# Quantification of Population of an Australian Termite, *Drepanotermes tamminensis* (Hill), within a Western Australian Wheatbelt

Park, Hyean Cheal

(Department of Plant Resources, Miryang National University, Miryang, Kyungnam 627-906, Korea)

# 서부 호주 밀 재배지역의 흰개미(Drepanotermes tamminensis (Hill)) 서식 밀도 조사

박 형 철

(국립밀양대학교 식물자원학과)

# ABSTRACT

This study estimated the mound and termite population density in the two study plots in Durokkopin Nature Reserve, Western Australia between 2003 and 2004. The mound density and size were greater in the woodland than in the shrubland. The annual growth rate of mounds was minimal. Some mounds decreased in volume during the 14 month observation period in both study plots. There were no significant differences in the termite population per mound or in the proportion of each caste between the two study plots. The size of the termite population in the mound progressively increased from the small to larger mounds. Overall, of the two favoured habitats, woodland appears to be more optimal for this termite species than the shrubland.

**Key words**: Population density, termites, isoptera, *Drepanotermes tamminenensis* 

# INTRODUCTION

Termites are found predominantly in the tropical and subtropical regions of the world. According to Watson and Gay (1991), there are over 2300 species world-wide. Many studies of termite ecology have been carried out in Africa and elsewhere (Robinson 1958, Johnson and Whitford 1975, Pomeroy 1976, Mastumoto and Abe 1979, Arshad 1981, 1982, Schaefer and Whitford 1981, Abe 1982, Badawi *et al.* 1982, Whitford *et al.* 1982, Wood *et al.* 1983, Anderson and Wood 1984, Ezenwa 1985, Silva *et al.* 1985, Elkins *et al.* 1986, Nutting *et al.* 1987, Okwakol 1987, Darlington 1982, 1990, 1991).

The role of termites in an ecosystem can be defined in terms of three essential features (Wood and Sands 1978). The first feature is their ability to divert a proportion of the total energy flow through the ecosystem. It relates to the density and dyna-

mics of termite populations. It also involves various parameters, such as foraging activity, feeding preferences and rates of food consumption. The second feature is their physical and chemical influence on the ecosystem. Termites often construct extensive and massive nest systems in response to food availability and other environmental factors. As a results, they have a profound effect on redistribution of soil particles, on physical and chemical properties of soils, and consequently on vegetation. The influence of termites on these aforementioned soil characteristics have been reported by many workers, including Robinson (1958), Lee and Wood (1971a, b), Johnson and Whitford (1975), Pomeroy (1976), Arshad (1981, 1982), Badawi et al. (1982), Holt and Coventry (1982), Culver and Beattie (1983), Spain et al. (1983), Anderson and Wood (1984), Ezenwa (1985), Elkins et al. (1986), Nutting et al. (1987), Coventry et al. (1988), Lobry de Bruyn (1991), and Whitford et al. (1992). The third feature is their interaction with other organisms. It involves a variety of direct and indirect effects, such as predatory, symbiotics and commensal

Corresponding author
 Phone: +82-55-350-5505, Fax: +82-55-350-5500
 E-mail: hepark@mnu.ac.kr

relationships. Little is known of the effect of these activities on the habitat in which termites live. These interactions within the termite-soil-vegetation system are complex and are not fully understood.

The influence of termites on plants and soils may be related to their population size and colony densities. However, in contrast to the wealth of quantitative information on the populations of other soil animals, such as earthworms, mites, collembola and ants, little information is available on termite population structure. This lack of information is partly due to the paucity of appropriate investigations and partly to the difficulties involved in sampling termite population (Sands 1972, Baroni-Urbani *et al.* 1978).

Estimating the density and population of mounds for mound-building termite species is easier than for subterranean termite species because their nests are visible. Subterranean species are more difficult to sample satisfactorily unless their presence is indicated by characteristic openings at the soil surface (Lee and Wood 1971a). There are even problems with mound-building species because there is always a certain proportion of the termite population which is foraging in the subterranean galleries.

The purpose of this study is primarily to determine the correlation between the size of mounds and the annual growth rate of mounds on the study area. Secondly, it is to find the correlation between the volume of mounds and the population of termites within the mound.

