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Harvesting rate of the termite, *Drepanotermes tamminensis* (Hill) within native woodland and shrubland of the Western Australian wheatbelt

H. C. Park,[1,*] J. D. Majer,[1] R. J. Hobbs[2] and T. U. Bae[3]

[1]*School of Environmental Biology, Curtin University of Technology, Bentley, Western Australia, 6102,* [2]*CSIRO, Division of Wildlife and Ecology, LMB 4, PO, Midland, Western Australia, 6056 Australia and* [3]*Dong-A University, Department of Agricultural Biology, Saha-Ku, Busan, Korea*

The Western Australian termite, *Drepanotermes tamminensis* (Hill), harvests various plant materials according to biomass availability. The main litter components harvested by this termite in a woodland dominated by *Eucalyptus capillosa* are bark and leaves of the major tree species, while in shrubland dominated by *Allocasuarina campestris*, shoots of this species are taken. Harvesting mainly occurs during the autumn (April–May) and spring (September–October) seasons. The commencement and duration of harvesting appears to depend partly on weather conditions, with harvesting taking place at temperatures between 15 and 25 °C after periods of rain. This species of termite harvests approximately 15.6 g m^{-2} $year^{-1}$ and 3.2 g m^2 $year^{-1}$ (dry weight of plant material) in the woodland and shrubland, respectively.

Key words: *Drepanotermes tamminensis*; harvesting rate; Isoptera; termite.

INTRODUCTION

The termite genus *Drepanotermes* (Isoptera: Termitinae) is confined to the Australian continent. All species are harvesters and they venture into the open by day or night to gather both freshly fallen and old leaf litter, grass or other vegetable debris which they store in underground nests or in mounds. *Drepanotermes tamminensis* (Hill) is confined to the agricultural regions of southwestern Australia. It is thus the only species of *Drepanotermes* in Australia which is restricted to an area of winter rainfall (Watson & Perry 1981). *Drepanotermes tamminensis* is a mound-building species. The mounds are irregularly conical or rounded, commonly 0.5–1.0 m high, although they can reach 2 m. All mounds are used for storing litter that has been harvested by the termites from the surrounding areas. This species is known to harvest a wide range of material, depending on what is available (Watson & Perry 1981).

Some field observations on foraging activity and harvesting rate by other termite species have already been reported (Sands 1961; Ohiagu & Wood 1976; Matsumoto & Abe 1979; Ohiagu 1979; Schaefer & Whitford 1981) but there is no quantitative information on harvesting rate and harvesting behaviour of *D. tamminensis*. This study was undertaken for three reasons: (i) to observe the harvesting behaviour; (ii) to estimate the diurnal and seasonal periodicity of harvesting; and (iii) to estimate the amount of litter harvested by *D. tamminensis*. It forms part of a wider investigation of the role of this species in the nutrient dynamics of the Western Australian wheatbelt (Park 1993).

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 (Fig. 1), between April 1991 and March 1992. Durokoppin Nature Reserve is an A-class reserve for the conservation of flora and

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

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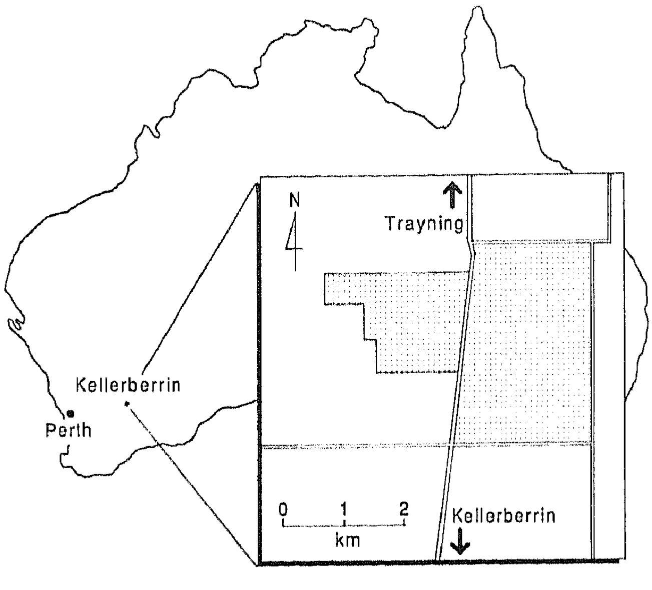

Fig. 1. Location of the study site. (□) Farmland; (▦) Durokoppin Nature Reserve.

fauna and contains a number of vegetation types, ranging from open low heath to tall woodland. A range of studies on different aspects of the biota is currently being performed in this area by the CSIRO Division of Wildlife and Ecology as part of the 'ecological dynamics of remnants of native vegetation' programme. The mean rainfall for the reserve is 333 mm $year^{-1}$ and mean minimum and maximum temperatures are 11.3 and 25.0°C, respectively. The most effective rains for plant growth are received in winter, from May to August.

