The significance of termites as decomposers in contrasting grassland communities of semi-arid eastern Australia

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ABSTRACT

Decomposition of various litter forms including dead tussocks of two native perennial grasses, woolly-butt (*Eragrostis eriopoda*) and mulga mitchell (*Thyridolepis mitchelliana*), as well as roots of woollybutt, dung of sheep and kangaroo, and bleached toilet rolls, was studied in contrasting grazing exclosures, half of which had termites excluded by biocide (termiticide) treatment. Dead mulga mitchell tussocks decayed more rapidly than woollybutt tussocks during the first 17 months post mortem. Thereafter, rate of decay differed little between species. After 3 years, only small amounts of tussock residues of either species remained and only then did the impact of biocide treatment become significant.

Decomposition of kangaroo pellets was typically bimodal with significantly higher decomposition recorded in the controls (no biocide) up to 40 months after treatment, and many intact pellets remaining in the biocide-treated plots. While decomposition of sheep pellets showed similar bimodality, decomposition remained significantly lower in the biocide treatments for the entire duration of the experiment. Results suggest that abiotic processes, including those induced by UV radiation, may be dominant influences mediating decomposition of litter in these semi-arid ecosystems, especially following high-rainfall seasons when abundant grass biomass has been generated providing a surfeit of potential forage for harvester termites.

1. Introduction

Vegetation patterning in Australian semi-arid woodlands is widely recognised as a response to the redistribution of rainwater and topsoil containing organic material and plant nutrients (Ludwig et al., 1997). Soil biota play a critical role in maintaining soil-based processes in semi-arid landscapes although direct links between such diverse taxa and rates and efficiency of various landscape functions are much less clear (Giller et al., 1997; Jones et al., 1994; Whitford, 2002; Whitford et al., 1992). Even though preliminary studies have shown clear spatial patterning of surface soil features 'engineered' by vertebrates such as the burrowing bettong (*Bettongia lesueur*) (Noble et al., 2007) and invertebrates such as the harvester termite (*Drepanotermes perniger*) (Noble et al., 1989), little is known of the relationships between vegetation mosaics and ecosystem processes and their mediation by soil invertebrates in semi-arid ecosystems of Australia.

Perennial grasses, particularly C$_3$ species such as bandicoot grass (*Monachather paradoxa*) and mulga mitchell (*Thyridolepis mitchelliana*) commonly provide highly nutritious forage for livestock in rangelands dominated by mulga (*Acacia aneura*). Once senescent they become valuable forage for herbivorous invertebrates as well, in particular the ubiquitous *Drepanotermes perniger* (Watson and Perry, 1981). Watson et al. (1973) suggested that mound-building harvester termites alone in central Australia could consume around 100 kg ha^{-1} dry matter of herbage annually. Because they also claimed that the biomass of harvester termites was comparable to that of domestic livestock grazing in the same area, *viz.* 10–15 kg ha^{-1}, there has been an underlying assumption amongst some observers that harvester termites had the potential to become major competitors with domestic livestock once such forage, despite its relatively low nutritive value, was all that was available for livestock. However, given that harvester termites feed primarily on 'fungal gardens' growing on senescent plant material stored in subterranean galleries (Watson et al., 1973), they are more specifically detritivores than herbivores.

While there is no evidence of a significant decline in soil invertebrate abundance in Australia's semi-arid rangelands this may simply reflect a dearth of relevant information. Giller et al.

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(1997) distinguished three broad functional groups of invertebrates: 'ecosystem engineers', 'litter transformers' and 'micropredators'. Soil microarthropods, for example, are important 'litter transformers' in Australian rangelands. Their populations have been shown to vary considerably between different parts of these landscapes, the highest numbers of 'litter transformers' usually being found in grass-dominated patches (Noble et al., 1996).

According to Whitford (2000), there is now sufficient scientific evidence available to confirm that two groups of social insects, termites and ants, play critical roles as 'webmasters' in desert ecosystems by controlling their structural and functional properties. Termites are amongst the most abundant invertebrates found throughout the Australian arid zone (Noble and Tongway, 1986) and, as 'litter transformers', have a significant influence on particular ecosystem processes including nutrient cycling (Noble and Tongway, 1988; Whitford et al., 1992). In addition to having an influential role in the decomposition of both above- and below-ground plant residues, they also produce macropores facilitating infiltration by rainwater (Eldridge, 1994; Elkins et al., 1986; Greene et al., 1990; Leonard and Rajot, 2001).

