Decomposition of woody debris in Western Australian forests

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Abstract: Changes in mass and nutrients in experimental logs of six tree species during 5 years of exposure in the three major forest production regions of southwest Western Australia were measured to determine how climate, substrate quality, and substrate size interact to regulate decomposition of woody debris in this Mediterranean-type climate. Branch (3–5 cm in diameter) and bole (10–15 cm in diameter) material of the six species was set out in representative areas of a regenerating clear-cut *Eucalyptus diversicolor* F. Muell. wet sclerophyll forest, selectively cut *Eucalyptus marginata* Donn ex Smith dry sclerophyll forest, and clear-cut areas of a former *Pinus pinaster* Aiton plantation. Experimental logs were collected at about 0.5, 2, and 5 years after placement and were separated into bark and wood components. Samples of initial material were analyzed for moisture content, water-soluble and NaOH-soluble extractives, and nutrient concentrations (N, P, K, Ca, and Mg). At each collection, moisture content and changes in mass and nutrient concentration were determined for the sample logs. *Eucalyptus calophylla* R.Br. the major associate of the two native forests, lost the most mass during this time, up to 65% of the initial mass (decomposition coefficient $k = 0.22$ year^{-1}). Decomposition was least in *P. pinaster* and *E. marginata*, at about 24–26% of original mass ($k = 0.05$ year^{-1} and 0.07 year^{-1}, respectively). Mass losses were greatest in Manjimup, the wettest site, and least at Gnangara, the driest site, but differences in overall levels of decomposition were small despite the range in climatic moisture regimes. Small logs decomposed faster than large logs. Changes in nutrient concentrations occurred in all logs at all sites, indicating activity by decomposer organisms and (or) leaching losses. Nitrogen was the only element to be immobilized over the 5-year period. Mineralization rates were of the order P ≈ Ca < Mg < K. Concentrations of compounds extractable in cold water and NaOH decreased during the 5 years of exposure. Differences in decomposition rates were partly explained by initial concentrations of N only; there appeared to be no relationship between decomposition and concentration of the other elements and extractives.

Résumé : Les variations de la masse et des éléments nutritifs dans les billes expérimentales de six espèces d'arbres, pendant 5 ans d'exposition dans les trois principales régions de production forestière du sud-ouest de l'Australie occidentale, ont été mesurées pour déterminer comment le climat, la qualité et la dimension du substrat interagissent dans la décomposition des débris ligneux sous ce type de climat méditerranéen. Des échantillons de branches (de 3 à 5 cm de diamètre) et de troncs (de 10 à 15 cm de diamètre) des six espèces ont été répartis dans les aires représentatives d'une coupe à blanc en régénération d'une forêt sclérophile humide d'*Eucalyptus diversicolor* F. Muell. dans une coupe sélective d'une forêt sclérophile sèche d'*Eucalyptus marginata* Donn ex Smith et dans les aires coupées à blanc d'une ancienne plantation de *Pinus pinaster* Aiton. Les billes expérimentales ont été récoltées à intervalles d'environ 0.5, 2 et 5 ans après leur installation et ont été séparées en composantes d'écorce et de bois. Des échantillons du matériel initial ont été analysés quant à leur teneur en eau, en extraits solubles à l'eau et au NaOH, et à leur concentration d'éléments nutritifs (N, P, K, Ca et Mg). À chaque récolte, la teneur en eau et les changements de la masse et de la concentration en éléments nutritifs ont été déterminés dans les échantillons de billes. L'*Eucalyptus calophylla* R.Br., l'associé principal des deux forêts indigènes, a perdu le plus de sa masse pendant cette période, jusqu'à 65% de la masse initiale (coefficient de décomposition $k = 0.22$ an^{-1}). La décomposition était moindre chez *P. pinaster* et chez *E. marginata* soit environ 24 à 26% de la masse originale ($k = 0.05$ an^{-1} et 0.07 an^{-1}, respectivement). Les pertes de masse étaient les plus élevées au Manjimup, site le plus humide, et les plus faibles au Gnangara, site le plus sec, mais les différences globales des niveaux de décomposition étaient faibles malgré les écarts entre les régimes climatiques d'humidité. Les petites billes se sont décomposées plus rapidement que les grosses. Les changements concernant les concentrations d'éléments nutritifs se sont produits dans toutes les billes de tous les sites, indiquant une activité des organismes décomposeurs et (ou) des pertes par lessivage. L'azote fut le seul

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élément immobilisé pendant la période de 5 ans. Les taux de minéralisation furent de l'ordre de P = Ca < Mg < K. Les concentrations des composés extractibles à l'eau froide et au NaOH ont diminué pendant les 5 ans d'exposition. Les différences relatives aux taux de décomposition ont été expliquées en partie par les concentrations initiales de N seulement; aucune relation n'a semblé exister entre la décomposition et la concentration des autres éléments et extraits.