# MATERIAL AND METHODS

# 1. Termite species studied and study area

Drepanotermes tamminensis is virtually confined to the agricultural regions of south-western Australia. It is thus the only species of *Drepanotermes* in Australia which is restricted to an area of winter rainfall. Therefore, *D. tamminensis* was chosen for this study due to the lack of information in the study area. Colonies are commonly found in eucalypt woodland, particularly that of *Eucalyptus capilosa* Blakely, but also occurs in mixed woodlands or shrublands and in dense thickets of *Melaleuca* spp. or *Allocasuarina campestris* Diels.

The study area was Durokoppin Nature Reserve (117° 45′ E, 31° 24′ S), which is located 250 km east of Perth, Western Australia, and covers an area of 1030 ha. This area forms a part of Western Australian wheatbelt and has been almost entirely cleared of native vegetation for farming. Since small

proportions of original native vegetation have been retained in numerous reserves, it is possible to study the nature of the original vegetation. Durokoppin Nature Reserve is a protected reserve which is vested in the Department of Conservation and Land Management (CALM), Australia. The surrounded area is farmland which was totally cleared many years ago.

On the basis of the results from the large-scale survey, two study plots were selected, one in a representative region of Wandoo woodland and the other in Cauarina shrubland. These areas were selected because of the density of mounds was high (>72 mounds per circular plot), thus enabling a range of mound sizes to be studied within a small area. This site also offered easy access from the main road.

# 2. Density and size of termite mounds

All termite mounds were mapped and counted in the two gridded study plots during January, 2003. Mounds were confirmed to be active by chipping them often and inspecting for termites, followed by replacement of the chipped portion. The size of the mounds was measured in July, 2003 and again February, 2004 in order to estimate the annual growth rate of mounds within each study plot. Height and mean width (the average of EW and NS width) were measured for all termite mounds within each study plot. Measurements were taken twice and the mean value was taken in order to achieve greater accuracy. Bacause the mounds of *D. tamminensis* tend to be conical, mound volume (V) may be estimated by the following formula:

$$V = (\pi \times R^2 \times H)/3$$

where  $\pi$  is the circular constant, R is the mean basal radius of the mounds and H is the height of mound.

In order to assess differencies in the volume of mounds between study plots, the non-parametric Mann-Whitney Utest (Zar 1984) was used. The statistical analysis which was used to compare the growth rate of mounds was the non-parametric Kramer's multiple caomparison test (Zar 1984). A regression analysis (Zar 1984) was used in order to estimate the relationship betweenmound volume and the rate of mound increment. The Mann-Whitney U-test (Zar 1984) was used in order to compare the mean growth rate between study plot.

# 3. Population density of termite mounds

Two approaches may be used to estimate the population of mounds. Firstly, the whole mound can be sampled and the total population within a mound can be counted. Alternatively, a portion of mound can be sampled and the resulting termite count can be extrapolated to give an estimate of numbers in the total mounds. The former method was used by Holdaway et al. (1935) on Eutermes exitiosus, Hill et al. on Nasutitermes exitiosus in Australia. The latter method was adopted by Hartwig (1956) on Trinervitermes ebenerianus in Africa.

The whole mounds sampling method was adapted in the present study in order to the termite population within mounds. This method, although laborious and time consuming, is more accurate than the latter method. It consists of digging up mounds and separating termites from the mound materials by flotation (Holdaway *et al.* 1935, Gay and Greaves 1940, Maldague 1964, Greaves 1967).

Mounds were dug up during the early morning in order to maximise the number of termites within the mounds (J. A. L. Watson, personal communication). In order to protect the reserve, 10 mounds, which were representative of the size category ranges which existed in the study plots, were selected and dug up from each of two areas which were adjacent to the reserve. These areas supported similar vegetation types to those of the study plots. For each mound, height, diameter and depth below ground were estimated prior to returning the material to the laboratory. All mounds were brought to the laboratory where they were broken up and sieved. Sieved material from each mound was soaked in alcohol for 24 hrs and then placed into a container of water where separation of termites and plant material occurred by flotation. After separation of termites and plant material, the number of termites was counted and the proportional composition of each caste (workers, soldiers, reproductives) was estimated.

The relationship between mound volume and termite population within each mound was elucidated using regres-sion analysis (Zar 1984). The t-test (Zar 1984) was used in order to estimate the differences between the mean termite density within the mounds associated with the two vegetation types.