Much of the evidence for their importance is based on overseas experience (e.g. Parker et al., 1982; Whitford et al., 1982) although subsequent research in Australia started to focus more on impacts by termites on soil ecology, particularly those relating to modification of soil (e.g. Lobry de Bruyn and Conacher, 1990). While mounds constructed by *Drepanotermes tamminensis* and *Amitermes obeuntis* and foraging galleries of *D. tamminensis* and *A. neogermanus* had significantly higher organic carbon contents with pH lower than the surface soil, such modified soil was regarded as essentially inaccessible for plant growth (Lobry de Bruyn and Conacher, 1995).

In semi-arid and arid regions, different termites may consume wood, herbaceous plants, and leaves of some shrubs and trees (Faragalla, 2002; Mando and Brussaard, 1999; Schuurman, 2005, 2006; Whitford, 1999; Zaady et al., 2003). In arid rangelands of the United States, subterranean termites were found to affect soil organic matter, water infiltration, soil nitrogen, plus the composition and productivity of the vegetation (Whitford, 2002). There the effects of termites on rangeland vegetation are the indirect result of their impacts as decomposers following their foraging activities. Because of the many effects of termites on arid ecosystems, they have also been referred to as 'keystone species' (Whitford, 1991).

In Australia, little is known about the role of termites in facilitating the decomposition of aerial litter represented by senescent grass tussocks, or indeed many other forms of organic detritus found throughout the semi-arid woodlands. While densities of dung pellets voided by different vertebrate herbivores have been used to estimate animal densities in semi-arid woodland landscapes (Landsberg and Stol, 1996; Landsberg et al., 1994), information detailing the comparative decomposition of such pellets is scant. This study examines the effects of termites by comparing decomposition of a variety of litter forms in the presence and absence of termites, as well as their influence on soil properties, in both runoff and runon zones located within a semi-arid mulga (*Acacia aneura*) woodland in northwestern New South Wales.

2. Methods and materials

Experimental sites were established on "Glenora" Station, c. 35 km north of Louth, New South Wales (30° 16′S, 144° 53′E) (Fig. 1) on two contrasting vegetation types representing the opposing extremes of a catenary sequence. One community, dominated by
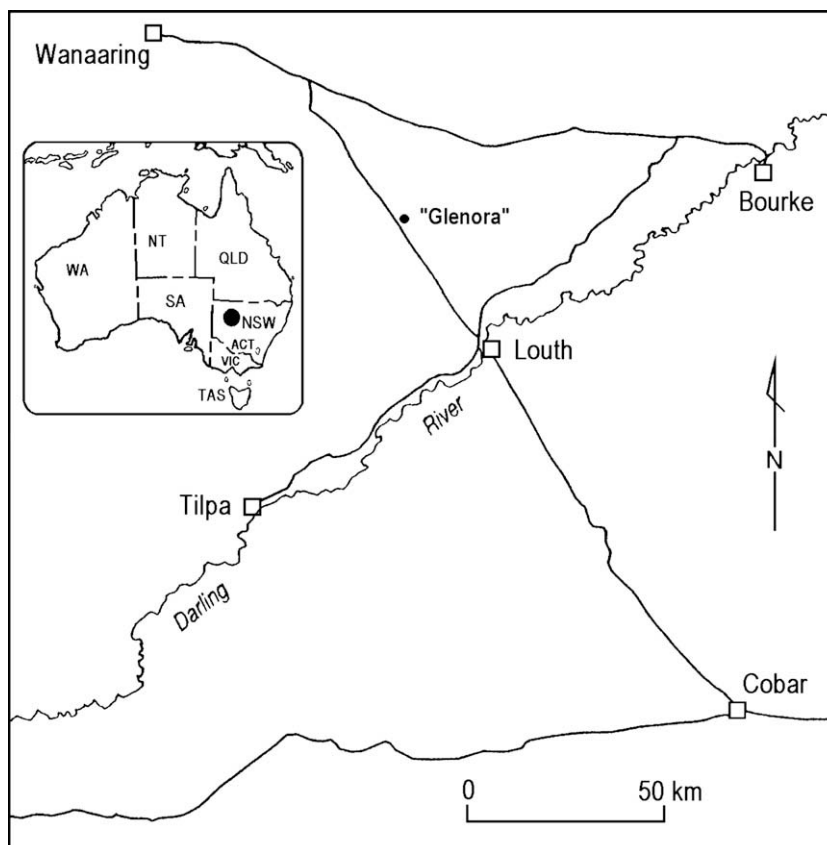

