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**STUDIES ON THE DISTRIBUTION AND ECOLOGICAL ROLE OF
TERMITES IN A LOWLAND RAIN FOREST OF WEST MALAYSIA
(3) DISTRIBUTION AND ABUNDANCE OF TERMITES IN PASOH FOREST
RESERVE^{1), 2)}**

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西マレーシアの低地多雨林におけるシロアリの分布と役割に関する研究

(3) パソフ多雨林におけるシロアリの分布・密度・現存量

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Synopsis

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The distribution and abundance of termites were studied in a lowland rain forest (Pasoh Forest Reserve) of West Malaysia. Fifty-two species were found in a 1-ha plot, 14 species in a 16 m² area and 10 species in a 2 m² area. Density and biomass of the entire termite population were estimated at 3000-4000/m² and 2.2-2.6 g. d.w./m² respectively. Dominant termites were *Macrotermes malaccensis*, *M. carbonarius* and *Dicuspitermes nemorosus*. More than half of the entire termites (in biomass) cultivated fungi in their nests. Termites occupied all strata of the forest from the height of more than 30 m on and in the standing trees down to the depth of 30 cm in the soil. Termites living deeper in the soil than 30 cm are very scarce. Termites making subterranean and intermediate nests shared about two thirds of the total termite population in the number of species, density and biomass. Mound builders are not predominant, though they are important termites. The populations of arboreal nest making termites were low. The termites occupied an overwhelmingly dominant position among soil macrofauna in Pasoh Forest.

Introduction

Termites are widely distributed through the tropical and subtropical regions. Some important studies were carried out on the abundance, distribution, and role of termites in the savannah ecosystems of West Africa (JOSENS, 1972; LEPAGE, 1974; WOOD et al., 1977), but only a little information has been available on the ecology of termites in tropical

rain forests. There have been no reliable estimates of total termite populations in a single area of tropical rain forest. We attempted to study the distribution and abundance of termites together with their role in the breakdown of dead plant materials in a tropical rain forest of West Malaysia.

This study was carried out as a part of the Joint Malaysia-Japan-U. K. IBP (International Biological Programme) Project of a lowland rain forest at Pasoh Forest Reserve in West Malaysia. The present paper deals with the distribution and abundance of termites in Pasoh Forest Reserve. Population density, biomass, nitrogen and carbon content, energy value and respiration rate of dominant termites in the forest were separately reported by

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MATSUMOTO (1976), faunal composition by ABE (1978) and feeding habits by ABE (1979) and leaf litter consumption by termites by MATSUMOTO & ABE (1979).

Study Area

The study was carried out at Pasoh Forest Reserve in the State of Negeri Sembilan, West Malaysia (ca. 2°59'N and 102° 18'E, alt. 75–190 m). The IBP Research Area (ca. 650 ha) occupied the central part of the Forest Reserve and was surrounded by a buffer zone consisting of undisturbed or selectively logged forest. Five 2-ha 100 m × 20 m plots (Plots 1, 3, 4, 6 and 7) and five 20 m × 200 m plots (Plots 2, 5, 8, 9 and 10) were established within the Research Area for the study of vegetation, primary production and soil fauna. Background information for IBP soil fauna study was given by KIRA (1976). The study on termite populations was carried out mainly in and around Plot 1.

The Research Area is covered by undisturbed lowland rain forest of *Shorea-Dipterocarpus* type (SOEPADMO, 1973). Giant trees of the topmost emergent layer reach a height range of 45–55 m, and a closed main canopy is formed at 25–35 m above the ground by the second layer trees.

The area receives an average precipitation of slightly less than 2,000 mm per year, representing the area with least amount of rainfall in West Malaysia. The air temperature near the forest floor ranged between 25°C and 27°C and the relative humidity was almost always close to saturation through the day (AOKI et al., 1975).

Methods

1) Density and dispersion of conspicuous termite nests

The distribution of dominant arboreal, epigeous and intermediate (ABE, 1978) nests was mapped in a 100 m × 100 m area (T-Plot) of Plot 1, a 40 m × 50 m area (M-Plot) and a 4 m × 4 m area (A-Plot) near Plot 1. Some species making arboreal nests higher than 10 m above the ground level were not recorded owing to technical difficulty. Some epigeous nests may have been overlooked but this was checked in a 10 m × 20 m area of M-Plot where soil was dug to a depth of 30 cm and the nests were confirmed after being enumerated by observation.

Soil was dug up to a depth of 20–30 cm to locate dominant subterranean nests in a 10 m × 20 m area (M'-Plot) of M-Plot and a 4 m × 4 m area (A-Plot)

after arboreal, epigeous and intermediate nests had been recorded. *Macrotermes malaccensis* (HAVILAND) and *Longipeditermes longipes* (HAVILAND) making big and concentrated subterranean nests were easy to locate, but many other subterranean nests were usually too diffuse to locate.

The nests in living trees were recorded in a 20 m × 100 m area (K-Plot) of Plot 1, where trees had been clear-felled for primary production studies 6 months before the study of termites commenced. It is possible that termites nesting in the living trees abandoned the nest after the trees were felled.

2) Population density and biomass of termites making conspicuous nests

The population density and biomass of termite populations making conspicuous nests (arboreal, epigeous, intermediate and subterranean nests) were calculated from a) abundance of the nests, and b) average number and biomass of the population inhabiting the nest. Forty-nine nests of 8 species were sampled from Plots 1, 5 and 10 to determine the population inhabiting the nests. They were as follows: 39 epigeous nests (4 of *Macrotermes carbonarius* HAGEN, 24 of *Dicuspiditermes nemorosus* (HAVILAND) and 11 of *Homallotermes foraminifer* (HAVILAND)), 6 arboreal nests (5 of *Bulbitermes singaporensis* (HAVILAND)? and 1 of *Hospitalitermes* sp.) and 4 subterranean nests (3 of *Macrotermes malaccensis* and 1 of *Longipeditermes longipes*). The population in a nest was usually very large and direct counting of whole individuals was not employed. The procedure and most of the results were separately reported by MATSUMOTO (1976).

3) Population density and dispersion of subterranean termites making diffuse nests

Most subterranean termites (except *Macrotermes malaccensis* and *Longipeditermes longipes*) made diffuse nests which were difficult to locate and their density and dispersion were studied by direct sampling from the soil. The density and vertical distribution of subterranean termites was studied in a 1 m × 2 m area of A-Plot where the dominant subterranean nests were also located. The area was divided into 8 quadrats, each measuring 50 cm × 50 cm, and one of them was further divided into 4 small quadrats, each measuring 25 cm × 25 cm. Soil in each quadrat was dug up successively to a depth of 25 cm and termites were extracted from every 5 cm layer of soil by hand-sorting. Small amounts of soil were put into a large basin (ca.