# **RESULTS**

# 1. Density and size of termite mounds

A total of 41 and 24 active mounds was recorded respectively, in the woodland and the shrubland plots. The mean sizes of mounds in each study plot are listed in summary form in Table 1, and the individual measurements are given in Table 2 and 3.

The data indicate that the height, diameter and volume of

Table 1. Mean measurements of the height, diameter, basal area, and volume of mounds in the two study plots. The significant differences between the two study plots were tested by the Mann-Whitney U-test. Each value is the mean and standard error

	Height (cm)	Diameter (cm)	Basal area (cm²)	Volume (cm³)	
Woodland (n = 41)	$46.2 \pm 0.3$	80.7±0.4	5541.0±6.5	$97526.0 \pm 39.0$	
Shrubland $(n=24)$	31.0±0.5	$61.7 \pm 0.5$	$3320.0 \pm 7.9$	$43129.4 \pm 47.0$	
Significance	***	***	***	***	

<sup>\*=</sup>p<0.005, \*\*=p<0.01, \*\*\*=p<0.001, and NS not significant.

mounds were significantly higher (P < 0.001) in the woodland than in the shrubland plot.

Mean volumes of mounds are 97526.0 cm<sup>3</sup> in the woodland and 43129.4 cm<sup>3</sup> in the shrubland plot, respectively. Mounds had a mean basal area of 5541 cm<sup>2</sup> and height of 46.2 cm (range of 23.1-73.9 cm) in the woodland and a mean basal area of 3320.0 cm<sup>2</sup> and a mean height of 31.0 cm (range of 15.9-62.3 cm) in the shrubland plot. It is of interest to note that the variability in mound sizes within each vegetation association was low; the woodland mounds were uniformly large and shrubland mounds were uniformly smaller than those in the woodland.

Table 2 and 3 show the changes in individual mound sizes within two study plots over the 14 month observation period. During the observation period in the woodland, 17 out of 41 mounds (41.5%) were observed to increase in size, and five mounds (12.2%) decreased in their volume (Table 2). In the shrubland plot, nine of 24 mounds (37.5%) increased in size, and three mounds (12.5%) decreased in size (Table 3). All other mounds remained at the original size.

The percentage change in volume was small, varying from -0.5 to 3.4% (average 0.6%) in the woodland and from -1.1 to 3.9% (average 0.8%) in the shrubland during the observation period. The pattern of growth was that most additions were made around the periphery of the mounds, rather than at the existing summit.

# 2. Population density of termites in mound

The population of termites in individual mounds within each study plot is shown in summary form in Table 4. Fig. 1 illustrates the proportions of each termite caste within each study plot. These figures are underestimates since, despite the fact that mounds were sampled at a time when less termites would be in underground tunnels, a proportion of the colony

Table 2. Mound sizes and the rate of changes in size during the observation period in the woodland plot

