

A model of litter harvesting by the Western Australian wheatbelt termite, *Drepanotermes tamminensis* (Hill), with particular reference to nutrient dynamics

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A series of papers have been published which describe the influence of vegetation and soil type on the Western Australian wheatbelt termite, *Drepanotermes tamminensis* (Hill), and also on its litter harvesting levels and contribution to the soil nutrient budget. This paper integrates these findings by means of a computer simulation model. The model consists of three modules which respectively describe the dynamics of litter on the ground, the dynamics of litter within termite mounds and how these in turn influence nutrient loads within the habitat. The outputs of the model suggest that this litter harvesting termite plays an important role in the nutrient dynamics of the area and it provides an estimate of the unmeasured variable, litter consumed in mounds by termites, which is consistent with measurements for other termite species with similar feeding habits.

Key words: *Drepanotermes tamminensis*; harvesting rate; Isoptera; nutrient dynamics; simulation model; termites.

INTRODUCTION

The mound-building termite, *Drepanotermes tamminensis* (Hill), is a common species in the Western Australian wheatbelt. It constructs conical or rounded mounds, generally up to 1 m in height, and workers forage above ground during humid conditions to harvest litter and other vegetable debris which they subsequently store in the mound.

Between 1990 and 1993 a study was performed on the contribution this termite makes to litter harvesting, and ultimately to the nutrient budget, in Wandoo (*Eucalyptus capillosa*) woodland and Casuarina (*Allocasuarina campestris*) shrubland in the Durokoppin Nature Reserve, Western Australia (Park 1993). This study comprised a series of

components, including characterization of the influence of vegetation and soil types on the distribution and density of mounds (Park *et al.* 1994a,b), quantifying the harvesting rate of termites in both of the above mentioned vegetation types (Park *et al.* 1993) and measuring the contribution of this termite to the soil nutrient budget (Park *et al.* 1994c). The study highlighted the important contribution which this termite can make to nutrient cycling in the wheatbelt, although it did not attempt to quantify the rate of breakdown of litter within the mounds.

The aims of this paper are to integrate the findings of the study in order to (i) represent the dynamics of litter harvesting by *D. tamminensis*, (ii) represent the impact that litter harvesting has on nutrient dynamics, (iii) follow the changes in the system through time, (iv) check the consistency of the field data, (v) estimate variables which were not measured directly in the field, and (vi) make suggestions for further studies and data collection. In order to achieve these aims we utilized the ITHINKTM computer package which enables the

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user to construct a model that simulates the interactions occurring in the field.

STRUCTURE OF MODEL

The specific biological components necessary to estimate litter dynamics by termites can be divided into three modules. The first module refers to the dynamics of litter on the ground, the second to the dynamics of litter in the mound and the third to the dynamics of nutrients in litter. A model is formed by the stocks, inflows, outflows, driving variables and constant coefficients. After characterizing stocks and flows, variables and constants which have been estimated experimentally are entered into the model. The results of simulation of each modelling run are illustrated as an output in the form of a graphical plot.

To construct the model, a number of simplifying assumptions were made. The assumptions were as follows: (i) the simulation is carried out using a monthly time step, (ii) the number of termites in a mound is constant throughout the year, (iii) all individual termites consume the same amount of litter, (iv) litter harvesting occurs only during spring (October–November) and autumn (April–May, see Park *et al.* 1993), and (v) the system is stationary from year to year (i.e. the amounts of litter and nutrients are equal at the beginning and end of a 12 month period). The model operated on a monthly time sequence as this corresponded to the time frame of availability of termite data collected from the field. The model was run over a 12 month period, although it was also used to investigate the behavior of the system over several years.

The detailed structure of the model is described in the following three sections. Measurement and derivation of the individual variables is described in Park (1993) and Park *et al.* (1993, 1994a,b,c). The code letters for each variable consist of two or three letters. In order to distinguish between related variables a lower case second letter indicates that the variable is in g and/or m^{-2} , while an upper case second letter indicates that it is expressed in kg and/or ha. It should be noted that in order to provide a uniform variable coding system in the model, the codes are not the same as in previous papers. The state and driving variables and constant coefficients are listed in alphabetical order in Appen-

dix 1, which also lists the constants that were calculated by the model.

Dynamics of litter on the ground

In this module (Fig. 1), the monthly variation in ground litter biomass has been estimated from experimental data described in Park (1993) and Park *et al.* (1993). The model is organized around the accumulation and loss of litter on the ground (L_g). The inflow is the monthly litter fall (L_f), while the outflows are the amount of litter harvested by *D. tamminensis* (L_h) and the amount of litter which has decayed as a result of agents other than this termite (L_d). Graphical functions were derived from experimental data on the monthly rate of litter fall, of litter harvested and of litter decayed (Park *et al.* 1993). The related equations are as follows:

$$\begin{aligned} L_g(t + \Delta t) &= L_g(t) + (L_f - L_d - L_h) \times \Delta t \\ L_{gi} &= L_g(0) \end{aligned} \quad (1)$$

