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Influence of vegetation and soil types on the wheatbelt termite, *Drepanotermes tamminensis* (Hill), in the Western Australian wheatbelt

H. C. Park,[1]* J. D. Majer[1] and R. J. Hobbs[2]

[1]*School of Environmental Biology, Curtin University of Technology, Bentley, Western Australia 6102 and* [2]*CSIRO, Division of Wildlife and Ecology, LMB 4, PO, Midland, Western Australia 6056, Australia*

A survey of the distribution and density of mounds of the harvester termite, *Drepanotermes tamminensis* (Hill), was carried out in the Durokoppin Nature Reserve, Western Australia in 1990. Vegetation and, to a lesser extent, soil type, appear to be important factors in determining density and distribution of termite mounds within the Reserve. A more detailed study of mounds in Wandoo (*Eucalyptus capillosa*) woodland and Casuarina (*Allocasuarina campestris*) shrubland indicated that the total number and size of mounds were significantly higher in the woodland than in the shrubland. The total wet weight biomass of *D. tamminensis* was calculated as 3.74 g m^{-2} (37.4 kg ha^{-1}) in the woodland and 1.69 g m^{-2} (16.9 kg ha^{-1}) in the shrubland. Thus, of the two favored habitats, Wandoo woodland appears to be more optimal for this termite species than the Casuarina shrubland.

Key Words: *Drepanotermes tamminensis*; habitat; Isoptera; soil type; termite; vegetation type.

INTRODUCTION

The termite genus *Drepanotermes* is confined to the Australian continent. All species are specialized harvesters, paralleling the Hodotermitidae harvesters of Africa. They forage in the open, often by day, storing the gathered material in mounds or underground galleries (Watson *et al.* 1978). *Drepanotermes tamminensis* (Hill) is confined to the agricultural regions of south-western Australia. It is thus the only species of *Drepanotermes* in Australia that is restricted to a winter rainfall area (Watson & Perry 1981).

In view of the apparent abundance of this species in the Western Australian wheatbelt, a study was performed on its local-scale distribution, its litter harvesting activities and its role in the nutrient dynamics of the area. The study reported in this paper had the following objectives: (i) to evaluate the influence of vegetation and soil types on mound distribution and density; (ii) to describe the mound size and density within study plots situated within the two most favored habitats of this species; and (iii) to provide an estimate of the population size and biomass of termites in the mounds and on an area basis. The harvesting activities of *D. tamminensis* have been described in Park *et al.* (1993) and the distribution of nutrients in and around *D. tamminensis* mounds are described in Park *et al.* (in press). The ultimate aim of this study is to provide inputs for a model that describes the role of *D. tamminensis* in litter harvesting and in nutrient cycling. This model will be presented in a subsequent paper (Park *et al.* unpubl. data).

METHODS

All experiments were conducted at the Durokoppin Nature Reserve (117°45′E, 31°24′S), which is located 250 km east of Perth. The area is an A-class reserve for the conservation of flora and fauna and contains a number of vegetation and soil types. Vegetation classification in the study area was carried out using a Landsat multi-spectral scanner

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*Present address: 355-5 (2/3), Sujeong 1 Dong, Dong-Ku, Busan, Korea.

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(MSS) by Hobbs *et al.* (1989). The survey recognized 10 main vegetation types. Table 1 shows the names of, and the dominant plant species within, each vegetation type in the Reserve. A detailed soil survey of a large section of the study area was published by Bettenay and Hingston (1961). The five soil types in the Reserve are Booraan (a yellow duplex soil), Collgar (a yellow duplex soil), Danberrin (yellow and red duplex soils), Merredin (a red duplex soil) and Ulva (a gravelly yellow earth). Names in brackets are the Great Soil Groups described in Stace *et al.* 1968).

Inspection of the vegetation and soil maps shows that, although locations of vegetation communities across the Reserve loosely reflect trends in soil types, there is no definite correlation between vegetation and soil (Table 2). Thus, although there are problems of cross-correlation between vegetation and soil type, this is not considered to adversely affect the elucidation of the relative influence of each factor on termite distribution.

Large scale survey

The Reserve was gridded out at 50 × 100 m intervals by the Australian Survey Office in June 1986. In March 1990 all *D. tamminensis* mounds were counted within a 25 m radius of every grid-point in the Reserve. Mounds were not checked to see if they were active or not. In order to compare the differences between vegetation and soil types in terms of mean density of mounds per point that supported mounds, one-way analysis of variance followed by Kramer's multiple comparison test (Zar 1984) was used. Chi-squared χ^2 analysis (Zar 1984) was then used to compare the effects of vegetation and soil types on mound frequency within each vegetation and soil category.

