

Contribution of the Western Australian wheatbelt termite, *Drepanotermes tamminensis* (Hill), to the soil nutrient budget

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The role of soil modification by the mound-building termite, *Drepanotermes tamminensis* (Hill), was studied during 1991 in the Durokoppin Nature Reserve, Western Australia. Soil chemical parameters were quantified for 'soils' in nests and for surrounding soil in both a Wandoo (*Eucalyptus capillosa*) woodland and a Casuarina (*Allocasuarina campestris*) shrubland plot. All 'soils' in nests were more acidic than the surrounding soil within each study plot. Generally, nutrient levels in the nested soils were higher than the un-nested soil within each study plot and were also higher in the woodland than in the shrubland plot. Depending on the nutrient concerned, the nested soil contained between 0.3 and 21.9% of the total nutrient load per hectare within each study plot. The quantities of nutrients per hectare in termite mounds were higher in the woodland than in the shrubland plot. It is concluded that mounds of this species of termite form a significant bank of nutrients, although time for release of such nutrients depends on the degree of erosion and on the longevity of mounds.

Key words: *Drepanotermes tamminensis*; isoptera; soil nutrients; termite.

INTRODUCTION

The termite *Drepanotermes tamminensis* (Hill) is a predominant mound-building species within certain areas of the Western Australian wheatbelt. It has been found that *D. tamminensis* is an important agent in litter harvesting and ultimately in nutrient cycling within this ecosystem (Park *et al.* 1993, Park *et al.* in press). Various studies that have been carried out on nutrient cycling indicate that soil chemical changes caused by termites are an important contributor to soil profile modification (Wood 1976; Holt *et al.* 1980; Schaefer & Whitford 1981; Badawi *et al.* 1982; Nutting *et al.* 1987; Coventry *et al.* 1988). In Australia, the effects of mound-building termites on the soil are still poorly understood, although some field observations on soil chemical and physical modification by various ter-

mite species have been reported (Lee & Wood 1971a,b; Watson 1977; Holt *et al.* 1980; Coventry *et al.* 1988; Lobry de Bruyn 1990). The objectives of this paper are to determine the effects of *D. tamminensis* on soil chemistry and to find the differences between nested and un-nested soils within two types of vegetation.

METHODS

Study site

This study was carried out near Kellerberrin in Durokoppin Nature Reserve (117°45'E, 31°24'S), which is located 250 km east of Perth, Western Australia. The mean rainfall for the area is 333 mm year⁻¹ and mean minimum and maximum temperatures are 11.3°C and 25.0°C, respectively.

Two study plots were selected, one in a representative region of Wandoo woodland (mainly dominated by *Eucalyptus capillosa* trees) and the other in

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Casuarina shrubland (dominated by *Allocasuarina campestris* shrubs). These areas were selected because the density of mounds was high, thus enabling a good variety of mounds to be studied within a small area. The size of each study plot was 2000 m² (40 m × 50 m) and each was gridded out at 10 m × 10 m intervals.

Assessment of the nutrient concentration in nested versus un-nested soil

Within each study plot, 10 mounds were randomly selected for the assessment of nutrients in soil. Three soil samples (from the centre of the mound, 1 m and 5 m distant from the mound) were collected from the selected mounds by the use of a soil-corer (radius = 2.5 cm, depth = 10 cm). All samples were sieved and analyzed for pH and macronutrient content by CSBP and Farmers Ltd, Bayswater, Western Australia.

Soil pH was estimated by the electrometric method (Cornell meter) using a pH instrument and a 1 : 5 mix of soil to 0.01 mol/L CaCl₂ (Peech 1965). Organic carbon (C) was determined using the dichromate oxidation procedure without external heating (Walkley & Black 1934). Inorganic nitrogen-nitrate (N-NO₃) and nitrogen-ammonium (N-NH₄) were measured in order to provide an indication of nitrogen availability. Colwell's method (1963, 1965) of extraction was used for the available phosphorus (P) and potassium (K). The phosphorus content was then determined colorimetrically using the Murphy and Riley method (1962) at 882 nm. The potassium content was determined from the same solution using atomic absorption at 766.5 nm.

