# Impacts of canopy cover on soil termite assemblages in an agrisilvicultural system in southern Cameroon

## L. Dibog<sup>1,2</sup>, P. Eggleton<sup>1\*</sup>, L. Norgrove<sup>3,4</sup>, D.E. Bignell<sup>5</sup> and S. Hauser<sup>3</sup>

<sup>1</sup>Termite Research Group, Entomology Department, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK: <sup>2</sup>NERC Centre for Population Biology, Imperial College, University of London, Silwood Park, Ascot, Berkshire, SL5 7PY, UK: <sup>3</sup>International Institute of Tropical Agriculture, Humid Forest Station, BP 2008 (Messa) Yaoundé, Cameroon: <sup>4</sup>Division of Life Sciences, King's College, University of London, London, W8 7AH, UK: <sup>5</sup>Tropical Biology and Conservation Unit, Universiti Malaysia Sabah, Kampus Jalan Tuaran, 88999 Kota Kinabalu, Sabah, Malaysia

## Abstract

Termites were sampled using randomized soil pits in 64 cropping plots, each  $25 \times 25$  m, forming an experimental agrisilvicultural system in both a 6- and an 18year-old Terminalia ivorensis plantation, in which canopy cover, crop, cropping system and land preparation were the principal treatment variables. The treatments were established in April 1995 and sampling was carried out in November 1995, February 1996 and July 1996. A total of 82 termite species were found, of which 67 were soil-feeders. Overall termite abundance and the abundance of soil-feeders increased between November 1995 and July 1996, reaching a mean of nearly 6000 m<sup>-2</sup>. Pooling termite data from these sampling dates, in the old plantation, the high canopy cover treatment (192 stems ha<sup>-1</sup>) had a greater abundance of termites, compared with the low canopy cover treatment  $(64 \text{ stems ha}^{-1})$  and this effect was independent of crop type (plantain or cocoyam), cropping system (single stands or mixed crops) and land preparation (mulch retained or burned, plantain only). The young tree plantation (same tree densities as in the old plantation) showed no significant difference in termite abundance between high and low canopy (levels of tree foliage) densities, though the high canopy sheltered a greater number of termites. Analysis of covariance showed that crop yield (both plantain and cocoyam) was not directly linked to the abundance of all termite populations, but that the cocoyam yield was positively correlated with the abundance of soil-feeding termites (the majority in the assemblage) in the young plantation. This may be due to the beneficial conditioning of soil resulting from the foraging and construction activities of soil-feeders.

## Introduction

The Humid Forest Zone (HFZ) of Africa covers significant parts of a broad swathe of countries, from Guinea

\* Author for correspondence. Fax: +44 171 938 8937 E-mail: pe@nhm.ac.uk in the west to the Congo basin in the east and south. The present zone is a mosaic of different types of land use: patches of secondary forest and fallow vegetation, some tree plantations and substantial remnants of primary vegetation (Swift & Mutsaers, 1992). The dominant soils are acidic (oxisols and ultisols derived from low activity clays), commonly exhibiting aluminium toxicity, low cation exchange capacity, low base saturation and low phosphorus availability. Consequently, they have low inherent fertility and, in many cases, low structural stability if soil organic matter is excessively depleted.

The traditional food production systems of the humid forest zone are those of shifting cultivation (slash and burn) and (increasingly) recurrent fallow rotation, with plantain, cocoyam, maize, groundnut and cassava as the principal staples, the last having a relatively low fertility requirement. In recent years, socioeconomic factors (including declining world prices for cocoa, oil-palm and other cash crops), population growth, the lack of urban employment opportunities and legal uncertainties over title to timber revenue, have led to an increase in the clearance of forest for food production and, concomitantly, an accelerated decline in the fertility of soils under cultivation as fallow periods have shortened (Woomer & Swift, 1994). Agricultural research in the humid forest zone has therefore been directed towards the improvement of sustainability, for example by the conservation of soil organic matter and the provision of better mulching regimes, and the development of flexible mixed cropping systems, for example, the combination of high-value tree crops with field-planted staples (Scholes et al., 1994). Multistrata systems provide an opportunity for the simultaneous production of timber (and/or other tree crops) and food, with a sustained supply of organic matter, maintaining soil structure and nutrient status.

The importance of macrofauna to the promotion of tropical soil fertility has been stressed in recent reviews (Fragoso et al., 1993; Lavelle et al., 1994; Garnier-Sillam & Harry, 1995; Nash & Whitford, 1995; Brussaard & Jumas, 1996; Wood, 1996). The distribution, protection and stabilization of organic matter, the genesis of soil macroaggregates and porosity, humification, the release of immobilized nitrogen and phosphorus, the improvement of drainage and aeration, and the increase in exchangeable cations have all been demonstrated in soils modified by termites and earthworms (e.g. Mulongoy & Bedoret, 1989; Lavelle et al., 1992). Depletion of termite abundance and diversity is now a well-established effect of forest clearance (Wood et al., 1982; Eggleton et al., 1995, 1996). Overall, the conservation of indigenous invertebrate biodiversity should be an integral part of land-management strategies (e.g. Smith et al., 1993) in the humid forest zone if the goal of increased crop yield sustainability (and indirectly forest conservation) is to be realized.

