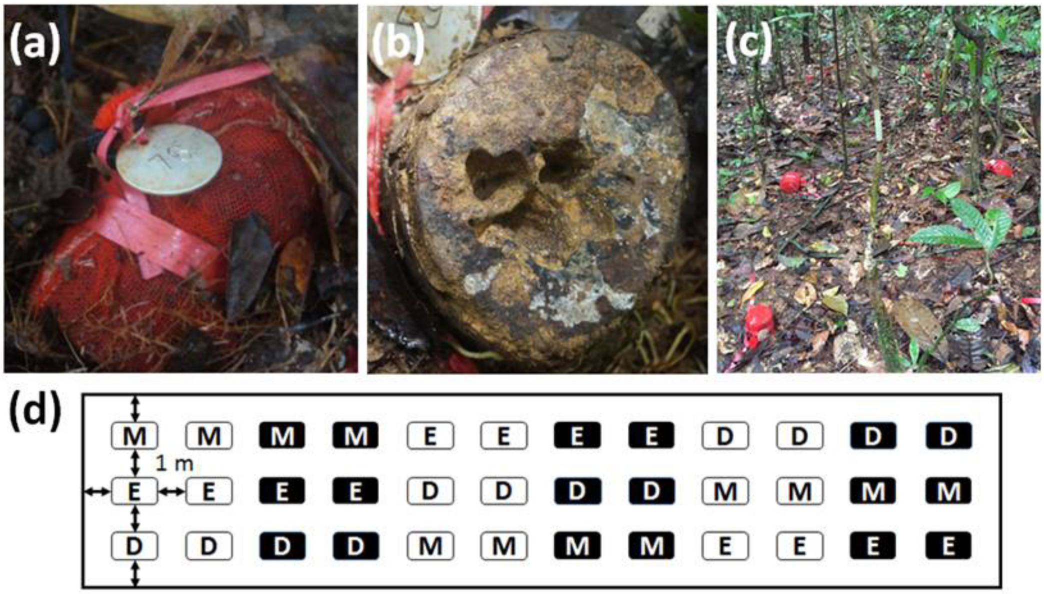

Fig 1. Photographs of *Dillenia beccariana* installed as (a) a mesh bag sample, and (b) a control sample in Jul., 2016 (after 18 months), and (c) a picture of the study site, and (d) a diagram of an experimental design of each subplot in Jan., 2015. Species: M = *M. bancana*; E = *E. tapos*; D = *D. beccariana*. Treatment: white box = control; black box = mesh bag.

samples) and 23 (43 samples) months from the beginning of the experiment. After the mesh was removed, the retrieved samples were air-dried for 48 h (Figs 2a & 2b), and the sprouts were removed using a scissors (Fig 2c). Termite-imported soils were also found in samples with termites as Ulyshen & Wagner (2013) stated (Fig 2d). Therefore, the soils were removed from the samples using forceps after air-drying, and then the surface of the dead wood samples was cleaned carefully using small brushes (Fig 2e). The mass remaining [%; (air-dried weight × 100)/initial air-dried weight] was determined. The difference in mass remaining between the treatments (control & mesh bag) was regarded as the contribution of termites to the mass loss (%). Because of limited electricity and time, and to keep the integrity of samples, an air-drying method was conducted, which might cause an error on the wood weight. However, the study site has relatively constant temperature and precipitation (Anderson-Teixeira et al., 2015), and all of the samples were air-dried at the same time (Collins, 1981). Thereby, we expected that the results of the termite contribution to mass loss of dead wood might not be distorted. When other invertebrates were found on samples, the time of occurrence was recorded. The meshes were checked at the time of measurements. Subsequently, the samples were laid again in the study site.

Sampling was conducted after 13 months (27 samples) and 23 months (20 samples) for carbon (C) and nitrogen (N) analyses. The collected samples were ground, and oven-dried at 103 °C. To determine the C/N ratio, an Elemental analyzer (vario Macro CHN, Elementar Analysensystem GmbH, Germany) was used.

To assess the effects of species, treatment, and their interaction, the mass remaining was analyzed using a two-way analysis of variance (ANOVA) at the time of measurements. To assess the differences in mass remaining between treatments, and the differences in C/N ratio of control among the species, a one-way ANOVA was conducted. All statistical tests were carried out using SAS 9.4 software (SAS system, Cary, USA).