The significance of differences in soil pH and the nutrient concentration of soil between the two study plots was tested by the *t*-test (Zar 1984). Comparisons of each element in soil between nested and un-nested soil within each study plot were made using Duncan's multiple comparison test (Zar 1984).

Comparison of total nutrient contents between nested and un-nested soil

The total mass of soil in the nested and un-nested areas was estimated in order to compare the total quantity of nutrients in nested and un-nested soil. Total mass (dry weight) of soil in each mound was

estimated for the mounds within each study plot. 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 which 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, sieved, dried for 24 h at 105 °C and the soil weighed. The mean mass of soil within a nest was then calculated from the woodland and shrubland separately. These values were multiplied by the number of mounds within each plot in order to estimate the soil mass within mounds. The resulting values were then corrected to represent an area of one hectare.

Bulk density for un-nested soil is the mass of a unit volume of dry soil. This volume includes both solids and pores. Twenty undisturbed soil samples were taken using a soil-corer (radius = 2.5 cm, depth = 10 cm) and oven-dried for 24 h at 105 °C. Bulk density, *B*, was calculated by the following formula:

$$B = W/V \quad (1)$$

where *W* is the dry weight of soil per unit area (g) and *V* is the volume of soil per unit area (cm³). The total mass of soil to a depth of 10 cm within one hectare was then calculated by multiplying soil bulk density by the volume of soil to a depth of 10 cm.

Nutrient content in nested soil (kg ha⁻¹), *N_n*, was calculated from the total weight of soil in the nested area (kg ha⁻¹), and the nutrient concentration of soil in the nested area (%). This was calculated by the following formula:

$$N_n = (W_n \times \%N_n)/100 \quad (2)$$

where *W_n* is the total mass of soil in nests within one hectare and %*N_n* is the nutrient concentration of soil occupied by termite mounds.

Nutrient content in the un-nested soil (kg ha⁻¹), *N_u*, was calculated from the mass of soil in the un-nested area, and the nutrient concentration of soil in the un-nested area (%). The relationship is as follows:

$$N_u = (W_u \times \%N_u)/100 \quad (3)$$

where *W_u* is the mass of soil (excluding nests) in one hectare and %*N_u* is the nutrient concentration of soil in the un-nested area. From the results of equations (2) and (3) it was possible on a hectare

basis to calculate the percentage of each nutrient which was contained within the nests and within the remaining un-nested soil.

RESULTS

Assessment of the nutrient concentration in nested versus un-nested soil

The mean values for soil pH and for each macro-nutrient in the nested and un-nested soils within each study plot are listed in Table 1. The pH of nested soils was lower than un-nested soils within each study plot. When comparing between the two study plots, the nested soils were more acidic in the woodland than the shrubland, although the acidity of un-nested soils in the shrubland was slightly higher than the woodland. The drop from 6.03 in the un-nested woodland soils down to 4.67 on mounds represents a major modification of soil pH, although this effect was less dramatic in the shrubland.

Except for N-NO₃ in the woodland and P in both plots, concentration values for each nutrient were significantly higher in nested soil than in un-nested soil 1 m off mounds within each study plot. All nutrients except P in the shrubland were significantly higher on the mound than 5 m off the mound. Each element within the nested soil of the woodland was higher than within the shrubland plot.

Within the un-nested area, the concentration of N-NO₃ in the soil 1 m from the mound was at least seven times higher than in soil at the 5 m distance from the mound within both study plots. Within

each study plot, N-NH₄ in the soil 1 m from the mound was also significantly higher than in the soil at 5 m distance from the mound. Although levels of N-NH₄ were highest on the mound and declined with increasing distance from the center, levels of N-NO₃ were highest 1 m off the mound. Phosphate levels declined with increasing distance from the mound within the woodland, although this trend was not observed within the shrubland. There was no difference between potassium or organic matter at 1 m and 5 m from mounds.

