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Litter production, decomposition and nutrient release in cleared and uncleared pasture systems of central Queensland, Australia

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Abstract: The temporal impact of clearing trees on litter production, litter decomposition and on C, N and P release through decomposition of litter was examined in the pasture systems of a semi-arid zone of central Queensland. Paired sites for cleared pastures (developed from clearing woodlands) and uncleared (intact woodland) pastures were selected to represent three dominant tree communities of the region i.e. *Eucalyptus populnea*, *E. melanophloia* and *Acacia harpophylla*, with three different time-since-clearing (5, 11–13 and 33 y) treatments. Yearly litter production was greater at uncleared sites (1732–1948 kg ha^{-1} y^{-1} for eucalypt and 2596 kg ha^{-1} y^{-1} for acacia communities) compared with cleared sites (1038–1282 kg ha^{-1} y^{-1} for eucalypt and 1100 kg ha^{-1} y^{-1} for acacia communities averaged over three time-since-clearing treatments). Rates of litter decomposition and of release of C, N and P from decomposing litter were higher at cleared than uncleared sites for all three tree communities. The cleared and uncleared sites did not differ significantly in total amount of C and N released per year since the concentrations of C and N were greater in litter from uncleared sites but the rate of release was less than that at cleared sites. Slow but continuous release of nutrients in eucalypt and acacia woodlands may be an adaptation of these communities to maintain the nutrient cycle and to avoid leaching of nutrients in the nutrient-poor soils of the region.

Key Words: Litter decomposition, litter production, nutrient release, pasture systems, tree clearing

INTRODUCTION

Litter maintains nutrient and energy flow at the soil–plant interface, provides habitat for various soil organisms and protects soil from erosion. Agren & Bosatta (1996) described litter as 'the bridge between plant and soil'. Litter production and decomposition varies with climate, season, substrate quality and type of vegetation (Hobbie 1992, Melillo *et al*. 1982, Upadhyay *et al*. 1989, Vitousek *et al*. 1994). Chemical composition of litter, which changes with type of plant community, influences structure and activity of microbial communities inhabiting soils (Kutsch & Dilly 1999), and biological and physicochemical properties of topsoil (Heal & Dighton 1986). Knowledge of litter production and decomposition rates is important when estimating nutrient turnover, C and N fluxes, and C and N pools in different ecosystems.

Conversion of woodlands/forests to open grasslands may negatively impact litter production and decomposition at the expense of quick monetary gains obtained from increased production in cleared pastures. The change in vegetation structure from woodlands to open grasslands may not only lead to changes in quantity and composition of litter, but also to other ecosystem properties (e.g. soil microclimate, Vetaas 1992; and nutrient return, Kochy & Wilson 1997) that could influence ecosystem processes.

In Queensland, 80 million ha of woodland communities (∼ 48% of the total area of the state) are used mainly to graze cattle for beef production. Since the beginning of the last century until 1985 various governmental policies and incentives for settlement schemes encouraged clearing of these woodlands on a large scale, to develop land for exotic pastures and cropping (Boulter *et al*. 2000). Clearing of woodlands continues at a high rate (528 000 ha y^{-1} cleared during 2001–2003; Department of Natural Resources and Mines 2005) to develop pastures. The economic gain from enhanced pasture

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production following clearing is the main reason for the land-holders to clear natural woodlands but this may compromise the sustainability of land resources because of nutrient runoff (Lawrence *et al.* 1988), soil erosion, changes in soil microclimate and nutrient mineralization that are linked to litter production, nutrient recycling and decomposition (Sangha 2003). Such impacts of clearing woodlands that affect the ecosystem processes and hence primary production and decomposition are often ignored while evaluating the monetary gains from cleared pastures in comparison to their uncleared pastures (Sangha 2003). Studies conducted in tropical woodlands/savannas suggest that production and decomposition of litter from trees and grasses play an important role in sustaining nutrient resources in nutrient-poor soils (Beard 1953, Belsky 1994, Belsky & Amundson 1998, Belsky *et al.* 1989, Tothill & Mott 1985). In Queensland, there is a paucity of data that relate to either the role of trees in maintaining a nutrient balance in woodland pastures, or the comparative nutrient cycling through litter in uncleared and cleared pastures. Burrows & Burrows (1992), Grigg & Mulligan (1999) and McIvor (2001) reported only on tree litter production in woodland communities (*Eucalyptus* spp. (*E. crebra, E. melanophloia, E. moluccana* and *E. drepanophylla*) and *Corymbia erythrophloia*) whereas two recent studies in Queensland reported only on litter decomposition. The first, by Wang *et al.* (2004) reports on decomposition in relation to N availability and plant material composition in controlled conditions for litter from woodlands (*Acacia aneura, A. harpophylla* and *Eucalyptus microcarpa*) and some agricultural crops (wheat (*Triticum aestivum*), buffel (*Cenchrus ciliaris*), sugarcane (*Saccharum officinarum*) and stylo (*Stylosanthes humilis*)). The second by Jalota *et al.* (in press) on *in situ* litter decomposition in *A. aneura* and *C. ciliaris* pastures in south-west of Queensland did not address the issues of litter production. No reports compare litter production, its decomposition and nutrient recycling *in situ* in woodland and cleared pastures of Queensland. It is important to quantify the role of trees in litter production, in nutrient recycling and in maintaining litter decomposition processes and nutrient mineralization when evaluating the integrated effect of clearing to develop pastures, for such processes provide land-holders with intangible services that sustain the land resources for long-term production gains.

Our research targets the influence of change in vegetation structure from native woodlands to open grasslands (largely monocultures of the grass *Cenchrus ciliaris* L.) on litter production, composition, decomposition and on release of N, P and C. The main objective was to quantify the role of these services when estimating gains in pasture production from clearing compared to uncleared (woodland) pastures. The effect of time since clearing on these parameters was also quantified. The role of soil properties i.e. microbial biomass for C and N, and organic carbon on litter decomposition was also examined. For this, three major woodland communities, each represented by a dominant tree species i.e. *Eucalyptus populnea* F. Muell. (poplar box), *Eucalyptus melanophloia* F. Muell. (silver-leaved ironbark) and *Acacia harpophylla* F. Muell. ex Benth. (brigalow), were selected in the central Queensland region.