Mound No.	Height	Diameter (cm)	Basal area (cm²)	Volume (cm <sup>3</sup> )		Changes	% of
WOUNG NO.	(cm)			2003	2004	in volume	change
1	45.3	89.8	6333.5	95635.6	95002.2	-633.4	-0.7
2	66.7	116.0	10568.3	234968.9	234968.9	0	0
2 3	44.8	99.1	7713.3	115184.5	114488.2	-696.3	-0.6
4	62.0	94.3	6984.2	144339.0	144339.0	0	0
5	46.4	67.3	3557.3	55019.5	55943.4	923.9	1.7
6	32.3	50.7	2018.9	21739.4	21736.4	0	0
7	24.2	64.5	3267.5	26357.5	27262.8	905.3	3.4
8	51.0	97.5	7466.2	126925.3	127920.7	995.4	0.8
9	46.8	60.2	2846.3	44402.5	45229.5	827.0	1.9
10	61.6	96.4	7298.7	149866.1	149866.1	0	0
11	33.9	53.5	2248.0	25402.5	26240.1	837.6	3.3
12	47.4	82.8	5384.6	85076.1	85973.5	897.4	1.1
13	51.3	68.1	3642.4	62284.5	62284.5	0	0
14	29.8	48.5	1847.5	18351.4	18351.4	0	0
15	40.9	59.2	2752.5	37526.3	38278.3	752.0	2
16	68.0	107.0	8992.0	203819.2	204581.9	762.7	0.4
17	40.6	73.3	4119.9	57108.7	56642.2	-466.5	-0.8
18	44.3	83.0	5410.6	79896.6	80475.3	578.7	0.7
19	50.0	84.5	5607.9	93465.7	93465.7	0	0
20	61.2	125.8	12429.4	253560.3	252317.4	-1242.9	-0.5
21	39.8	78.5	4839.8	64208.3	64208.3	0	0
22	30.6	42.5	1418.6	11470.0	14470.0	0	0
23	28.4	41.0	1320.3	12498.4	12718.5	220.1	1.8
24	61.3	117.8	10898.9	222699.7	222699.7	0	0
25	28.2	66.6	3483.7	32746.6	33443.3	696.7	2.1
26	73.9	122.8	11843.7	291749.3	291749.3	0	0
27	62.7	89.5	6291.2	131486.8	131486.8	0	0
28	63.3	109.4	9399.9	198338.5	198338.5	0	0
29	36.0	58.5	2687.8	32254.0	32807.7	553.7	1.7
30	44.0	80.8	5127.6	75204.5	75204.5	0	0
31	46.8	76.0	4536.5	70768.8	71974.1	1205.3	1.7
32	39.3	62.9	3107.4	40706.4	40706.4	0	0
33	34.2	61.5	2970.6	33864.5	34105.9	241.4	0.7
34	65.6	119.5	11215.7	245249.6	243201.6	-2048.0	-0.8
35	56.6	98.5	7620.1	143766.4	143766.4	0	0
36	66.0	95.5	7163.0	157586.6	158541.7	955.1	0.6
37	54.3	109.0	9331.3	168896.8	168896.8	0	0
38	29.0	64.5	3267.5	31585.4	31585.4	0	0
39	23.1	52.5	2164.8	16668.4	17143.4	474.8	2.9
40	34.3	73.3	4219.9	48247.0	49076.4	829.4	1.7
41	28.2	68.5	3685.3	34641.7	34641.7	0	0
Mean	46.2	80.7	5541.0	97526.0	97710.6	184.6	0.6
S.E.	0.3	0.4	6.5	38.8	38.7	7.3	0.2

is still outside of the mound (Abensperg-Traun and de Boer 1990). There would also be a tendency for termites to move out of the mound during excavation (Darlington 1982).

Workers are the most abundant caste in the colony, followed by soldiers and reproductives. Numbers of individuals per mound in all castes tended to be greater in the woodland than the shrubland plot, although the differences were not significant. This may in part be due to the high degree of vari-

ance in the data set.

The total mean number of termites in mounds was 28903 per mound in the woodland and 22106 in the shrubland (Table 5). The proportion of each caste were: workers - 78.59%, soldiers - 16.15% and reproductives - 5.26% in the woodland, and workers - 78.23%, soldiers - 16.09% and reproductives - 5.68% in the shrubland.

To investigate the relationship between mound volume and

Table 3. Mound sizes and the rate of changes in size during the observation period in the shrubland plot

Mound No. Height (cm)	Height	Diameter	Basal area	Volume (cm³)		Changes	% of
	(cm)	(cm <sup>2</sup> )	2003	2004	in volume	changes	
1	46.8	86.2	5835.9	91039.3	90036.5	-1002.8	-1.1
2	28.0	65.4	3359.3	31353.2	32028.0	674.8	2.2
3	18.3	34.4	929.4	5669.4	5570.9	-98.5	-1.7
4	30.0	69.2	3761.0	37609.9	37609.9	0	0
5	44.3	93.0	6792.9	100308.6	100761.5	452.9	0.5
6	32.7	62.6	3077.8	33547.9	33547.9	0	0
7	21.6	59.8	2808.6	20222.0	20222.0	0	0
8	36.1	62.5	3068.0	36917.8	37869.0	951.2	2.6
9	26.0	44.2	1534.4	13298.0	13298.0	0	0
10	23.3	52.5	2164.8	16812.9	16812.9	0	0
11	20.1	36.0	1017.9	6819.8	7087.6	267.8	3.9
12	21.3	55.0	2375.8	16868.4	17373.2	504.8	3.0
13	19.7	45.5	1626.0	10677.2	10677.2	0	0
14	22.3	36.5	1046,4	7777.8	8056.2	278.4	3.6
15	36.1	78.3	4815.2	57942.8	58834.2	891.4	1.5
16	61.5	104.3	8560.3	175486.9	175486.9	0	0
17	48.1	89.5	6291.2	100869.5	100869.5	0	0
18	62.3	98.0	7543.0	156642.2	156642.2	0	0
19	33.1	67.5	3578.5	39482.5	40430.3	947.8	2.4
20	24.6	49.6	1932.2	15844.1	15844.1	0	0
21	15.9	34.0	907.9	4812.0	4812.0	0	0
22	24.0	57.8	2623.9	20991.1	21726.1	735.0	3.5
23	26.9	60.4	2868.3	25691.8	25691.8	0	0
24	21.7	38.5	1164.2	8420.7	8226.7	-194.0	-2.3
Mean	31.0	61.7	3320.0	43129.4	43313.1	183.7	0.8
S.E.	0.5	0.5	7.9	46.7	46.5	6.6	0.4