Comparison of total nutrient contents between nested and un-nested soil

The total mass of soil and total nutrients in nested and un-nested soil are listed in Table 2. Total mass of nested soil to a depth of 10 cm was 17.0 and 7.8 t ha⁻¹ within the woodland and shrubland plot, respectively. Total mass of un-nested soil was 1720.2 and 1733.1 t ha⁻¹ within the woodland and shrubland, respectively. Thus, the mass of mounds represented 1.0% and 0.4% of the total mass of soil within the woodland and shrubland plots, respectively. The difference in total mass between the two study plots was related to differences in the size and density of termite mounds (Park *et al.* in press).

Organic carbon in the nested soil was calculated as 0.54 and 0.21 t ha⁻¹ within the woodland and shrubland plots, respectively. Within the un-nested soil, the mass of C was 28.26 and 12.02 t ha⁻¹ within the woodland and shrubland plots, respectively. Thus, 1.9% and 1.7% of total C were contained in the nested soil within the woodland and shrubland plots, respectively.

Table 1. Comparison of the soil pH and nutrient concentration between the nested and un-nested soil within each study plot.

	On-mound	Shrubland		Woodland		
		Off-mound		On-mound	Off-mound	
		1 m	5 m			1 m
pH	5.18 + 0.06 (a*)	5.31 + 0.09 (b)	5.55 + 0.08 (b)	4.67 + 0.04 (a)	5.61 + 0.08 (b)	6.03 + 0.07 (c)
Carbon (%)	2.66 + 0.15 (a)	0.90 + 0.11 (b)	0.68 + 0.05 (b)	3.17 + 0.07 (a)	1.44 + 0.10 (b)	1.67 + 0.13 (b)
N-NO ₃ (ppm)	7.70 + 0.40 (a)	14.60 + 2.05 (b)	1.47 + 0.23 (c)	13.60 + 1.40 (a)	14.60 + 1.28 (a)	1.90 + 0.28 (b)
N-NH ₄ (ppm)	20.00 + 0.00 (a)	12.10 + 2.29 (b)	5.10 + 0.75 (c)	20.00 + 0.00 (a)	10.20 + 2.41 (b)	4.10 + 0.72 (b)
P (ppm)	3.70 + 0.47 (a)	4.80 + 0.83 (a)	5.40 + 0.72 (a)	12.00 + 1.76 (a)	8.90 + 0.62 (a)	4.80 + 0.79 (b)
K (ppm)	117.7 + 13.82 (a)	64.6 + 8.37 (b)	52.6 + 5.10 (b)	218.2 + 12.91 (a)	130.2 + 11.94 (b)	116.7 + 8.72 (b)

*Within each soil chemical characteristic, means with the same letter do not differ significantly ($P < 0.05$).

The significance of differences was tested by the Duncan's multiple comparison test. Each value is the mean and standard error ($n = 10$).

Table 2. Total mass of soil and associated nutrients in the nested and un-nested soil within each study plot.