60 cm in diameter) and transported to a large table which was brought into the forest near the study site. Five specially trained workers extracted termites from the soil sample by hand-sorting. This method ensured that few termites died in the soil samples and consequently made it easy to rapidly separate the live termites from soil. However, it is possible that the disturbance caused by taking a soil sample would affect the number of termites in subsequently sampled adjacent areas, resulting in termites escaping from the sampling area before the soil was completely dug up, because the whole sampling process took four days.

The present survey was carried out in February–August 1972, October 1973–January 1974 and in August 1974 by ABE and in August 1972–January 1973 and May–October 1973 by MATSUMOTO.

Results

(1) Nest sites of termites

Fifty-seven species of 23 genera belonging to 2 families and 6 subfamilies have been found in the Pasoh Forest Reserve and 52 species in a 1-ha plot (T-Plot). Termite nests were classified into five types by NOIROT (1970); a) nests within wood, b) subterranean nests, c) epigeous nests, d) arboreal nests and e) inquilinies. ABE (1978) examined the nests of termites in Pasoh Forest and added another, the intermediate type, which is intermediate among subterranean, epigeous, arboreal nests and nests within wood. Nest site composition of each subfamily is shown in Table 1 and nest sites of the dominant 18 genera in Pasoh Forest are schematically shown in Fig. 1. Intermediate and subterranean nests were dominant in the number of species in Pasoh Forest, though epigeous and arboreal nests were conspicuous.

There was a rich variety of nest sites, including all strata of the forest from the height of more than 30 m on and in the standing trees down to the depth of 30 cm in the soil. The termites were, however, hardly observed deeper than 30 cm in the soil where many small stones were distributed. There were some correlations between the taxonomic position of the species and their nest sites. The nest sites of both Coptotermitinae and Rhinotermitinae of the Rhinotermitidae, a relatively primitive group of termites in Pasoh Forest, were restricted in or around standing and fallen trees. On the other hand, the 4 subfamilies of Termitidae had a wide variety of nest sites and termites of each subfamily differed in their vertical distribution of nest sites. The Amitermitinae, including *Microcerotermes*, constituted a dominant arboreal termite group. Many species of Termitinae showed no dependency on trees, though some species nested in and around fallen logs or dead stumps. The Termitinae made epigeous, subterranean (shallow layer) and intermediate nests which were mainly distributed on or near the ground surface. The Macrotermitinae constituted a dominant subterranean (deep layer) group, though *Macrotermes carbonarius* made the biggest mound in Pasoh Forest. The nests of Macrotermitinae had no direct relation with trees. Affinity to trees was again found in the nests of Nasutitermitinae, which was the richest of all subfamilies of the forest in the variety of the nest habitat as well as the number of species (ABE, 1978).

(2) Dispersion of the arboreal and epigeous nests

The dispersion of the arboreal and epigeous nests in T-Plot (1 ha) is shown in Fig. 2. The nests higher than 10 m above the ground level are not shown in the figure. According to the observation

Table 1 Nesting habits of termites in Pasoh Forest

Subfamily	Nesting habits	Nest in trees	Arboreal nest	Intermediate nest	Epigeous nest	Subterranean nest	Unknown	Number of species
Rhinotermitidae		2		4			1	6
Coptotermitinae				1			1	2
Rhinotermitinae		2		3				4
Termitidae		1	9	15	7	25	1	50
Amitermitinae			4			1		5
Termitinae				8	5	7		14
Macrotermitinae					2	10		12
Nasutitermitinae		1	5	7		7	1	19
Unidentified						1		1
Total No. of species		3	9	19	7	26	2	57

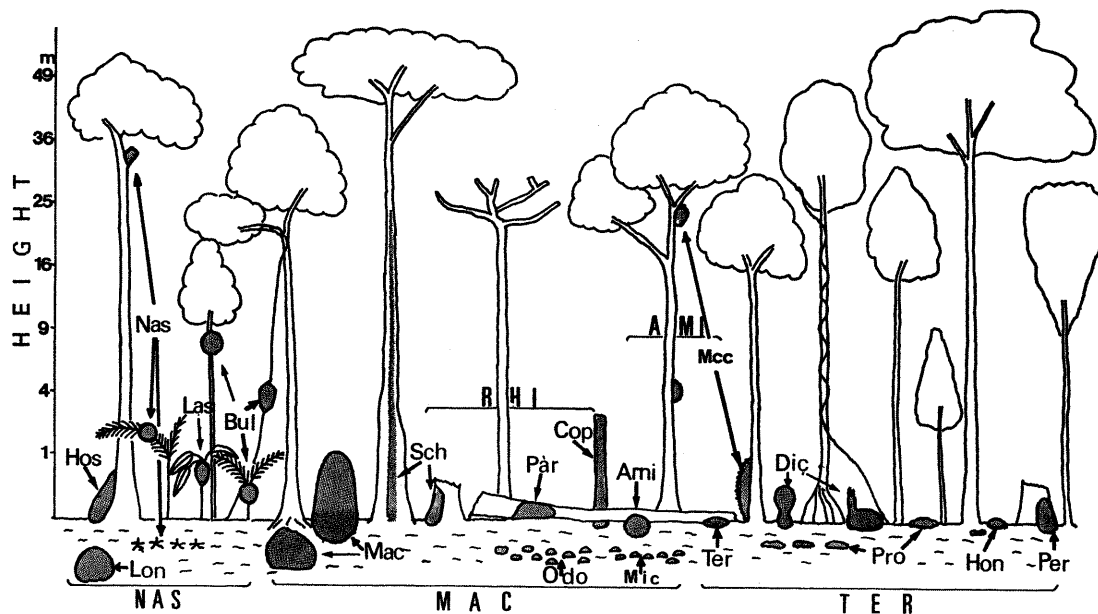


Fig. 1. Vertical distribution of termite nests in Pasoh Forest. Abbreviation: Rhinotermitidae (RHI): Sch = *Schedorhinotermes*, Par = *Parrhinotermes*, Cop = *Coptotermes*, Amitermitinae (AMI): Ami = *Amitermes*, Mcc = *Microcerotermes*, Termitinae (TER): Ter = *Termes*, Per = *Pericapritermes*, Dic = *Dicuspiditermes*, Pro = *Procapritermes*, Hom = *Homalotermes*, Macrotermitinae (MAC): Mac = *Macrotermes*, Odo = *Odontotermes*, Mic = *Microtermes*, Nasutitermitinae (NAS): Hos = *Hospitalitermes*, Lon = *Longipeditermes*, Nas = *Nasutitermes*, Lac = *Lacessititermes*, Bul = *Bulbitermes*.