Results

During the study period, termites were found in a few of mesh bag samples, because the use of 1.4 mm opening was not enough to block all of the termite access. To deal with this issue, all of the mesh bag samples were checked before measuring air-dried weight, and then the mesh bags having termites or traces of termites were excluded from the data analyses.

Throughout the study period, species had a significant effect on the mass remaining (Table 1). When termites were not excluded, the mass loss of dead wood increased by 4.17-29.59% in *M. bancana*, 2.20-6.49% in *E. tapos*, and 0.74-10.78% in *D. beccariana* (Figs 3a, 3b & 3c). The difference in mass remaining between treatments was highest after 7 months in *M. bancana* and *E. tapos*, whereas it was highest after 23 months in *D. beccariana* (Fig 3d). Resprouting occurred only in *D. beccariana* after 7 months, and the sprouts were not found afterward (Fig 2c).

Until 7 months, the interaction effect of species and treatment was significant (Table 1). During this period, the contribution of termites to mass loss increased the highest in *M. bancana*, followed by *E. tapos,* and then *D. beccariana*, i.e.,

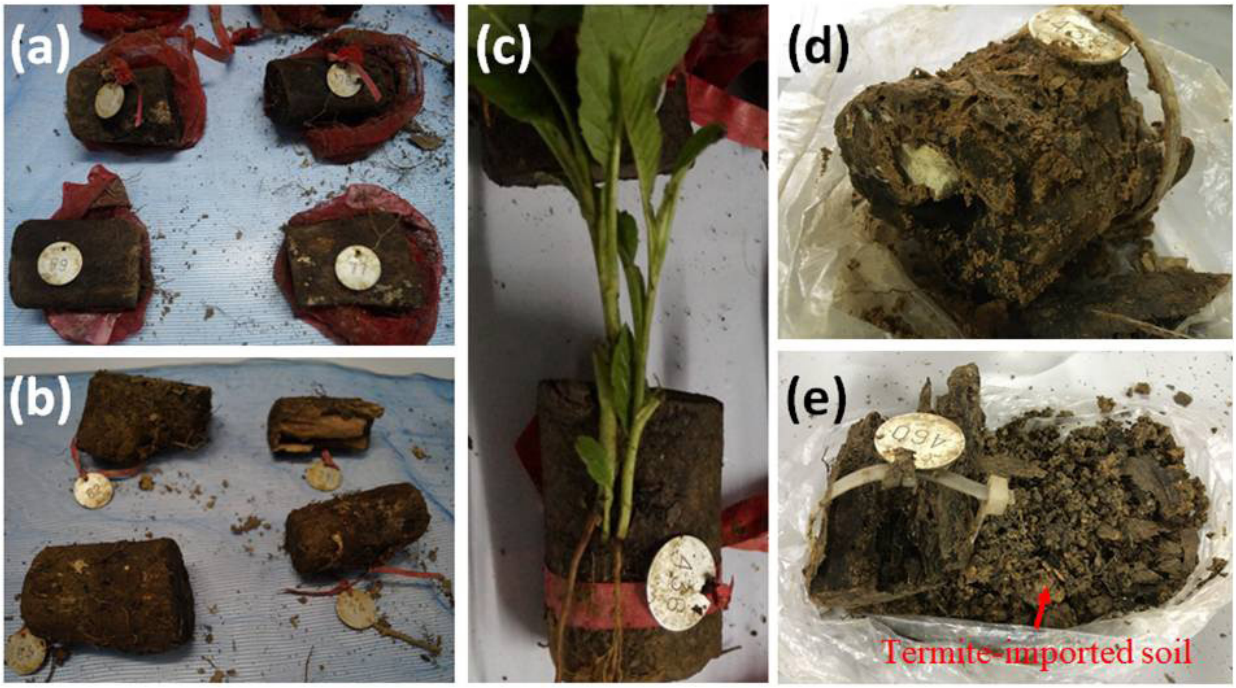

Fig 2. Photographs of an air-dried (a) mesh bag samples and (b) control samples, and (c) a resprout in a control sample, and control samples (d) before removing termite-imported soils, and (e) after removing the soils.

Table 1. Two-way ANOVA of the mass remaining on the effect of species, treatment, and their interaction after 3, 7, 13, and 23 months.The number of samples was 108, 108, 104, and 50 for 3, 7, 13, and 23 months, respectively. The values highlighted in bold indicate statistical significance ($p < 0.05$).