**Table 4.** Summary of mound termite population sizes, broken down into castes, in the two study plots. Each value is the mean and standard error (n = 10). Means were compared by the t-test

	T				
	Worker	Soldier	Repro- ductive	Total	
Woodland	$22714 \pm 3823$	$4669 \pm 843$	$1521 \pm 260$	$28903 \pm 4891$	
Shrubland	$17293 \pm 2702$	$3556 \pm 515$	$1257 \pm 224$	$22106 \pm 3416$	
Significance	NS	NS	NS	NS	

<sup>\*=</sup>p < 0.005, \*\*=p < 0.01, \*\*\*=p < 0.001, and NS not significant.

**Table 5.** Summary of the sampled mound sizes and termite populations within each study plot

		Height (cm)	Diameter (cm)	Depth (cm)	Volume (cm <sup>3</sup> )	No. termites
Woodland	Mean	37.9	69.0	18.8	92019.3	28903
	S.E.	4.3	7.0	2.6	27873.9	4891
Shrubland	Mean	36.7	63.6	17.0	74011.0	22106
	S.E.	4.7	6.1	2.6	21904.6	3416

population of termites in individual mounds, a regression analysis of the combined plot data was used. Table 5 shows the

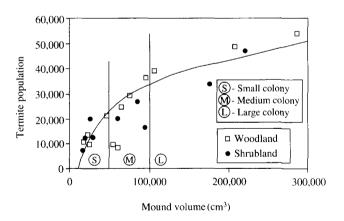


Fig. 1. Regression of the population of termites on the mound volume (cm<sup>3</sup>).

size of mound and termite population.

The regression for the termite population of mounds (Fig. 1) is described by the equation:

$$Y = 10^4 \times (2.87 \log X - 11.05)$$

where Y is the termite population in the mound and X is the volume of mounds ( $cm^3$ ). The st andard error of the regression

coefficient for this equation is 0.843 logarithmic units. The mounds were arbitrarily subdivided into three categories by mound volume; small colony (0-50,000 cm³, S), medium colony (50,001-100,000 cm³, M) and large colony (>100,000 cm³, L). This equation indicates that the termite population increased progressively as the volume of the mounds increased. Within small colony bands (S), the population increased more rapidly than other sections (M, L). In the large colony band (L), the rate of increase fell when the size of the mound increased.

# **DISCUSSION**

There were difficulties in comparing the population and biomass of termites because of the lack of comparable data. Also, the validity of making mound growth rate predictions based on limited short-term experience is questionable because mounds seem to take an extremely long period to increase in size.

## 1. Density and size of termite mounds

The total number and size of mounds were significantly higher in the woodland than in the shrubland. Furthermore, the proportion of mounds, which exhibited an annual increment (41.4% in the woodland and 37.5% in the shrubland) was also greater in the woodland than in the shrubland. From these results, D. tamminensis appears to have the potential to carry out more biological activity in the woodland than in the shrubland. In the former study (Park et al. 1994), the vegetation type is the predominant factor in determining density and distribution of termites in a study area. In other words, woodland appears to be a more optimal habitat for D. tamminensis than does shrubland. This may be related to the quantity and nutrient concentration of the vegetation. Furthermore, greater food availability in the woodland than the shrubland, may be the key factor for this termites' preference to the former habitat. In another Australian termite study, Calaby and Gay (1959) investigated the distribution of the Genus Coptotermes and found that all species, (except one) were dependent on Eucalyptus spp. for food. Thus, D. tamminensis may not be the only termite species which prefer Eucalyptus spp. dominated vegetation.