The present study focused on: (i) understanding the potential influence of the association of trees and crops with different cropping systems and soil management on the termite assemblage; (ii) estimating the effect of tree umbrages (high and low degree of canopy cover) on the abundance and species richness of soil termites; as well as (iii) measuring the interaction between termites and crop yields, as some termite species are assumed to be either pests of certain crops (Harris, 1968; Sands, 1973; Roonwal, 1979; Wood & Cowie, 1988) or to have beneficial effects on soil fertility (Harris, 1954; Das, 1957; Lee & Wood, 1971; Collins, 1983). In this paper, we report the results of quantitative termite sampling in two agrisilvicutural experiments in a 6- and an 18-year-old plantation of Terminalia ivorensis (Combretaceae), derived from old growth secondary tropical forest in southern Cameroon.

#### Materials and methods

## Study area

The Mbalmayo Forest Reserve (MFR), southern Cameroon  $(11^{\circ}25'-11^{\circ}31' \text{ E}, 3^{\circ}23'-3^{\circ}31' \text{ N}, approximately 640 m above sea level, 9500 ha) is an area of lightly to highly disturbed semi-deciduous tropical pre-montane moist forest (Holdridge$ *et al.*, 1971) with annual rainfall averaging 1520 mm, falling in two wet seasons March–June and August–November inclusive (Lawson*et al.*, 1990, Dibog*et al.*, 1998). Soils are classified as kandiudults derived from schists, typically with loamy sand to sandy loam overlying clay subsoils, moderately drained with weak to moderate structure, strongly acid and leached of bases, with low cation exchange capacities and low nitrogen, phosphorus and potassium status (Holland*et al.*, 1992). Mean monthly temperatures range from 22.5 to 25.0°C.

Developmental projects being undertaken in the Mbalmayo Forest Reserve follow the broad guidelines of the Reserve Management Plan (Ministère de l'Environement et des Forêts, MINEF, Cameroon) and include clonal forestry (Office National de Développement des Eaux et Forêts, ONADEF), the management of short-fallow subsistence agricultural regimes (International Institute of Tropical Agriculture, IITA), and multistrata systems, i.e. underplanting agricultural crops in forestry plantation (IITA, King's College London and ONADEF).

## Site preparation and treatments

The experiments were established in two Terminalia ivorensis (local name: framiré) plantations, 6 and 18 years old, in the Mbalmayo Forest Reserve. Initial land clearance in 1989 (6-year-old plantation) and 1978 (18-year-old plantation) was manual for both plantations (Lawson, 1995). Both experimental plantations had an incomplete two factorial split plot design in four blocks, with three timber stand treatments as main plots: an undisturbed T. ivorensis control stand; T. ivorensis with cropping at 192 stems ha-1 (high canopy cover, both plantations) and T. ivorensis with cropping at 64 stems ha<sup>-1</sup> (low canopy cover, old plantation) or 40 stems ha<sup>-1</sup> (low canopy cover, young plantation) (Norgrove & Hauser, in press). In the older plantation, canopy cover ranged from 48 to 78% in the high and 11 to 29% in the low canopy treatments. In April 1995, mean girth and height were 87.2 cm and 21.5 m, respectively (Norgrove & Hauser, in press). In the younger plantation, canopy cover ranged from 25 to 32% in the high and 0 to 20% in the low canopy treatment. In April 1995, mean girth of trees was 35.8 cm; mean tree height was 9.8 m (Norgrove & Hauser, in press). Different crop management treatments were: sole plantain, intercrop of plantain-cocoyam and sole cocoyam all mulched with the slashed material, and sole plantain, where the slashed material was burned before planting. Subplots were  $25 \times 25$  m.

The experiments were established in April 1995. The understorey of the plantations was manually slashed without removing slash crosscut trunks. Timber stand densities were imposed by thinning according to standard silvicultural practice. In the plots to be burned (plantain only), slash was removed at least 50 cm away from standing tree trunks to avoid scorch damage. Planting density for plantain was 1600 plants ha<sup>-1</sup> on a 2.5  $\times$  2.5 m square

configuration, thus 100 plants per sub-plot. Cocoyam planting density was 20,408 plants  $ha^{-1}$  on a 0.7 m square configuration. Cocoyams were harvested in April 1996, plantains in January 1997.

This describes the experimental design as originally set up to assess the effects of canopy on crop yield (Norgrove & Hauser, in press). For the termite studies, the control plots were not employed because of the lack of information on their location at the period of our investigations. For the termite analyses, the mulch retained and the slash burned plantain treatments were analysed as part of the crop systems. This gave rise to four treatments (high and low canopy cover per crop and per plantation), and five crop treatments, per plantation. The preparation of plots and treatments selected for termite studies are summarized in table 1.