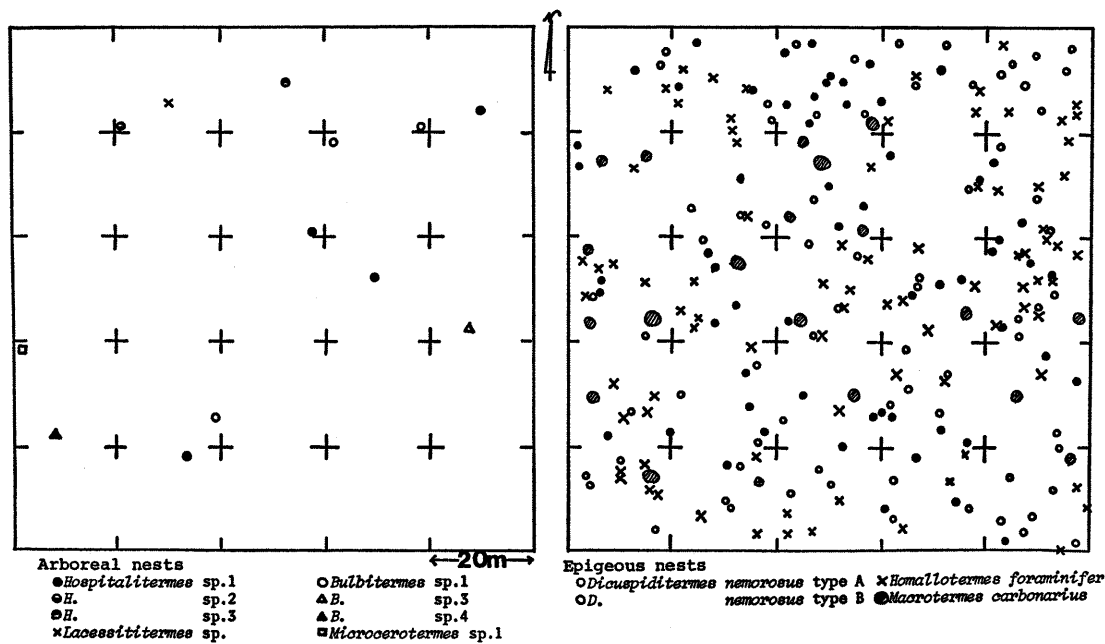


Fig. 2. Dispersion of arboreal, epigeous and conspicuous intermediate nests. Arboreal nests located higher than 10m, small epigeous or intermediate nests such as *Procapritermes* spp. and *Termes* spp. are omitted.

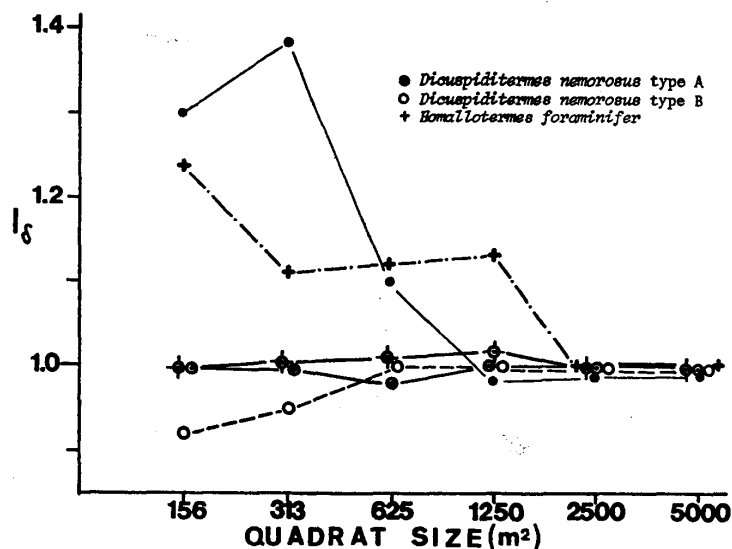


Fig. 3. $I\delta$ -quadrat size curve for *Dicuspiditermes nemorosus* type A, type B and *Homalotermes foraminifer* nests in T-Plot (100 m \times 100 m).

from a wooden walk-up tower which was constructed around a big trunk of *Shorea leprosula* near Plot 4 up to the height of 36 m just below the tree crown, some nests of *Microcerotermes* were recognized on the tree trunk at a height of more than 10 m around the tower, but their density could not be estimated. Thirteen arboreal nests of 8 species were found in the 1-ha plot. There was a large number of arboreal nesting species with a low number of nests per species.

Macrotermes carbonarius made a big mound, and *Dicuspiditermes nemorosus* (type A and type B) and *Homalotermes foraminifer* made conspicuous epigeous nests of medium size. Their shape, size and weight were reported by MATSUMOTO (1976) and ABE (1978). Two hundred and thirty-six epigeous nests of these species were distributed in 1-ha plot (Fig. 2). Their distribution pattern was examined by means of the area- $I\delta$ curve (MORISITA, 1959) shown in Fig. 3. The nests of *D. nemorosus* type A and *H. foraminifer* showed a somewhat aggregated distribution, while *D. nemorosus* type B was distributed more or less uniformly. The pattern of distribution, however, became random if all of these medium size nests were put together. *Macrotermes* nests were reported to exclude the presence of other termites in their immediate environment (BOUILLON, 1970), but such a relation was not necessarily apparent in Pasoh Forest.

(3) Distribution of subterranean nests

Many species made nests in the soil, which were

usually difficult to locate except for *Macrotermes malaccensis* and *Longipeditermes longipes* which made concentrated subterranean nests. *Odontotermes* spp. and *Microtermes* sp. made diffuse subterranean nests composed of small chambers containing fungus combs. The distribution of the nests of *M. malaccensis* and *L. longipes* together with the fungus combs of *Odontotermes* and *Microtermes* is shown in Figs. 4 and 5.

(a) Vertical distribution

The vertical distribution of the nests in a 4 m \times 4 m area (A-Plot) is shown in Fig. 4.

i) Shallow layer (ground surface and 0–5 cm in depth): *D. nemorosus*, *H. foraminifer* and *Procapritermes* sp. 1 (all Termitinae) made their nests on the ground surface. The nests of *Procapritermes* sp. 1 were not easy to find owing to their small size, flat shape, dark colouration and because they were covered with leaf litter. The subterranean part of these epigeous nests extended by 0–10 cm below the ground level. Many larvae and nymphs of the other species of Termitinae occurred, but their nests were difficult to locate.

ii) Middle layer (5–15 cm): Many workers, soldiers and larvae of Termitinae and Nasutitermitinae occurred in this layer. This suggested that some species nested in this layer, but their nests were difficult to distinguish from mere soil, even when queens were found. The shaded area in Fig. 4c indicates where many workers, soldiers and larvae of *Procapritermes* sp. 4 were observed. *Nasutitermes* sp. 1, whose soldiers were dimorphic,