Mound size and density

A plot in each of the two vegetation types that were most favored by *D. tamminensis* was then marked out for detailed investigation of mound distribution and for analysis of termite population density. Plots were selected in areas where mound density was greatest in order to maximize the chance of detecting litter harvesting by this species (see Park *et al.* 1993). These 40 × 50 m plots were gridded out at 10 m × 10 m intervals during April 1990. All termite mounds within the study plots were mapped and counted. Mounds were confirmed to be active by chipping them open and inspecting for termites, followed by replacement of the chipped portion. Height and mean width (the average of E–W and N–S width) were measured for all mounds within each study plot. Measurements were taken twice and the mean value was taken in order to achieve greater accuracy. Because the mounds of *D. tamminensis* tend to be conical, it is possible to use the following formula for estimating mound volume (V):

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

where π is the circular constant, R is the mean basal radius of the mounds and H is the height of the mounds. The Mann-Whitney U-test (Zar 1984) was used in order to assess the differences in the size of mounds between study plots.

Table 1. The main vegetation types and the dominant plant species associated with each one in the study area (adapted from Hobbs *et al.* 1989)

Vegetation type	Dominant plant species
Acacia woodland	*Acacia acuminata*, *Eucalyptus loxophleba*
Salmon gum woodland	*Eucalyptus salmonophloia*, *E. capillosa*
Wandoo woodland	*Eucalyptus capillosa*
Casuarina shrubland	*Allocasuarina* spp., *Acacia* spp.
Dense heath	*Allocasuarina campestris*
Leptospermum heath	*Leptospermum erubescens*
Mallee	Dominated by several species, including *Eucalyptus redunca* and *E. erythronema*
Mixed heath	No dominant species, characterized by a high diversity of shrubs
Open low heath	Dominated by sedges, mainly *Ecdiocolea monostachya*
Rock outcrops	Sparse cover of mosses, lichens and small annuals (<10 cm height)

Table 2. Percentage frequency of vegetation types associated with soil types in the Durokoppin Reserve

	Soil type				
Vegetation type	Booraan	Collgar	Danberrin	Merredin	Ulva
Acacia woodland	9.5	0.0	14.3	0.0	76.2
Salmon gum woodland	69.6	30.4	0.0	0.0	0.0
Wandoo woodland	44.2	4.2	5.3	4.2	42.1
Casuarina shrubland	50.8	11.9	0.0	0.0	37.3
Dense heath	59.4	3.1	25.0	0.0	12.5
Leptospermum heath	20.0	0.0	0.0	0.0	80.0
Mallee	89.3	0.0	0.0	0.0	10.7
Mixed heath	0.0	4.1	0.0	0.0	95.9
Open low heath	20.2	0.0	1.5	1.5	76.8
Rock outcrops	87.5	0.0	12.5	0.0	0.0

Population and biomass of termites in the mounds

The whole-mound sampling method (Holdaway *et al.* 1935; Gay & Greaves 1940; Gay & Wetherly 1970) was used in order to assess the termite population within mounds. This consisted of digging up mounds and separating termites from the mound materials by a flotation method (Holdaway *et al.* 1935; Gay & Greaves 1940; Maldague 1964; Greaves 1967). Mounds were dug up in late winter during the early morning in order to maximize the number of termites within the mounds (J. A. L. Watson, pers. comm. 1990). In order to protect the Reserve, 10 mounds, representative of the size category ranges that existed in each study plot, were selected and dug up from each of two areas that were just outside the Reserve and which supported similar vegetation types to those of the study plots. 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 h and then placed into a container of water where flotation and separation of termites and plant material occurred. After separation, termites were counted and the proportional composition of each caste (worker, soldier and reproductive nymph) was estimated.

The biomass of termites per unit area was estimated from the total number of termite mounds per unit area, the population of termites per mound and the individual dry weight of termites. The individual biomass of each caste (soldier, worker and nymph) was obtained by weighing 100 termites. Thus, the total biomass of termites per unit area, B, can be expressed as:

$$B = n \times P \times \{(Bw \times Cw) + (Bs \times Cs) + (Bn \times Cn)\}$$

where n is the total number of mounds per unit area, P is the population of termites per mound, Bw, Bs and Bn (g) are the biomass of individual workers, soldiers and nymphs, respectively, while Cw, Cs and Cn (%) are the proportional composition of workers, soldiers and nymphs, respectively. The t-test (Zar 1984) was used in order to assess differences in termite biomass and population size within the mounds that were associated with the two vegetation types.