Fig. 1. Map showing the location of "Glenora" Station, west of Bourke, N.S.W., Australia (after Noble et al., 2007).

woollybutt (*Eragrostis eriopoda*), represented the upper or runoff zone while the other grassland community, located in the runon zone at the lowest point of the soil catena, was dominated by mulga mitchell. Both communities have been described in detail elsewhere (Hodgkinson and Müller, 2005; Noble et al., 1998; Tongway and Ludwig, 1990).

This study was located in the Landsdowne land system comprising undulating stony ridges of Cretaceous sandstones and shales with low tablelands of Tertiary silcretes (Walker, 1991) ranging up to 20 m in relief with narrow to broad dendritic drainage lines; slopes are less than 0.5%. The soil is classified as a massive red earth Gn 2.12 (Northcote, 1979), and consists of a red-brown clay loam surface soil overlying a massive red texture B horizon (Greene, 1992).

Four plots (each 6×3 m) were selected at random locations within four replicate blocks in both communities. Large vertebrate herbivores, i.e. kangaroos (*Macropus* spp.) and domestic livestock, were excluded from two plots in each block by means of steel weldmesh panels (each panel 3 m long and 1.8 m high). Termites were eliminated in October 1988 from one vertebrate plot and one non-vertebrate plot in each block by applying chlorpyrifos as an emulsion (200 mL Dursban P.C. in 10 L water) at 5.68 L m^{-2} with Comprox® used as a wetting agent to enhance infiltration. Control (non-termiticide) plots also had the wetting agent only applied. A galvanised tin barrier (14 cm high) was erected around termite-free plots by inserting 6 cm of the original 20 cm high sheet into the surface soil to eliminate entry by surface foraging parties. Shortly afterwards, all live grass plants in both experiments were killed by spraying Roundup CT® (450 g L^{-1} glyphosate at 1:100 concentration) at 0.68 L m^{-2} to ensure simultaneous mortality. The woollybutt plots required a follow-up spray 4 weeks later to ensure complete mortality.

Randomly selected grass tussocks (ten per plot) were individually identified by a numbered metal tag attached to a steel pin inserted into the ground; woollybutt tussocks in the plots in the runoff zone and mulga mitchell tussocks in the plots in the runon zone. Tussock biomass was monitored regularly from October 1998 (more frequently in the first year and then at least annually) using a double sampling technique similar to the Adelaide technique (Andrew et al., 1979). At each sampling, a single tussock of each species was selected as a standard. The individual mass of each tagged tussock was then visually estimated as a percentage of the appropriate standard. When leaf remained on tussocks, the percentage biomass of leaf present on each tussock was also visually estimated. Visual estimates were converted to actual biomass by regressions established at each sampling, when a minimum of ten tussocks of both species were each visually estimated as percentages of the standards then cut, oven-dried and weighed. The percentage of leaf present was also estimated by regressions relating visually estimated percentages from the calibration samples to actual percentages determined by separation of the leaf fraction and subsequent oven-drying and weighing.

In December 1995, series of dung baits were laid out in the non-vertebrate plots in both the woollybutt and mulga mitchell communities. Five individual dung samples of both kangaroos and sheep, each comprising 20 and 80 pellets per sample respectively, were randomly located within the two treatments inaccessible to vertebrates in each of the four blocks in both communities. These dung samples were of uniformly recent origin based on criteria, e.g. degree of bleaching, defined by Landsberg and Stol (1996). Individual dung samples were weighed before being placed on the soil surface beneath squares (*c.* 15×15 cm) of 2 mm fibreglass mesh fixed by metal pins inserted into the soil at each corner. Each bait sample was identified by a numbered aluminium tag attached to one of the metal pins.

During subsequent monitoring, the mesh was carefully lifted from each dung sample and the number of intact pellets recorded. In November 1996 and April 1997 numbers of intact pellets remaining were counted for each sample, and in April 1999 and April 2000 intact pellets remaining were counted beneath mesh covers that could still be located. In November 1996 and November 1997 a small number of pellet samples, generally one per plot, were also weighed.

