

Effects of termite exclusion on decay of heavy and light hardwood in a tropical rain forest of Peninsular Malaysia

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ABSTRACT. Wood pieces of a heavy hardwood *Neobalanocarpus heimii* (King) P. S. Ashton and a light hardwood *Shorea macroptera* Dyer were used in decomposition experiments with termite-exclusion and control trays on the forest floor of the Pasoh Forest Reserve, West Malaysia to determine effects of wood quality on termite-mediated wood decay. *Shorea macroptera* had a significant loss of C in the presence of termites while *Neobalanocarpus heimii* showed no significant termite effect. *Neobalanocarpus heimii* and *S. macroptera* both accumulated N in the absence of termites, but *S. macroptera* lost it when termites were present. The C/N ratio decreased with and without termites as decay proceeded in both species. *Neobalanocarpus heimii* accumulated P, but *S. macroptera* lost it with and without termites. The C/P ratio decreased in *N. heimii*, but did not change in *S. macroptera*. Decomposition was considerably enhanced by termites in *S. macroptera*, but not in *N. heimii*, indicating that termite foraging activity was affected by the different wood qualities of the two trees. The qualities responsible for the differences and how different wood qualities affect nutrient cycling in the tropical rain forest ecosystem are discussed.

KEY WORDS: carbon, decomposition, hardwood, *Neobalanocarpus heimii*, nitrogen, phosphorus, *Shorea macroptera*, termite, wood quality

INTRODUCTION

Termites in tropical forests show varied contributions to wood decay, depending on wood size and quality. For example, Abe (1980) and John (1973) reported faster decomposition of wood litter in smaller diameter logs than in larger ones. These variations in wood litter traits within forests may affect the contribution of termites to wood decay as a whole, probably resulting in variations not only in nutrient cycling, but also in patterns of faunistic diversity that use resources and refuges in decaying wood litter.

Heavy woods seem, a priori, to be difficult to decompose and light woods

relatively easy. Although wood durability to termites has been tested in view of wood density in the field of wooden architecture, it has not been assessed whether heavy woods are actually harder for termites to decompose than light woods under natural conditions. There are trees of both heavy and light hardwood in lowland tropical rain forests of Southeast Asia. For tropical forest ecosystem management, it is important to know how variation in wood quality affects decomposition and nutrient cycling processes through wood-foraging of termites in the forest. Here I compare experimentally the contribution of termites to the decomposition rates of heavy and light hardwoods.

METHODS

The study was conducted at the Pasoh Forest Reserve, Negeri Sembilan, Malaysia, where the annual precipitation is at its lowest within West Malaysia (Tjia 1988). These relatively dry conditions are reflected in the termite community with fungus-growing Macrotermitinae being dominant (Abe & Matsumoto 1979, Collins 1983).

Furthermore, over half of the termite species recorded at Pasoh are wood feeders (Jones & Brendell 1998). The Pasoh forest is composed of natural and regenerating parts. Termite exclusion experiments were made at a natural forest site (site N) at the centre of the forest and a regenerating forest site (site R) at the periphery of the forest. The regenerating area had been selectively logged in 1955.

Open-top stainless steel trays of two types were used. They were 12-cm square at the upper rim, 11-cm square at the lower rim and 5 cm in height. The bottom panel had a 5-cm square opening and a facing pair of open side-panels in the lower margin at 1 cm height. These openings were covered with stainless steel net with a mesh size of 1 mm in exclusion trays and not covered in control trays. The trays were fixed with nails in the ground.

Neobalanocarpus heimii (the Malay name chengal) and *Shorea macroptera* (the Malay name melantai) were the tree species used. *N. heimii* is a heavy hardwood tree and *S. macroptera* is a light hardwood one. Each piece of wood was 10 cm × 7.5 cm × 1 cm. Six pieces were bundled, wrapped with a stainless-steel wire and put in either type of tray. At each site, 36 bundles of wood pieces were placed within the 2-m × 2-m area of the forest floor. Each combination of species and treatment comprised nine bundles.