where L_g is the amount of litter on the ground after a period of time Δt ($\Delta t = 1$ month in the case of this model), L_{gi} is the initial amount of litter on the ground (610 g m^{-2} and 315 g m^{-2} for woodland and shrubland, respectively, as measured in the field, Park 1993, L_f is the amount of litterfall, L_d is the amount of litter decay by other agents and L_h is the amount of litter harvested by *D. tamminensis*. L_d was calculated from the rate of litter decay per month by other agents (% L_d , % per month) and the amount of litter on the ground (L_g). It was calculated as follows:

$$L_d = (\% L_d \times L_g) / 100 \quad (2)$$

The variable L_h , which is the amount of litter harvested by *D. tamminensis*, was calculated from the rate of litter harvested by termites (% L_h , % per month) and the amount of litter on the ground (L_g). It was calculated as follows:

$$L_h = (\% L_h \times L_g) / 100 \quad (3)$$

Dynamics of litter in the mound

The links in this module are illustrated in Fig. 1. The model is based around the amount of litter inside a mound (LM). It operates on a kilogram basis, rather than the grams used in module 1. The inflow is the amount of litter harvested by *D. tamminensis* per mound (LH), while the outflow is

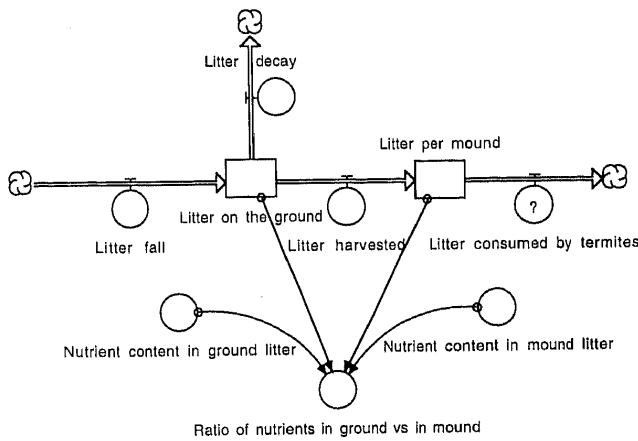


Fig. 1. Schematic diagram showing the relationships between the three modules of the model, which respectively describe: (i) the dynamics of litter on the ground; (ii) the dynamics of litter in termite mounds; and (iii) the flow of nutrients from leaf litter on the ground to that in termite mounds. The rectangles indicate stocks, circles indicate driving variables and double arrows indicate flows.

the litter consumed in mounds by termites (LC). The inflow was calculated from the proportion of a hectare where termites are active at any given time (FA), the number of mounds per hectare (MO) and the amount of litter harvested monthly by termites per hectare (LH). The outflow was calculated from the amount of daily litter consumed by termites (L_t ; $g [g \text{ of termite}]^{-1} \text{ day}^{-1}$) and the biomass of termites per mound (B_t). Most variables and parameters were measured in each study site (Park 1993; Park *et al.* 1993). The exception was the amount of litter consumed by termites inside the mound (L_t), as measurement of this parameter was beyond the scope of the study. Consequently, the rate of litter consumption by individual termites was calculated from the model using sensitivity analysis with the assumption that the system is stationary (see Results section). The resulting estimate was then compared with data on termite food consumption from comparable studies.

The related equations for the amount of litter within the mound, LM, are:

$$\begin{aligned} LM(t + \Delta t) &= LM(t) + (LH - LC) \times \Delta t \\ LM_i &= LM(0) \end{aligned} \quad (4)$$

where LM_i is the initial amount of litter per mound (2.2 and 2.0 kg mound^{-1} in woodland and shrubland plots, respectively; Park 1993), LH is the amount of litter harvested by termites monthly per

mound and LC is the amount of litter consumed monthly by termites per mound.

LH was calculated from L_h , the amount of litter harvested by termites monthly per square meter (equation 3), FA and MO. FA and MO values were estimated experimentally from field studies (Park 1993; Park *et al.* 1993). The related equation is:

$$LH = \{(L_h \times 10\,000/1000) \times FA\}/MO \quad (5)$$

LC was calculated from L_t , the amount of litter consumed daily per gram of termite per day and B_t , the biomass of termites per mound, which was calculated from laboratory data (Park 1993). L_t was derived from the sensitivity analysis (see Results section) and then converted to a monthly value. The equation is:

$$LC = \{(L_t \times B_t) \times 30\}/1000 \quad (6)$$

B_t was calculated from the number of termites per mound (P) and the biomass and relative composition of each termite caste, namely workers, soldiers and nymphs. The equation is:

$$\begin{aligned} B_t &= P \times \{(B_w \times C_w) + (B_s \times C_s) \\ &\quad + (B_n \times C_n)\} \end{aligned} \quad (7)$$

where B_w , B_s , B_n are the mean weights (g) of workers, soldiers and nymphs, respectively. C_w , C_s and C_n (%) indicate the mean proportion of workers (79%), soldiers (16%) and nymphs (5%) in mounds, as measured in the laboratory (Park 1993).