Two study plots were selected, one in a representative region of wandoo woodland (mainly dominated by *Eucalyptus capillosa* trees) and the other in casuarina shrubland (dominated by *Allocasuarina campestris* shrubs). Vegetation descriptions are given in Hobbs and Atkins (1988) and Hobbs *et al.* (1989). These plots are hereafter referred to as woodland and shrubland, respectively. 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 m^2 (40 m × 50 m) and each was gridded out at 10 m × 10 m intervals.

Within each study plot, all termite mounds were counted and a total of 41 and 24 mounds was recorded in the woodland and shrubland plots, respectively (Park 1993). In early April 1990 and again in May 1991, ten 1 m^2 quadrats were randomly selected from within each of the two study plots. All aboveground litter was collected from within these quadrats and weighed. The total amount of litter on the woodland floor was 610.2 g m^{-2} in 1990 and 697.1 g m^{-2} in 1991, while the shrubland supported 315.3 g m^{-2} in 1990 and 303.1 g m^{-2} in 1991. The differences in litter biomass between 1990 and 1991 within both study plots were not significant (Park 1993). It is therefore assumed that litter biomass was stable from year to year. Litter decay by agents other than *D. tamminensis* was assessed by measuring the loss from known quantities of litter confined in mesh containers (McColl 1966; Attiwill 1968; Park 1975; Rogers & Westman 1977; Birk 1979). The annual amount of litter decay by other agents was found to be extremely small in both study plots (Park 1993).

Field observation of litter harvesting

In April 1991, ten 1 m^2 quadrats were randomly selected in each study plot. All litter was removed from the quadrats and these were then covered with a nylon net to protect them from litterfall. Weighed quantities of three major litter components (*E. capillosa* bark, 150 g; *E. capillosa* leaves, 150 g; *A. campestris* shoots, 200 g dry weight) were then placed in each quadrat. The slightly higher mass of *A. campestris* shoots was used in order to produce a volume of litter similar to that of the more dense *E. capillosa* litter.

During the field programme, termite behavior was observed on a monthly basis. When termite harvesting occurred, the activity of *D. tamminensis* was monitored and the 10 harvesting quadrats were scored for presence or absence of harvesting activity every 2 h until harvesting ceased. Air temperature during harvesting was also measured every 2 h in order to assess the relationship between harvesting and temperature. Daily rainfall recordings were also taken in the field.

Harvesting rate

The litter components in each quadrat were replaced with fresh pre-weighed litter every 2 months during the field programme. All litter remaining after each 2 month period was placed in separate plastic bags according to litter fraction and returned to the laboratory for oven-drying at 60°C prior to weighing. Any visible soil adhering to litter was brushed off before weighing.

For each plot, differences in the rate of harvesting of each litter component between sampling periods were tested for significance by *t*-test. A *t*-test was also used to compare the differences in harvesting rate between the two study plots within each sampling period. Comparisons of the rate of harvesting of each litter component during the sampling period within the study plots were made using one-way analysis of variance along with a Duncan's multiple comparison test.

RESULTS

Field observation of litter harvesting

Harvesting occurred during the autumn (April–May) and spring (September–October) seasons only. Figures 2 and 3 show the harvesting activity and air temperatures recorded when foraging was observed. The commencement and duration of the harvesting appeared to depend partly on weather conditions. For instance, harvesting was usually stimulated during or after moderate rainfall and there was no harvesting under hot and dry, or cold and heavy rain conditions.

Harvesting by *D. tamminensis* was first observed on 10 April 1991. On this date, a maximum of six quadrats with termites harvesting was recorded in the woodland plot, while a maximum of three quadrats with termites harvesting was recorded in the shrubland plot. Harvesting followed afternoon rainfall and lasted for approximately 6 h in the woodland (16.00–22.00 h) and 4 h in the shrubland (18.00–22.00 h; Fig. 2a). Air temperature during harvesting ranged between 15 and 18 °C.