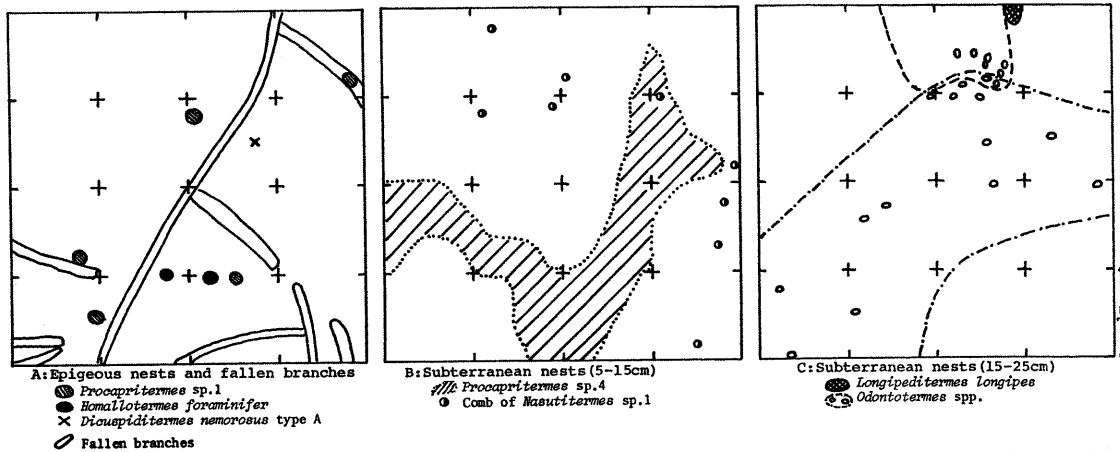


Fig. 4. Distribution of epigeous and subterranean nests in A-Plot (4 m x 4 m). The shaded area shows the site where many workers, soldiers and larvae of *Procapritermes* sp. 4 were observed.

also seemed to nest in this layer. Passageway of this species expanded into small chambers where many workers, soldiers, larvae and strange constructions of soil (2.5 cm x 2.5 cm x 2.5 cm in size), similar to the fungus combs of Macrotermitinae, were observed.

iii) Deep layer (15-25 cm): Termitinae were hardly observed in this layer. Two species of *Odontotermes* were observed to make diffuse nests composed of small oval chambers containing fungus combs connected by galleries. There was little dif-

ference in the vertical distribution of their fungus combs, but their horizontal distribution was clearly separated (the shape and size of fungus combs of the two species were different from each other). Twenty-two fungus combs were found in 4 x 4 m area. A nest of *L. longipes* was also observed in this layer.

(b) Horizontal distribution

The horizontal distribution of dominant subterranean nests in a 10 m x 20 m area of M-Plot is shown in Fig. 5. About 10 nests of *Odontotermes*

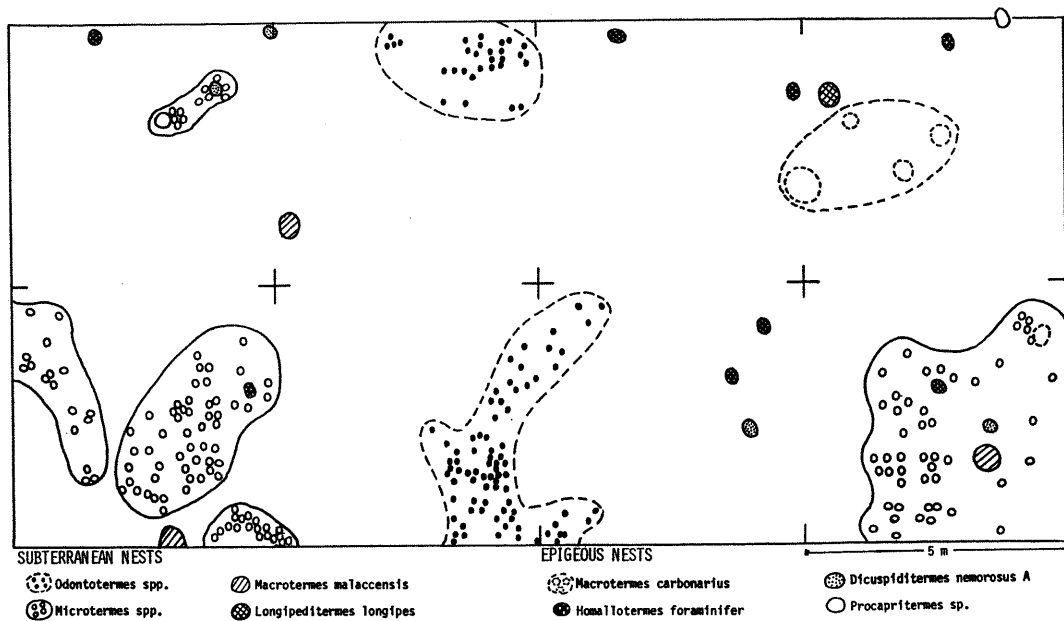


Fig. 5. Nests of dominant subterranean species in M-Plot (10 m x 20 m). Dominant epigeous nests are also shown. Open and closed circles show fungus combs.

spp., *Microtermes* sp., *Macrotermes malaccensis* and *Longipeditermes longipes* were found in this area. No overlapping was observed in the range of distribution of fungus combs of *Odontotermes* spp. and *Microtermes* sp. The study of subterranean termite populations is still in its earliest stages (SANDS, 1972) and there are few studies on their nest abundance. HARTWIG (1966) estimated the density of nests of *Odontotermes latericius* in South Africa at about 1/ha. NEL (1968) estimated the density of *Hodotermes mossambicus* at 110/ha.

(4) Abundance of nests

The abundance of nests of different types are shown in Table 2. It goes without saying that the total number of nests can never be known without completely digging up soil and felling all trees in the study area. Owing to this technical difficulty, the enumeration of Table 2 could not cover arboreal nests located higher than 10 m, many intermediate nests such as those of *Termes* spp., *Parrhi-*

notermes sp., *Schedorhinotermes* spp., *Pericapritermes* spp. and *Oriensubulitermes* spp. and various subterranean nests.

The incidence of overlooking the nests was studied in a 10 m × 20 m area of M-Plot, where the soil was dug up to the depth of 30 cm and nests were confirmed after the enumeration of the epigeous nests by eye observation. *D. nemorosus* type A and B nests were conspicuous and were not overlooked at all, while 25% of *H. foraminifer* nests had been missed at the first census, owing to their flat shape, dark colouration and because they were covered with leaf litter. The number of *H. foraminifer* nests in T-Plot given in Table 2 refers to the result of eye observation.