Based on previous studies in Australia (French et al., 1981) where unbleached toilet rolls had been successfully employed as attractants to assess the potential impact of xylophagous termites such as *Amitermes* spp. on various wood baits, five such toilet rolls were also randomly located in each of the non-vertebrate plots in December 1995. Before placement, each roll was first wrapped in aluminium foil to reduce external weathering and to facilitate termite foraging by reducing temperature extremes as much as possible. After initial weighing, each roll was kept in place by means of a numbered metal pin passing through the centre and inserted into the soil. In December 1996, November 1997 and April 1999 one roll from each plot was recovered from the foil and weighed, and in April 2000 all remaining rolls that could be located were recovered and weighed.

Finally, five subterranean baits, each comprising 12 g of washed and air-dried woollybutt roots enclosed within 2 mm-fibreglass mesh sachets, were also buried in December 1995 at a shallow depth in each non-vertebrate plot in the woollybutt community. Decomposition of these baits was monitored in November 1996, November 1997 and April 2000. Similar measurements of root decomposition of mulga mitchell were not possible due to difficulties in obtaining sufficient quantities of root material. Due to some major runoff events and subsequent flooding and leaching of termiticide in the lowest replicate block in the mulga mitchell community, all data collected from this block relating to animal dung and toilet roll baits were subsequently discarded.

Because of apparent slaking of the surface soil in the woollybutt community following application of the termiticide (hereafter referred to as biocide) and wetting agent in 1988, duplicate samples for bulk density and infiltration determinations were taken in April 2000 in each of the four replicates of both biocide and control plots in this community to determine whether there were any differences in soil physical structure still persisting after 12 years. Bulk density was determined by taking undisturbed cores (70 mm in diameter and 50 mm deep) and drying them at 105 °C while infiltration rates were measured at the same sites with disc permeameters (200 mm in diameter) at supply potentials of +10 mm of water (i.e. ponded conditions) using the methodology described by Greene (1992). Measurements of both bulk density and infiltration rate were made independently by two observers within each replicate plot. Due to logistical constraints, it was not possible to undertake similar measurements in the mulga mitchell community.

3. Statistical analyses

3.1. Grass tussocks

Grass tussock biomass values, estimated using the double sampling technique, were all converted to biomass remaining per 100 g of the initial biomass in October 1988. Separate analyses of variance were performed on the biomass data at each of the seven sampling times from February 1989 to March 1993 to examine differences between the four treatments (vertebrate herbivores present/absent × termites present/absent), two species and the treatment × species interaction. All biomass values were log-transformed (log$_e$) before analysis.

3.2. Kangaroo pellets

As the numbers of kangaroo pellets remaining at each sampling time were generally close to either 0 or 20, the response was effectively binary, with 10 pellets or more remaining regarded as 'not decomposed' and 9 or fewer remaining as 'decomposed'. Logistic regressions were fitted as generalised linear models with binomial errors and logit link (GenStat for Windows, 2007) to these binary responses at each of the four sampling times to examine the effect of treatment, differences between communities, and their interaction.

Data for kangaroo pellet weight were available at two times, *viz.* 11 and 23 months after treatment (i.e. November 1996 and November 1997 respectively). As these measurements were destructive, a single analysis of variance was performed with time (11 and 23 months after treatment) as a factor in addition to treatment (termites present/absent) and community. The variable analysed was % weight remaining, calculated as

$$100 \times \text{final mass / initial mass}.$$

To stabilise the variation, a logistic transformation (Atkinson, 1985)

$$\log_e ((\% \text{ weight remaining} + 10)/(110 - \% \text{ weight remaining}))$$

was applied before analysis. Adjusted means were obtained by back-transforming the transformed means and approximate standard errors by back-transforming the transformed means ± SE and calculating half that interval.