#### *Termite sampling and identification*

Sampling of the experimental plots was carried out in November 1995, February 1996 and July 1996. Preliminary sampling of the old plantation experimental site was carried out in August 1995, to verify the sampling methods and for taxonomic screening, but the data are not included in the analysis. In each plot, two randomly located soil cores, each of  $20 \times 20 \times 10$  cm (depth) were dug out (including surface litter, but not larger woody items or timber) and immediately hand-sorted on large tables under cover by a team of six experienced field assistants. Termites were preserved in 80% ethanol and identified (worker and soldier castes only), using facilities and reference collections provided by Institut de Recherche Agricole pour le

Table 1. Summary of treatment applications in the multistrata agrisilvicultural experiment and plots selected for termite studies in Mbalmayo Forest Reserve, Cameroon.

	No. of plots
Classification of plots per site	
Total	32
High tree density Low tree density Plantain planted Plantain mulch retained Plantain slash-burned Cocoyam planted Plantain and cocoyam planted (mixed crops)	16 16 16 8 8 8 8 8
Treatments imposed per site	
High canopy cover, plantain mulch retained Low canopy cover, plantain mulch retained High canopy cover, plantain slash-burned Low canopy cover, plantain slash-burned High canopy cover, cocoyam	4 4 4 4 4
Low canopy cover, cocoyam High canopy cover, mixed crops Low canopy cover, mixed crops	4 4 4

Thirty two plots, each of  $25 \times 25$  m, were randomly allocated combinations of four cropping treatments with four replications per treatment, in each site: plantain (mulch retained); plantain (slash-burned); cocoyam (mulch retained); mixed crops (mulch retained, plantain + cocoyam). The plots were further divided equally between high and low tree densities shading, making a total of eight treatments.

Développement (IRAD Cameroon) and The Natural History Museum (UK). Data (pooled between the two soil cores per plot per sampling) were recorded as abundance (termites  $m^{-2}$ ), total species richness and trophic group (numbers of soil- and non soil-feeding species, *sensu* Eggleton *et al.*, 1995; Bignell *et al.*, 1997).

Despite the fact that cocoyam was harvested in April 1996, data were pooled from the whole period of sampling. This is justified because: (i) termites have semi-permanent colonies with longevity up to 70 years in the soil (Lobry de Bruyn & Conacher, 1995); and (ii) serial randomized sampling is prone to indicate high species turnover, which may be an artefact (i.e. pseudo-turnover) arising from the marked patchiness of termite distribution and their foraging territories. Pooling data from the whole period of sampling therefore gives the best overall estimate of the level of termite activity.

#### Crop yields

Cumulative crop yields were determined as follows: cocoyam, dry weight of tubers (kg  $ha^{-1}$ ); plantain, fresh weight of fruits (tonnes  $ha^{-1}$ ). Plantain fruits from fallen (uprooted) plants were excluded.

#### Statistical treatments

The influences of canopy, crop and sampling period on termite abundance and species richness were measured, as well as the influence of those factors on functional groups (soil-feeding termites and non soil-feeders including fungusgrowing termites and wood and litter foragers), in the young and the old plantation separately.

For the termite data we employed a three-way repeated measures ANOVA, to assess significant differences between the plot parameters. The independent (grouping) variables were: (i) canopy with two levels for each site (high and low); (ii) crop with four levels in each plantation (cocoyam, plantain, plantain burned plots and mixed crops); and (iii) time (November 1995, February 1996 and July 1996) as repeated measures. A *post hoc* Tukey HSD test was used to identify significant differences between treatments, when a particular effect was significant overall.

The tested dependent variables were:

**1.** Termite abundance: the abundance of termites from soil cores generally fit a negative binomial distribution, revealing a high degree of dispersion of the samples (see Eggleton *et al.*, 1996). The mean abundances were log(x + 1) transformed, to normalize the distribution.

**2.** Species richness: the observed values were used for the ANOVAs to compare the plot parameters. Additionally, the  $\alpha$ -diversity Tukey's Jack-knife estimate (Whittaker, 1972) was used to quantify the potential number of species in both sites, and within the canopy gradient levels.

**3.** Soil- and non soil-feeders: log-transformed soil- and non soil-feeding termite abundance were analysed separately to measure the influence of the independent variables on the two feeding groups.

**4.** An Analysis of Covariance (ANCOVA) was used to test separately the correlation between overall termite abundance, soil-feeder and non soil-feeder termite abundance, and cocoyam and plantain yield, in both plantations independently of treatment effects.

## Results

Across all the sampling periods and sites, we recorded a total of 85 species belonging to two families: 83 species of Termitidae, and two species of Rhinotermitidae (see appendix). In the old plantation, 61 species were sampled, with 50 species from the high canopy cover plots and 37 species from the low canopy cover plots. From the young plantation 62 termite species were recorded, with 45 species from the high canopy closure plots and 43 from the low canopy closure plots.