	On-mound	Shrubland		Woodland		
		Off-mound		On-mound	Off-mound	
		1 m	5 m		1 m	5 m
Area occupied (m ² ; total = 1 ha)	40.0 (0.4)	605.5	9354.5 (93.5)	113.6 (1.1)	1155.0 (11.6)	8731.4 (87.3)
Total mass (t) in 1 ha to 10 cm depth	7.8 (0.4)	105.4 (6.1)	1627.7 (93.5)	17.0 (1.0)	201.1 (11.6)	1519.1 (87.4)
Nutrient content						
Organic C (t ha ⁻¹)	0.21 (1.7)	0.95 (7.8)	11.07 (90.5)	0.54 (1.9)	2.90 (10.1)	25.36 (88.0)
N-NO ₃	0.1 (2.5)	1.5 (37.5)	2.4 (60.0)	0.2 (3.4)	2.9 (48.3)	2.9 (48.3)
N-NH ₄	0.2 (2.0)	1.3 (13.3)	8.3 (84.7)	0.3 (3.5)	2.1 (24.4)	6.2 (72.1)
P	0.03 (0.3)	0.5 (5.4)	8.8 (94.3)	0.2 (2.2)	1.8 (19.3)	7.3 (78.5)
K	0.9 (1.0)	6.8 (7.3)	85.6 (91.7)	3.7 (1.8)	26.2 (12.6)	177.3 (85.6)

Figures in parentheses represent percentage values.

Inorganic N-NO₃ and N-NH₄ within the woodland plot were 0.2 kg ha⁻¹ and 2.5 kg ha⁻¹, respectively, in the nested soil, as opposed to 5.8 kg ha⁻¹ and 8.9 kg ha⁻¹ in the un-nested soil of the same plot. As a consequence of these findings, 3.4% of total N-NO₃ and 21.9% of total N-NH₄ were respectively contained in the nested soil. Within the shrubland, the quantities of N-NO₃ and N-NH₄ were 0.1 kg ha⁻¹ and 1.0 kg ha⁻¹, respectively, in the nested soil, as opposed to 3.9 kg ha⁻¹ and 11.1 kg ha⁻¹ in the un-nested soil. Therefore, 2.5% and 8.3% of total N-NO₃ and total N-NH₄ were respectively contained in the nested soil within the shrubland.

Within the woodland plot, available P and K were 0.2 kg ha⁻¹ and 3.7 kg ha⁻¹, respectively, in the nested soil. The corresponding values were 9.1 kg ha⁻¹ and 203.5 kg ha⁻¹ in the un-nested soil. Thus, 2.2% of the total P and 1.8% of total K were contained in the nested soil within the woodland plot. Available P and K within the shrubland contributed 0.03 kg ha⁻¹ and 0.9 kg ha⁻¹ in the nested soil. In the un-nested soil, 9.3 kg ha⁻¹ and 92.4 kg ha⁻¹ of P and K were recorded. Within the shrubland plot, the corresponding values were 0.3% of total P and 1.0% of total K in the mounds.

DISCUSSION

The soil of *D. tamminensis* mounds exhibited significantly lower pH values and generally higher nutrient concentrations than the surrounding soil within each study plot. The depression of pH in the nested

soil was particularly marked in the woodland. Lee and Wood (1971a) also found that the mounds of *Drepanotermes rubriceps* had a lower soil pH (i.e. pH = 5.5) than the surrounding soil (i.e. pH = 6.4). The more acidic nested soil may be due to the process of organic matter decomposition which releases carbon dioxide and forms carbonic acid (Breeusma & de Vries 1984). Possibly the more dramatic change in pH in woodland mounds was associated with the greater harvesting rate (Park *et al.* 1993), and therefore presumably organic matter decomposition, in woodland than in shrubland mounds.

The percentage of organic carbon in the nested soil was at least twice as high as the un-nested soil within the woodland plot. It was three times higher than the un-nested soil within the shrubland plot. *Drepanotermes tamminensis* are active harvesters of various plant materials (Park *et al.* 1993). With termites' saliva as a cementing agent, plant material is incorporated in the mound as well as the lining of gallery walls. Gillman *et al.* (1972) analyzed the organic constituents of a *Coptotermes acinaciformis* nest and found that glycoprotein was present and probably of salivary origin. Thus, both organic material and the saliva probably elevate the amount of organic carbon which is found in the soil of the mounds.