The nests of *Macrotermes* were sometimes difficult to distinguish from a mere heap of soil, especially near the base of a big tree. Only the number of confirmed nests is shown in Table 2, so that the figures might be somewhat underestimated. The size of sample quadrats for estimating the density of

Table 2 Abundance of nests of different types

Type of nest	Plot (Area studied)	T-Plot (1 ha)	M-Plot(No/ha) (0.2 ha)	A-Plot(No/ha) (16 m ²)	M ² -Plot(No/ha) (0.02 ha)	K-Plot(No/ha) (0.2 ha)
Arboreal nests		8	4(20)			
<i>Bulbitermes</i> sp. 1		3	0			
<i>B.</i> sp. 3		1	4(20)			
<i>B.</i> sp. 4		1	0			
<i>Lacessititermes</i> sp. 1		1	0			
<i>L.</i> sp. 2		1	0			
<i>Microcerotermes</i> sp. 1		1	0			
Epigeous nests						
Big size		20	3(15)			
<i>Macrotermes carbonarius</i>		20	3(15)			
Medium size		216	74(370)			
<i>Dicuspiditermes nemorosus</i> A		60	19(95)			
<i>D. nemorosus</i> B		71	22(110)			
<i>Homalotermes foraminifer</i>		85	33(165)			
Small size				4.5(2800)		
<i>Procapritermes</i> sp. 1				4.5(2800)		
Intermediate nests		5				
<i>Hospitalitermes</i> sp. 1		4				
<i>H.</i> sp. 2		1				
Subterranean nests					9.5(480)	
Fungus growers					8.5(430)	
<i>Macrotermes malaccensis</i>					3 (150)	
<i>Odontotermes</i> spp.					3.5(180)	
<i>Microtermes</i> sp. (<i>pallidus</i> ?)					2 (100)	
Not fungus growers					1 (50)	
<i>Longipeditermes longipes</i>					1 (50)	
Nests in living tree trunks						2(10)
<i>Schedorhinotermes</i> sp.						2(10)

subterranean nests and especially of small mounds (*Procapritermes* sp. 1) was not large enough to get good estimates. The nests in living tree trunks could not be enumerated until about 6 months after the felling, so that only the number of those nests confirmed by their traces was given in Table 2.

In spite of the expected difference in the accuracy of estimating nest density of different species, some conclusions may be drawn from Table 2. The density of arboreal nests, big epigeous nests (mounds) and medium-sized epigeous nests obtained in the two different plots fell within the range of 5–20/ha, 5–20/ha and 200–400/ha respectively. An inverse correlation seems to exist between the size and the abundance of epigeous nests. The density of small epigeous nests was greater than that of medium-sized nests by one decimal place, and the latter was in turn more than ten times as large as the density of big nests. The nest density of *Odontotermes* and *Microtermes*, which are diffuse fungus growers, was similar to that of medium-sized nests, and the total number of arboreal nests was similar to that of big mounds.

The abundance of termite mounds in Pasoh Forest was compared and discussed with that in various ecosystems of the world by MATSUMOTO (1976).

(5) Abundance and distribution of subterranean termites

The number of individuals and biomass of subterranean termites in a 1 m × 2 m area of A-Plot are shown in Table 3 and Fig. 6. Epigeous nests were

Table 3. Species composition of subterranean termites in a 2 m × 1 m area

Species	No. of termites	Biomass (mg in wet weight)
Macrotermitinae	308	1279.2
<i>Macrotermes malaccensis</i>	32	433.8
<i>Macrotermes carbonarius</i>	4*	503.5*
<i>Odontotermes</i> sp. 5 (soldiers)	48	81.5
<i>Odontotermes</i> sp. 6 (soldiers)	3	5.5
<i>Odontotermes</i> (workers)	221	254.9
Termitinae	1141	2038.1
<i>Procapritermes</i> sp. 1 (soldiers)	36	33.8
<i>Procapritermes</i> sp. 6 (soldiers)	20	39.2
<i>Pericapritermes</i> sp. 1 (soldiers)	93	435.1
<i>Pericapritermes</i> sp. 2 (soldiers)	32	60.5
Termitinae (workers)	960	1469.5
Nasutitermitinae	1045	1141.4
<i>Nasutitermes</i> sp. 1 (soldiers)	259	234.2
<i>Bulbitermes</i> sp. 2 (soldiers)	182	143.6
Nasutitermitinae (workers)	604	763.6
Unidentified	6	2.0
Total	2500	4460.7

* Two reproductives were included.

not found, but some foraging workers and reproductives of epigeous nest-making termites were found in this area. They are treated as subterranean termites. Ten species of subterranean termites were found in the area, and their density and biomass were 1250/m² and 2.23 g w.w./m² respectively. Termitinae constituted about half of the subterranean termite population. The species-area relation of epigeous and subterranean termites in A-

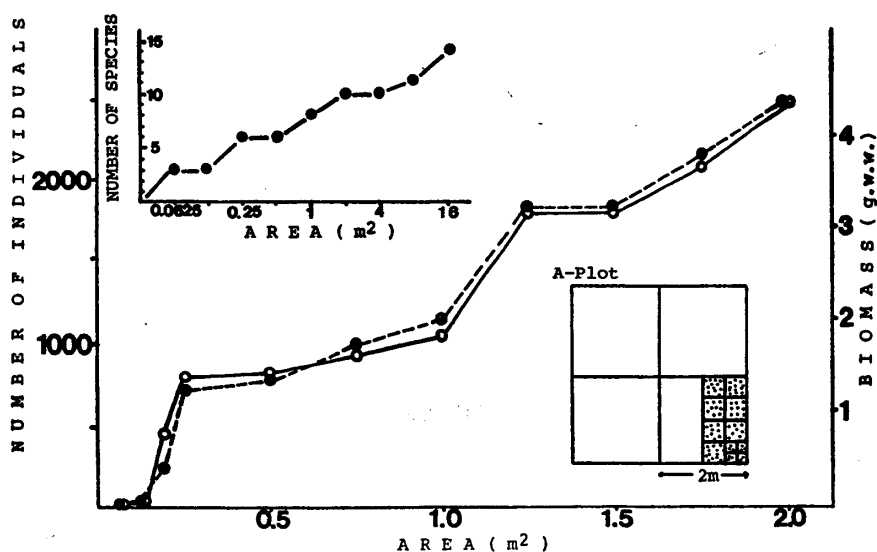


Fig. 6. Number of individuals, biomass (1 m × 2 m) and species-area relation (4 m × 4 m) in A-Plot. Biomass is shown in broken line.