3.3. Sheep pellets

As the numbers of sheep pellets remaining were close to either 0 or 80 for the majority of samples at each sampling time, the response was effectively binary rather than binomial. For consistency with the kangaroo pellets and due to the binomial assumption being violated, the sheep pellet counts were modelled as a binary response, where 40 pellets or more remaining was categorised as 'not substantially decomposed' and 39 or less remaining as 'substantially decomposed'. As for kangaroo pellets, logistic regressions were fitted to these binary responses at each of the five sampling times to examine the effect of treatment (termites present/absent), differences between communities, and their interaction. No analyses were performed on sheep pellet weights, as these data were found to be unreliable due to the difficulty of separating pellet residues from termite carton (developmental cellulose excreted by termites which they then mix with soil to form feeding galleries).

3.4. Toilet rolls

As the measurement of toilet roll weight was destructive each roll could only be measured once. As with sheep pellets, due to difficulties separating roll residues from other material, accurate weights could not be obtained for many of the rolls. Where satisfactory weights were obtained the time of exposure (months since December 1995) was noted. All roll weights were converted to the percentage of original mass remaining. To stabilise the variation, a logistic transformation (Atkinson, 1985)

$$\log_e ((\% \text{ weight remaining} + 1)/(101 - \% \text{ weight remaining}))$$

was applied to these percentages before analysis. Due to unequal numbers of rolls recovered from each block at each time, transformed percentages were analysed using the method of residual maximum likelihood (REML) (Patterson and Thompson, 1971), with

treatment (termites present/absent) × community × time of exposure as the fixed effects and blocks within community as the random effect.

3.5. Roots of woollybutt

As for toilet rolls, measurement of root weight was destructive. For each sample, time of exposure following burial (months since December 1995) was noted and all root weights were converted to the percentage of original weight remaining. These percentages were then transformed using the same logistic transformation and method of analysis employed for toilet rolls. However, as roots were only obtained from one grass species there was a simpler structure for the analysis, with treatment (termites present/absent) × time of exposure as the fixed effects and blocks within community as the random effect.

3.6. Bulk density and infiltration rate

Differences in bulk density and infiltration rate between the two treatments were examined by performing a two-way analysis of variance for each variable, with treatment (termites present/absent), observer and the treatment × observer interaction as terms in the analysis. Neither variable required transformation before analysis.

4. Results

As all woollybutt tussocks were in the runoff zone and all mulga mitchell tussocks in the runon zone, comparison of species incorporates comparison of the zones where they were measured. Analyses of log-transformed percentages of tussock residues (leaf + stem) found no significant species × treatment interactions at any observation time. Accordingly, species were compared using means over the four treatments and treatments were compared using means over the two species. Mulga mitchell tussocks in the runon zone were found initially to decay more rapidly than woollybutt tussocks in the runoff zone with significantly less tussock mass of the former species remaining in the first two samplings ($P < 0.001$), as well as later in the third ($P = 0.02$) and fifth ($P = 0.003$) ones (Fig. 2a). No significant treatment differences in residual tussock biomass were evident until the final four samplings where, except for April 1992 ($P = 0.006$), differences between controls and other treatments were all highly significant ($P < 0.001$) (Fig. 2b). Decomposition of leaves of both grass species, irrespective of treatment, was comparatively rapid and only trace amounts remained 18 months after herbicide application (March 1990) whereas 30% of the original tussock still remained as stem.

The number of kangaroo pellets remaining in the samples was essentially bimodal with many more samples of ∼20 pellets remaining for the biocide treatment than for the control (no biocide) treatment. This is illustrated for the pellet counts after 16 months of exposure (April 1997) in Fig. 3a. Data for sheep pellets demonstrated similar clustering of samples, with numbers of pellets remaining near 80 (i.e. little decomposition) or near 0 (i.e. maximum decomposition) (see Fig. 3b). However the bimodality was not as pronounced as for the kangaroo pellets. In both cases treatment differences were essentially due to more samples near zero for no biocide than biocide.