Dynamics of nutrients in litter

The module for the relationship between macro nutrients (N, P, K) in the mound and ground litter is shown in Fig. 1. The percentage of nutrients in mounds, expressed as a percentage of total nutrients, %NM, is estimated from the absolute amount of nutrients in the ground (NG) and in the mound (NM) litter (see Park *et al.* 1994c). The required variable for the model inputs were the concentration of nutrients in the ground litter (%NG), the concentration of nutrients in the mound litter (%NU), the amount of litter on the ground (LG), the amount of litter in the mound (LM) and, finally, the number of mounds per hectare (MO). The amount of litter in mounds per hectare (LMH) was derived from the latter two variables. The related equations are:

$$\%NM = \{NM/NM + NG\} \times 100 \quad (8)$$

$$NG = (\%NG \times LG)/100 \quad (9)$$

$$NM = (\%NU \times LMH)/100 \quad (10)$$

$$LMH = MO \times LM \quad (11)$$

The ratio of nutrient concentration in mound relative to that in ground litter, NC, was calculated from the following formula:

$$NC = (\%NM \times 0.01) \times BA \quad (12)$$

where BA is the basal area of the mounds (ha).

RESULTS

Dynamics of litter on the ground

Model predictions

The monthly variation in the amount of litter on the ground, the amount of litter fall, litter decay and litter harvested by termites for woodland and shrubland plots are shown in Fig. 2a,b, respectively. The

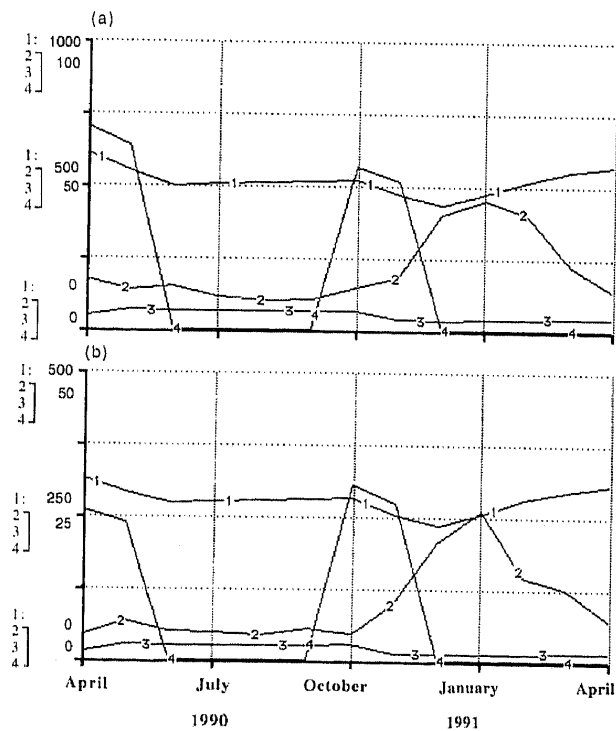


Fig. 2. Monthly variation in the amount of litter on the ground, litter fall, litter decay by other agents and the amount of litter harvested by termites, in: (a) Wandoo (*Eucalyptus capillosa*) woodland and (b) Casuarina (*Allocasuarina campestris*) shrubland. Key to x-axis: 1, weight of litter on ground (g m^{-2}) (Lg); 2, litter fall ($\text{g m}^{-2} \text{ month}^{-1}$) (Lf); 3, litter decay ($\text{g m}^{-2} \text{ month}^{-1}$) (Ld); 4, litter harvested by *Drepanotermes tamminensis* ($\text{g m}^{-2} \text{ month}^{-1}$) (Lh).

amount of litter on the ground displays a similar pattern in both study plots. The troughs in the line for litter on the ground occurred as a result of decreased availability of litter during the harvesting periods of termites. The lowest litter level on the ground was between November and January, just after the second harvesting period. After this period, the litter level increased rapidly in comparison with the level between the first and second harvesting period. This was due to an increase in litter fall and an absence of harvesting by termites.

The variation in the amount of litter harvested by termites exhibited different patterns in the woodland and shrubland plots. In the woodland plot the amount of litter harvested by termites was higher during the first period (between April and May) than the second harvesting period (between October and November). By contrast, it was higher during the second than the first harvesting period in shrubland. The annual amount of litter decayed by other agents was extremely small in both study plots. The amount of litter on the ground increased between the harvesting periods (between June and September), despite some litter decaying. Consequently, the amount of litter on the ground in both study plots appeared to remain fairly stable during this period.

The stationarity of the system was investigated using the sensitivity analysis procedure. This investigates the behavior of the model for a range of values of a given parameter. The outputs can be displayed graphically, thus providing insight into the behavior of this particular variable in the system. It was carried out for a range of initial values of litter on the ground (Lgi). The results shown in Fig. 3a,b demonstrate that there is an equilibrium for a particular amount of litter on the ground in each study plot. The model was run for the woodland plot using values for initial litter on the ground ranging from 0 to 1000 g m^{-2} in 100 g m^{-2} increments. If the initial amount of litter on the ground is below 600 g m^{-2} , the amount of litter on the ground at the end of each 12 month period will increase until the equilibrium value of 600 g m^{-2} is reached. If the initial amount of litter is above 600 g m^{-2} , the value of the amount of litter will decrease by the end of each 12 month period until it reaches the same equilibrium value of 600 g m^{-2} (Fig. 3a). This result shows that the value of 600 g m^{-2} is the amount of litter on the ground which represents a stationary state for the system.