The experiments were run from December 1992. At 1-y intervals, three bundles were retrieved from each combination of site, tree species and treatment. Thus, the decay periods were 1, 2 and 3 y starting at the same time. Because of animal disturbance, data for *S. macroptera* in exclusion trays at site N for the 3-y period are missing. Termites were collected from the bundles every 3–7 mo and identified according to Tho (1992).

All wood pieces used, with additional six pieces of each species, were weighed

at the same time before the experiments. Retrieved wood pieces, and the additional ones that were used to estimate their original conditions, were dried to a constant weight at 95 °C and sampled by boring holes with a 6-mm diameter electric drill. The boring was arranged to evenly cover the whole of the remaining pieces of wood. The bored part was at least 3.4% of the total volume. From the resulting chips, C and N concentrations were determined with a furnace-equipped C-H-N analyser (Sumigraph NC-90A) and phosphorus concentration was determined by a colorimetric method (Murphy & Riley 1962) after nitric acid digestion in Teflon bottles (Okamoto & Fuwa 1984).

Annual mass loss rates of these elements were calculated as k (y^{-1}) in an exponential equation,

$$X_t = X_0 e^{-kt}$$

where t is the decay period in years, X_0 is the initial mass at the start of the experiment, X_t is the mass remaining in t years. The single exponential model was applied as one of the best models that describe the decline in mass during the decay process (Wieder & Lang 1982). The coefficient k was calculated for the periods of 1, 2, 3 y, respectively. The mass ratios C/N and C/P were calculated for the ends of these periods.

Data were compared statistically between the exclusion and control treatments, between the two tree species, between the two sites, and between the two decay periods using a four-way ANOVA. Neither data for the 3-y period were used in the test because those for *S. macroptera* were incomplete. Before the comparison, the data were transformed logarithmically using the equation $X' = \log(X + 1)$ because their variances tended to increase with the mean values (Zar 1984).

RESULTS

The wood density of *N. heimii* was 0.79 g cm^{-3} and that of *S. macroptera* was 0.53 g cm^{-3} in a dried condition. Carbon in *N. heimii* wood pieces did not decrease with time after a 10–20% loss in the initial mass in the first year (Figure 1a). The average loss rate was between 0.166 and 0.260 y^{-1} for the 1-y period, but only $< 0.100 \text{ y}^{-1}$ for longer periods (Figure 1b). In contrast, *S. macroptera* wood pieces lost C remarkably fast in the presence of termites (Figure 1c). Carbon decreased to less than half the initial mass in the 3-y period. Loss rates without termites were lower than 0.1 y^{-1} , but those with termites were higher except at site N in the 1-y period (Figure 1d). The enhanced loss of C by termites was indicated by the ANOVA as significant effects of the treatments on loss rate ($F_{1,31} = 12.4$, $P = 0.0014$). A significant interaction between treatments and tree species ($F_{1,31} = 7.44$, $P = 0.0104$) showed that C loss was enhanced by termites only for *S. macroptera*.

Nitrogen did not decrease, but increased markedly with time in *N. heimii* (Figure 2a). Loss rates were negative and decreased abruptly in the 2-y period