MATERIALS AND METHODS

Research sites and design

The sites were selected as pairs for uncleared and cleared treatments, clearing having taken place at different times in the past i.e. 5, 11–13 and 33 y for each of three tree species (*Eucalyptus populnea*, *E. melanophloia* and *Acacia harpophylla*), in a 3 (tree species) × 3 (time-since-clearing) × 2 (paired plots for cleared and uncleared) design. The 5-, 13- and 33-y-old cleared sites are referred to in the text as Ep5y, Ep13y, Ep33y for *E. populnea*; Em5y, Em11y, Em33y for *E. melanophloia*; and Ah5y, Ah13y and Ah33y for *A. harpophylla*.

The paired cleared and uncleared sites were selected in close proximity with the assumption that they had similar biophysical characteristics (soil type, slope and vegetation) before clearing (according to the information provided by the landholder), and to some extent to minimize variation in grazing management since the same cattle grazed the cleared and their paired uncleared sites. Plots were pull-chain cleared. Details on timing of clearing and stocking rate at each site are presented in Table 1.

All the sites were selected at a grazing property ‘Avocet’ of a total area about 5000 ha (23.83°S, 148.14°E) in

Table 1. Details of time of clearing (all sites were chain pulled) and annual average stocking rate (SR) (adult cattle per ha) at cleared and uncleared sites for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla*

	Cleared treatments		Uncleared treatments
Tree community	Time of clearing	SR	SR
Eucalyptus populnea			
Ep5y	May 1996	0.2	0.2
Ep13y	December 1987	0.3	0.2
Ep33y	July 1967	0.2	0.2
Eucalyptus melanophloia			
Em5y	May 1996	0.2	0.2
Em11y	October 1990	0.3	0.3
Em33y	July 1967	0.16	0.16
Acacia harpophylla			
Ah5y	May 1996	0.2	0.1
Ah13y	December 1987	0.3	0.2
Ah33y	July 1967	0.16	0.2

central Queensland. The property is located 30 km south of Emerald, Queensland. In this semi-arid climate, the average annual rainfall is 600 mm, with sporadic summer storms during November–February. Average (over the 136 y from 1865–2001) minimum and maximum temperatures during winter (June–August) are 6–8 °C and 23–25 °C, and during summer (December–February) are 22–24 °C and 33–36 °C respectively.

All three woodland communities have an open canopy structure, and are colonized with understorey of native grass species, generally *Aristida* spp. in *E. populnea*; *Themeda triandra* in *E. melanophloia*; and *Dichanthium sericeum*, *Paspalidium caespitosum*, *Eragrostis* sp. in *A. harpophylla*, and some shrubs and legumes (*Rhynchosia* spp., *Indigofera* spp.). Cleared sites were dominated by the grass species *C. ciliaris*. All three tree species grow to the same height, *c.* 10–15 m. Details on species and associated land zones are presented by Sattler *et al.* (1999). *Eucalyptus populnea* grows on sandy soils, *E. melanophloia* on sandy-loam and *A. harpophylla* grows on clay soils. Vegetation of the woodland communities is similar to that of savannas with upper storey of less-dense trees (10–30% foliage cover, and 10–30 m tree height) and understorey of grasses (characteristics of savannas as described by Fox *et al.* 2001).

Since the tree density and herbaceous biomass influence litter production, data on these parameters were quantified. Tree density and tree basal area were studied using transect method (TRAPS (Transect Recording And Processing System); Back *et al.* 1997). At each site three transects of 50 × 4 m area were laid within a selected total area of 1 ha. All the woody trees and shrubs > 1.5 m height were considered for measurements. Tree basal area was estimated from the circumference 30 cm above the ground with a measuring tape and tree density was estimated by counting the number of trees and shrubs per unit area. Above-ground biomass of herbaceous plants was measured using the quadrat method. Five quadrats of 1 × 1 m area were laid within 1-ha marked area at each site. Measurements were taken throughout 1 y; starting from March 2001 at regular 4-mo intervals, in July 2001, November 2001 and March 2002. Quadrats were located at different positions at each sampling date. Plant samples from each quadrat were harvested just above the ground level, taken to the laboratory and dried at 60 °C for 48 h and weighed for biomass measurements.

Measurements for litter production

At each site a representative area of 1 ha was marked to study production of ground litter (mostly leaves, branches and twigs < 1 cm in circumference) during different seasons through sampling at 4-mo intervals through 1 y. Decomposition was quantified (as detailed below) over the same time intervals. The amount of litter produced at each site was studied under the normal grazing regime while decomposition was quantified in the fenced plots (10 × 10-m area at the centre of each 1-ha plot) to avoid disturbance from cattle.

The seasonal data on litter production and decomposition were then summed to estimate annual amounts of litter production. Annual amounts of litter produced at each site were then used to calculate the amount of C, N and P released over the year for which decomposition was studied.

The paired-plot technique (Wiegert & Evans 1964) was adopted to measure the amount of litter produced on the ground during different seasons. In March 2001, three quadrats of 1 × 1 m were selected randomly in three different directions and marked at each site. The standing green herbage was removed and dead litter on the soil surface was then collected from each quadrat. The litter samples were air dried and screened to exclude large sticks of circumference > 1 cm. For the next sampling date in July 2001, litter was collected from adjacent plots paired to the marked plots used in March 2001 and processed in the same way as in March 2001. The same procedure was followed in November 2001 and March 2002.

Based on seasonal decomposition rates and the amount of litter collected during the different seasons, litter production per season was computed as presented in Table 2.