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Introduction

Decomposition of forest litter and the subsequent mineralization of essential nutrient elements is of primary importance for maintaining forest productivity (Swift et al. 1979; Charley and Richards 1983). Leaf litter decomposition has been widely studied (Facelli and Pickett 1991), but the breakdown of woody debris has received only limited consideration (Harmon et al. 1986; Vogt et al. 1986). Woody debris is a conspicuous component of the forest floor in most forest ecosystems. As a result of its relatively large size and low nutrient concentrations, it decomposes more slowly than fine litter and may require decades to become mixed into the forest soil (Harmon et al. 1986; Fahey et al. 1991). Woody debris may contain a large portion of the nutrient pool despite the low concentrations in wood, and the long-term productivity of forested ecosystems is likely influenced by the slow return of available nutrients from this material.

In addition to its role in nutrient cycling, woody debris also represents a large and potentially long-term storage of carbon. If decomposition rates are slower than rates of biomass accumulation of replacement trees, the forest becomes a carbon sink that may be important when extrapolated over large forest landscapes (Lugo and Brown 1992). However, because there is so little information on wood decomposition rates for a variety of forest types, these extrapolations cannot be made at this time.

Current understanding of the influence of climate on decomposition processes of woody debris of hardwood species is derived mainly from studies of forests growing in climates in which temperatures favorable for microbial activity coincide with moisture availability. Decomposition processes in forests of Western Australia operate under a Mediterranean-type climate. The rainy period of late autumn to early spring is a season of relatively low temperatures (but frost-free). When temperature conditions for microbial activity improve in late spring and summer, the moisture regime is reduced, which may limit microbial activity (Kaarik 1974; Flanagan and Bunnell 1976), suggesting slow rates of decomposition for woody debris.

Improved knowledge of the rates of decomposition of woody debris and some of the factors affecting these rates is important for better long-term management of forests in Western Australia as well as in many other parts of the world. The major aim of our study was to determine how climatic gradients, substrate quality, and size of woody debris, represented by the dominant species of the three major productive forest regions of Western Australia, affect decomposition of woody debris. In this paper we discuss our results in relation to the following hypotheses: decomposition rate, as measured by mass loss, is regulated by (*i*) climatic constraints, (*ii*) the quality of the substrate, and (*iii*) the dimensions of the substrate, particularly diameter.

Materials and methods

Study sites

Three study sites were chosen to represent a gradient of moisture and temperature conditions (Table 1). The Gnangara *Pinus pinaster* Aiton plantation is the warmest and driest site, with a virtually rain free summer (November to March). The intermediate site was located in the *Eucalyptus marginata* Donn ex Smith forest (jarrah forest) region near the town of Dwellingup. Like Gnangara, there is very little rain during the summer months. The wettest and coolest site was located in the *Eucalyptus diversicolor* F. Muell. forest (karri forest) region near the town of Manjimup. The annual rainfall is similar to that of Dwellingup, but its more even distribution throughout the year and cooler temperatures makes the Manjimup site the wettest of the three sites.

This gradient of temperature and moisture conditions was enhanced by placing the experimental logs in sites with different management practices. The Gnangara site was in a newly clear-cut location. The Dwellingup site was in an area of selective logging that retained an open canopy of remaining trees. The Manjimup site was placed in an area that had been clear-cut 4 years prior to the start of our study and that at the start of the experiment had a closed canopy of trees to 5 m tall and a dense understory of native shrubs.

Field methods

The six species selected for this study were chosen to represent the three dominants of the major forests, *E. diversicolor*, *E. marginata*, and *P. pinaster* (non-native), and the common subordinate trees of the native forests, *Allocasuarina fraseriana* (Miq.) L. Johnson, *Banksia grandis* Willd., and *Eucalyptus calophylla* R.Br.

Fresh material was cut from trees of these six species into pieces approximately 75 cm long from bole wood (10–15 cm in diameter) and branch wood (3–5 cm in diameter). Each experimental log was numbered and tagged and its fresh weight determined. The two diameter classes of wood used in this study (referred to hereafter as small log and large log) bound the common sizes of slash produced during logging operations in the forests of Western Australia. Five subsamples per species of all the initial fresh woody material were randomly selected to measure their initial chemical and physical characteristics.

Experimental logs of the two diameter classes and six species were placed in each of the three study sites so that five replicates per species and diameter class (for a total of 180 logs per collection date) could be picked up at future collection dates. The samples were placed in the field in mid-February to early March 1988, just prior to the start of the wet season.