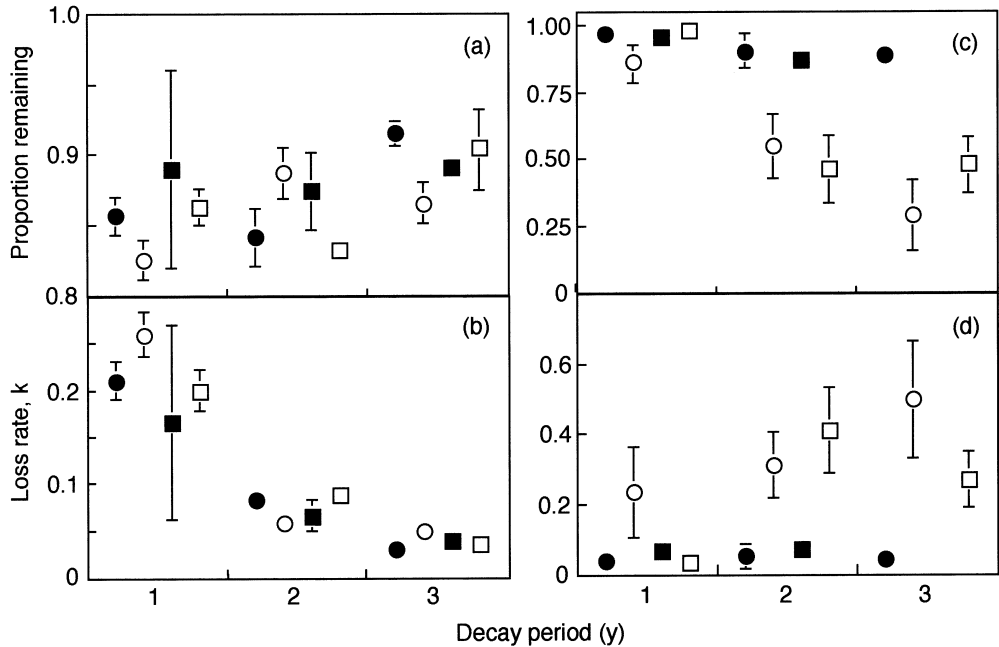


Figure 1. Changes in C content with length of decay period in sawn pieces of *Neobalanocarpus heimii* and *Shorea macroptera* wood. (a) Remaining proportion of the initial mass, *N. heimii*; (b) annual mass loss rate, *N. heimii*; (c) remaining proportion of the initial mass, *S. macroptera*; (d) annual mass loss rate, *S. macroptera*. Means and SEs are shown. Circles, regenerating forest site; squares, natural forest site; closed symbols, termite exclusion trays; open symbols, control trays.

(Figure 2b), suggesting that external N was immobilized. C/N ratios decreased with the decay period (Figure 2c) as expected from hardly lost C and accumulated N. Nitrogen in *S. macroptera* increased in the absence of termites, but it decreased in the presence of termites (Figure 2d). As a result, loss rates differed greatly between the treatments (Figure 2e). C/N ratio was originally 319 on average and then declined towards < 250 in 2 and 3 y with and without termites (Figure 2f). Treatments, decay periods and tree species had significant effects on loss rates of N ($F_{1,31} = 11.24$, $P = 0.0021$; $F_{1,31} = 10.88$, $P = 0.0024$; $F_{1,31} = 26.80$, $P < 0.0001$). A significant interaction between treatments and tree species ($F_{1,31} = 10.59$, $P = 0.0028$) supported that N loss was enhanced by termites only for *S. macroptera*. Decay periods and tree species also gave significant effects on C/N ratio ($F_{1,31} = 195.0$, $P < 0.0001$; $F_{1,31} = 53.4$, $P < 0.0001$), but treatments did not ($F_{1,31} = 0.09$, $P = 0.765$). The overall decline of C/N with time suggests that N was immobilized in both tree species.

In *N. heimii* wood, phosphorus was also accumulated (Figure 3a). Accumulation was fairly considerable in the 1-y, but slowed in the 2- and 3-y periods (Figure 3a, b). C/P ratios were originally $c. 5 \times 10^4$ and decreased by about a half in 1 y mainly due to P accumulation (Figure 1a, 3c). In *S. macroptera* wood, P was hardly accumulated (Figure 3d, e). Although C/P ratios increased with high variances in 2 y at site N, no overall trend was observed (Figure 3f). Decay