## Effects of canopy

## *Termite abundance*

Termite populations under all treatments (fig. 1, table 1) were variable from plot to plot (generally in the range of 200 to >4000 individuals  $m^{-2}$ ). The high and low canopy plots were significantly different from each other in the old plantation (with high canopy > low canopy), but were not significantly different in the young plantation.

## Species richness

The ANOVA (table 2) and the Jack-knife estimates (table 3, see also fig. 2) showed significant differences between the two canopies in the old plantation, with the high canopy sheltering more termite species than the low one (Tukey HSD test table 2, see also table 3). In contrast, no significant difference was found between the two canopy densities in the young plantation, although more species were sampled under high canopy than low canopy (table 3).

#### Feeding groups

Within the old plantation there were significantly more soil-feeders under the high canopy than the low canopy (fig. 1). In contrast, the difference between the two canopy cover levels in the young plantation site was not significant. The abundance of non soil-feeder termites whose diets are predominantly free of soil did not differ significantly between canopy treatments in either plantation (table 2).

#### Crop, cropping system and biomass management

#### Termite abundance and species richness

Crop treatment alone had no significant effect on termite abundance in either plantation site. However, the interaction crop\*canopy was significant in the young plantation for the abundance of all termite species. The *post hoc* tests revealed idiosyncratic responses (table 2). The species richness results were essentially the same as the abundance results (see table 2).

#### Feeding groups

Crop type had no significant effect at either site on soil- or non soil-feeder abundance. However, the young plantation again revealed significant effects of the interaction canopy\*crop on both soil- and non soil-feeding termite abundance (table 2).

## Time of sampling

In the old plantation, significant effects of the sampling periods were observed in the abundance of all termite



Fig. 1. Mean termite abundance in the plantation plots (Old Plantation, OP and Young Plantation, YP) under two levels of canopy cover (high, H and low, L) in Mbalmayo Forest Reserve, Cameroon. Open boxes, total abundance; black boxes, non soil-feeder abundance; diagonal hatching, soil-feeder abundance. Error bars are standard errors around the mean.



Fig. 2. Mean species richness in the plantation plots (Old Plantation, OP and Young Plantation, YP) under two densities of canopy cover (high, H and low, L) in Mbalmayo Forest Reserve, Cameroon.

species, species richness and the abundance of soil- and non soil-feeders (table 2). The young plantation did not show any statistical difference between sampling periods (table 2).

#### *Crop yields and termite abundance*

Cumulative mean crop yields for the two sites, the two canopy treatments and the cropping systems were: (i) plantain; lower in the old tree plantation (high canopy closure = 0.08 t ha<sup>-1</sup>, and low canopy closure = 1.85 t ha<sup>-1</sup>) than in the young plantation (high canopy = 2.70 t ha<sup>-1</sup>, and low canopy = 6.65 t ha<sup>-1</sup>) (Norgrove & Hauser, unpublished); (ii) cocoyam showed a similar response, with old plantation, high canopy = 17.6 kg ha<sup>-1</sup> and low canopy = 24.6 kg ha<sup>-1</sup>; young plantation, high canopy = 68.6 kg ha<sup>-1</sup>

128

Table 2. ANOVA summary table with Tukey honest significant difference (HSD) test pairwise comparison, showing the effects of
treatments, time of sampling and associated interaction terms on all termite species abundance (log mean abundance), soil- and non
soil-feeders abundance (log mean abundance), and species richness (No. spp. $=$ mean no. plot <sup><math>-1</math></sup> ).

Old Plantation				Young Plantation				
Effect	Total abundance	Soil-feeders abundance	Non soil- feeders abundance	No. spp.	Total abundance	Soil-feeders abundance	Non soil- feeders abundance	No. spp.
ANOVA								
Canopy	6.24*	4.33*	0.82	4.33*	0.94	1.41	0.00	2.50
$(F_{(1,24)})$ Crop	0.49	0.83	1.93	2.09	0.85	0.22	0.57	0.85
(F <sub>(3,24)</sub> ) Time	5.78**	4.94**	3.82*	5.51**	0.05	0.13	0.00	0.03
(F <sub>(2,48)</sub> ) Canopy/crop	0.35	0.11	0.41	0.03	4.75**	5.04**	3.63*	0.71
(F <sub>(3,24)</sub> ) Canopy/time	0.38	0.33	0.79	0.31	0.89	0.68	0.75	0.48
$(F_{(2,48)})$ Crop/time	0.72	0.59	2.00	1.64	1.09	2.05	0.92	1.09
$(F_{(6,48)})$ Canopy/crop/time $(F_{(6,48)})$	0.49	0.40	1.85	0.29	0.23	0.67	0.35	0.99
Tukey HSD test Canopy Canopy/crop	hc>lc	hc>lc		hc>lc	co <sub>hc<lc< sub=""> co<sub>hc</sub><pl<sub>hc</pl<sub></lc<></sub>	co <sub>hc<lc< sub=""> co<sub>hc</sub><pl<sub>lc</pl<sub></lc<></sub>	co <sub>hc<lc< sub=""> co<sub>hc</sub><pl<sub>hc</pl<sub></lc<></sub>	
					co <sub>lc</sub> >pb <sub>lc</sub> pl <sub>hc</sub> >pl <sub>lc</sub> pl <sub>hc</sub> >pb <sub>lc</sub>	$co_{lc} > pl_{lc}$ $co_{lc} > pb_{lc}$ $pl_{hc>lc}$ $pl_{hc} > pb_{lc}$	co <sub>lc</sub> >mx <sub>hc</sub> co <sub>lc</sub> >pb <sub>lc</sub>	
Time	Nv <jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td></td><td></td><td></td><td></td></jl<></jl </td></jl<></jl </td></jl<></jl </td></jl<></jl 	Nv <jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td></td><td></td><td></td><td></td></jl<></jl </td></jl<></jl </td></jl<></jl 	Nv <jl Fb<jl< td=""><td>Nv<jl Fb<jl< td=""><td></td><td></td><td></td><td></td></jl<></jl </td></jl<></jl 	Nv <jl Fb<jl< td=""><td></td><td></td><td></td><td></td></jl<></jl 				