The growth rate of mounds was extremely small, varying from -0.5 to 3.4% per annum (average 0.6%) in the woodland and from -1.1 to 3.9% (average 0.8%) in the shrubland

during the study period. This result comparable to findings from another termite study which was carried out in the same region (Lobry de Bruyn 1991). Lobry de Bruyn (1991) estimated the growth rate of D. tamminensis mounds, and found that it varied from 0.3 to 4.2% during a 17 months observation period. There is little information on the growth rate of termite mounds. One reason for the lack of data is that increases in the mound size are difficult to estimate. Estimates based on visual observations at the site, or on photographs, are also difficult to transcribe into actual growth rates. Furthermore, changes in mound size are very slight over a short period of time. Watson et al. (1988) studied the mound longevity of a Drepanotermes perniger (Froggatt) mound in northern New South Wales, Australia. They found the mound was stable in size during a 10 year period. They also observed that there was no obvious decrease in standing mound was mass over a 2.5 year period.

## 2. Population density of termites in mounds

Members of the worker caste were most abundant within both vegetation habitats (i.e. 78.59% in the woodland and 78.23% in the shrubland). When investigating the relationship between mound volume and termite population, the population increased progressively with increasing mound volume. In the regression graph (Figure 1), the population increased rapidly as the volume reached 50,000 cm³ (small mound) and thereafter it grew at a reduced rate. Thus, the growth rate of a mound's population in the early stages is rapid but is slows down, and may become stable in the later stages. Collins (1981) studied the population and age structure of *Macrotermes bellicosus* (Smeathman) in Nigeria. He noted that the juvenile period (0-4/6 years) was a time of exponential growth in colony and mound size. During the adult period (4/6-10/12 years), mound and population growth tends to stabilize.

There are few reliable estimates of the total numbers of termites within any habitats. Wood and Sands (1978) reviewed the role of termites in ecosystems, and discussed the abundance and live-weight biomass of termites in different ecosystems of the world. Their survey of the literature indicates upper limits of termite population and biomass in any ecosystem at around 15,000 termite m<sup>-2</sup> and 50 g m<sup>-2</sup>, although values in most ecosystems, are considerably lower than this. For example of the Australian studies which Wood and Sands (1978) note, the study of Lee and Wood (1968) estimated the population and density of the mound-building *Nasutitermes exitosus* (Hill) as 600 termite m<sup>-2</sup> and 3 g m<sup>-2</sup>, respectively, a

value which is within the biomass range for *D. tamminensis*. Wood and Sands' review also discussed the reproductivity of termites in various ecosystems and compares termite productivity with that of other soil and litter invertebrates and of the vertebrates fauna. Their discussion indicates that the biomass values, and the associated productivity of termites can exceed that of other epigaeic invertebrates and can approach, or even exceed, that of certain vertebrates.

# 적 요

본 연구는 서부 호주의 Durokkopin 자연 보호 구역에 서식하고 있는 흰개미의 개미집과 서식 밀도를 조사하기 위해수행되었다. 조사결과, Woodland에서의 흰개미 집의 분포와서식밀도가 Shrubland보다 월등히 높았으며, 일부 흰개미집의 경우 조사기간인 14개월 동안 크기가 감소한 것으로 조사되었으나, 일반적으로 조사기간 중 흰개미집의 크기변화는 거의 없었다. 또한, 두 조사 지역에서 각 개미집 내의 흰개미 개체수의 변화는 거의 없었으며, 계급별 구성비율 또한 거의 변화가 없는 것으로 조사되었다. 그러나, 흰개미 개체수는 개미집이 작을수록 증가율이 높은 것으로 조사되었다. 본 연구결과를 토대로 종합해 보면, 두 조사지역 중 Woodland가 Shurubland보다 공시 흰개미인 Drepanotermes tamminensis (Hill)에 보다 나은 서식처를 제공하는 것으로 사료된다.