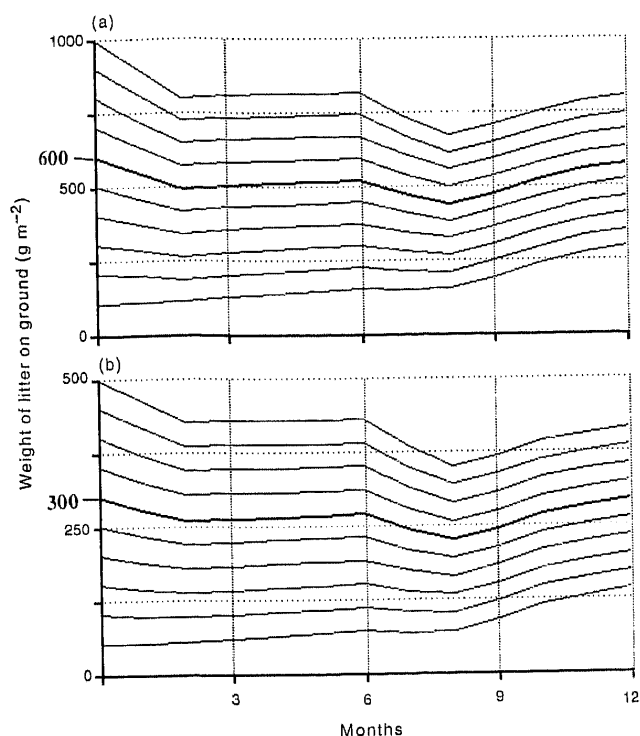


Fig. 3. Sensitivity analysis conducted on the initial amount of litter on the ground in each study plot (g m^{-2}) (Lgi) in: (a) Wandoo (*Eucalyptus capillosa*) woodland and (b) Casuarina (*Allocasuarina campestris*) shrubland.

The model was run for the shrubland plot using a range of values between 0 and 500 g m^{-2} in increments of 50 g m^{-2} . In this case it was found that a stationary state is reached at a value of 300 g m^{-2} (Fig. 3b). The predictions of the model are in agreement with field measurements, since initial litter biomass measured in the field was found to be 610 g m^{-2} in the woodland and 315 g m^{-2} in the shrubland plot (Park 1993; Park *et al.* 1993).

Dynamics of litter in the mound

Model predictions

The monthly variation in the amount of litter in the mound, of litter harvested and of litter consumed by termites in each study plot is shown in Fig. 4a,b. The variation in the amount of litter in the mound exhibited similar patterns in both study plots. However, there was a greater variability throughout the year in the woodland than in the shrubland plot. The amount of litter harvested by termites in each plot increased during the harvesting periods and decreased after harvesting. This was related to the quantity of litter taken and to the absence of food

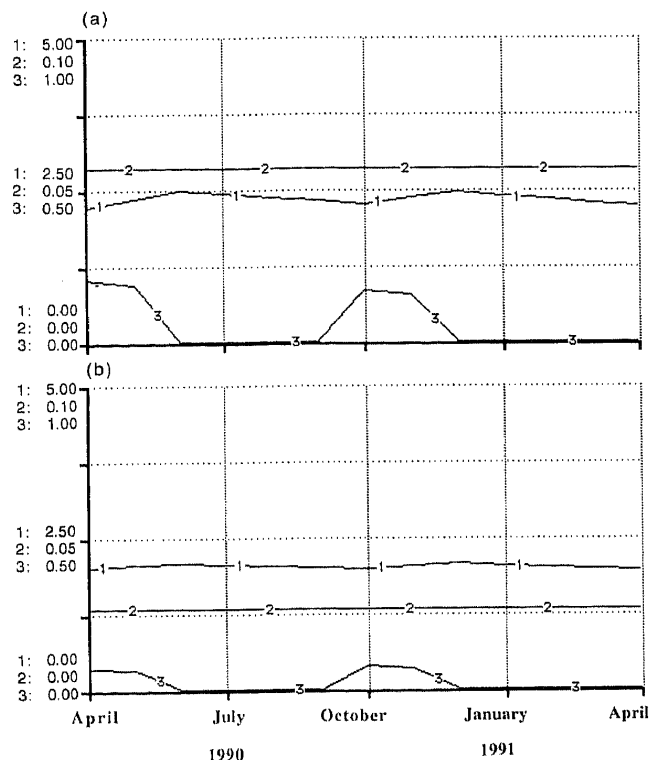


Fig. 4. Monthly variation in the amount of litter in the mound, the amount of litter consumed and the amount of litter harvested by *Drepanotermes tamminensis* in: (a) Wandoo (*Eucalyptus capillosa*) woodland and (b) Casuarina (*Allocasuarina campestris*) shrubland. Key to x-axis: 1, weight of litter per mound (kg mound^{-1}) (LM); 2, litter consumption by *D. tamminensis* ($\text{kg mound}^{-1} \text{ month}^{-1}$) (LC); 3, litter harvested by *D. tamminensis* ($\text{kg mound}^{-1} \text{ month}^{-1}$) (LH).

gathering by termites at other times of the year.