Significant effects are marked \* when P<0.05, and \*\* when P<0.01. Subscript brackets show d.f., and the data are the F value. Key for tukey test: hc, high canopy; lc, low canopy; Nv,= November 1995; Fb, February 1996; Jl, July 1996; co, cocoyam; pl, plantain (mulch retained); pb, plantain slash-burned; mx, mixed crops (plantain + cocoyam).

Table 3. Species richness comparison.

	Old	Plantation	Young	Young Plantation		
	Obs.	Jack-knife estimate	Obs.	Jack-knife estimate		
Entire plantation	61	81 ± 8	62	83 ± 12		
High canopy	50	$62 \pm 6$	45	$54 \pm 8$		
Low canopy	37	$45 \pm 5$	43	$54 \pm 9$		
Canopy ratio (high/low)	1.4	$1.40\pm0.03$		$01 \pm 0.04$		

The numbers are the observed values (Obs.) and the potential species (including the common and the scarce species sampled) estimated using an  $\alpha$ -diversity Jack-knife estimate (Whittaker, 1972),  $\pm$  standard deviation. The canopy ratio measures the disproportionality in the termite species richness between the two canopy densities per site.

Table 4. Results of ANCOVA showing F-values for the within cell regressions of log termite abundance on log cumulative yield for the plantain and cocoyam plots.

	Old Plantation	Young Plantation
Plantain		
Total	0.42	0.62
Soil-feeders	0.53	1.00
Non soil-feeders	0.00	0.04
Cocovam		
Total	0.05	3.00
Soil-feeders	0.12	5.84*
Non soil-feeders	0.36	0.07

F values without superscripts are not significant, \* P<0.05.

and low canopy = 92.0 kg ha<sup>-1</sup> (Hauser *et al.*, unpublished). A one-way ANCOVA using the data from the two plantations separately (with canopy density as the independent variable and termite abundance as the covariate) showed a significant effect of canopy for the two

crops. The within-cells regressions (table 4) were insignificant for termite abundance and crop yield in all cases, except for the regression of soil-feeder termite abundance on cocoyam yield in the young plantation, which was significant (P = 0.03).

130

## Discussion

Previous studies of the abundance, biomass and species richness of termites in the Mbalmayo Forest Reserve (Eggleton et al., 1995, 1996) have revealed higher termite diversity in forest-like systems (i.e. near primary and secondary forest, young plantation) than in cleared areas without canopy cover. This study has shown that agrisilvicultural schemes constructed where a significant proportion of the canopy cover is retained, preserve soil termite assemblages with a forest-typical character (see Eggleton et al., 1995, 1996). This applies especially to soil-feeding termites which are strongly affected by the disturbance and drying of the soil, as well as the removal of potential nesting sites, that occur when large trees are removed from habitats. The absence of differences in termite abundance between high and low canopy densities in the young plantation site, however, also suggests that when canopy cover drops below a threshold the forest-like soil-feeder assemblage may become attenuated.

No crop treatment factors had a significant effect on soilfeeder diversity, even though the soil in the plantain burned plots must have been heavily modified by the burning. However, this is in agreement with other studies of the effects of burning on termite assemblages (Abensperg-Traun & Milewski, 1995; Davies, 1997), suggesting that short-term small-scale burning may have relatively little effect on termite density in humid tropical forest regions, perhaps due to a combination of high annual rainfall and rapid recolonization from surrounding areas. The overall lack of differences between crop treatments may also be partially due to the absence of termite crop pests from this part of Cameroon (Eggleton *et al.*, 1995). The significant interaction terms (table 2) are hard to interpret, and probably have little biological significance.

The significant differences in termite diversity found between sampling times appear to follow closely seasonal changes observed on other parts of the Mbalmayo Forest Reserve (Dibog *et al.*, 1998), and do not appear to be due to any obvious post-manipulation changes. This study hints at some significant correlation between termite diversity and crop yield, although only between soil-feeder abundance and cocoyam yield in the young plantation (see table 3).