Analysis of kangaroo pellet counts indicated that there were significant differences between treatments (±biocide) but not between communities or a treatment × community interaction. Accordingly, only pellet data averaged over both grassland communities are presented. Initially decomposition of kangaroo pellets was significantly greater ($P < 0.001$) in the control (no biocide) treatments for the first three samplings (November 1996,
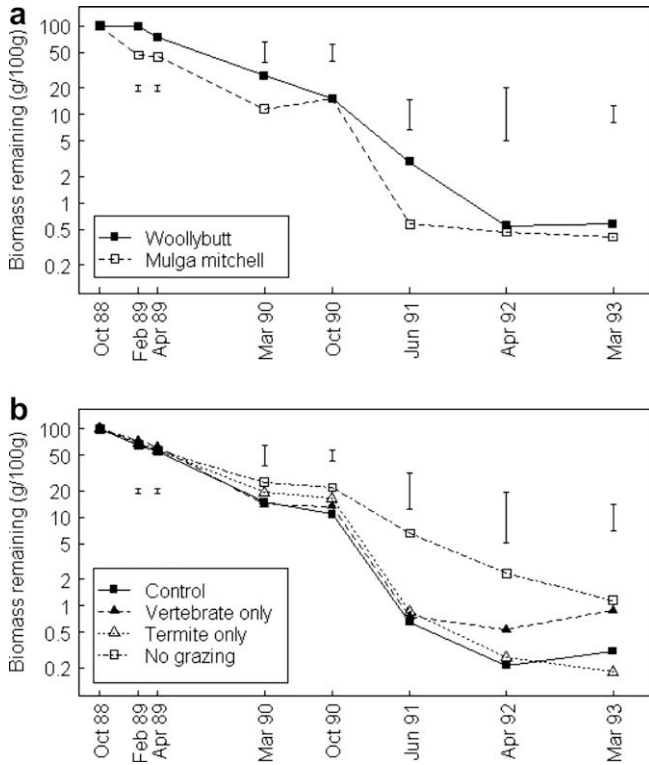
Fig. 2. Grass tussock weight loss over time under contrasting regimes: (a) species means (over four treatments) and (b) treatment means (over two species). Vertical bars are Least Significant Differences (5%) for comparison at each sampling time of (a) species and (b) treatments.

April 1997 and April 1999) however by April 2000 there was no significant treatment difference evident (Fig. 4a). Unlike the kangaroo pellet data, decomposition of sheep pellets remained significantly lower ($P < 0.001$) in the biocide treatments for the
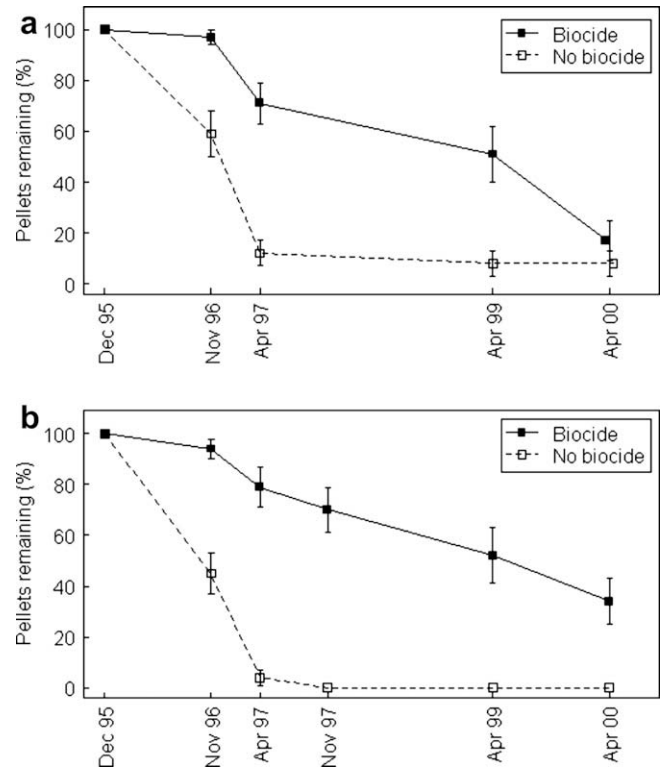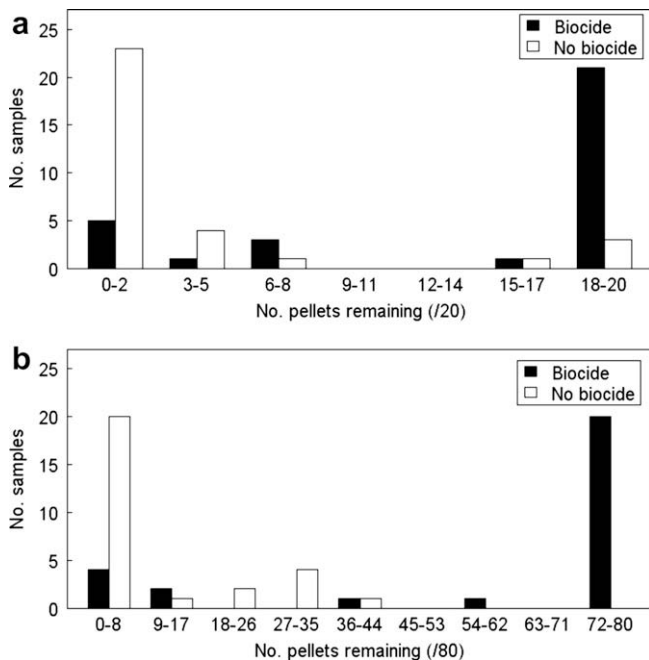