Effect	Df	3 months		7 months		13 months		23 months	
		F	p	F	p	F	p	F	p
Species (S)	2	51.78	**<.0001**	5.42	**0.0059**	6.57	**0.0022**	3.49	**0.0409**
Treatment (T)	1	15.24	**0.0002**	13.3	**0.0004**	5.27	**0.0240**	1.32	0.2585
S × T	2	3.45	**0.0359**	5.88	**0.0039**	2.28	0.1082	0.33	0.7245

× = interaction effect

in the order of species with lowest initial wood densities (Fig 3d). After 7 months, the interaction effect was not significant anymore (Table 1). The contribution of termites to mass loss began to decline in *M. bancana* and *E. tapos*, whereas it still increased in *D. beccariana* (Fig 3d). Especially between 13 and 23 months, the mass remaining of control samples did not decrease in *M. bancana*, whereas it showed a greater decrease than before in *D. beccariana* (Figs 3a & 3c). During this period, the control samples of *M. bancana* and *E. tapos* had a significantly lower C/N ratio than those of *D. beccariana* (n = 9, F = 18.36, $p < 0.05$; Fig 4). After 23 months, termite contribution still decreased in *M. bancana* and *E. tapos*, whereas it increased in *D. beccariana*, without a significant difference in C/N ratio among the species (n = 9, F = 0.83, $p > 0.05$; Fig 4). Simultaneously, ant colonies were found at 40% of the control samples of *M. bancana* and *E. tapos*. The coexistence of termites and ants on dead wood was not observed.

Discussion

Termites contributed to the mass loss of dead wood differently among the species. This result might be due to the differences in wood density. The wood density is a representative property, indicating resistance from fungi and pathogens. Previous studies have found that termites