Direct beneficial links between the activities (nestbuilding, foraging, runway and gallery construction) of non-pest species of termites and the growth of crop plants have been suggested previously (e.g. Adamson, 1943; Maldague, 1967; Wood & Sands, 1978), but data are scarce and the question remains speculative. As all termites feed on plant tissues or their direct derivatives, with occasional supplementation from other materials such as dung or living roots, the overall impact of termites can be expected to be a reduction in the total organic matter and other nutrients incorporated into soil (see Jones, 1990). Some evidence of this has been reported in a savanna-derived system (Veeresh & Belavadi, 1986), but there is again a shortage of data, partly explained by the difficulty of achieving experimental crop treatments where termites are completely excluded. Losses of nutrients to termites may be counterbalanced by the conditioning of soil that results from their foraging and constructional activities. The data presented here are somewhat ambiguous, and more detailed studies of the interaction between termites and soil fertility are evidently required to separate these potential positive and negative factors.

## Acknowledgements

We thank Institut de Recherche Agricole pour le Développement (IRAD Cameroon) for providing laboratory facilities; International Institute for Tropical Agriculture (IITA) for logistical support and laboratory facilities. We thank Dr S. Weise (IITA) and Dr P. Ngeh (ONADEF) and his staff for help in planning and establishment, Dr B. Duguma (ICRAF) and Dr G. Lawson (Institute of Terrestrial Ecology, ITE) were involved in the initial conception of the multistrata project, and also thanks to Dr D.T. Jones and Mr R.G. Davies for their comments on the manuscript. The Natural Environment Research Council (UK) provided financial support under the Terrestrial Initiative in Global Environment Research (award GST/02/625) to David E. Bignell, and research support for Luc Dibog. Lindsey Norgrove was supported by a King's College London Association scholarship.

## References

- Abensperg-Traun, M. & Milewski, A.V. (1995) Abundance and diversity of termites (Isoptera) in unburnt versus burnt vegetation at the Barrens in Mediterranean Western Australia. Australian Journal of Ecology 20, 413–417.
- Adamson, A.M. (1943) Termites and the fertility of soil. *Tropical Agriculture, Trinidad* **20**, 107-112.
- Bignell, D.E., Eggleton, P., Nunes, L. & Thomas, K.L. (1997) Termites as mediators of carbon fluxes in tropical forest: budgets for carbon dioxide and methane emissions. pp. 109–134 *in* Watt, A.D., Stork, N.E. & Hunter, M.D. (*Eds*) *Forests and insects*. London, Chapman and Hall.
- Brussaard, L. & Jumas, N.G. (1996) Organisms and humus in soils. pp. 329–359 in Piccolo, A. (Ed.) Humus substances in terrestrial ecosystem. Amsterdam, Elsevier.
- **Collins, N.M.** (1983) The utilization of nitrogen resources by termites (Isoptera). pp. 381–412 *in* Lee, J.A., McNeill, S. & Rorison, I.H. (*Eds*) *Nitrogen as an ecological factor*. Oxford, Blackwell Scientific Publications.
- Das, G.M. (1957) How to utilise mound site for growing tea. News literature. *Indian Tea Assessment, Tocklai* 4, 8–9.
- **Davies, R.G.** (1997) Termite species richness in fire-prone and fire-protected dry deciduous dipterocarp forest in Doi Suthep-Pui National Park, northern Thailand. *Journal of Tropical Ecology* **13**, 153–160.
- Dibog, L., Eggleton, P. & Forzi, F. (1998) The seasonality of a soil termite assemblage in a humid tropical forest, Mbalmayo, southern Cameroon. *Journal of Tropical Ecology* 14, 841–850.
- Eggleton, P., Bignell, D.E., Sands, W.A., Waite, B., Wood, T.G. & Lawton, J.H. (1995) The diversity of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve Southern Cameroon. *Journal of Tropical Ecology* **11**, 85–98.
- Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, J.H., Wood, T.G. & Bignell, N.C. (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. *Philosophical Transactions of* the Royal Society of London B 351, 51–68.
- Fragoso, C., Barois, I., González, C., Arteaga, C. & Patrón, J.C. (1993) Relationship between earthworms and soil organic matter levels in natural and managed ecosystems in Mexican tropics. pp. 231–240 in Mulongoy, K. & Merckx, R. (Eds) Soil organic matter dynamics and sustainability of tropical agriculture. Chichester, John Wiley and Sons.