On 4 May 1991, termites again commenced harvesting after an afternoon shower and continued for 2 h (16.00–18.00 h) in both study plots (Fig. 2b). Harvesting ceased at the onset of heavy rainfall (46 mm). Harvesting was observed in eight quadrats within the woodland plot and five quadrats within the shrubland plot on this date. Air temperature ranged between 17.5 and 19.5 °C. On the following day (5 May), harvesting again commenced and continued for 28 h (06.00 h on 5 May to 10.00 h on 6 May) in the woodland and 22 h (06.00 h on 5 May to 04.00 h on 6 May) in the shrubland (Fig. 2c). The maximum number of quadrats where harvesting was observed was 7 and

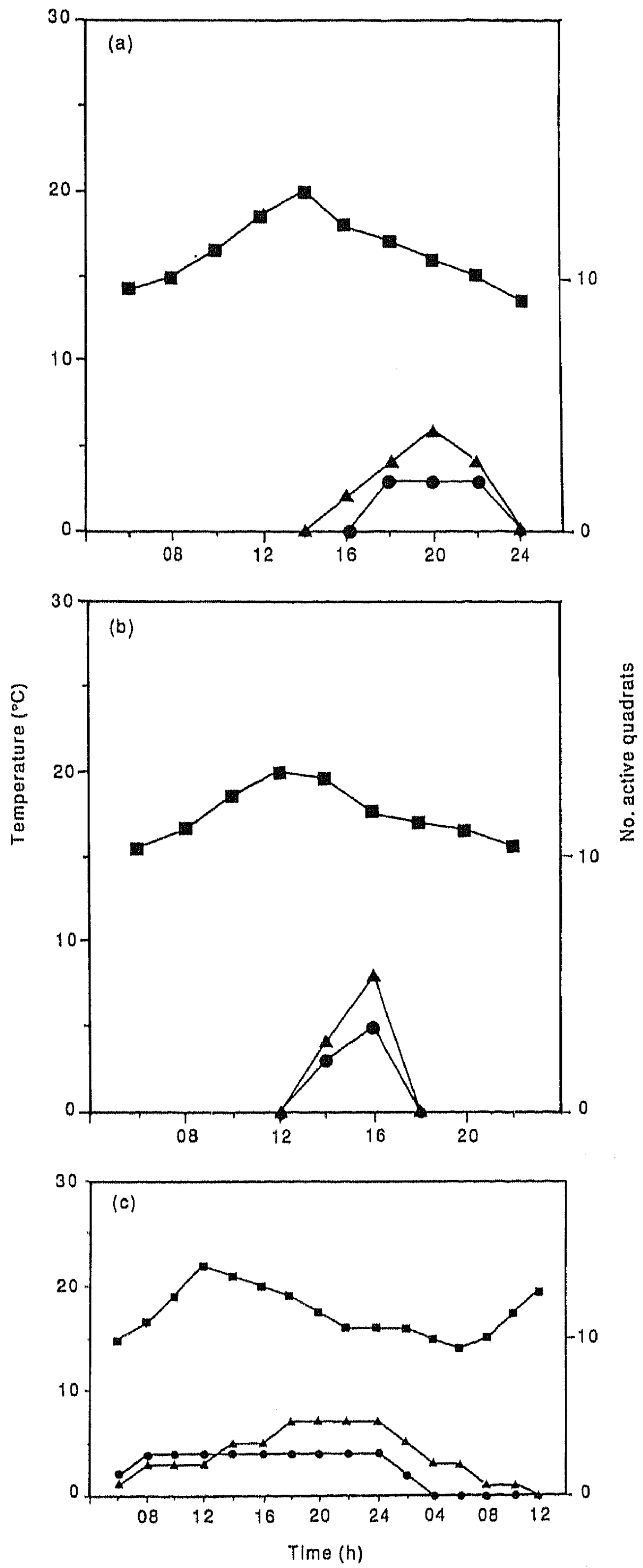

Fig. 2. Hourly counts of the number of quadrats where harvesting activity was observed and corresponding air temperatures for the three autumn days when harvesting was observed. (a) 10 April; (b) 4 May; (c) 5–6 May 1991. (–■–) Air temperature; (–▲–) woodland; (–●–) shrubland.