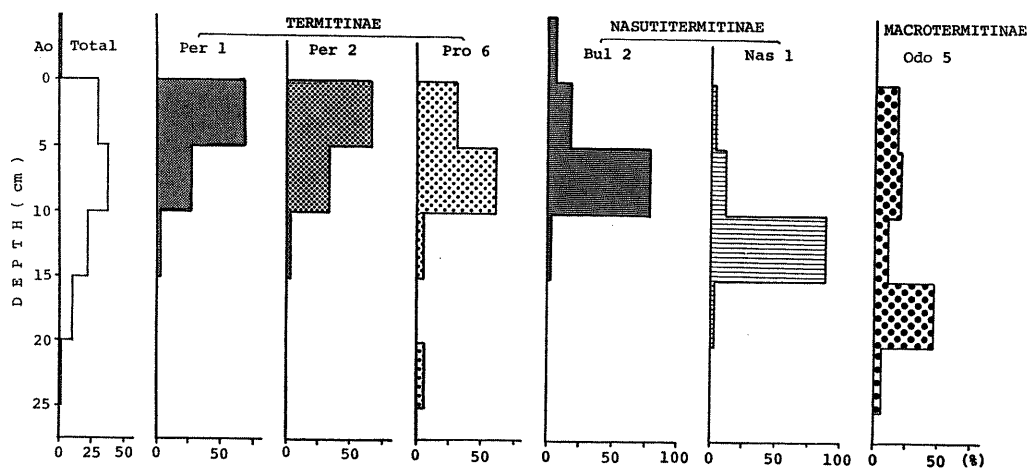


Fig. 7. Vertical distribution of dominant subterranean termites (only soldiers) in A-Plot. Abbreviation: Per 1 = *Pericapritermes* sp. 1, Per 2 = *Pericapritermes* sp. 2, Pro 6 = *Procapritermes* sp. 6, Bul 2 = *Bulbitermes* sp. 2, Nas 1 = *Nasutitermes* sp. 1, and Odo 5 = *Odontotermes* sp. 5.

Plot (4 m × 4 m) are also shown in Fig. 6. Fourteen species were found in the small area of 16 m².

The vertical distribution of subterranean termites (only soldiers) in the 1 m × 2 m area is shown in Fig. 7. The termites were mainly distributed in the 0–15 cm layer and were hardly observed in the layers deeper than 25 cm. A correlation was found between the taxonomic position of the species and their distribution pattern. Termites of the Termitinae such as *Pericapritermes* sp. 1, *Pericapritermes* sp. 2 and *Pericapritermes* sp. 6 were mainly distributed in the shallow layer (0–10 cm), those of Nasutitermitinae, such as *Bulbitermes* sp. 2 and *Nasutitermes* sp. 1, were in the middle layer (5–10 cm) and those of Macrotermitinae, such as *Odontotermes* sp. 5, were in the deep layer (15–20 cm).

The distribution of subterranean termites in Pasoh Forest was characterized by the concentration of termites in the shallow layer and the vertical segregation of their habitats as stated above. According to WOOD et al. (personal communication), many subterranean termites are distributed to the depth of 1–2 m in the savannah of West Africa in the dry season. As regards the horizontal distribution at similar depth, no overlapping was observed among the range of distribution of fungus combs of *Odontotermes* spp. and *Microtermes* sp. as shown in Figs. 4 and 5. On the other hand many species of Termitinae which made diffuse subterranean nests seemed to overlap each other at 0–15 cm depth in the soil.

(6) Density and biomass of the entire termite population

The termites were divided into six groups to estimate their population density and biomass: 1) Termites making conspicuous mounds, 2) Termites making arboreal nests, 3) Termites making conspicuous intermediate nests, 4) Termites making concentrated subterranean nests (subterranean termites A) and 5) Other subterranean termites making diffuse nests (subterranean termites B) and 6) Termites in living or dead trees. The last group is not dealt with here. Termites such as *Procapritermes* sp. 1 and *Termes* spp. which make inconspicuous epigeous or intermediate nests are included in subterranean termite B. The density and biomass of termites in Pasoh Forest are shown in Table 4. Average population density and biomass of dominant termites were separately reported by MATSUMOTO (1976) and those of macrofauna by CHIBA (1974). In spite of the expected difference in the accuracy of estimation of population and biomass among the five groups of termites, some conclusions may be drawn from Table 4.

The most abundant species were *Macrotermes malaccensis* and *Dicuspitermes nemorosus*; *M. carbonarius*, *Homalotermes foraminifer* and *Longipeditermes longipes* were also abundant. The abundance of mound making termites, subterranean termites A and subterranean termites B was similar; approximately 1000/m². In comparison, the populations of arboreal nest making termites were low. Termites making arboreal nests higher than

Table 4. Population in a nest, nest density, population density, live weight and dry weight biomass of termites in Pasoh Forest. Number and weight of termites in a nest are after MATSUMOTO (1976) except for *Hospitalitermes* sp.

Category	No. of samples	Soldier	Worker	Larva	Nymph Alate	Total	No. of nests per ha	No. of termites per m ²	Biomass g w.w. per m ²	Biomass g d.w. per m ²
Mound making termites										
<i>Macrotermes carbonarius</i>	4	4200	26800	56900	600	88500	15-20	130-180	1.21-1.62	0.33-0.43
<i>Dicuspitermes nemorosus</i> type A	15	560	12350	22000	0	45000	60-95	270-430	0.37-0.58	0.08-0.12
<i>Dicuspitermes nemorosus</i> type B	9	1300	28700	17000	0	47000	71-110	330-520	0.63-0.97	0.15-0.24
<i>Homalotermes foraminifer</i>	11	1000	9000	2600	0	12600	85-165	110-210	0.15-0.29	0.04-0.07
Arboreal nest making termites										
<i>Bulbitermes</i> sp. 1 (<i>singaporensis</i> ?)	5	7300	35100	—	0	42400	8-20 ^{a)}	30-80 ^{a)}	0.04-0.10 ^{a)}	0.01-0.02 ^{a)}
Intermediate nest making termites										
<i>Hospitalitermes</i> sp.	1	43000	124000	38000	2000	207000	0-5	0-100	0.00-0.28 ^{b)}	0.00-0.08 ^{b)}
Subterranean termites A										
<i>Macrotermes malaccensis</i>	3	2700	27700	13000	0	43400	150	650	4.06 ^{c)}	1.06 ^{c)}
<i>Longipedermes longipes</i>	1	23300	44400	11000	0	78700	50	390	—	—
Subterranean termites B										
Total										
								3160-3810	8.69-10.13	2.23-2.58

a) Nests of some other arboreal species than *Bulbitermes* sp. 1 (*singaporensis*?) are included.

b) Larvae and nymphs were not included.

c) Larvae were not included.

d) Wet weight

e) Dry weight/wet weight = 1/4 was used.

10 m above the ground were not included in Table 4, but observations from a 36 m walk-up tower indicated that they were scarce. Total termite population density was estimated to be about 3,000–4,000/m². The density of subterranean termites (both A and B) was 2,290/m² and constituted 66% of the total termite population. The density of conspicuous mound making termites was 840–1,340/m² and constituted about 30% of the total termite population. The most abundant genera were *Macrotermes* and *Dicuspitermes* which constituted about 45% of the total termite population. Approximately two thirds of the total termite population were subterranean and one third epigeous.