- Garnier-Sillam, E. & Harry, M. (1995) Distribution of humic compounds in mounds of some soil-feeding termite species of tropical rainforests: its influence on soil structure stability. *Insectes Sociaux* 42, 167–185.
- Harris, W.V. (1954) Termites and tropical agriculture. *The Journal* of Imperial College of Tropical Agriculture **31**, 11–18.
- Harris, W.V. (1968) Termites of the Sudan. University of Khartoum, Sudan Natural History, B 4, 113–131.
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.H. (1971) Forest environments in tropical life zones. Oxford, Pergamon Press.
- Holland, M.D., Allen, R.K.G., Campbell, K., Grimble, R.J. & Stickings, J.C. (1992) Natural and human resource studies and land use options. Department of Nyong et So'o, Cameroon. Natural Resources Institute, Chatham, UK.
- Jones, J.A. (1990) Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *Journal of Tropical Ecology* 6, 291–305.
- Lavelle, P., Blanchard, E., Martin, A., Spain, A.V. & Martin, S. (1992) Impact of soil fauna on the properties of soils in the humid tropics. pp. 157–185 in Lal, R. & Sanchez, P.A. (Eds) Myths and science of soils of the tropics: proceedings SSSA 17 October 1993 Las Vegas, Nevada. Soil Science Society of America. Inc, Madison USA.
- Lavelle, P., Lattaud, C., Trigo, D. & Barois, L. (1994) Mutualism and biodiversity in soils. *Plant and Soil* **170**, 23–33.
- Lawson, G.J. (1995) Growth of indigenous tree plantations in the Mbalmayo Forest Reserve. Report. Institute of Terrestrial Ecology, Edinburgh, UK.
- Lawson, G.J., Mason, P.A., Ngeh, P.A, Musoko, M., Eamus, D. & Leakey, R.R.B. (1990) Endomycorrhizal and nutrient cycling in indigenous hardwood plantations in Cameroon – effects of different systems of site preparation. Final Report to UK Overseas Development Authority (ODA).
- Lee, K.E. & Wood, T.G. (1971) Physical and chemical effects on soils of some Australian termites, and their pedological significance. *Pedobiologia* 11, 376–409.
- Lobry de Bruyn, L.A. & Conacher, A.J. (1995) Soil modification by termites in the central wheatbelt of western Australia. *Australian Journal of Soil Research* **33**, 179–193.
- Maldague, M.E. (1967) Importance des populations de termites dans les sols equatoriaux. pp. 743–752 in *Transactions of the eighth International Congress of Soil Science, Bucharest – Romania 1964.* vol. 3. Publishing House of the Academy of the Social Republic of Romania.

- Mulongoy, K. & Bedoret, A. (1989) Properties of worm castes and surface soils under various plant covers in the humid tropics. *Soil Biology and Biochemistry* 21, 197–203.
- Nash, M.H. & Whitford, W.G. (1995) Subterranean termites: regulators of soil organic matter in the Chihuahuan desert. *Biology and Fertility of Soils* 19, 15–18.
- **Norgrove, L. & Hauser, S.** (1998) Effects of tree density and crop management upon growth of plantain in low-input agrisilvicultural system. *Acta Horticulturae* (in press).
- **Roonwal, M.L.** (1979) *Termite life and termite control in tropical South Asia.* India, Scientific Publishers.
- Sands, W.A. (1973) Termites as pests of tropical food crops. *Pest* Articles and News Summaries **19**, 167–177.
- Scholes, M.C., Swift, M.J., Heal, O.W., Sanchez, P.A., Ingram, J.S.I. & Dalal, R. (1994) Soil fertility research in response to the demand for sustainability. pp. 1–14 in Woomer, P.J. & Swift, M.J. (Eds) The biological management of tropical soil fertility. Chichester, John Wiley and Sons.
- Smith, F.D.M., Pellew, R., Johnson, T.H. & Walter, K.R. (1993) How much do we know about the current extinction rate? *Trends in Ecology and Evolution* 8, 375–378.
- Swift, M.J. & Mutsaers, H.J.W. (1992) IITA research for Humid Forest Zone, 1993–1998. International Institute of Tropical Agriculture, Ibadan, Nigeria.
- Veeresh, G.K. & Belavadi, V.V. (1986) Influence of termite foraging on the fertility status of the soil. *Journal of Soil Biology and Ecology* 6, 53–66.
- Whittaker, R.H. (1972) Communities and ecosystems. New York, Macmillan.
- Wood, T.G. (1996) The agricultural importance of termites in the tropics. *Agricultural Zoology Reviews* 7, 117–155.
- Wood, T.G. & Cowie, R.H. (1988) Assessment of on-farm losses in cereals in Africa due to soil insects. *Insect Science and Its Application* 9, 709–716.
- Wood, T.G. & Sands, W.A. (1978) The role of termites in ecosystems. pp. 245–292 in Brian, M.V. (Ed.) Production ecology of ants and termites. Cambridge, Cambridge University Press.
- Wood, T.G., Johnson, R.A., Bacchus, S., Shittu, M.O. & Anderson, J.M. (1982) Abundance and distribution of termites in a Riparian forest in the southern Guinea savanna vegetation zone of Nigeria. *Biotropica* 14, 25–39.
- Woomer, P.L. & Swift, M.J. (1994) The biological management of tropical soil fertility. Chichester, John Wiley and Sons.