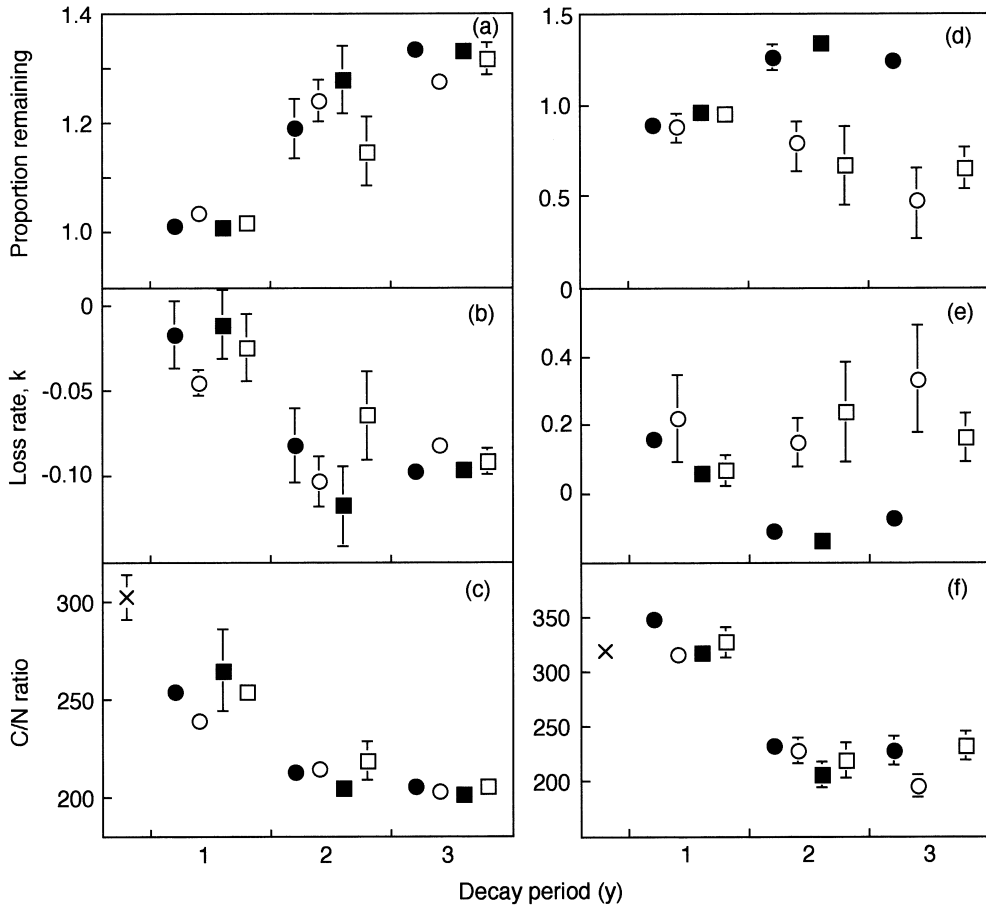


Figure 2. Changes in N content with length of decay period in sawn pieces of *Neobalanocarpus heimii* and *Shorea macroptera* wood. (a) Remaining proportion of the initial mass, *N. heimii*; (b) annual mass loss rate, *N. heimii*; (c) C/N ratio, *N. heimii*; (d) remaining proportion of the initial mass, *S. macroptera*; (e) annual mass loss rate, *S. macroptera*; (f) C/N ratio, *S. macroptera*. Symbols as in Figure 1, except crosses in (c) and (f) representing intact wood pieces.

period and tree species had significant effects on loss rates of P ($F_{1,31} = 7.64$, $P = 0.0095$; $F_{1,31} = 35.75$, $P < 0.0001$), but treatments did not ($F_{1,31} = 0.80$, $P = 0.377$). Only tree species had a significant effect on C/P ratios ($F_{1,31} = 52.30$, $P < 0.0001$).

For all these analyses, sites did not have any significant effects. Decomposition of these heavy and light hardwoods did not proceed differently at the natural and regenerating forests as far as loss rates of C, N and P and their ratios were concerned.