RESULTS

Large scale survey

During the survey, 4643 mounds were encountered at the 407 circular points within the Reserve. Some of these mounds would undoubtedly be inactive so this figure must be regarded as an overestimate of mound density within the Reserve. The data were then expressed for each vegetation and soil type as the total number of points, total number of mounds, total number of mounds per point, the percentage of points with mounds, mean density of mounds per point (where present) and expected number of points.

Influence of vegetation types on mound density and distribution

Table 3 illustrates the summary of mound density parameters within each vegetation type. According

Table 3. Summary of density of mounds within specific vegetation types. The significance of the differences in mound density between vegetation types was tested by Kramer's multiple comparison test

	Vegetation type							
	Woodland	Casuarina shrubland	Mallee	Open low heath	Dense heath	Mixed heath	Leptospermum heath	Rock outcrops
Total no. points	139	67	28	69	32	49	15	8
Total no. mounds	1990	1538	294	271	123	369	7	51
Total no. points with mounds	90	62	21	18	14	35	2	6
Percentage points with mounds	64.8	92.5	75.0	26.1	43.8	71.4	13.3	75.0
Mean density of mounds per point (where present)	22.1	24.8	14.0	15.1	8.8	10.5	3.5	8.5
Significance	ab*	a	abc	abc	c	bc	c	c

*Means with the same letter do not differ significantly ($P < 0.01$).

to Kramer's test, differences among vegetation types in terms of the mean density of mounds per point that supported mounds were significant ($P < 0.01$). Density values were highest in Casuarina shrubland (24.8 mounds per circular plot), second highest in Wandoo woodland (22.1 mounds per circular plot) and lowest in Leptospermum heath (3.5 mounds per circular plot).

Table 4a shows the results of the χ^2 analysis of vegetation types on mound frequency. Since the calculated χ^2 was 34.1, the impact of vegetation types on mound distribution is highly significant ($P < 0.001$). The size of the χ^2 value in individual cells provides an indication of the magnitude of influence of vegetation type on mound frequency. Thus, of particular note was the fact that the observed number of mounds in Casuarina shrubland was considerably more than expected, while it was less in open low heath and Leptospermum heath vegetation types. A subsequent χ^2 analysis was

Table 4. Comparison between the observed and expected frequency of points where mounds occur within (a) each broad vegetation type. The significance of the differences was evaluated using the Chi-squared test and the woodland was further broken down into (b) acacia plus salmon gum woodland and wandoo woodland

(a)

	Vegetation type								
	Woodland	Casuarina	Mallee	Open low heath	Dense heath	Mixed heath	Leptospermum heath	Rock outcrops	Total
Observed no. (O)	90	62	21	18	14	35	2	6	248
Expected no. (E)	84.7	40.8	17.1	42.0	19.5	29.9	9.1	4.9	248
$\chi^2 = (O-E)^2/E$	0.33	11.0	0.89	13.71	1.55	0.87	5.54	0.25	34.1
d.f. = 7									$P < 0.001$

(b)

	Vegetation type		
	Acacia and Salmon	Wandoo	Total
Observed no. (O)	7	83	90
Expected no. (E)	30.9	59.1	90
$\chi^2 = (O-E)^2/E$	18.49	9.67	28.16
d.f. = 1			$P < 0.001$

performed in which the woodland vegetation was further subdivided into two groups (Acacia + Salmon gum woodland and Wandoo woodland). At this level of separation, the type of woodland was also significant ($P < 0.001$), with more mounds than expected in Wandoo woodland and less than expected in Acacia + Salmon gum woodland (Table 4b).

To summarize so far, *D. tamminensis* mounds appear to be predominantly associated with Wandoo woodland and Casuarina vegetation types in the Reserve and they reach the highest densities in these two vegetation associations.