Table 2. Sampling dates for litter production, decomposition (seasonal and longer term), and calculations for amount of litter produced during different seasons

Litter production	Seasonal litter decomposition with litter bags:		Seasonal decomposition rate	Longer-term litter decomposition with litter bags:		Amount of litter produced during different seasons
	left on	collected on		left on	collected on	
18–24 March 2001 = X_0	1 April 2001	12 August 2001	April–August 2001= R_1	1 April 2001	12 August 2001	
24–30 July 2001 = X_1	12 August 2001	13 December 2001	August–December 2001= R_2	1 April 2001	13 December 2001	March 2001–July 01 = X_1-X_0+R_1
26–30 Nov 2001 = X_2	13 December 2001	11 April 2002	December 2001–April 2002 = R_3	1 April 2001	11 April 2002	July 2001–November 01 = X_2-X_1+R_2
24–30 March 2002 = X_3						November 2001–March 02 = X_3-X_2+R_3

The method assumes that the amount of litter produced at a particular time of sampling in paired plots is similar. For each sampling date, litter was collected from one of the paired plots and left uncollected in the adjacent paired plot for a particular time (t_0). For the next sampling date (time t_1), the amount of litter added to the plot that was left uncollected at t_0 represents the amount of litter produced during that period (t_0-t_1) (e.g. at time t_0, X_0 is the amount of litter in a quadrat, after time t_1 the paired quadrat to the previously sampled one had X_1, so the amount of litter produced for time t_0-$t_1 = X_1$-X_0). Since the previous amount of litter (X_0) underwent decomposition during time t_0-t_1, the seasonal rates of decomposition were of necessity computed and used to account for decomposed litter when calculating precisely the total amount of litter produced in a season (Table 2).

Measurements for seasonal and long-term decomposition, and release of C, N and P

Decomposition was studied seasonally from litter collected during different seasons and annually from litter collected at the start of the study. In each season, litter collected from three different quadrats per plot was mixed well; litter with mixed species composition was used for decomposition studies. Seasonal decomposition data for one date (April 2002) were lost for Em5y due to accidental mild and patchy burning.

Litter bags made of nylon mesh (mesh size 1 × 1.5 mm) were used for the study of seasonal and annual decomposition. The size of a litter bag and the weight of litter per bag were calculated based on the amount of litter distributed per unit area in the field. An average weight of 5 g in each 15 × 15-cm bag was used for all the sites. Litter collected in March 2001 was kept for seasonal decomposition from April 2001 until August 2001 (Table 2). For decomposition from August 2001 to December 2001 litter collected in July 2001 was used and so on for December 2001 to April 2002. Longer-term decomposition from April 2001 until April 2002 was studied on litter collected in March 2001, with regular sampling at 4- (August 2001), 8- (December 2001) and 12-mo (April 2002) intervals (Table 2).

Litter bags were placed on the soil surface for decomposition in a fenced area of 10 × 10 m located centrally at each site to avoid disturbance due to grazing. Three litter bags per site were collected at the end of each specified time period, cleaned of soil, and dried to a constant weight. Likewise three bags were removed at 4-mo intervals for the longer-term decomposition trial.

The coefficient of variation for litter production and litter decomposition measurements for all data over a year and for data within each sampling date ranged from 17–35%. The rate of litter decomposition (R) for time period t (mo) was calculated as:

$$R = \frac{X_0 - X_t}{X_0 \times t}$$

where X_0 = original weight of litter left for decomposition (g), X_t = weight of litter remaining at time period t (g), t = time period.

The decay constant (k) for the annual rate of decomposition was calculated from $X_t/X_0 = e^{-kt}$, where t = time (y) and k = the annual decay constant (Olsen 1963).

After each of 4, 8 and 12 mo of litter decomposition, the samples from three litter bags for each sampling date were separately dried, manually cleaned to remove soil particles, bulked and ground for analysis of C, N and P. Litter samples collected in March 2001 (without decomposition) from each site were also thoroughly mixed, ground and analysed for C, N and P, and data were used to calculate their total amount released over a year.

Percent nutrient remaining in undecomposed litter at t time was computed according to Blair (1988) as:

$$= \frac{\text{Litter mass remaining (\%)} \times \text{nutrient concentration in the remaining mass (g per 100 g)}}{\text{Initial concentration of a nutrient (g per 100 g)}}$$

The total amount of nutrient released in relation to total amount of litter produced at each site was calculated from the amount of litter decomposed from time t_0 to t and nutrient content associated with decomposed litter at t_0 and t time, as follows:

$$\text{Amount of nutrients at time } t_0 \text{ in litter } (Y_0) = \text{Amountof litter } (X_0) \times \text{Initial nutrient concentration}$$

$$\text{At time t, amount of litter decomposed} = X_t,$$

$$\text{Thus the nutrient content at time t in the remaining litter } (Y_1) = \text{Amount of litter left undecomposed } (X_0\text{-}X_t) \times \text{Nutrient concentration at t.}$$

$$\text{The amount of nutrients released during } t_0 \text{ to t time} = Y_0\text{-}Y_1$$

Decomposition of litter was examined in relation to soil properties i.e. soil organic carbon (analysed following the Walkley and Black method, using H_2SO_4 and $K_2Cr_2O_7$ in 1:100 dilution, measured colorimetrically), and soil microbial biomass (C and N using Chloroform extraction method, Vance *et al.* 1987). Eight soil samples were taken randomly in each plot from the top 0–5 cm depth during January–March 2001, and bulked for analysis.

Statistical analysis

The amount of litter production, its decomposition, and its nutrient composition and nutrient release were analysed using residual maximum likelihood technique (REML; Patterson & Thompson 1971) in Genstat software ver 6.0 (Genstat Committee 2002). REML is a specific analytical tool to deal with unbalanced data sets (Genstat Committee 2002). In the present analysis, all the uncleared treatments of a tree species were considered as replicates while the cleared treatments for each age group were taken as such with no replication within a tree species, but replicated across different tree species.

The residual variation was calculated based on the three uncleared replicates of each of the tree species (i.e. 3 replicates × 3 tree species = 9 'plots' representing 3 treatments) allowing comparisons between these and the unreplicated cleared community 'plots' (1 replicate × 3 tree species × 3 clearing treatments = 9 'plots' representing 9 treatments). There are, therefore, 12 treatments in total (uncleared, and 5-, 11–13- and 33-y-old pastures, each for three tree species).