Termites collected both from *N. heimii* and *S. macroptera* were *Macrotermes malaccensis* (Haviland), *Ancistrotermes pakistanicus* (Ahmad) and *Odontotermes sarawakensis* Holmgren. Collected only from *N. heimii* was *Dicuspiditermes nemorosus* (Haviland). Nine of 10 collections had *M. malaccensis* with another collection of

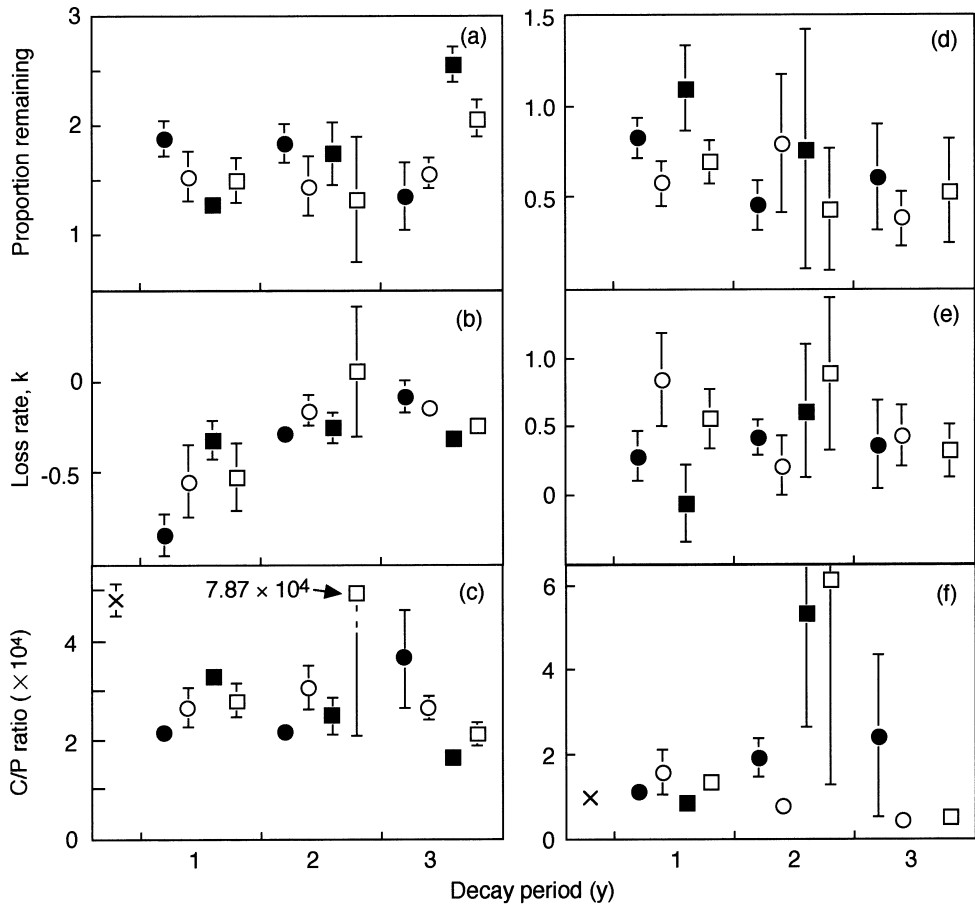


Figure 3. Changes in P content with length of decay period in sawn pieces of *Neobalanocarpus heimii* and *Shorea macroptera* wood. (a) Remaining proportion of the initial mass, *N. heimii*; (b) annual mass loss rate, *N. heimii*; (c) C/P ratio, *N. heimii*; (d) remaining proportion of the initial mass, *S. macroptera*; (e) annual mass loss rate, *S. macroptera*; (f) C/P ratio, *S. macroptera*. Symbols as in Figure 2.

O. sarawakensis at site N. At site R, 15 of 19 collections had *A. pakistanicus*. This clear faunal difference in termites did not produce site effects. These wood-foraging termites are likely to be comparable in the ability of decomposing wood litter in this size category.