Influence of soil types on mound distribution and density

Table 5 summarizes the mound distribution parameters on each soil type. Using Kramer's test procedure, differences in the mean density of mounds per point that supported mounds within each soil type were significant ($P < 0.01$). Mound density was highest on the Merredin soil type (34.2 mounds per circular plot), intermediate on the Collgar and Booraan soil types (26.9 and 20.9 mounds per circular plot, respectively) and lowest on the Danberrin and Ulva soil types (15.2 and 15.1 mounds per circular plot, respectively).

Table 6 shows the results of the χ^2 analysis of the influence of soil types on mound frequency. Since the calculated χ^2 analysis was 4.19 ($P > 0.9$), there appears to be no influence of soil type on mound frequency. In summary then, although there is some influence of soil type on mound density, the frequency of mounds is apparently unaffected by substrate. The tendency for Wandoo woodland and Casuarina shrubland to occur on the Booraan soil type indicates that there could be some intercorrelation between the influence of soil and vegetation on mound density. However, the nature of the data did not permit an exploration of this possibility in more detail.

Mound size and density

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 Casuarina shrubland. These are hereafter referred to as woodland and shrubland plots, respectively. The distance between each study plot was approximately 300 m.

A total of 41 and 24 active mounds was recorded in the woodland and the shrubland plots, respectively. The mean sizes of mounds in each study plot are listed in Table 7. The data indicate that the height, diameter and volume of mounds were significantly higher ($P < 0.001$) in the woodland than in the shrubland plot. It is of interest that the variability in mound sizes within each vegetation association was low; the woodland mounds were uniformly large and the shrubland mounds were uniformly smaller than those in the woodland.

Population and biomass of termites in the mounds

The population of termites and the proportion of each caste in mounds, within each study plot, is shown in Table 8. 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 was still outside

Table 5. Summary of density of mounds within specific soil types. The significance of the differences between soil types was tested by Kramer's multiple comparison test

			Soil type		
Vegetation type	Booraan	Collgar	Danberrin	Merredin	Ulva
Total no. points	162	22	18	5	200
Total no. mounds	2262	377	198	171	1635
Total no. points with mounds	108	14	13	5	108
Percentage points with mounds	66.7	63.6	72.2	100.0	54.0
Mean density of mounds per point (where present)	20.9	26.9	15.2	34.2	15.1
Significance	ab*	ab	bc	a	c

*Means with the same letter do not differ significantly ($P < 0.05$).

Table 6. Comparison of the observed and expected frequency of points where mounds occur within each soil type. The significance of the differences was evaluated using the Chi-squared test

Vegetation type	Soil type Booraan	Collgar	Danberrin	Merredin	Ulva	Total
Observed no. (O)	108	14	13	5	108	248
Expected no. (E)	98.7	13.4	11.0	3.0	121.9	248
$\chi^2 = (O-E)^2/E$	0.88	0.03	0.36	1.33	1.59	4.19
d.f. = 4						NS*

*NS = not significant.

Table 7. Mean measurements of height, diameter and volume of mounds within the two study plots. The significance of differences between the two study plots was tested by Mann-Whitney *U*-test. Each value is the mean and standard error

	Height (cm)	Diameter (cm)	Volume (cm^3)
Woodland (n = 41)	46.2 ± 0.3	80.7 ± 0.4	97 526.0 ± 39.0
Shrubland (n = 24)	31.0 ± 0.5	61.7 ± 0.5	43 129.4 ± 47.0
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$

Table 8. Summary of mound population sizes, broken down into castes, in the two study plots. Each value is the mean ± standard error (n = 10) and, in brackets, the proportion of each termite caste (%). Means were compared by the *t*-test

	Termite castes			
	Soldier	Worker	Nymph	Total
Woodland	4669 ± 843 (16.15)	22 714 ± 3823 (78.59)	1521 ± 260 (5.26)	28 903 ± 4891
Shrubland	3556 ± 515 (16.09)	17 293 ± 2702 (78.23)	1257 ± 224 (5.68)	22 106 ± 3416
Significance	NS*	NS	NS	NS

*NS = not significant.

the mound (Abensperg-Traun & de Boer 1990) and there would also be a tendency for termites to move out of the mound during excavation (see comments in Darlington 1982). Workers are most abundant in the colony, followed by soldiers and then nymphs. 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 an artefact of the high degree of variance in the data.