The REML model included the effects of tree species (*E. populnea*, *E. melanophloia* and *A. harpophylla*), clearing treatment (i.e. 5, 11–13 and 33 y) and their interaction. The interactions between tree species and clearing treatments were significant ($P = 0.05$), so the results are presented for each tree species for uncleared and for cleared (5-, 11–13- and 33-y-old) pastures. The model undergoes an iterative process through the fixed and the random effects to estimate the residual variance, which is then used to calculate least significant difference of means (LSD) between treatments. Pair-wise comparisons of means between any two treatments were conducted using the LSD test at $P = 0.05$. The means and LSDs from REML analysis are used in presenting all the results.

RESULTS

Tree density and herbage biomass

Tree density at uncleared sites was greatest for *Acacia harpophylla* followed by *Eucalyptus populnea* and *E. melanophloia* (Table 3). Overall, cleared sites had more above-ground biomass of herbaceous plants compared to uncleared sites. Between cleared sites of a tree species, the annual above-ground biomass of herbaceous plants was greatest at the Ep13y and Ah13y, and at Em5y sites (Table 3).

Litter production

The amount of litter production varied during different seasons for different tree species and their cleared treatments (Table 4). Uncleared sites generally produced more litter than did the cleared sites.

Eucalyptus populnea and *Acacia harpophylla* woodlands produced the maximum amounts of litter during November 2001 to March 2002 (Table 4). There was no significant difference in the amount of litter produced between cleared and uncleared sites of *E. melanophloia*, irrespective of season. In contrast, uncleared *A. harpophylla* produced significantly (at $P < 0.05$) more litter compared with most cleared sites in all the seasons (e.g. litter produced at the uncleared site in March–July 2001 was more than double that of the cleared sites). In *E. populnea*, only during July–November 2001 was litter produced at uncleared close to twice the amount at the cleared sites (Table 4).

The total amount of litter produced per annum (calculated from summing data for all seasons over a year) was greatest for all the tree species in their uncleared

Table 3. Tree parameters and annual average above-ground biomass for herbaceous plants at uncleared and cleared (5 y, 13 y and 33 y) sites for *Eucalyptus populnea, Eucalyptus melanophloia* and *Acacia harpophylla*

Tree community	Parameter	Uncleared	5 y	13 y	33 y
Eucalyptus populnea	Tree density (ha^{-1})	1583	–	–	–
	Basal area ($m^2\ ha^{-1}$)	37	–	–	–
	Above-ground biomass (herbaceous plants) ($kg\ ha^{-1}\ y^{-1}$)*	2107^{b}	2817^{ab}	3792^{a}	2748^{ab}
Eucalyptus melanophloia	Tree density (ha^{-1})	1216	–	–	–
	Tree basal area ($m^2\ ha^{-1}$)	21	–	–	–
	Above-ground biomass ($kg\ ha^{-1}\ y^{-1}$)	3761^{b}	6335^{a}	3743^{b}	2816^{b}
Acacia harpophylla	Tree density (ha^{-1})	3622	–	–	–
	Tree basal area ($m^2\ ha^{-1}$)	21	–	–	–
	Above-ground biomass ($kg\ ha^{-1}\ y^{-1}$)	1823^{b}	3030^{ab}	4259^{a}	2803^{ab}

*Different superscripts in a row represent significant differences at $P < 0.05$ between treatments within a tree community.

Table 4. Litter production (kg ha^{-1}) at uncleared and cleared sites (5 y, 13 y and 33 y) for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla*

		Eucalyptus populnea	*Eucalyptus melanophloia*	*Acacia harpophylla*	LSD*
March–July 2001	Uncleared	448	523	883	379.9
	5 y	211	234	365	
	13 y	482	351	322	
	33 y	189	313	231	
July–November 2001	Uncleared	786	583	774	380.2
	5 y	383	401	259	
	13 y	265	520	497	
	33 y	401	416	516	
November 2001–March 2002	Uncleared	498	842	939	427.9
	5 y	272	472	722	
	13 y	552	645	372	
	33 y	360	496	336	
Total ($\text{kg ha}^{-1}\ \text{y}^{-1}$)	Uncleared	1732	1948	2596	873.3
	5 y	866	1107	1346	
	13 y	1299	1515	1191	
	33 y	949	1226	1084	

*LSD represents average value of least significant differences of means ($P < 0.05$) for all three communities at any one sampling date.

treatments, although the differences between cleared and uncleared treatments were not all significant. The cleared treatments did not differ significantly from each other in the total amount of litter produced per year (Table 4).

Litter decomposition

Seasonal decomposition. The decomposition of litter was faster during August–December compared with other seasons throughout a year in *E. melanophloia*, while the rate did not vary much between seasons in *A. harpophylla* and *E. populnea* (Figure 1). The cleared sites of 5 y age in all the tree species supported significantly ($P < 0.05$) greater rates of litter decomposition than the uncleared sites, with few exceptions. There were no notable differences in decomposition of litter at uncleared and 11–13-y-old or 33-y-old sites in *E. populnea* and *E. melanophloia*. Uncleared *A. harpophylla* had lower rates of decomposition than Ah33y sites during August–December 2001 and December 2001–April 2002 (Figure 1).

Longer-term decomposition. The proportion of litter remaining after 1 y of decomposition was greatest at the uncleared sites (i.e. litter decomposition proceeded more slowly at uncleared than at cleared sites). The average litter loss over 1 y at uncleared sites was 15–20 per cent of original mass while cleared sites had 25–35 per cent mass loss (Figure 2). The maximum proportion of litter was decomposed in 5-y-old pastures for all woodland types, followed by 33-y-old sites in *E. melanophloia* and *A. harpophylla*.