Sensitivity analysis

This was carried out in order to provide an estimate of the amount of litter consumed by termites (on a per mound and per gram of termite basis; LC and Lt) in each study plot (Fig. 5a,b). This estimate was necessary because, in the scope of this study, it was not possible to measure this parameter directly in the field.

It has already been demonstrated that the amount of litter in mounds is closely related to the mound volume (Park 1993). According to the field measurements of annual increment in mound volume, increases were so slight that there was effectively no increment in mound volume over the 15 month interval from 1990 to 1991 (Park 1993). Thus, mound volume and the amount of litter in the mounds may be assumed to be relatively stable from

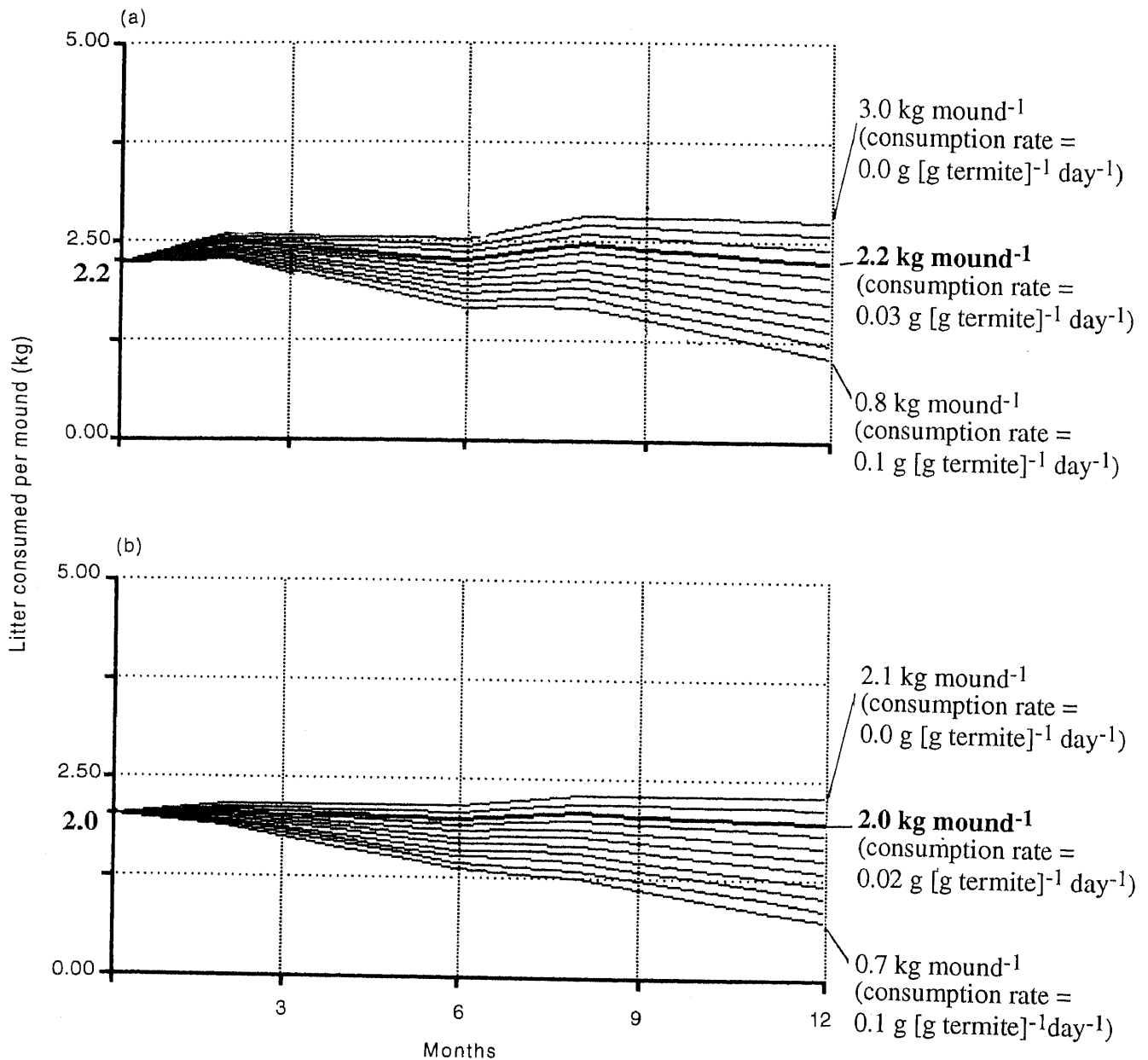


Fig. 5. Sensitivity analysis conducted on litter consumption by *Drepanotermes tamminensis* (in kg mound⁻¹ month⁻¹ and g [g termite]⁻¹ day⁻¹) (LC and Lt) in: (a) Wandoo (*Eucalyptus capillosa*) woodland and (b) Casuarina (*Allocasuarina campestris*) shrubland.

year to year in the study plots. From this, it may be deduced that the input (the amount of litter harvested by termites) and the output (the amount of litter consumed by termites) have probably reached equilibrium.