Table 1 Comparison of litter harvesting rate ($\bar{x} \pm SE$, $n = 10$) between the harvesting seasons and among litter components within each study plot

Study plot	Harvesting season	Dry weight loss (%)		
		E. capillosa		*A. campestris*
		Leaves	Bark	Shoots
Woodland	Autumn	$27.6 \pm 1.2^{a\dagger}$	18.2 ± 1.2^{b}	23.1 ± 1.3^{ab}
	Spring	28.7 ± 1.4^{a}	14.6 ± 1.8^{b}	21.3 ± 1.4^{ab}
Shrubland	Autumn	16.5 ± 2.0^{ab}	10.6 ± 1.9^{a}	22.1 ± 2.3^{b}
	Spring	21.2 ± 1.8^{a}	13.3 ± 0.9^{b}	30.4 ± 1.9^{c}

Means between the two harvesting seasons were compared by *t*-test. The significance of the differences among litter components was tested by the Duncan's multiple comparison test.
†Within each group, means with the same letter do not differ significantly ($P < 0.05$).

4 in each study plot, respectively. Air temperature on this occasion ranged between 15 and 22 °C.

In spring, harvesting generally took place in the morning. The first harvesting was observed on 12 October 1991. A maximum of four quadrats was recorded as active in the woodland and three in the shrubland. Harvesting started in the morning and lasted for approximately 4 h (08.00–12.00 h) in both study plots (Fig. 3a). Air temperature during this period ranged between 17 and 23 °C. Rain fell before and during this harvesting period (10 mm). On 15 November 1991 harvesting commenced after a shower and lasted for 18 h (10.00–04.00 h) in the woodland and 20 h (08.00–04.00 h) in the shrubland (Fig. 3b). A maximum of six and five quadrats were recorded as active in the woodland and shrubland plots, respectively. Air temperature during this activity period ranged between 19 and 25 °C.

Harvesting rate

The mean rates of litter harvesting by *D. tamminensis* within each study plot are listed in Tables 1 and 2. Table 1 shows the differences in the rate of litter harvesting between the autumn and spring seasons and the differences among litter components within each study plot. During the autumn, eight woodland quadrats were visited by termites, and 27.6% of *E. capillosa* leaves, 18.2% of *E. capillosa* bark and 23.1% of *A. campestris* shoots were harvested. During the spring season, six woodland plot quadrats were visited, and 28.7% of *E. capillosa* leaves, 14.6% of *E. capillosa* bark and 21.3% of *A. campestris* shoots were harvested. The average harvesting rate for all litter components combined was 23.0% and 21.5% during the autumn and spring seasons, respectively. There were no significant differences between the two seasons in any of the three components, although the harvesting rate was slightly higher during the autumn than in spring. There were significant differences ($P < 0.05$) among litter components harvested within each season, with termites harvesting more *E. capillosa* leaves than other litter material.

In the shrubland plot, five quadrats were visited during the autumn season. The amount of harvested material was: *E. capillosa* leaves, 16.5%; *E. capillosa* bark, 10.6%; and *A. campestris* shoots, 22.1%. During the spring season, five quadrats were visited and the amount harvested was: *E. capillosa* leaves, 21.2%; *E. capillosa* bark, 13.3%; and *A. campestris* shoots, 30.4%. The average harvesting rate for all litter components combined was, respectively, 16.4 and 21.6% during the autumn and spring seasons. There were no significant differences between the two seasons in any of the three components, although the harvesting rate was slightly higher during the spring than in autumn. There were significant differences ($P < 0.05$) in harvesting rate of the litter components within each season. More *A. campestris* shoots were harvested than any other litter material.

There were no significant differences in the rate of litter harvesting between the two study plots within each season, although the harvesting rate was slightly higher in the woodland than in the shrubland plot (Table 2).