The decay constant (k) reflected the faster rate of litter decomposition at 5-y-old sites with k values of −0.25 to −0.38 and half lives of 1.8 to 2.6 y, compared with k values of −0.19 to −0.20 and half lives of 3–4 y for uncleared sites (Table 5).

Table 5. Decay constants (k) and half lives calculated over 1-y period of decomposition of litter at cleared and uncleared sites for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla* communities

Tree community	Treatment	k	Half life (y)
Eucalyptus populnea	Uncleared	−0.19	3.64
	5 y	−0.38	1.83
	13 y	−0.22	3.08
	33 y	−0.22	3.08
Eucalyptus melanophloia	Uncleared	−0.20	3.41
	5 y	−0.26	2.65
	13 y	−0.17	3.09
	33 y	−0.25	2.76
Acacia harpophylla	Uncleared	−0.20	3.41
	5 y	−0.26	2.65
	13 y	−0.17	3.09
	33 y	−0.25	2.76

C, N and P concentrations in litter during longer term decomposition

At the beginning of the experiment (March 2001) C and N concentrations in litter were greater at uncleared than those at cleared sites for *E. populnea* (except N concentrations at Ep5y site) and *A. harpophylla*, whereas P concentrations in litter were greater at cleared than uncleared sites with few exceptions (data not presented). In contrast, *E. melanophloia* showed no notable difference for C, N and P concentrations between cleared and uncleared sites. Overall, mean C : N ratio in undecomposed litter for all the cleared (irrespective of age) and uncleared treatments for each tree community was more in litter produced at cleared than uncleared sites, but only significantly so for *A. harpophylla* (Table 6).

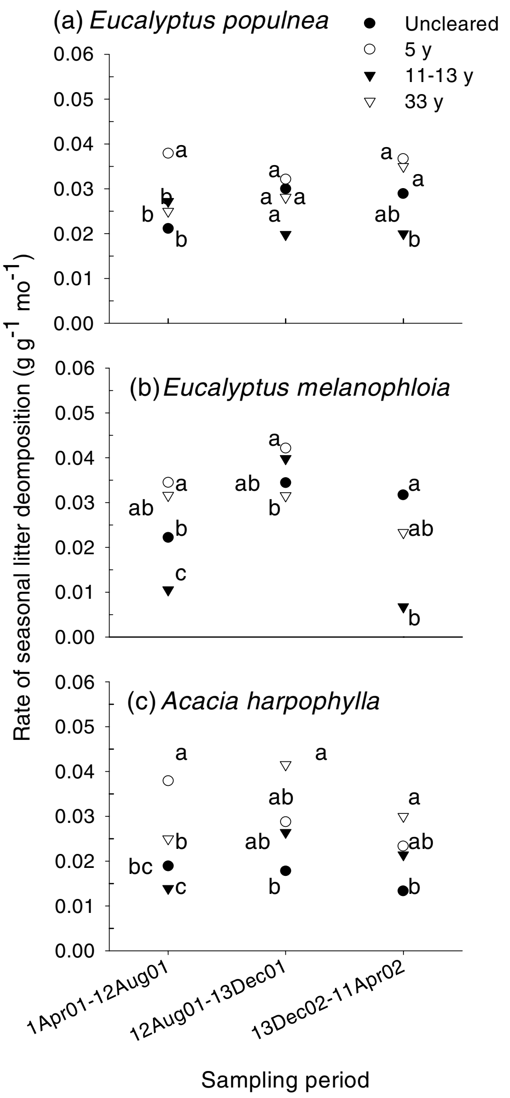

Figure 1. Seasonal decomposition rate for litter produced at cleared and uncleared sites for (a) *Eucalyptus populnea*, (b) *Eucalyptus melanophloia* and (c) *Acacia harpophylla* communities. Any two treatments with different letters on any one sampling date within a tree community denote significant difference at P< 0.05.

Based upon the content of nutrients (i.e. litter mass × concentration) remaining in the litter at any time, it was clear that there was a net release of C, N and P as decomposition proceeded at all sites, with few exceptions (Figure 3). There was no release of C at the 33-y-old pastures, nor of N except a small initial decline at uncleared sites for *E. populnea* (Figure 3). P was released at all the sites except at uncleared *E. populnea* and *A. harpophylla* (Figure 3). The smaller release of P and N than expected based upon the litter mass at uncleared compared with cleared sites occurred because the rate of their incorporation into decaying litter exceeded the loss of litter mass over the duration of decomposition (Figure 3).

Table 6. Mean (± SE) C: N ratio in undecomposed litter at cleared (average for all the three time-since-clearing treatments) and uncleared sites for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla*

	Cleared	Uncleared
Eucalyptus populnea	61 ± 13.8	55 ± 6.51
Eucalyptus melanophloia	72 ± 13.2	70 ± 5.24
Acacia harpophylla	70 ± 9.39	38 ± 1.76

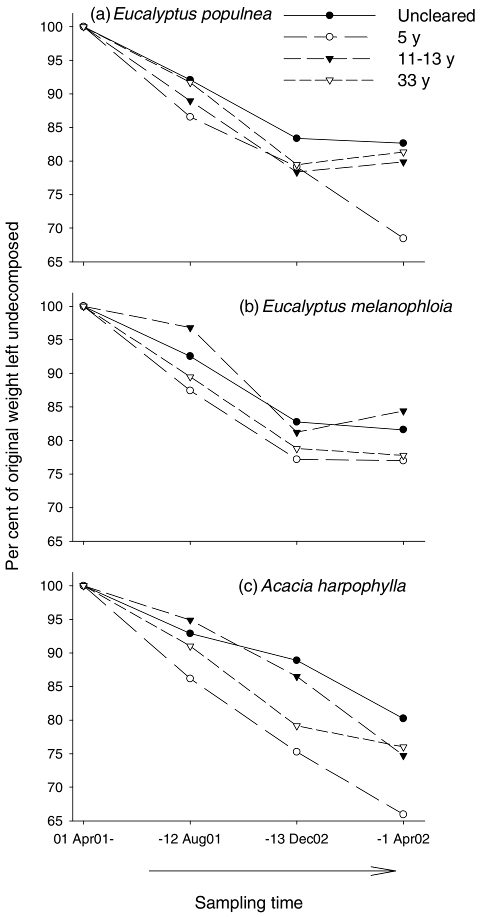

Figure 2. Decomposition of litter at cleared and uncleared sites over 1 y for (a) *Eucalyptus populnea*, (b) *Eucalyptus melanophloia* and (c) *Acacia harpophylla* communities. Average LSD for decomposition period 01April 2001–12 August 2001 = 6.33, for 12 August 2001–13 December 2001 = 6.94, and for 13 December–1 April 2002= 10.68, denotes significant difference of means among any two treatments for a particular sampling time at P < 0.05.