Fig. 3. Histograms illustrating the distribution of numbers of (a) kangaroo and (b) sheep dung pellets remaining in April 1997 in samples originally containing 20 (kangaroo) or 80 (sheep) pellets.

Fig. 4. Decomposition over time in biocide and no biocide treatments of (a) kangaroo and (b) sheep dung pellets. Vertical bars are $\pm$ SE of each mean % remaining.

entire duration of the study (Fig. 4b). The difference between grass communities was marginal for sheep pellets for two of the samplings but showed no overall trend, and there was no treatment × community interaction.

Kangaroo pellet weight showed significant differences between treatments (55 $\pm$ 10% remaining for biocide and 14 $\pm$ 6% remaining for no biocide; $P = 0.002$) and times of exposure (50 $\pm$ 9% remaining and 13 $\pm$ 6% remaining for 11 and 23 months respectively; $P = 0.003$).

Many of the toilet rolls, especially those located in the control ('no biocide') treatments, were heavily ramified with carton. As with sheep pellets, because of difficulties in separating carton from residual paper, toilet roll data were also highly variable. There were no significant treatment effects; only a decrease in weight over time was evident. Therefore data are not presented.

There was a significant decrease in woollybutt root weight across time ($P < 0.001$) but differences between the two treatments and the time × treatment interaction were not significant (Table 1). The rate of decomposition of roots was much slower than that for grass tillers and for kangaroo or sheep pellets.

There were no treatment or observer differences or observer × treatment interaction for either bulk density or infiltration rate. Mean bulk density was 1.65 ($\pm$0.02) Mg m^{-3} and mean infiltration rate was 17.6 ($\pm$2.5) mm h^{-1}.

Table 1
Effect of time of exposure and biocide treatment on decomposition of woollybutt roots.

Exposure time (months)	% roots remaining	
	Biocide	No biocide
11	97 (3.41 $\pm$ 0.42)	94 (2.99 $\pm$ 0.42)
23	83 (1.58 $\pm$ 0.42)	84 (1.63 $\pm$ 0.42)
52	75 (1.34 $\pm$ 0.29)	76 (1.16 $\pm$ 0.29)

Values in brackets are means of logistic transformed percentages $\pm$ SE.

5. Discussion

There are two discrete stages in the decomposition process: fragmentation and mineralisation, both of which may be separated spatially and temporally (Whitford, 2002). The former stage may involve both abiotic and biotic agencies while the latter, based on chewing and digestion through enzyme lysis, together transform the size and chemical status of the material originally consumed. Mineralisation processes involve the conversion of such fragmented material into microbial biomass and eventually the breakdown of carbon compounds in this material by deamination of proteins and excretion of ammonia.

In the studies reported in this paper, we have focussed on the fragmentation phase by offering a series of alternative baits to termites resident in two contrasting grassland communities. While some, i.e. senescent grass tussocks, were subjected to initial fragmentation by harvester termites such as *Drepanotermes perniger* other baits, i.e. dung pellets voided by native and exotic herbivores, contained herbage residues that had already gone through an initial comminution and digestion phase before being subjected to further digestive treatment by non-harvester, dung-feeding guilds of termites. The more rapid decomposition of kangaroo dung compared with that of sheep may have resulted from the evolution of microbes specialising in their decay (Ayres et al., 2006).