The individual biomass of each caste was: soldier 5.0 mg, worker 6.0 mg and reproductive nymph 15.0 mg. Based on the population of termites in a mound and the number of termite mounds per hectare, the wet weight biomass of termites in each study plot was calculated as: soldiers 0.48 g m^{-2} (4.8 kg ha^{-1}), workers 2.79 g m^{-2} (27.9 kg ha^{-1}) and nymphs 0.47 g m^{-2} (4.7 kg ha^{-1}) in the woodland. The corresponding values for shrubland were: soldiers 0.21 g m^{-2} (2.1 kg ha^{-1}), workers 1.25 g m^{-2} (12.5 kg ha^{-1}) and nymphs 0.23 g m^{-2} (2.3 kg ha^{-1}). Thus, the total biomass of termites was 3.74 g m^{-2} (37.4 kg ha^{-1}) in the woodland and 1.69 g m^{-2} (16.9 kg ha^{-1}) in the shrubland, respectively. On an area basis, the biomass of termites in the woodland was approximately twice that of the shrubland habitat.

DISCUSSION

Vegetation and, to a lesser extent, soil type, appear to be important factors in determining density and distribution of termite mounds within the Reserve. The trends between different vegetation and soil types can be summarized as follows. *Drepanotermes tamminensis* appears to be able to build its mounds on all soil types, although it does attain higher densities on certain substrates. In particular, higher densities are attained on the Merredin, Collgar and Booraan soil types. Watson and Perry (1981) noted that *D. tamminensis* occurs most commonly on hard-setting or clayey loams, which are characterized by a gradual or duplex texture profile. Unfortunately, the specific soil types associated with this termite's distribution were not monitored by the aforementioned authors so it is not possible to directly compare their observations with the present study. In addition, mound densities and mound frequencies are highest on the Wandoo woodland and Casuarina shrubland. Mounds are generally present at much lower densities or frequencies within the heathland associations. This finding is consistent with Watson and Perry's observation (1981) that colonies of *D. tamminensis* are commonly found in eucalypt forests, in mixed woodlands or in shrublands.

The total number and size of mounds were significantly higher in the woodland than in the shrubland. Thus, for this species of termite, the woodland appears to be a more optimal habitat than the shrubland. This fact may be related to the quantity and nutrient concentration of vegetation. Certainly, the biomass and nutrient concentration of the above-ground plant material and of the litter are much higher in the woodland than in the shrubland (Park unpubl. data, Park *et al.* 1993).

Members of the worker caste were most abundant within both vegetation habitats (i.e. 78.6% in the woodland and 78.2% in the shrubland, respectively). The overall biomass values for this species of termite were 3.74 g m^{-2} and 1.69 g m^{-2} for the woodland and shrubland, respectively. Although these values are at the uppermost range that this termite may attain within this particular area, they are considerable and highlight the potentially important role that this termite may play in these ecosystems. Even in areas of lower mound density, the biomass would be significant and the impact of this termite undoubtedly of importance. In addition, since other harvester termites are also present within the Reserve (Abensperg-Traun and de Boer 1990), the role of *D. tamminensis* may be taken over by other species in areas where it is absent or at a low density.

There are few reliable estimates of the total numbers of termites within any habitats in Australia. Wood and Sands (1978) review the role of termites in ecosystems and present a table of 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 of around 15 000 termites m^{-2} and 50 g m^{-2}, although values in most ecosystems are considerably lower than this. Of the Australian studies that they quote, Lee and Wood (1968) estimated the population and density of the mound-building *Nasutitermes exitiosus* as 600 termites m^{-2} and 3 g m^{-2}, a value which is within the biomass range reported by the present authors for *D. tamminensis*. Wood and Sands' review also discusses the productivity of termites in various ecosystems and compares termite productivity with that of other soil and litter invertebrates and of the vertebrate 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. Since the biomass values of *D. tamminensis* are within the range of the termite communities that were reviewed by Wood and Sands, the present authors believe that the contribution of *D. tamminensis* to productivity must also be proportionately high within Durokoppin Nature Reserve.

The ultimate objective of this investigation was to estimate the contribution of *D. tamminensis* to nutrient cycling within the Durokoppin Nature Reserve. The data in this paper indicate the fact that this termite can attain particularly high mound density and biomass values, particularly in Wandoo woodland and Casuarina shrubland. A companion paper in the series (Park *et al.* 1993) has also indicated the large contribution of this termite to litter harvesting in these two habitats. In a later paper in this series (Park *et al.* unpubl. data) these findings will be integrated with the aid of a computer model in order to quantify the overall contribution of *D. tamminensis* to nutrient cycling throughout the year in the Durokoppin Nature Reserve.

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