The content of nutrients released after 1 y of decomposition as a per cent of their original content in undecomposed litter can be derived from the final (April 2002) data presented in Figure 3. Subtracting the final data point from the original 100% content gives the values, and shows a greater loss of C, N and P at the 5-y sites than at the uncleared sites especially for *E. populnea*. In a comparison between cleared sites, the nutrient loss after 1 y of decomposition was at a maximum in the 5-y-old pasture compared with those 13 or 33 y since

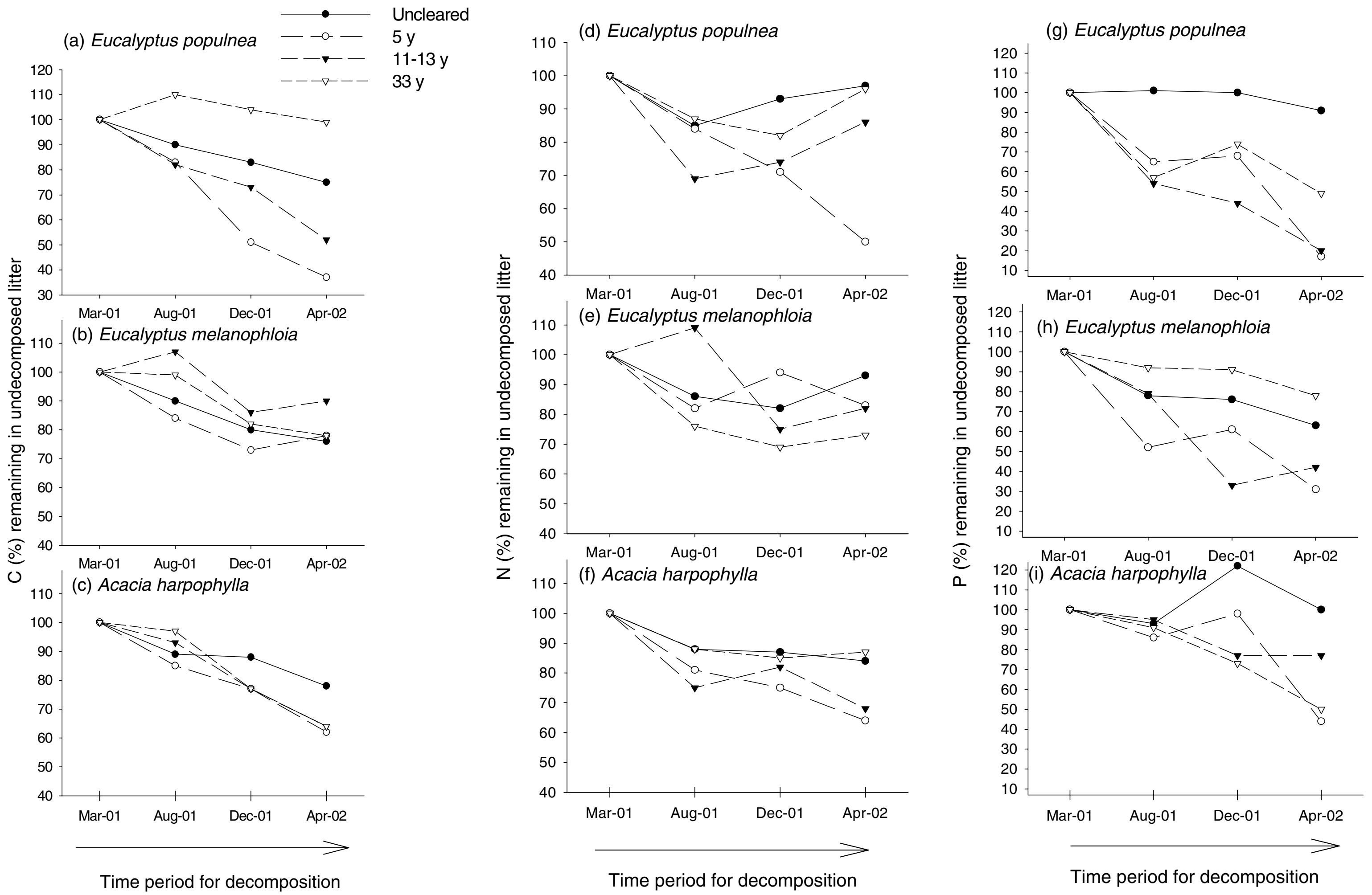

Figure 3. The per cent content of carbon (a–c), nitrogen (d–f) and phosphorus (g–i) in undecomposed litter at any sampling date during 1 y of decomposition at cleared and uncleared sites for *Eucalyptus populnea* (a, d, g), *Eucalyptus melanophloia* (b, e, h) and *Acacia harpohhylla* (c, f, i) communities.

Table 7. Release of C, N and P on an annual basis (kg $\text{ha}^{-1}\text{y}^{-1}$) according to total amount of litter produced at uncleared sites and those cleared for 5 y, 13 y and 33 y for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla*

	Uncleared	5 y	13 y	33 y	LSD*
C	214	95.8	173	105	248
N	2.14	2.22	1.11	1.41	5.57
P	0.19	0.42	0.56	0.23	0.39

*LSD denotes the least significant difference of means in a row at $P < 0.05$, in the absence of significant interaction between tree community and time-since-clearing. The values are presented for a common response among all the communities.