With the exception of P in the shrubland, values for other nutrient concentrations were significantly higher in the nested soil, as opposed to the surrounding soil. In the woodland, P was significantly more concentrated at 1 m from the mound than in the

surrounding soil. Thus, even this nutrient can be elevated by termite activity in certain vegetation associations. Lobry de Bruyn (1990) also found that both available P and K in the nested soil of *D. tamminensis* was approximately twice as high as in the un-nested soil. These trends have also been noted for other types of termites, such as the fungus cultivating Termitidae of Africa. For instance, Arshad (1981) found that exchangeable bases, organic carbon and nitrogen were generally higher in mound samples of *Macrotermes subhyalinus* and *M. michaelseni* than in the surrounding subsoil.

The tendency for N-NO₃ to be more concentrated immediately around, rather than on the mound is particularly interesting. In comparison with N-NH₄ which tends to become bound to the substrate, N-NO₃ is more mobile and may be leached off the mound more readily. Alternatively, although many elements of the microflora are known to be more numerous on the mounds of certain termite species than in the surrounding soil (Meikeljohn 1965; Pathak & Lehri 1959; Lee & Wood 1971b), it may be that re-ingestion of mound material during nest reconstruction (Lee & Wood 1971b) could inhibit the activity of nitrifying bacteria and hence the production of N-NO₃.

In the current study, all nutrients in nested and un-nested soil within the woodland were generally higher than the shrubland plot. The differences between the two study plots reflect the slightly richer soils associated with woodlands in the wheatbelt, and may also be due to different nutrient concentrations in available plant material within each study plot. The nutrient concentrations of above-ground plant material were generally higher in the woodland than the shrubland habitat (Park unpubl. data). Harvesting of litter by *D. tamminensis* in the two study plots brings nutrient-rich plant material into the mound. It is then released into the soil as a result of termite and microbial activity. At this stage we are unable to quantify the relative roles of termites and the associated mound microbial populations in nutrient release from harvested material.

Overall, nutrients in mounds made up between 0.3 and 21.9% of the total nutrient load per hectare within each of the study plots. If the 1 m ring of soil around the nest is also included, the contribution of nests to total nutrient load is between 5.7 and 51.7%. These values are high in relation to Holt's (1988) finding that the north Queensland termite,

Amitermes laurensis, accounted for at least 5% of total carbon mineralized in the ecosystem which he studied. In the present study each nutrient analyzed within the nested soil in the woodland plot exhibited a significantly greater quantity per hectare than in the shrubland plot. All nutrient content values per hectare in the nested soil were between 2–7 times higher in the woodland than the shrubland plot. The difference between the two study plots is probably due to the greater mound density (Park *et al.* in press) and nutrient concentration of the nested soils in the woodland than in the shrubland plot.

The high nutrient loads in the 1 m ring of soil around the nests indicates that nutrients are slowly released from live termite mounds to the surrounding area. This is evidenced by the fact that N-NO₃, N-NH₄ and, in the woodland, P levels were significantly elevated at 1 m when compared to levels at 5 m.

The potential for mound nutrients to be made available to the ecosystem also depends on the longevity of the colony and on the duration of resistance to erosion of their abandoned mounds. Lee (cited in Holt *et al.* 1980) stated that it is reasonable to assume that an *Amitermes vitosus* mound would have a life span of 20–40 years followed by 5–10 years after senescence of the colony. Lobry de Bruyn (1990) also commented that erosion rates of uninhabited mounds are slow and, for *D. tamminensis*, mounds take a minimum of 30 years to erode to ground level. While a *D. tamminensis* mound is occupied, erosion is probably slower. Therefore, although these mounds form a significant store of nutrients, some of which may be continuously released as a result of erosion, considerable quantities of nutrients may only become available to the ecosystem in periods greater than 30 years following death of the colony.

Nevertheless, given the nutrient-poverty of the wheatbelt soils, *D. tamminensis* represents an important agent of nutrient redistribution within the plant communities studied. The effects of the resulting patchy distribution of nutrients on community dynamics have yet to be studied.

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