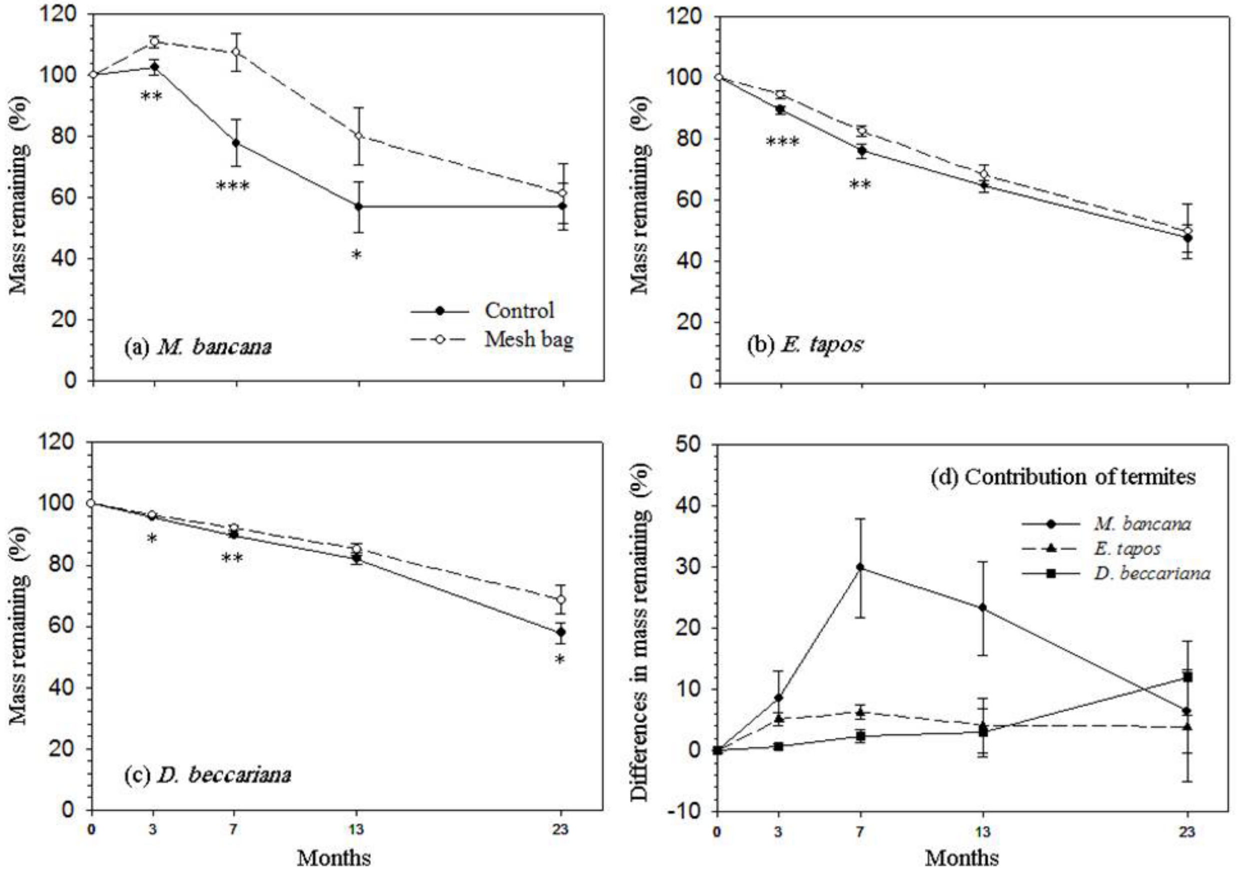

Fig 3. Mean mass remaining for (a) *M. bancana*, (b) *E. tapos*, and (c) *D. beccariana*, and (d) the contribution of termites during the 23 months. Contribution of termites = Differences in mass remaining between treatments. Vertical bars represent the standard error. Asterisks indicate significant differences (*$p < 0.1$, ** $p < 0.05$, *** $p < 0.01$).

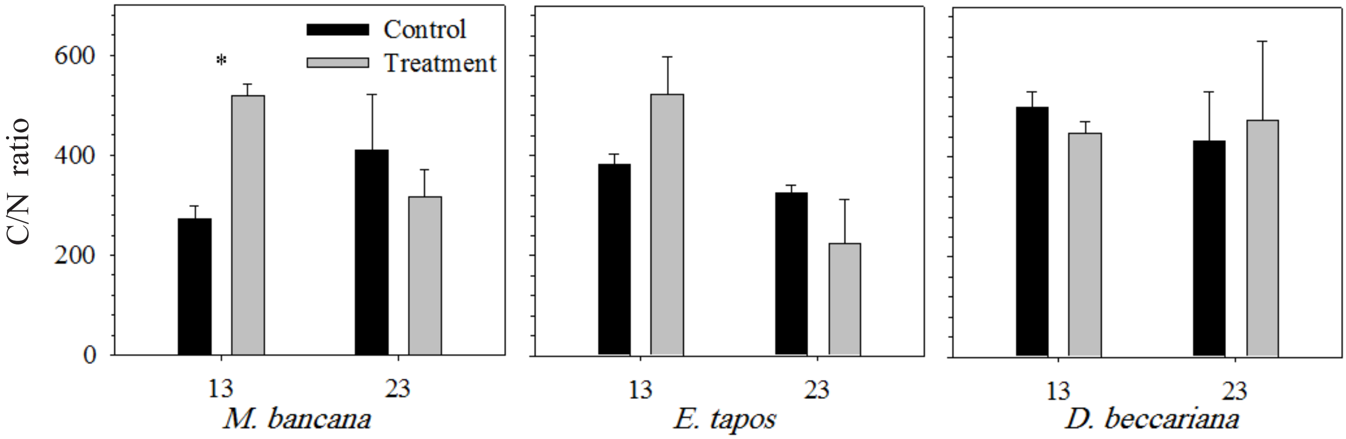

Fig 4. Mean C/N ratio across the species after 13 months and 23 months. Vertical bars indicate the standard error. Asterisks indicate significant differences (* p < 0.05).

preferentially feed on dead wood with low wood density (Gentry & Whitford, 1982; Takamura et al., 2001). Another possible explanation is the difference in chemical composition of stems among species. Species having high resprouting potential, such as *D. beccariana*, is known to have several strategies to protect their stems against decomposers (Just et al., 2017; Poorter et al., 2010). Especially, stems of *D. beccariana* might contain high lignin or secondary metabolites such as phenols, which possibly hamper termite feeding (Freschet et al., 2012; Guérard et al., 2007; Just et al., 2017). The termites might feed more on *D. beccariana* after these metabolites were sufficiently degraded by fungi (Ulyshen, 2016).