Table 8. The potential content of nutrients (kg ha^{-1}) stored in litter produced at uncleared sites and sites cleared for 5 y, 13 y and 33 y for *Eucalyptus populnea*, *Eucalyptus melanophloia* and *Acacia harpophylla* communities

Site		Uncleared	5 y	13 y	33 y
Eucalyptus populnea	C	812	296	542	289
	N	15.3	8.04	6.63	4.49
	P	0.58	0.60	1.10	0.50
Eucalyptus melanophloia	C	792	354	583	479
	N	11.4	4.38	6.56	10.4
	P	0.84	0.50	0.95	0.51
Acacia harpophylla	C	1149	367	485	423
	N	29.9	6.55	5.49	6.32
	P	0.87	0.55	0.63	0.67

clearance for all tree species, but significantly so only for *E. populnea*.

There was no difference between cleared and uncleared treatments in any tree community in the amount of C, N and P released from litter produced over a year (Table 7). However, it is important to note that the decomposition process was most likely not complete after 1 y. The potential content of C, N and P stored in litter produced at uncleared sites, were it to be completely released over time, was greater than at cleared sites (Table 8).

Relationship between litter decomposition and soil parameters

Soil microbial biomass and organic carbon were analysed (once in January–March 2001) to determine their relationship with litter decomposition. Rates of litter decomposition were weakly correlated with the amount of soil microbial biomass of carbon ($r = 0.30$ at $P = 0.05$, $df = 12$) and nitrogen ($r = 0.56$; $P = 0.05$, $df = 12$), and soil organic carbon content ($r = 0.30$; $P = 0.05$, $df = 12$).

DISCUSSION

In contrast to tropical forest ecosystems, there have been relatively few studies on nutrient dynamics in the semi-arid savannas (Frost 1984, Lamotte & Bourliere 1983), and major gaps still exist in our current knowledge on this topic (Mistry 2000). In Queensland, with the exception of Jalota *et al.* (in press) there have been no detailed studies that compare total ground-litter decomposition and nutrient dynamics in natural woodland and developed pasture systems. The present study fills this gap, and reveals decomposition behaviour and release of nutrients from ground litter in open grassland and woodland pastures.

Tree clearing for pasture development in central Queensland does provide production benefits (as reported by Burrows 1993), but fails to maintain litter production and nutrient release in cleared pasture systems. Uncleared *E. populnea*, *E. melanophloia* and *A. harpophylla* produced more litter per annum (range of 1732–1948 kg $\text{ha}^{-1}\text{y}^{-1}$ for eucalypt and 2596 kg $\text{ha}^{-1}\text{y}^{-1}$ for acacia) compared with their cleared or open grassland (755–1586 kg $\text{ha}^{-1}\text{y}^{-1}$). Similar values over the range of 900–2700 kg $\text{ha}^{-1}\text{y}^{-1}$ for tree litter in eucalypt and corymbia communities of central Queensland were reported by Burrows & Burrows (1992) and Grigg & Mulligan (1999), but they did not report comparable data for cleared pasture systems. Studies conducted in South Africa on *Burkea africana*, *Terminalia sericea* and *Ochna pulchra* savannas indicate similar amounts of plant litter production (1859 kg $\text{ha}^{-1}\text{y}^{-1}$, Frost 1984; 1700–1790 kg $\text{ha}^{-1}\text{y}^{-1}$, Morris *et al.* 1982). The values reported here are greater than those for tree litter production (720–1270 kg $\text{ha}^{-1}\text{y}^{-1}$) in eucalypts (*Eucalyptus crebra*, *E. drepanophylla*, *C. erythrophloia*) of northern Queensland (McIvor 2001).

The greater production of ground litter in woodlands than the open grasslands was mainly due to litter derived from trees as well as from understorey vegetation in woodlands. The litter produced at cleared sites from grass and other herbaceous species is generally less lignified compared to some of the litter (herbaceous and woody species) obtained from vegetation at uncleared sites. The herbaceous nature of litter in open grasslands was primarily responsible for faster rates of litter decomposition – this was especially apparent at 5-y-old sites compared with uncleared sites – whereas the presence of a waxy coating on eucalypt leaves contributes to their slow rates of decomposition (Bernhard-Reversat 1999). This accords with data of Frost (1984) and Morris *et al.* (1982) that showed that grass litter decomposed faster than tree litter in savannas. In our study, on average, about 25–35% of total mass was lost over 1 y from cleared sites compared to 15–20% in litter from woodlands, values not dissimilar to those of Jalota *et al.* (2005) who reported a 40% loss in *C. ciliaris* pastures and 28% loss in *Acacia aneura* woodlands over 1 y in south-west Queensland with 516 mm annual rainfall. Such differences in decomposition rates between woodland communities are likely to be due to differences between species in chemical composition and morphology; the smaller and thinner leaves of *A. aneura* may have contributed to faster decomposition compared to the three tree species studied here. The decomposition rates for litter from woodlands in our study were greater compared with those of *Eucalyptus obliqua* forest (5–15%) in south-east Australia (a relatively cold climate) (Attiwill 1968), but for *Burkea* savannas in south Africa (annual rainfall 600 mm), Bezuidenhout (1980) reported a much greater loss in grass litter mass (60%) compared to 11–26% loss in tree litter over 1 y. These differences are due to differences in composition of plant material, soil microclimate and climate (Kutsch & Dilly 1999, Vetaas 1992). A more recent study by Wang *et al.* (2004) in controlled conditions highlighted the importance of type of C (C functional groups) as decomposition was initially (2–4 wk) related positively to carbonyl C content, and then negatively to aryl and O-aryl C content over a longer term, the latter regulated the rate of decomposition after the initial phase of decomposition.