The amount of litter on the ground and the proportion of ground visited by termites during

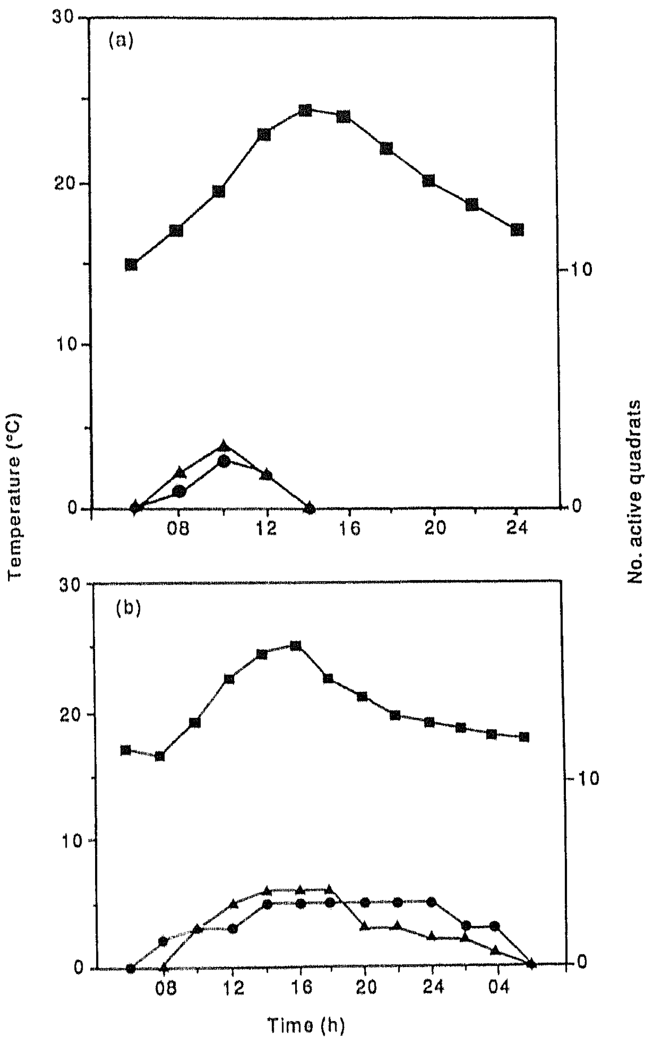

Fig. 3. Hourly counts of the number of quadrats where harvesting activity was observed and corresponding air temperatures for the two spring days when harvesting was observed. (a) 12 October; (b) 15–16 November 1991. (–■–) Air temperature; (–▲–) woodland; (–●–) shrubland.

harvesting have been measured for each plot (Park 1993) and will be reported in separate papers. These measurements were combined with the data on the rate of litter harvested by termites per quadrat per month (% m^{-2} $month^{-1}$) in order to express the amount of litter harvested by *D. tamminensis* in terms of the overall quadrats per square meter per month (g m^{-2} $month^{-1}$). This was calculated for each month by the following formula:

$$H = ([(\%H \times L)/100] \times F)/100$$

Where H is the amount of litter harvested by *D. tamminensis* per square meter per month, $\%H$ is the percentage of litter harvested by termites in one square meter quadrat per month, L is the amount of litter on the ground (i.e. 610.2 g m^{-2} in the woodland and 315.3 g m^{-2} in the shrubland plot) and F is the percentage of the study plot area that is foraged by termites (i.e. 5.75% in the woodland and 2.70% in the shrubland plot). It is assumed that the termite does not discriminate the age of the litter when it selects food items. The results indicate that the total amount of litter harvested by termites was much greater in the woodland than in the shrubland plot. After summing the monthly calculations for H, the amounts of litter harvested throughout the year were calculated as 15.6 g m^{-2} $year^{-1}$ in the woodland and 3.2 g m^{-2} $year^{-1}$ in the shrubland plot.

DISCUSSION

Harvesting was confined to the autumn (April–May) and spring (October–November) seasons in both study plots. The commencement and duration of harvesting was partly dependent on weather conditions. Most harvesting was observed after or during rain. In the autumn season, harvesting was usually an afternoon activity but it was restricted to the morning in spring. Foraging air temperatures ranged from 15 to 22 °C in autumn and 19 to 25 °C

Table 2 Comparison of litter harvesting rate ($\bar{x} \pm$ SE, n = 10) between two study plots within each harvesting season