DISCUSSION

The contribution of termites in the loss of C and N from *S. macroptera* wood was considerable, but not from *N. heimii*. This difference might be related to the difference in the wood density. A large proportion of studies has suggested, however, that wood density is not among the main factors that control termite foraging, rather they demonstrated that allelochemicals are operating, as reviewed by Scheffrahn (1991). In comparison with the high density wood of

Paranephelium macrophyllum King (Takamura & Kirton 1999), the C loss rate with termites of *N. heimii* (0.04–0.26 y^{-1}) was lower than that of *P. macrophyllum* (0.37–0.62 y^{-1}), although the wood density of *N. heimii* (0.79 g cm^{-3}) was lower than that of *P. macrophyllum* (1.02 g cm^{-3}). The C loss rate of *S. macroptera* was intermediate (0.03–0.50 y^{-1}) whereas its wood density was 0.53 g cm^{-3} . On the other hand, the loss rate of dry weight of *Shorea parvifolia* (wood density = 0.52 g cm^{-3}) was as high as 0.61 and 1.07 y^{-1} (Abe 1980). Thus the wood density does not correlate linearly with decay rate in the presence of termites. *N. heimii* wood is extremely durable without preservation treatment (Wong 1982). Malaysian heavy hardwoods are durable because most of them contain toxic chemicals that deter decomposers (Menon 1993). Therefore, the clear difference in decay rates between *N. heimii* and *S. macroptera* may plausibly be hypothesized to be partially due to chemicals that deter termite attack.

The relative low rates of decomposition in the present citation may also be accounted for by differences in nutrient concentrations. In my previous study (Takamura & Kirton 1999) and that of Abe (1980), test wood consisted of cut pieces of logs or branches covered with phloem and cambium rich in nutrients. In the present study, wood pieces of *N. heimii* as well as of *S. macroptera* were sawn from logs so that they lacked phloem and cambium parts. The C/N and C/P ratios of *P. macrophyllum* (Takamura & Kirton 1999) were 257 and about 5×10^3 , respectively, and lower than the values of *N. heimii* and *S. macroptera*, indicating that the woods used in the present study may have been less attractive to termites.

Once a *N. heimii* tree falls, it accumulates nutrients. There appears to be no release of the accumulated nutrients in 3 y (Figure 3a, b). Fallen *N. heimii* trees may therefore be nutrient sinks in tropical rain forest. Generally speaking, wood decay fungi have a key role in immobilizing nutrients and increasing nutrient concentrations in wood litter as indicated by C/N and C/P (Boddy & Watkinson 1995). But in this case, a slight increase of C seems to have also occurred, which is not probable by heterotrophic fungi (Figure 1a). Tentative calculations of increase in C and N masses in the second and third years from these figures gave the C/N ratio of 40–50 for the increased biomass. These ratios are not so far from those of the food ball of *Hospitalitermes* termites that comprises epiphytes like lichens, algae and mosses (Miura & Matsumoto 1997), but very different from that of *N. heimii* wood. Those autotrophic or mixotrophic organisms could cause an accumulation of nutrients.

Once a *S. macroptera* tree falls, it loses nutrients in the presence of termites. The magnitude of this increase in rate of loss was up to 12.3 times. This tree is a source of nutrients. If termite activity is suppressed, accumulation of nutrients can occur (Figure 2d). The fate of woods that accumulate nutrients is important in nutrient cycling within forest ecosystems since nutrients retained by them cannot be utilized directly by trees unless tree roots invade them, as has been observed in billets of *P. macrophyllum* (Takamura & Kirton 1999). Matsumoto & Abe (1979) and Yamashita & Takeda (1998) show the significant

role of termites in decomposition of leaf litter in Pasoh. This study reveals that termites should be even more important for nutrient cycling in preventing immobilization and accumulation of nutrients in wood litter.

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