Due to the faster rate of decomposition at cleared sites, the rate of release of C, N and P was also faster at cleared sites than in woodlands, with few exceptions. Similarly, Frost (1984) reported faster release of N, P and K from herbaceous litter than from tree litter in *Burkea* savannas. In the present study, the rate of release of nutrients tended to decline with age of cleared pastures. This raises concern for maintenance of a steady release of nutrients with age of cleared pastures. Litter in the 5-y-old pastures lost 20–50% of N and 50–80% of P stored therein over a year (Figure 3) but lower proportions were lost 13 y and 33 y after clearing. The uncleared treatments lost only 10–20% of the total stored content of N or P. However, the amounts of C, N and P released over a year from the total amount of litter produced per annum at each site did not differ significantly between cleared and uncleared systems due to the large error in the estimates (Table 7). The proportion of C released was lower at cleared compared with uncleared sites, hence soil organic matter from litter may not be sustained following clearing. At uncleared sites, although the proportion of nutrients released was lower (Figure 3), a steady nutrient flow was still maintained in natural systems due to the greater amounts of litter produced there. Zucker (1983) suggested that slowly decomposing leaves are in fact an advantage in nutrient-poor environments such as in semi-arid savannas/woodlands, since they reduce the possibility of nutrient loss due to rapid decomposition.

Plant chemical composition significantly impacts on decomposition processes (e.g. microbial immobilization and nitrification) and nutrient cycling, as these ecosystem functions improve with increased plant diversity (Hooper 1996, Hooper & Vitousek 1998). We believe that the monoculture of *C. ciliaris* in cleared pastures, through its low quantity and fast release of nutrients, is responsible for nutrient run down. This is evidenced by the decline in return of C, N and P at any time after clearing compared with that in woodland pastures where diverse species contribute to the efficient return of nutrients. Probably, variation in species composition would contribute to differences in chemical composition and to the release of different proportions of nutrients over a given time in systems more diverse than a monoculture. In support of this, the soil nutrients N and P were more abundant in uncleared compared with cleared pasture soils (Sangha *et al.* 2005).

The amount of C, N and P released from annual litter production over 1 y was in fact underestimated in Table 7, since the amount of total litter that decomposed was only 15–20% in woodlands and 25–35% in cleared pastures, given that the decomposition process was still incomplete after 1 y. The release of nutrients from total litter production at a site would have been greater if the litter had been completely decomposed. In 1 y of the present decomposition study there was a loss of P compared with the initial concentration in undecomposed litter while N and C barely declined. Indeed, there was accumulation of N and C at a few sites, especially uncleared ones. Release of N in beech litter (*Fagus sylvatica*) over 3 y of decomposition was studied in detail by Zeller *et al.* (2000), and in *Eucalyptus diversicolor* forest by O'Connell (1988). They explained that, contrary to expectation, incorporation of N in decomposed litter occurs for the initial years of decomposition and that this is derived from external sources such as throughfall, soil fauna, fungi and bacteria.

Decomposition of litter and release of nutrients not only depends upon litter composition but also upon soil type, microbial communities and soil properties (Kutsch & Dilly 1999, Scholes & Walker 1993, Vitousek & Matson 1984). The positive relationship between decomposition rate and soil organic carbon, and with soil microbial biomass suggests that microbial activity may enhance the decomposition process. A strong seasonal pattern in microbial activity (higher in mid-summer and least in the dry season) that coincided with litter decomposition patterns was reported for South African savannas by Bezuidenhout (1978). Microbial and other decomposition processes depend upon the type of material available for decomposition and on other factors such as climate and water availability (Bardgett *et al.* 1999). Thus, the quality of litter influences microbial processes (microbial immobilization) and nutrient retention in a system (Vitousek & Matson 1984). The effects of soil properties, for example water availability or pH, on litter decomposition or on growth of particular microbes and their activities responsible for litter decomposition, vary with seasons and can play an important role in moderating nutrient return to a system. Any tree clearing or management activity that affects soil properties, thus, may influence litter decomposition and nutrient release in cleared and uncleared pastures systems.

Besides clearing trees to manage land for production gains, other management practices such as grazing pressure and fire also significantly affect the amount of litter production, and hence the return of nutrients to a system. Birk & Simpson (1980) and O'Connell (1988) highlighted the role of fire in nutrient dynamics in Australian eucalypt forests. Studies conducted elsewhere suggested that high stocking rates lead to reduced litter production and root biomass (Cantarutti *et al.* 2002, Christie 1979) and slow rates of decomposition (Shariff *et al.* 1994) and reduced C and N pools (Mapfumo *et al.* 2002). The reduction in litter and root biomass, and change in litter composition can consequently affect microbial communities that are responsible for decomposition processes and thus release of nutrients to soil.

In woodlands, nutrient cycling is steady but slow compared with the faster rate of cycling in cleared pastures. In eucalypt woodlands, the toxic effects of allelochemicals on soil microbes (Chander *et al.* 1995, Dellacassa *et al.* 1989) contribute to slow nutrient cycling from litter, although we are not aware of reports that refer to these effects in native woodlands. The slow rates of decomposition at uncleared eucalypt and acacia sites may reflect their adaptation in resource use efficiency on Australian soils, as Zucker (1983) has suggested that slow decomposition reduces the possibility of nutrient run down. From an ecological perspective, Grubb (1989) explained with examples from different ecosystems that poor soils support vegetation communities which are adapted to poor nutrient status. There is a two-way relationship between structure or type of vegetation communities and soils, and it is still not clear which plays a greater role in determining the other (Grubb 1989). The sclerophyllous nature of eucalypt and acacia communities growing in central Queensland is probably an adaptation to nutrient-poor soils and to the semi-arid climate. Slow but continuous release of nutrients from litter is a further feature of this adaptation that protects the system from leaching of nutrients, a problem in many ecosystems (Whitmore 1989). Nevertheless, the potential content of C and N stored in litter produced at uncleared sites, were it to be completely released over time, was greater than at cleared sites (Table 8). The steady characteristic return of nutrients at uncleared sites, was disturbed by clearing; cleared sites had less production of ground litter and what was there was decomposed faster. Thus change in vegetation from woodlands to cleared grasslands led to a change in the natural equilibrium of nutrient return to the system that over the long term could obviate the gains in pasture production.

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