Using the sensitivity analysis procedure, an estimate can be derived of the daily litter consumption per gram of termite which produces a stationary state in terms of the amount of litter in the mound. Figure 5a,b represents the monthly values of litter in mound which result from values of litter consumed by termites ranging between 0 and 0.1 g (g of

termite)⁻¹ day⁻¹. This range was derived by referring to comparable studies on other termites (see references in Discussion). In the woodland plot, a stationary litter value of 2.0 kg mound⁻¹ is reached for a consumption value of 0.03 g (g of termite)⁻¹ day⁻¹ (Fig. 5a). Thus, since the litter content of the mound is fairly stable from year to year, it can be assumed that the amount of litter consumed by termites in the woodland is approximately 0.03 g (g of termite)⁻¹ day⁻¹. Similarly, the equilibrium in the shrubland plot was reached at approximately 0.02 g (g of termite)⁻¹ day⁻¹ (Fig. 5b).

Using the previously derived values of litter consumption, a sensitivity analysis was carried out to investigate the stationarity of the system for a range of initial values LM_i (amount of litter in mound) in each study plot (Fig. 6a,b). Using the same approach as in the previous sensitivity analyses, it can be demonstrated that a stable equilibrium is reached at 2.0 and 1.5 kg mound^{-1} in woodland and shrubland, respectively. It is worth noting that the predictions of the model are reasonably consistent with the field measurement of 2.2 kg mound^{-1} and 2.0 kg mound^{-1} in woodland and shrubland, respectively.

Dynamics of nutrients in litter

The annual variation in the quantity of nutrients in the mound is shown for woodland and shrubland respectively in Figs 7a,b,c and 8a,b,c. The variation in the percentage and quantity of nutrients in the mound litter showed a similar pattern within both study plots. The quantity of nutrients in the mound

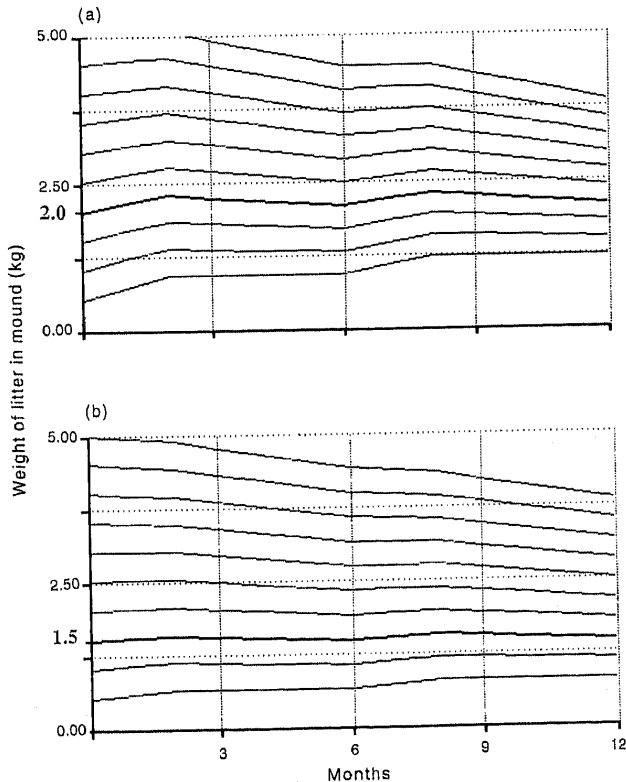


Fig. 6. Sensitivity analysis conducted on the initial amount of litter in *Drepanotermes tamminensis* mounds (kg mound^{-1}) (LM_i) in: (a) Wandoo (*Eucalyptus capillosa*) woodland and (b) Casuarina (*Allocasuarina campestris*) shrubland.