# REFERENCES

- Abe, T. 1982. Ecological role of termites in a tropical rain forest. In. Breed, M. D., Michenner, C. D. and Evans, H. E. (eds.). The biology of social insects, Proceedings of the 9th Congress of the International Union for the Study of Social Insects, Boulder, Colorado. Westview Press, Boulder, Colorado. pp. 71-75.
- Anderson, J.M. and T.G. Wood. 1984. Mound composition and soil modification by two soil-feeding termites (Termitinae, Termitidae) in a riparian Nigerian forest. *Pedobiologia* **26**: 77-82.
- Arshad, M.A. 1981. Physical and chemical properties of termite mounds of two species of Macrotermes (Isoptera, Termitidae) and the surrounding soils of the semi-arid savanna of Kenya. Soil Sci. 132: 161-174.
- Arshad, M.A. 1982. Influence of the termites Macrotermes michaelseni (SjÖst) on soil fertility and vegetation in a semi-arid savanna ecosystem. Agro-ecosystem. 8: 47-58.
- Badawi, A., A.A. Faragalla and A. Dabbour. 1982. The role of termites in changing certain chemical characteristics of the soil (*Psammotermes hybostoma Desneaux*). *Sociobiology*. 7: 135-143.
- Baroni-Urbani, C., G. Josens and C. Peakin. 1978. The role of termites in changing certain chemical characteristics of the soil (*Psammotermes hybostoma* Desneaux). *Sociobiology*, 7: 135-143.

- Calaby, J.L. and F.J. Gay. 1959. Aspects of the distribution and ecology of Australian termites. In. Keast, R. L., Crocker, R. L. and Chisrian. C. S. (eds.). *Biogeography and Ecology* in Australia. Junk Publishers. Netherlands. pp. 211-213.
- Collins, N.M. 1981. Population, age structure and survivorship of colonies of *Macrotermes bellicosus* (Isoptera: Macrotermitinae). *J. of Anim. Ecol.* 50: 293-311.
- Coventry, R.J., J.A. Holt and D.F. Sinclair. 1988. Nutrient cycling by mound-building termites in low-fertility soils of semi-arid tropical Australia. *Aust. J. Soil Res.* 26: 375-390.
- Culver, D.C. and A.J. Beattie. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology.* 64: 458-492.
- Darlington, J.P.E.C. 1982. Population dynamics in an African fungus-growing termite. In. Breed, M. D., Michener, C. D. and Evans, H. E. (eds.). The biolugy of social insect, Proceedings of the 9th Congress of the International Union for the Study of Social Insect, Boulder, Colorado. Westview Press, Boulder, Colorado. pp. 54-58.
- Darlington, J.P.E.C. 1990. Population in nests of the termite Macrotermes subhyalnus in Kenya. Insectes Sociaux. 37: 158-168.
- Darlington, J.P.E.C. 1991. Turnover in the populations within mature nests of the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux*. 38: 251-262.
- Elkins, N.Z., G.V. Sabol, T.J. Ward and W.W. Whitford. 1986. The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia*. **68**: 521-528.
- Ezenwa, M.I.S. 1985. Comparative study of some chemical characteristics of mound materials and surrounding soils of different habitats of two species in Nigerian savanna. *Geo-Eco-Trop.* 9: 29-38.
- Hartwig, E.k. 1956. The determination of the population distribution in Trinervitermes nests as a basis for control measures. Bullettino del Laboratrio di Zoologia generale e agraria R. Scuola superiore d'agricoltura Portici. 33: 629-639.
- Holdaway, F.G., F.J. Gay and T. Greaves. 1935. The termite population of mound colony of *Eutermes exitiosus* Hill. J. Coun. Sci. Indust. Res. Aust. 8: 42-46.
- Holt, J.A. and R.J. Coventry. 1982. The effects of mound-building termites on some chemical properties of soils in north-eastern Australia.
  In. Lee, K.E. (ed.). Proceeding of the 3rd Australian Conference on Grassland Ecology. Adelaide, 30 November- 4 December. S. Aust. J. Soil Res. 18: 97-109.
- Johnson, K.A. and W.G. Whitford, 1975. Foraging ecology and relative importance of subterranean termites in Chihuahuan Desert ecosystem. *Environ. Entomol.* 4: 66-70.
- Lee, K.E. and T.G. Wood. 1968. Preliminary studies of the role of *Nasutitermes exitiosus* (Hill) in the cycling of organic matter in a yellow podzolic soil under dry sclerophyll forest in South Australia. Transactions of the 9th International Congress of Soil Science, *Adelaide*. 2: 11-18.
- Lee, K.E. and T.G. Wood. 1971a. Termites and soils. Academic Press, New York and London.
- Lee, K.E. and T.G. Wood. 1971b. Physical and chemical effects on soils of some Australian termites, and their pedological significance. *Pedobiolgia.* 11: 376-409.
- Lobry de Bruyn, L.A. 1991. The role of ants and termites in modifying soil properties in naturally vegetaed and agricultural environments. PhD. Thesis, University of Western Australia. Perth.
- Matsumoto, T. and T. Abe. 1979. The role of termites in a equatorial rain forest ecosystem of West Malaysia. II. Leaf litter consumption on the