There were changes in the contribution of termites to the mass loss of dead wood over time. Until 7 months, the termite feeding might depend on the initial traits of dead wood, such as initial wood density and secondary metabolites. After 7 months, the termites might forage from *M. bancana* and *E. tapos* to *D. beccariana*, in response to the differences in C/N ratio among the species. Mortality of termites, which feed on sound wood, increases with a decreasing C/N ratio of the substrate, owing to an imbalanced symbiotic system with gut microbes or the accumulation of ammonia in the guts (Majeed et al., 2015). After 23 months, the decreasing trend of termite foraging might be caused by appearance of ants, which would have accelerated termite emigration. Ants are known termite predators and non-tree specific invertebrates that nest on small dead wood (Levings & Franks, 1982). When ants are present on dead wood, the decomposition activities of termites and fungi decrease (Warren & Bradford, 2012). Wang et al. (2003) also found ant colonies in the branches hollowed out by termites in a temperate forest.

Overall, termites accelerated the mass loss of dead wood, and the acceleration depended on the dead wood species. These results are in accordance with the findings of Liu et al. (2015), who reported the role of termites in enhancing the effect of wood traits on decomposition. Moreover, root foraging occurs more on dead wood hollowed by termites, thereby, accelerating nutrient cycling (Lu et al., 2013). Based on these previous findings, we expected that the effects of dead wood on C and nutrient cycles in forest ecosystems would be enhanced by termites, and the effects would be different depending on the dominant dead wood species.

In this study site, termites contributed to 0.74-29.59% mass loss of dead wood within 23 months. Gentry and Whitford (1982) also reported a wide range of termite-driven mass loss in dead wood (3-20%) in Savanna. These wide ranges in these results suggest that there is an uncertainty in quantifying the contribution of termites to the mass loss of dead wood in terrestrial ecosystems. Three explanations are possible for this uncertainty. First, termite feeding is highly affected by dead wood species, which have developed various defense strategies against attacks from herbivores and pathogens, such as mutualism or secondary metabolites. These various traits differently affect the termites, thereby, reducing or enhancing termite feeding (Verma et al., 2009). Second, ants are also abundant in tropical rainforests (Levings & Franks, 1982). There is a possibility that the amount of termite-driven mass loss in dead wood is overestimated without considering the predator effects. It could lead to incorrect extrapolation if the measurement was conducted once or stopped in the middle of mass loss process. The last possibility might be the different accessibility of termite among the dead wood samples. The magnitude of wood decomposition could vary with the number and type of termite colonies near the dead wood, because these factors could control accessibility of termites and influence mass loss caused by termite feeding accordingly (Ulyshen et al., 2016).

This study demonstrated that termites contribute to mass loss of dead wood, thereby, affecting C and nutrient cycles in forest ecosystems. In addition, the contribution varies by not only species but changing factors such as wood traits and predators. Therefore, the changes should be considered to estimate the termite contribution to dead wood decomposition precisely.

Acknowledgment

We thank the staffs at UBD and KBFSC for their support during the study. We also thank UBD and CTFS for allowing us to conduct this study at the site. This study was supported by research grants from Korea Forest Service (S121315L130110) and National Research Foundation of Korea (2015R1D1A1A01057124).

Author Contribution

Yowhan Son and Kamariah Abu Salim conceived and designed the experiments; Yujin Roh, Sohye Lee, Guanlin Li, Seongjun Kim, Seung Hyun Han, and Jongyeol Lee were responsible for the collection of data from the study site; Yujin Roh, Guanlin Li and Hanna Chang analyzed the data; all authors participated in the discussion of results; Yujin Roh wrote the manuscript.

References

Anderson-Teixeira, K.J., et al. (2015). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Global Change Biology, 21: 528-549. doi: 10.1111/gcb.12712.

Ashton, P.S. & Hall, P. (1992). Comparisons of structure among mixed dipterocarp forests of north-western Borneo. Journal of Ecology, 80: 459-481. doi: 10.2307/2260691.

Bradford, M.A., Warren II, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., Wieder, W.R., Wood, S.A. & King, J.R. (2014). Climate fails to predict wood decomposition at regional scales. Nature Climate Change, 4: 625-630. doi: 10.1038/nclimate2251.

Bultman, J.D. & Southwell, C.R. (1976). Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica, 8: 71-95. doi: 10.2307/2989627.

Collins, N.M. (1981). The role of termites in the decomposition of wood and leaf litter in the southern Guinea savanna of Nigeria. Oecologia, 51: 389-399. doi:10.1007/BF00540911.