The biomass of the total termite population was estimated at 2.2–2.6 g d.w./m² (8.6–10.2 g w.w./m²). The biomass of both *Macrotermes malaccensis* and *M. carbonarius* was 1.39–1.49 g/m² and constituted about 58% of the total biomass. The biomass of both *Macrotermes* and *Dicuspitermes* was 1.74 g/m² and constituted about 72% of the total termite biomass. The biomass of epigeous nest making termites was 0.60–0.86 g/m² and constituted about 30% of the total biomass. In comparison, the bio-

mass of arboreal termites was low, although there were several species.

Recently WOOD & SANDS (1978) reviewed and discussed the role of termites in ecosystems. They summarized the abundance and live weight biomass of termites in different ecosystems. Abundance and biomass of termites in Pasoh Forest are compared in Table 5 with those in other tropical regions, based on the study of WOOD & SANDS (1978). There is considerable variation in the figures for abundance in natural ecosystems of tropical regions. Maximum populations in rain forest were recorded in Trinidad by STRICKLAND (1944) from soil cores only 7.5 cm deep and did not include the mound and arboreal nest making termites. The abundance of termites in Trinidad seems to be much higher than in Pasoh Forest. It is evident that more studies in tropical rain forest are necessary to compare the density and biomass of termites between forest and savannah, where some intensive ecological studies have been carried out in West Africa (JOSENS, 1972; LEPAGE, 1974; WOOD et al., 1977). The density of arboreal termites in Pasoh Forest is the highest of all ecosystems that have been studied. The domi-

Table 5. Abundance and live weight biomass of termites in different ecosystems of tropical regions (partly cited from WOOD & SANDS (1978), Table 9–5)

Ecosystem	Subterranean termites*	Mound-building termites	Arboreal nest making termites	Total no. per m ²	Biomass g.w.w. per m ²	Author
Forest						
Rain forest						
Malaysia	2290	1090	105 ^{a),b)}	3485 ^{a)}	9.4 ^{a)}	ABE & MATSUMOTO (present paper)
Trinidad	4450					STRICKLAND (1944)
<i>Brachystegia</i> forest						
Congo	500	338		1000	11.0	MALDAGUE (1964)
Semi-deciduous forest						
West Africa	3163	0	0	3163	8.0	WOOD & SANDS (1978)
Savannah						
Ivory Coast ^{c)}				861	1.7	JOSENS (1972)
Nigeria						
Primary woodland	2558	971	0	3528		WOOD et al. (1977)
Secondary woodland	2509	0	0	2509		WOOD et al. (1977)
Senegal	161 ^{a)}	66	0	229 ^{a)}	1.0 ^{a)}	LEPAGE (1974)
Agro-Ecosystem						
Maize, Nigeria	6825	0	0	6825	18.9	WOOD et al. (1977)

* Termites making nests in the trees are included.

a) Underestimated because some species of termites are not included.

b) *Hospitalitermes* spp. (intermediate nest-making termites) are included.

c) Mean of facies D1 (open savannah woodland) and D2 (moderately open savannah woodland) (after WOOD & SANDS, 1978)

nance of subterranean termites seems to be greater in savannah than in rain forest.

Discussion

The species composition, population density and biomass of dominant termites, and feeding habits of termites in Pasoh Forest were reported in previous papers (ABE, 1978; MATSUMOTO, 1976; ABE, 1979) and the distribution and abundance of termites were given in the present paper. Though the identification and abundance estimates of total termite populations are not completed, an outline of the fauna, habitat, feeding habits, distribution and abundance of termites in Pasoh Forest may be drawn.

Termites in Pasoh Forest seem to be characterized as follows; 1) richness in the number of species, 2) dominance of the Termitidae and inferiority of the Kalotermitidae in the number of species, density and biomass, 3) the dominance of *Macrotermes* and *Dicuspitermes*, 4) the dominance of fungus growing Macrotermitinae, 5) richness in the variety of habitats, especially the existence of arboreal nests at more than 30 m above the ground level, 6) dominance of subterranean and intermediate nest making termites, 7) scarcity of termites in living trees, 8) richness in the variety of feeding habits, especially the existence of lichen-

feeders, 9) dominance of wood feeders and humus feeders, 10) dominance of termites among the soil macrofauna.

The subfamily composition of termites in various habitats is shown in Table 6. It is evident that Pasoh Forest had the greater number of species. There are more species of Termitidae in tropical region than in subtropical and temperate regions. On the other hand, the Kalotermitidae were absent in Pasoh Forest, while being present in subtropical and temperate regions. There were more species of Termitinae and Nasutitermitinae in Pasoh Forest than in tropical savannah. All species of Termitinae are soil feeders, which suggests the importance of soil feeders in tropical rain forest.

Two species, *Macrotermes malaccensis* and *M. carbonarius* occupied more than half of the total biomass of termites. *Dicuspitermes nemorosus* was also abundant. Thus Pasoh Forest can be described as *Macrotermes malaccensis-carbonarius* forest or *Macrotermes-Dicuspitermes* forest. The fact that *Macrotermes* is dominant leads the 4th characteristic of termites in Pasoh Forest: dominance of fungus growing Macrotermitinae. Termites of *Macrotermes*, together with *Odontotermes* and *Microtermes*, cultivate fungi in their nests. The role of fungi cultivated by *M. carbonarius* on their fungus combs was discussed in relation to the nutrition

Table 6. Subfamily composition of termites in various habitats

Region	Tropical region				Subtropical reg. Temperate reg.	
	Habitat	Savannah			Various ecosystems	
Locality	Rain Forest	Ivory Coast	Nigeria	Senegal	Ryukyu Isls.	Japan Isls.*
Latitude (N)	Malaysia 2°58'	6°18'	9°18'	16°16'	24°-30°	30°-44.5°
Author	Present paper	JOSENS	WOOD et al.	LEPAGE	IKEHARA	IKEHARA
Subfamily	(1979)	(1972)	(1977)	(1974)	(1966)	(1966)
Kalotermitidae						
Kalotermitinae	0	4	0	0	4	3
Hodotermitidae						
Hodotermitinae	0	0	0	0	1	1
Rhinotermitidae						
Rhinotermitinae	4	1	0	0	0	0
Coptotermitinae	2	2	1	2	2	2
Psammotermitinae	0	0	0	1	0	0
Termitidae						
Amitermitinae	5	12	7	6	0	0
Termitinae	14	10	5	5	1	0
Macrotermitinae	12	12	11	4	1	0
Nasutitermitinae	19	13	7	5	1	0
Not identified	1					
Total	57	54	31	23	10	5

* Including *Glyptotermes nakajimai* recorded by MORIMOTO (1973).

of termites and the decomposition of leaf litter with special reference to their nitrogen metabolism by MATSUMOTO (1976). The association between termites and fungi was reviewed by SANDS (1969) and discussed with reference to the role of fungi by NOIROT & NOIROT-TIMOTHÉE (1969), LEE & WOOD (1971), JOSENS (1971), WOOD (1976, 1978), LA FAGE & NUTTING (1978) and WOOD & SANDS (1978). WOOD (1978) considered that cultivation of fungi on the fungus combs, followed by re-ingestion of old portions of the fungus comb containing material degraded by fungi leads to the complete or near-complete utilization of food by termite-fungus system.