- forest floor. Oecologia. 38: 261-274.
- Nutting, W.L., M.I. Haverty and J.P. La Fage. 1987. Physical and chemical alteration of soil by two subterranean termite species in Sonaran Desert grassland. *J. Arid Envir.* 12: 233-239.
- Okwakol, M.J.N. 1987. Effects of Cubitermes testacus (Williams) on some physical and chemical properties of soil in a grassland area of Uganda. Afr. J. Ecol. 25: 147-153.
- Park, H.C., J.D. Majer and R.J. Hobbs. 1994. Influence of vegetation and soil types on the mound density and distribution of the wheatbelt termite, *Drepanotermes tamminensis* (Hill), in the Western Australian wheatbelt. *Eco. Res.* 9(2): 151-158.
- Pomeroy, D.E. 1976. Some effects of mound-building termites on soils in Uganda. *J. Soil Sci.* 27: 377-394.
- Robinson, J.B.D. 1958. Some chemical characteristics of 'termite soils' in Kenya coffee fields. J. Soil. Sci. 9: 58-65.
- Sands, W.A. 1972. Problems in attempting to sample tropical subterranean termite population. *Ekologia Polska*. **20**: 23-31.
- Schaefer, D.A. and W.G. Whitford. 1981. Nutrient cycling by the subterranean termite, Gnathamitermes tubiformans in a Chihuahuan Desert Ecosystem. Oecologia. 48: 277-283
- Silva, S.I., W.P. MacKay and W.G. Whitford. 1985. The relative contributions of termites and micro-arthropods to fluff grass litter disappearance in the Chiuahuan Desert. *Oecologia*. 67: 31-34.
- Spain, A.V., R.D. John and T. Okello-Oloya. 1983. Some pedological effects of selected termite species at three locations in north-eastern

- Australia. In. LeBurn, P. L., André, H. M., Di Medts, A., Gregoire-Wido, C. and Wauthy, G. (eds.). Proceedings of the 8th International Congress of Soil and Zoology, Louvain-la-Neuve (Belgium). Dieu Brichart, Louvain-la-Neuve. pp. 143-149.
- Watson, J.A.L., R.A. Barrett and J.P. Green. 1988. Growth of the mounds of the Australian harvester termite, *Drepanotermes perniger* (Froggatt) (Termitinae). *Sociobiology*. 14: 217-244.
- Watson, J.A.L. and F.J. Gay. 1991. Isoptera (Termites). In Commonwealth, Scientific and Industrial Research Organisation (eds.) The insects of Australia. Vol. 1. 2nd Edition. Melbourne University Press, Calton, Victoria. pp. 330-347.
- Whitford, W.G. 1978. Y. Steinberger and G Ettershank. 1982. Contributions of subterranean termites to the "economy" of Chihuahuan Desert ecosystem. *Oecologia*. 55: 298-302.
- Whitford, W.G., J.A. Ludwig and J.C. Noble. 1992. The importance of subterranean termites in semi-arid ecosystems in South-Eastern Austalia. J. Arid Envir. 22: 87-91.
- Wood, T.G. and W.A. Sands. 1978. The role of termites in ecosystems.
  In. Brain, M. V. (ed.). Production ecology of ants and termites.
  Cambridge University Press, Cambridge. pp. 245-292.
- Wood, T.G., A.A. Johnson and J.M. Anderson. 1983. Modification of soil in Nigerian savanna by soil-feeding *Cubitermes* (Isoptera, Termitidae). *Soil Biol. Biochem.* 15: 575-579.
- Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, New Jersey.