Harvesting season	Study plot	Dry weight loss (%)		
		E. capillosa		*A. campestris*
		Leaves	Bark	Shoots
Autumn	Woodland	27.6 ± 1.2	18.2 ± 1.2	23.1 ± 1.3
	Shrubland	16.5 ± 2.0	10.6 ± 1.9	22.1 ± 2.3
Spring	Woodland	28.7 ± 1.4	14.6 ± 1.8	21.3 ± 1.4
	Shrubland	21.2 ± 1.8	13.3 ± 0.9	30.4 ± 1.9

in spring. From these results, it appears that the optimal air temperature for harvesting ranges between 15 and 25 °C. However, adequate moisture conditions are also required. In addition to prevailing rainfall conditions, litter moisture may also be important since this may make litter more suitable for cutting prior to its removal. Quantitative field evaluation of the relationships between harvesting by *D. tamminensis*, temperature and moisture is limited by the low number of days on which foraging was observed. However temperature has been observed to be important for other harvesting species. For instance, Ohiagu (1979) noted that the duration of foraging by *Trinervitermes geminatus* (Wasmann) is partly dependent on temperature, with a lower temperature threshold of 20 °C and an upper threshold of 35 °C. Foraging is restricted below or above these temperatures.

The harvesting activity of *D. tamminensis* was generally higher in the woodland than in the shrubland plot. In the woodland plot, harvesting activity by termites was observed in eight quadrats in autumn and six quadrats in spring. In the shrubland plot, five quadrats were harvested by termites in each season. Comparison of the rates of litter harvesting between the two study plots shows there were no significant differences, but the harvesting rate per quadrat was nevertheless slightly higher in the woodland than in the shrubland. However, when the greater extent of foraging in the woodland compared to the shrubland is taken into account, termites were found to harvest approximately 15.6 g m^{-2} $year^{-1}$ and 3.2 g m^{-2} $year^{-1}$ in the woodland and shrubland plots, respectively. The higher activity in the woodland may well be related to the differences of litter quantity and litter nutrient concentration in this plot. As mentioned earlier, litter quantity and also the associated nutrient levels are significantly higher in the woodland than in the shrubland (Park 1993).

In the woodland plot, there were no significant differences in the rate of litter harvesting between the two harvesting seasons. However, the harvesting rate was slightly higher during the autumn than in spring. There were also no significant differences between the two seasons in the shrubland, but the harvesting rate was slightly higher during the spring than in autumn. Comparison of the quantities of each litter component harvested within each season showed significant differences in harvesting rate among litter components in the woodland, where more *E. capillosa* leaves were harvested than any other litter component. In the shrubland, significantly more *A. campestris* shoots were harvested than any other litter component. According to these results, termites appear to feed on the most abundant resources. Where *E. capillosa* leaves are the most abundant litter resource (20–30% in the woodland plot [Park 1993]), these are taken in greater quantities than other litter components. Where *A. campestris* shoots are the most abundant litter resource (60–70% in the shrubland [Park 1993]), more of these are harvested than other litter components. This is despite the fact the termites had a choice in the experimental feeding quadrats that were installed in each study plot. This phenomenon may be due to the termites learning to take the most abundant litter component in each study plot.

Quantitative field estimates of harvesting by termites are limited, even though many instances of termites feeding on vegetation have been documented (Nel 1968; Josens 1972; Ohiagu & Wood 1976; Ohiagu 1979). Nel (1968) noted that *Hodotermes mossambicus* (Hagen) removed about 1.46 g m^{-2} $year^{-1}$ from South Africa. Josens (1972) estimated the amount of grass consumed by *Trinervitermes* spp. to be in the order of 0.6–4.4 g m^{-2} $year^{-1}$ in the Ivory Coast, while Bodine (1973) estimated that the desert termite, *Gnathamitermes tubiformans* (Buckley), removed 3.6 g m^{-2} $year^{-1}$ in West Texas. Ohiagu and Wood (1976) estimated the grass harvesting termite, *Trinervitermes geminatus*, harvested grasses at the rate of between 4.02 g m^{-2} $year^{-1}$ to 30.30 g m^{-2} $year^{-1}$ in Nigeria. Thus, harvesting by *D. tamminensis* is generally within the same order as that reported for other termites elsewhere in the world.

This study has indicated the importance of one species of termite as a harvester of vegetation and, ultimately, as an agent of nutrient cycling in this Western Australian ecosystem. The role of this termite takes on particular importance in view of the fact that Western Australian soils are notoriously impoverished in nutrients (Bettenay & Mulcahy 1972). Thus, any agent that enhances the return of nutrients, which are locked in the litter, back to the soil is of special importance. Furthermore, *D. tamminensis* is only one of 36 species of litter harvesting or wood-feeding termites in this study area (Abensperg-Traun 1990). The cumulative role of all these species in recycling nutrients would be considerably higher than the figure given for this species alone.

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