Termites in Pasoh Forest occupy a variety of habitats. Termites occupied all strata of the forest from the height of more than 30 m on and in the standing trees down to the depth of 30 cm in the soil. Termites living deeper in the soil than 30 cm are very scarce in Pasoh Forest, while in some arid region such as north India (ROONWAL, 1970) and Nigeria (WOOD et al., personal communication) subterranean termites are distributed to the depth of 2 m from the ground surface. Termites making subterranean and intermediate nests shared about two thirds of the total termite populations in the number of species, density and biomass. Mound builders were not predominant in the number of species, density and biomass, though they were conspicuous and were also important termites.

The absence or scarcity of the Kalotermitidae, referred to as dry wood termites because they nest primarily in wood (KRISHNA, 1970), is related to the 7th characteristic; scarcity of termites in living trees. According to HARRIS (1966), foresters in general appear to agree with the view expressed by MACGREGOR (1950): "There is nothing in published literature or unpublished reports to suggest that termites constitute a serious pest except in the case of *Eucalyptus* plantation or in the forest nurseries". Result of the present study seems to support the view expressed by MACGREGOR (1950).

The range of food materials eaten by termites had been reviewed by ADAMSON (1943), NOIROT & NOIROT-TIMOTHÉE (1969), LEE & WOOD (1971) and WOOD (1978). WOOD (1978) distinguished the following kind of food: 1) living vegetation, 2) fresh, dead vegetation, 3) decomposing vegetation, 4) humus, 5) fungi, and 6) special or incidental food (including lichen). The termites in Pasoh Forest consumed all kind of materials described by WOOD (ABE, 1979). The existence of lichen feeders is a

characteristic of the forest in Oriental and Papuan region, because lichen feeding termites are not distributed in other regions (ROONWAL, 1970). Roughly speaking, the termites consuming mainly wood, humus and fallen leaves occupied 60%, 25% and 15% of total biomass of termites respectively in Pasoh Forest (ABE, 1979). WOOD & SANDS (1978) compared the number of species of termites and their feeding habits in different ecosystems in West Africa and showed the dominance of soil feeders in the number of species in the tropical region, but did not show the density and biomass of termites with different feeding habits.

The last and probably the most important characteristic of termites in Pasoh Forest is their overwhelming dominance among soil macrofauna. CHIBA (1974) estimated the biomass of soil macrofauna including subterranean termites at 0.7–11 g w.w./m² in Pasoh Forest, but excluded termites which made epigeous, arboreal and concentrated subterranean nests. Considering that the termite biomass in the present study seemed to be equal to that of total soil macrofauna in CHIBA's data, it was evident that termites occupied an overwhelmingly dominant position among soil macrofauna in Pasoh Forest. On the other hand earthworms, which are usually abundant in temperate regions, were scarce (0–44/m² and 0–0.2 g w.w./m²) in Pasoh Forest.

Owing to the scarcity of information on species composition, feeding habits and abundance of termites in other tropical rain forests, it is difficult to separate the characteristics of the Pasoh termite fauna into those which are characteristic of Pasoh alone and those which are characteristic of rain forest in general.

Summary

1. The distribution, density and biomass of termites were studied in a lowland rain forest (Pasoh Forest Reserve) of West Malaysia. Pasoh Forest was very rich in the number of species, density and biomass of termites.

2. Fifty-two species of termites were distributed in a 1-ha plot, and 14 species in a 16 m² area.

3. Termites inhabited almost all strata of the forest, ranging from the top layer of trees taller than 30 m down to a depth of 30 cm in the soil. Termites living in the soil deeper than 30 cm were very scarce.

4. The density and biomass of the total termite population were estimated at 3,000–4,000/m² and

2.2–2.6 g d.w./m² respectively. The termites occupied an overwhelmingly dominant position among soil macrofauna in Pasoh Forest.

5. Approximately two thirds of the termites were subterranean and one third epigeous. The populations of arboreal nest making termites were low.

6. Dominant termites were *Macrotermes malaccensis*, *M. carbonarius* and *Dicuspiditermes nemorosus*, and their biomass were 1.06, 0.33–0.43, 0.23–0.36 g/m² respectively. Thus Pasoh Forest may be described as *Macrotermes malaccensis-carbonarius* forest or *Macrotermes-Dicuspiditermes* forest.

7. More than half of the termites (in biomass) cultivated fungi on the fungus combs in their nests.

8. Analysis with MORISITA'S I δ Index revealed that the two-dimensional distribution of the epigeous nest of each species was either uniform or clumped, although the nests of all species put together were more or less randomly distributed.

9. The characteristic of termites in Pasoh Forest was discussed in comparison with those in savannah and other ecosystems.

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摘 要

1. 西マレーシアの低地熱帯多雨林(パソ保護林)において、シロアリの分布・密度・現存量を調べた。この森ではシロアリの種数・密度・現存量のいずれも極めて豊富であった。
2. 52種のシロアリが1-ha内から、14種が16m²内から、また10種がわずか2m²内から見出された。
3. シロアリは樹上高さ30mを越えるところから地中30cmまで分布していたが、地中30cm以深のところにはほとんど見られなかった。
4. シロアリ全体の密度と現存量は3000-4000/m²と2.4-2.6g d. w./m²と推定され、シロアリはパソの森において、大型土壌動物の中で現存量の上で圧倒的に重要な位置を占めていた。
5. シロアリを生息場所別に見ると、全体の約2/3は地中、1/3が地表にある塚の中であり、樹上性のシロアリは種数は必ずしも少なくないが、密度・現存量のいずれも低かった。
6. 現存量の上から重要なシロアリは *Macrotermes malaccensis* (マラッカオオキノコシロアリ), *M. carbonarius* (スミオオキノコシロアリ), *Dicuspiditermes nemorosus* で、それらの現存量は、1.06, 0.33-0.43, 0.23-0.36 g. d. w./m²であった。それ故、パソの森のシロアリは *Macrotermes malaccensis-carbonarius* あるいは *Macrotermes-Dicuspiditermes* によって特徴づけられているといえる。
7. 優勢な種である *Macrotermes malaccensis* や *M. carbonarius* を始めとして、シロアリ全体の半分以上(現存量)のものは巣内においてキノコを培養する習性をもっていた。
8. 地表に中型の巣をつくる数種のシロアリの分布を MORISITA (1959) の Id を用いて調べると、それぞれの種は一樣か集中型を示したが、これらを全部いっしょにするとその分布はランダムとなった。
9. パソの森のシロアリをサバンナや他の生態系におけるものと比較検討した。