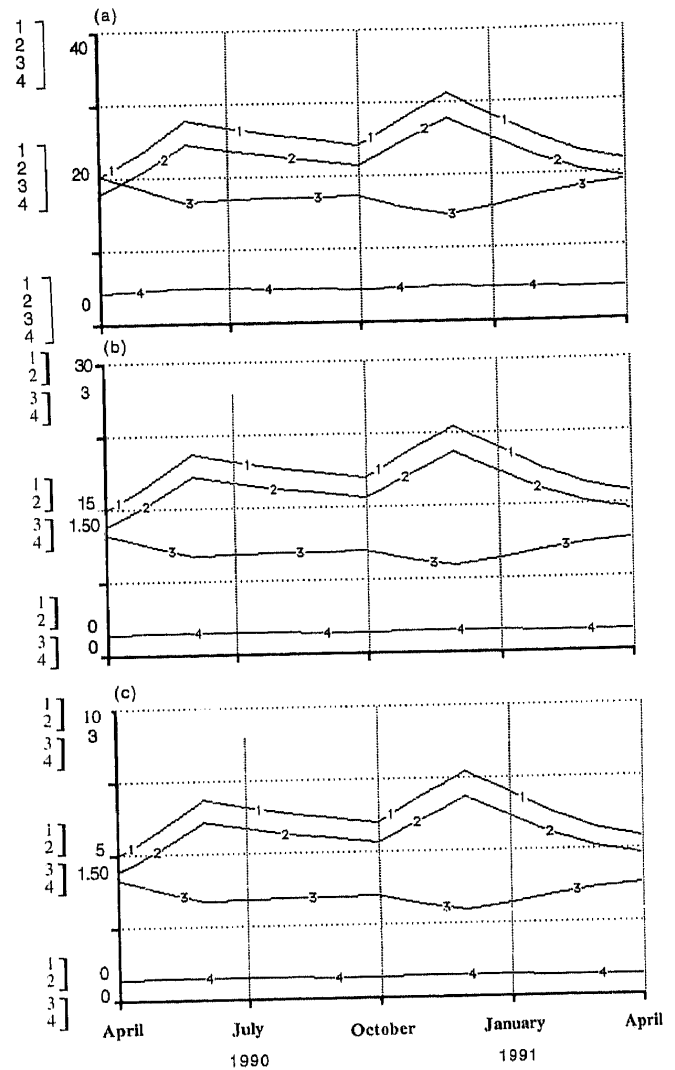


Fig. 7. Percentage of (a) nitrogen, (b) phosphorus and (c) potassium in mound-stored litter, actual concentration of nutrients in mound litter, and also the amount of nutrients in ground and mound litter within the Wandoo (*Eucalyptus capillosa*) woodland. Key to x-axis: 1, mound nutrients as percentage of total litter nutrients (%NM); 2, concentration of nutrients in mound litter (%) (%NU); 3, amount of nutrients in ground litter (kg ha^{-1}) (NG); 4, amount of nutrients in mound litter (kg ha^{-1}) (NM).

litter increased, while the quantity of nutrients in the ground litter decreased during the harvesting period of termites. The amount of nutrients in the mound litter was stable throughout the year as the amount of litter harvested and the amount of litter consumed by termites within mounds were equal to each other.

Within the woodland plot the quantity of N, P and K in the mound litter per unit area was approximately 20, 15 and 40 times higher than that in the surrounding ground litter (Fig. 7a,b,c,

respectively). In the shrubland plot the corresponding levels were at least 10, 20 and 35 times higher than that in the surrounding ground litter (Fig. 8a, b, c, respectively).

DISCUSSION

A number of conclusions may be drawn from the application of this model. Firstly, the amount of litter on the ground varies throughout the year and

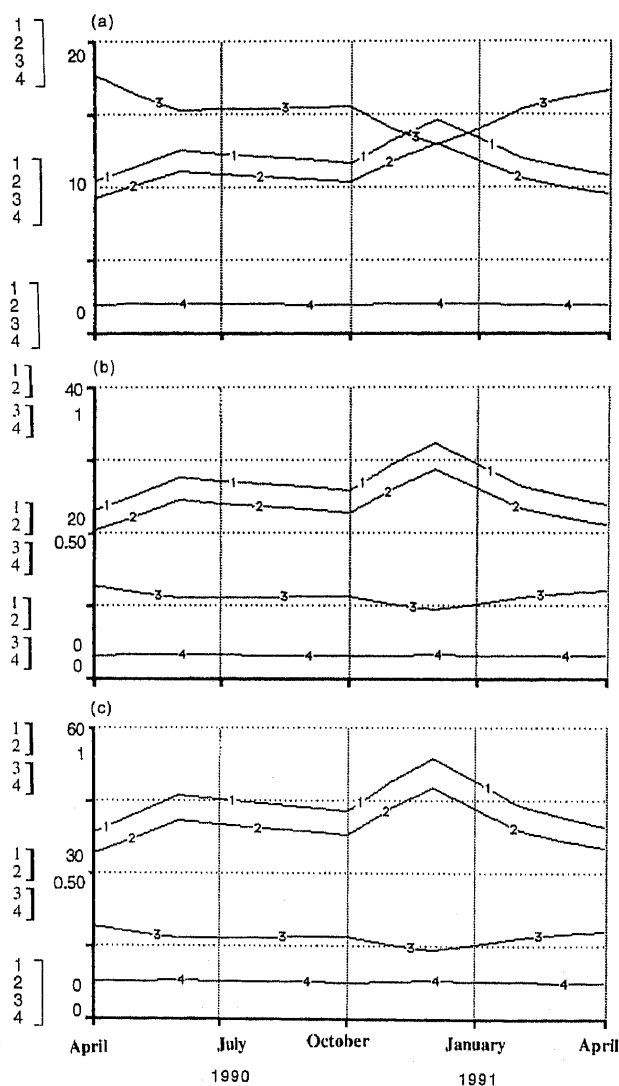


Fig. 8. Percentage of (a) nitrogen, (b) phosphorus and (c) potassium in mound-stored litter, actual concentration of nutrients in mound litter, and also the amount of nutrients in ground and mound litter within the *Casuarina* (*Allocasuarina campestris*) shrubland. Key to x-axis: 1, mound nutrients as percentage of total litter nutrients (%NM); 2, concentration of nutrients in mound litter (%) (%NU); 3, amount of nutrients in ground litter (kg ha^{-1}) (NG); 4, amount of nutrients in mound litter (kg ha^{-1}) (NM).

shows similar monthly patterns in both study plots. Within both plots the amount of litter on the ground decreased during harvesting periods and increased after harvesting by termites ceased. In particular, the amount of litter increased rapidly after the second harvesting period due to significant increases in litter fall and to the absence of harvesting by termites. The amount of litter decay by other agents, such as earthworms, micro-arthropods, other insects and micro-organisms did not appreciably influence the amount of litter on the ground. Therefore, it appears that *D. tamminensis* is a major agent of litter removal in the study plots. Sensitivity analysis of the variation in the amount of litter on the ground supports these field measurements.