Cornwell, W.K., Cornelissen, J.H., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C. & Zanne, A.E. (2009). Plant traits and wood fates across the globe: rotted, burned, or consumed?. Global Change Biology, 15: 2431-2449. doi: 10.1111/j.1365-2486.2009.01916.x.

Eggleton, P. (2000). Global patterns of termite diversity. In Abe, T., Bignell, D. E. & Higashi, M. (Eds.), Termites: evolution, sociality, symbioses, ecology (pp. 25-51). Kluwer Academic Publishers, Dordrecht. doi: 10.1007/978-94-017-3223-9_2.

Fiala, B. & Maschwitz, U. (1992). Domatia as most important adaptations in the evolution of myrmecophytes in the paleotropical tree genus *Macaranga* (Euphorbiaceae). Plant Systematics and Evolution, 180: 53-64. doi: 10.1007/BF00940397.

Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R. & Cornelissen, J.H. (2012). Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. Journal of Ecology, 100: 161-170. doi: 10.1111/j.1365-2745.2011.01896.x.

Gentry, J. & Whitford, W.G. (1982). The relationship between wood litter infall and relative abundance and feeding activity of subterranean termites *Reticulitermes* spp. in three southeastern coastal plain habitats. Oecologia, 54: 63-67. doi: 10.1007/BF00541109.

Guérard, N., Maillard, P., Bréchet, C., Lieutier, F. & Dreyer, E. (2007). Do trees use reserve or newly assimilated carbon for their defense reactions? A ^{13}C labeling approach with young Scots pines inoculated with a bark-beetle-associated fungus (*Ophiostoma brunneo ciliatum*). Annals of Forest Science, 64: 601-608. doi: 10.1051/forest:2007038.

Heil, M., Feil, D., Hilpert, A. & Linsenmair, K.E. (2004). Spatiotemporal patterns in indirect defence of a South-East Asian ant-plant support the optimal defence hypothesis. Journal of Tropical Ecology, 20: 573-580. doi: 10.1017/S0266467404001567.

Just, M.G., Schafer, J.L., Hohmann, M.G., & Hoffmann, W.A. (2017). Wood decay and the persistence of resprouting species in pyrophilic ecosystems. Trees, 31: 237-245. doi: 10.1007/s00468-016-1477-3.

Kim, S., Yoon, T.K., Han, S., Han, S.H., Lee, J., Kim, C., Lee, S.-T., Seo, K.W., Yang, A.R. & Son, Y. (2015). Initial effects of thinning on soil carbon storage and base cations in a naturally regenerated *Quercus* spp. forest in Hongcheon, Korea. Forest Science and Technology, 11: 172-176. doi: 10.1080/21580103.2014.957357.

Levings, S.C. & Franks, N.R. (1982). Patterns of nested dispersion in a tropical ground ant community. Ecology, 63: 338-344. doi: 10.2307/1938951.

Liu, G., Cornwell, W.K., Cao, K., Hu, Y., Van Logtestijn, R.S., Yang, S., Xie, X., Zhang, Y., Ye, D. & Pan, X. (2015). Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. Journal of Ecology, 103: 1214-1223. doi: 10.1111/1365-2745.12427.

Lu, M., Davidescu, M., Sukri, R.S. & Daskin, J.H. (2013). Termites facilitate root foraging by trees in a Bornean tropical forest. Journal of Tropical Ecology, 29: 563-566. doi: 10.1017/S0266467413000631.

Majeed, M.Z., Miambi, E., Riaz, M.A. & Brauman, A. (2015). Characterization of N_2O emission and associated bacterial communities from the gut of wood-feeding termite

Nasutitermes voeltzkowi. Folia Microbiologica, 60: 425-433. doi: 10.1007/s12223-015-0379-x.

Poorter, L., Kitajima, K., Mercado, P., Chubiña, J., Melgar, I. & Prins, H.H. (2010). Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. Ecology, 91: 2613-2627. doi: 10.1890/09-0862.1.

Shellman-Reeve, J.S. (1994). Limited nutrients in a dampwood termite: nest preference, competition and cooperative nest defence. Journal of Animal Ecology, 4: 921-932. doi: 10.2307/5269.

Small, A., Martin, T.G., Kitching, R.L. & Wong, K.M. (2004). Contribution of tree species to the biodiversity of a 1ha Old World rainforest in Brunei, Borneo. Biodiversity and Conservation, 13: 2067-2088. doi: 10.1023/B:BIOC.0000040001.72686.e8.