Removal of termites had a significant impact on decomposition rate of both kangaroo and sheep dung pellets. For kangaroo dung, it took just 12 months for 50% of the original pellet samples to decompose in control treatments exposed to termites whereas a further 2.5 years was required for half the pellet samples in the biocide treatments to disappear. Similarly, over 50% of sheep pellets in the 'no biocide' treatments had decomposed after 12 months had elapsed with another 2.5 years required for 50% of pellets to decompose in the 'biocide' treatments (Fig. 4a,b). By the final sampling decomposition of sheep dung was slower than kangaroo dung in the biocide treatments, suggesting that even abiotic agents may be less effective in recycling dung of exotic herbivores.

While termites are important processors of dung of both native and non-native herbivores, breakdown of dung in the termite gut may reduce the potential contribution of the dung to soil organic matter by abiotic transformation (Nash and Whitford, 1995) with photodegradation and intermittent rainfall acting independently of termites (Whitford, 2002).

The absence of a distinct treatment effect on decomposition of grass foliage may be the indirect effect of the herbicide treatment. It is possible that herbicide and wetting agent residues on the foliage caused the termites to avoid this source of carbon. In Western Australia, the harvester termite, *Drepanotermes tamminensis* harvested bark and leaves of *Eucalyptus capillosa* in a woodland and the shoots of shrubs in a shrubland dominated by *Allocasuarina campestris* (Park et al., 1993). These authors suggest that *D. tamminensis* harvests plant materials according to biomass availability. In our study, the large quantity of tree and shrub leaves, stems and bark, especially in the mulga mitchell community, may have contributed to the lack of harvesting of dead grass tussocks.

Thurow (1989) studied the decomposition of both standing-dead and ground-litter of herbage in coastal savanna of southern Somalia. He found the rate of entry into the surface-litter component was significantly faster for forbs than grasses while decomposition of dead litter that was still standing was considerably slower (50% disappearing in 1 year) than surface litter (95% annual disappearance). Data on seasonality and rates of feeding by harvester termites on different herbage diets, and in different habitats in semi-arid Australia, are sparse. The data presented in this paper indicate that decomposition of grass tussock residues may vary significantly between species and/or from one grassland community to another, as well as over time. While it is acknowledged that the design of these experiments involved internal replication within contrasting grassland communities, Hargrove and Pickering (1992) have pointed out that landscapes need not necessarily be replicated (and probably cannot be) in order to achieve a relational understanding of an ecosystem's response to environmental characteristics.

Using nylon-mesh litter bags anchored to the soil surface, Christie (1979) followed the decomposition of current season's litter produced by mitchell grass (*Astrebla* spp.), a C_4 species widespread throughout the grasslands of western Queensland. He estimated that the projected time required for this litter to decompose completely was around 3.3 years however he was unable to identify how much of this decomposition was the result of feeding by harvester termites and how much was due to the activity of diverse surface soil microarthropods present throughout the semi-arid zone (Noble et al., 1996). In the studies reported in this paper, removal of termites had little impact on the initial decomposition rates of both grass species. Only once residual litter mass had reached comparatively low levels did termite presence become a significant factor. This result may have been due, partially at least, to a form of predator satiation (O'Dowd and Gill, 1984) whereby termites were swamped by the sudden abundance of food on offer.

As Lobry de Bruyn and Conacher (1990) have pointed out, there are two contrasting theories as to whether termites have any impact on soil aeration and water infiltration. One theory proposes that their impact is negative because they compact the soil whereas the other proposes that infiltration is facilitated by incorporating soil organic matter and the construction of subterranean galleries. While biocide treatment at "Glenora" initially appeared to induce some slaking of the surface soil in the woollybutt plots, no significant differences in either bulk density or water infiltration were recorded. Bulk density values were similar to those recorded in another study on "Glenora" in soils adjacent to warrens constructed by the burrowing bettong (*Bettongia lesueur*) (Noble et al., 2007). The lack of any significant soil physical differences between biocide and control treatments may indicate that the effectiveness of the biocide had been significantly diminished simply through leaching by rainfall in the intervening period of 10 years between biocide application and soil sampling. Furthermore, macropores constructed by termites and other soil biota may have provided a stronger than expected legacy-effect.

Biotic decomposers such as harvester termites may become important only with time as the decay-resistant fraction in the litter increases. The results of the studies reported in this paper add further weight to the conclusions emanating from a re-examination of litter decomposition data gathered in a North American desert suggesting that abiotic processes, such as photochemical degradation of lignins, may be more important than previously thought (Moorhead and Reynolds, 1989; Whitford, 2002).

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