Secondly, the amount of litter in the mound varies throughout the year. Litter in the mound increased during harvesting periods and decreased after harvesting periods due to litter consumption by termites in the absence of litter harvesting. Sensitivity analysis graphs indicated that *D. tamminensis* consumed approximately $0.03 \text{ g (g of termite)}^{-1} \text{ day}^{-1}$ in the woodland plot and $0.02 \text{ g (g of termite)}^{-1} \text{ day}^{-1}$ in the shrubland plot. These values are consistent with those reported in the literature for termites with similar ecological requirements (e.g. Nel *et al.* 1970; Josens 1972; Lepage 1974; Ohiagu & Wood 1976; Ohiagu 1979). These studies have reported that harvesting termites consume between 0.003 and $0.059 \text{ g (g of termite)}^{-1} \text{ day}^{-1}$ of grass or litter. For example, Lepage (1974) estimated that *Macrotermes subhyalinus* (Rambur) consumed $0.003 \text{ g (g of termite)}^{-1} \text{ day}^{-1}$ of litter while Ohiagu and Wood (1976) noted that *Trinervitermes geminatus* (Wasmann) consumed between 0.007 and $0.055 \text{ g (g of termite)}^{-1} \text{ day}^{-1}$ of grass. Further experiments are now required to verify the amount of litter consumed within the mounds of *D. tamminensis*.

The differences in litter consumption levels between the two study plots may be associated with the differing environment, micro-climate, nutrient levels or differing quantity and quality of litter between the woodland and shrubland plots (Park 1993; Park *et al.* 1994a, b).

Finally, this modelling exercise has confirmed that the role of *D. tamminensis* in nutrient cycling appears to be important in the study area. The quantity of nutrients in the mound litter per unit area was at least 10 to 40 times higher than of the litter on

the adjacent ground. Nutrient turnover in termite mounds depends on the longevity of termite colonies and on the resistance of their abandoned mounds to weathering (Bonell *et al.* 1986). In the case of abandoned *D. tamminensis* mounds, a period of at least 30 years would be required for nutrients to be returned to the ecosystem (Lobry de Bruyn 1991). In the absence of erosion, the mounds may serve as a temporary nutrient reservoir in the ecosystem.

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APPENDIX I

List of variables and constants in alphabetical order

State variables

- Lg/LG Amount of litter on the ground (g m^{-2} or kg ha^{-1}).
- LM Amount of litter inside mound (kg mound^{-1}).

Driving variables, constants

- Determined experimentally or from the literature
- %Ld Litter decayed as a result of agents other than termites as a percentage of the amount of litter on the ground (Lg) ($\% \text{ month}^{-1}$).
- %Lh Litter harvested by termites as a percentage of the amount of litter on the ground (Lg) ($\% \text{ month}^{-1}$).
- %NG Percentage of nutrients in the ground litter, expressed as a percentage of total nutrients (%).

%NM	Percentage of nutrients in mounds, expressed as a percentage of total nutrients (ground litter + mounds) (%).	Ld	Litter decayed as a result of agents other than termites ($\text{g m}^{-2} \text{ month}^{-1}$).
BA	Basal area of the mounds (ha).	LH	Litter harvested by termites per mound ($\text{kg mound}^{-1} \text{ month}^{-1}$).
Bt	Biomass of termites per mound (g mound^{-1})	Lh	Litter harvested by termites ($\text{g m}^{-2} \text{ month}^{-1}$).
Bw, Bs, Bn	Mean weight of workers, soldiers and nymphs, respectively (g).	LMH	Amount of litter in mounds per hectare (kg ha^{-1}).
Cw, Cs, Cn	Mean proportion of workers, soldiers and nymphs in mound (%).	NC	Ratio of nutrient concentration in mound relative to that in ground litter.
FA	Proportion of a hectare where termites are active at any given time (%).	NG	Total amount of nutrients in the ground (kg ha^{-1}).
Lf	Litter fall ($\text{g m}^{-2} \text{ month}^{-1}$).	NM	Total amount of nutrients in the mound (kg ha^{-1}).
MO	Number of mounds per hectare.		Constants obtained by determining the stationary state of the system
P	Number of termites per mound.	Lgi	Initial amount of litter on the ground ($\text{g m}^{-2} \text{ month}^{-1}$).
Calculated by the model		LMi	Initial amount of litter inside mound (kg mound^{-1})
%NU	Concentration of nutrients in the mound litter (%).	Lt	Amount of litter consumed daily by termites ($\text{g [g of termite]}^{-1} \text{ day}^{-1}$).
LC	Litter consumed by termites per mound ($\text{kg mound}^{-1} \text{ month}^{-1}$).		