Stoklosa, A.M., Ulyshen, M.D., Fan, Z., Varner, M., Seibold, S. & Müller, J. (2016). Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. Basic and Applied Ecology, 17: 463-470. doi: 10.1016/j.baae.2016.03.001.

Takamura, K. (2001). Effects of termite exclusion on decay of heavy and light hardwood in a tropical rain forest of Peninsular Malaysia. Journal of Tropical Ecology, 17: 541-548. doi: 10.1017/S0266467401001407.

Traniello, J.F. & Leuthold, R.H. (2000). Behavior and ecology of foraging in termites. In Abe, T., Bignell, D.E. & Higashi, M. (Eds.), Termites: evolution, sociality, symbioses, ecology (pp. 141-168). Kluwer Academic Publishers, Dordrecht. doi: 10.1007/978-94-017-3223-9_7.

Ulyshen, M.D. (2016). Wood decomposition as influenced by invertebrates. Biological Reviews, 91: 70-85. doi: 10.1111/brv.12158.

Ulyshen, M.D., Müller J. & Seibold, S. (2016). Bark coverage and insects influence wood decomposition: Direct and indirect effects. Applied Soil Ecology, 105: 25-30. doi: 10.1016/j.apsoil.2016.03.017.

Ulyshen, M.D., Wagner, T.L. & Mulrooney, J.E. (2014). Contrasting effects of insect exclusion on wood loss in a temperate forest. Ecosphere, 5: 1-15. doi: 10.1890/ES13-00365.1.

Ulyshen, M.D. & Wagner, T.L. (2013). Quantifying arthropod contributions to wood decay. Methods in Ecology and Evolution, 4: 345-352. doi: 10.1111/2041-210x.12012.

Verma, M., Sharma, S. & Prasad, R. (2009). Biological alternatives for termite control: a review. International Biodeterioration and Biodegradation, 63: 959-972. doi: 10.1016/j.ibiod.2009.05.009.

Wang, C., Powell, J.E. & Scheffrahn, R.H. (2003). Abundance and distribution of subterranean termites in southern Mississippi forests (Isoptera: Rhinotermitidae). Sociobiology, 42: 533-542. doi: 10.1.1.495.4859.

Warren, R. & Bradford, M. (2012). Ant colonization and coarse woody debris decomposition in temperate forests. Insectes Sociaux, 59: 215-221. doi: 10.1007/s00040-011-0208-4.

Supplement

Table S1. Mean mass remaining (± SD; %) of *M. bancana*, *E. tapos*, and *D. beccariana* during the 23 months. n = the number of samples.

Species	Treatment	3 months		7 months		13 months		23 months	
		Mean	n	Mean	n	Mean	n	Mean	n
M. bancana	Control	102.47 (2.52)	18	77.76 (7.55)	18	56.86 (8.40)	16	57.01 (7.84)	5
	Mesh bag	110.88 (1.81)	16	107.35 (6.26)	16	79.94 (9.49)	15	61.18 (9.83)	5
E. tapos	Control	89.46 (1.20)	18	76.08 (2.38)	18	64.61 (1.94)	17	47.47 (4.50)	10
	Mesh bag	94.52 (1.26)	14	82.57 (1.59)	14	68.28 (3.34)	14	49.68 (8.93)	5
D. beccariana	Control	95.58 (0.27)	18	89.62 (0.64)	18	82.11 (1.87)	18	57.89 (3.40)	9
	Mesh bag	96.33 (0.33)	17	92.06 (0.96)	17	85.16 (1.90)	17	68.67 (4.63)	9

Table S2. Mean contribution of termites (± SD; %) for *M. bancana*, *E. tapos*, and *D. beccariana* during the 23 months. Contribution of termites = Differences in mass remaining between treatments. n = the number of samples.

Species	3 months		7 months		13 months		23 months	
	Mean	n	Mean	n	Mean	n	Mean	n
M. bancana	8.51 (4.46)	3	29.84 (8.04)	3	23.27 (7.66)	3	6.39 (6.77)	3
E. tapos	5.11 (1.10)	3	6.29 (1.24)	3	4.14 (4.44)	3	3.92 (8.89)	3
D. beccariana	0.71 (0.41)	3	2.37 (0.97)	3	2.91 (3.91)	3	11.88 (6.04)	3