132

## Appendix

List of termite species recorded from the agrisilvicultural experimental plots, Mbalmayo Forest Reserve, Cameroon.

## RHINOTERMITIDAE

Rhinotermitinae

- 1. Schedorhinotermes putorius (Sjöstedt) Coptotermitinae
- 2. Coptotermes sjoestedti (Holmgren) TERMITIDAE
- Nasutitermitinae
  - 3. Nasutitermes latifrons (Sjöstedt)
  - 4. Nasutitermes fulleri (Emerson)
  - 5. Nasutitermes arborum (Smeathman)
  - Macrotermitinae
    - 6. Microtermes spp.
    - 7. Pseudacacanthoterrnes militaris (Hagen)
    - 8. Acanthotermes acanthothorax (Sjöstedt)
    - 9. Synacanthotermes heterodon (Sjöstedt)
    - 10. Sphaerotermes sphaerothorax (Sjöstedt)
    - 11. Protermes prorepens (Sjöstedt)
    - 12. Odontotermes sp. 1

    - 13. Odontotermes sp. 2
    - 14. Odontotermes sp. 3
  - Apicotermitinae
    - Apicotermes-group
    - 15. Eburnitermes sp. nov. 1
    - 16. Duplidentitermes furcatidens (Emerson)
    - 17. Phoxotermes cerberus (Collins)
    - 18. Labidotermes sp. nov. 2
    - 19. Machadotermes rigidius (Weidner)
    - 20. New genus 1
    - 21. New genus 5 near Eburnitermes
    - Anoplotermes-group
    - 22. Adaiphrotermes sp. nov. 1
    - 23. Adaiphrotermes sp. nov. 2
    - 24. Anenteotermes polyscolus (Sands)
    - 25. Anenteotermes ateuchestes (Sands)
    - 26. Anenteotermes sp. nov. 1
    - 27. Aderitotermes sp. nov. 1 (near fossor)
    - 28. Aderitotermes sp. nov. 2
    - 29. Aderitotermes sp. nov. 3
    - 30. Adentotermes cavator (Sands)
    - 31. Amicotermes sp. nov. 1
    - 32. Amicotermes sp. nov. 2
    - 33. Acholotermes sp. nov. 1
    - 34. Ateuchotermes sp. nov. 1
    - 35. Ateuchotermes sp. nov. 2
    - 36. Ateuchotermes sp. nov. 3

    - 37. Ateuchotermes ctenopher (Sands)
    - 38. Acidnotermes praus (Sands)
    - 39. Amalotermes phaeocephalus (Sands)

https://doi.org/10.1017/S0007485399000206 Published online by Cambridge University Press

- 40. Alyscotermes sp. nov 1
- 41. Astratotermes spp.
- 42. Astalotermes quietus (Silvestri)
- 43. Astalotermes sp. nov. 2
- 44. Astalotermes sp. nov. 3
- 45. Astalotermes sp. nov. 5
- 46. Astalotermes sp. nov. 6 47. Astalotermes sp. nov. 7
- 48. Astalotermes sp. nov. 8
- 49. Astalotermes sp. nov. 9
- 50. Astalotermes sp. nov. 10
- 51. Astalotermes sp. nov. 11
- 52. Astalotermes sp. nov. 12
- 53. Astalotermes sp. nov. 13
- 54. Amicotermes sp. nov. 3
- 55. Amicotermes sp. nov. 4
- 56. New genus 3
- 57. New genus 4

Termitinae

- 58. Fastigitermes jucundus (Sjöstedt)
- 59. Mucrotermes spp.
- 60. Orthotermes depressifrons (Silvestn)
- 61. Basidentitermes aurivilli (Sjöstedt)
- 62. Proboscitermes sp. nov. 1
- 63. Microcerotermes parvus (Silvestri)
- 64. Unguitermes trispinosus (Ruelle)
- 65. Unguitermes sp. nov. 1
- 66. Unguitermes sp. nov. 2
- 67. Unguitermes sp. nov. 3
- 68. Unguitermes sp. nov. 4
- 69. Pericapritermes sp. nov. 1
- 70. Pericapritermes minimus (Weidner)
- 71. Pericapritermes chiasognathus (Sjöstedt)
- 72. Pericapritermes nigerianus (Silvestri)
- 73. Ophiotermes grandilabius (Sjöstedt)
- 74. Foraminitermes valens (Silvestri)
- 75. Foraminitermes tubifrons (Holmgren)
- 76. Foraminitermes sp. nov. 1
- 77. Furculitermes winifredae (Emerson)
- 78. Apilitermes longiceps (Sjöstedt)
- 79. Noditermes indoensis (Sjöstedt)
- 80. Tuberculitermes bycanistes (Sjöstedt)
- 81. Basidentitermes diversifrons (Silvestri)
- 82. Basidentitermes demoulini Harris
- 83. Basidentitermes mactus (Sjöstedt)
- 84. Profastigitermes putami (Émerson)
- 85. New genus 6

(Accepted 8 February 1999) © CAB International, 1999