The first collection was made in the 1st week of September 1988, after about 6–7 months of exposure, at the tail end of the wet season. A second collection was made in the last week of December 1989, after about 22 months and two wet seasons of exposure. The third collection occurred in mid-December 1992, approximately 58 months and five wet seasons after the start of the experiment. At each collection time, the mass of each log collected for that time period was measured in the field (wet weight). These logs were then placed in plastic bags

Table 1. Characteristics of study sites in the major forest regions of Western Australia.

Characteristic	Gnangara	Dwellingup	Manjimup
Latitude (S)	31°46′	32°44′	34°20′
Longitude (E)	115°52′	116°08′	116°07′
Elevation (m)	50	250	260
Mean annual rainfall (mm/year)	744	1306	1055
No. of rain days	100	131	153
Mean temperature range (°C)	10.9–25.0	9.5–21.6	9.7–20.2
Soil type	Deep sands	Lateritic gravel	Red earth
Dominant forest species	*Pinus pinaster*	*Eucalyptus marginata*	*Eucalyptus diversicolor*
Treatment	Fresh clearcut	Selectively logged	5-year-old succession

Note: Climatic data are from the Bureau of Meteorology (1975).

to prevent moisture loss and returned to the laboratory. For logistical reasons, all logs were then subsampled by cutting and pooling a cross-sectional piece from the middle and end of each one (about 8 cm thick from the small log and 5 cm thick from the large log) to determine dry to wet weight ratios for converting the field weights to dry weights. These subsamples were also used to determine nutrient concentrations.

Laboratory methods

The initial density of the large logs was determined from subsamples and was calculated as the ratio of the ovendry mass (including bark) to green volume, with volume determined by the water displacement method. The subsamples of all experimental logs (initial and subsequent collections) were used to determine dry to fresh weight ratios. All subsamples were dried at 65°C to constant weight. Bark was separated from wood and each component reweighed to obtain their relative proportions. Bark and wood samples were then ground to pass through a 1.00-mm mesh screen. The ground material was digested using a nitric-perchloric acid technique (modified from Zasoski and Burau 1977). Nitrogen concentrations of the samples were determined using the micro-Kjeldahl method. Phosphorus was determined by the molybdate blue method using an autoanalyzer (Zasoski and Burau 1977). Potassium, calcium, and magnesium were determined using atomic absorption spectrophotometer methods. Nutrient analyses of samples from the first collection were done in the Department of Botany, University of Western Australia. Nutrient analyses of all the other samples were carried out commercially by a professional laboratory (CSBP Ltd., in Perth, WA, specializing in analysis of plant and soil materials). Random samples analyzed in the Department of Botany were also included in the batch analyzed by CSBP Ltd. to insure comparability of results.

Concentrations of cold water (labile and leachable compounds) and NaOH (polyphenolics: Iiyama and Wallis 1988; L. Simpson, unpublished data[2]) extractives were measured on the initial and final samples only. Cold-water extractives were determined according to the methods of American Society for Testing and Materials (1978). Removal of polyphenolic extractives was accomplished by treating the samples with 0.1 M NaOH (Bland and Menshun 1971; Iiyama and Wallis 1988; L. Simpson, unpublished data (see footnote 2)) according to the Appita standard method (Appita 1973). Although it has been suggested that the use of NaOH as an extractant may also solubilize lignin, no evidence for this has been found for eucalypt species (Iiyama and Wallis 1988; L. Simpson, personal communication). Thus we are confident that the NaOH extractives represent the total polyphenolics present in the six species.

Data analysis

The moisture content was calculated on a dry mass basis as the difference between the wet and dry mass divided by the dry mass, expressed as a percentage. Mass loss of all experimental logs over time, by species, site, and component, was calculated as the ratio of the mass at each collection date divided by the original mass, and the results expressed as a percentage. Taylor and Parkinson (1988) and Sinsabaugh et al. (1992) suggested that loss in mass from slowly decomposing substrates such as large woody material is expected to be linear in contrast with the exponential pattern typically seen for fast decomposing material such as leaf litter (Olson 1963). We tested the fit of both the linear and single exponential models to our results.

Changes in nutrient concentrations were calculated by the same method as for mass. To calculate changes in the quantity of nutrients in the experimental logs, we first estimated the amount of bark and wood present in each log by multiplying the mean mass of the logs, by species and site initially and at each collection date, by the corresponding mean bark and wood fractions. We then multiplied the mean mass of each fraction by the corresponding mean nutrient concentration to obtain an estimate of the nutrient content of each log. Finally, we expressed the change in nutrient content as the ratio of the mean nutrient content at a given time by the mean initial content, expressed as a percentage of the original remaining.

To test for significant differences in the initial chemical characteristics of the experimental logs among species, we used analysis of variance followed by Fisher's protected least significant difference test. Main effects of site, species, component, and time, and their interaction, on mass loss (as percentage of original mass remaining) and change in nutrient concentrations (as percentage of original concentration remaining) were determined in a four-way analysis of variance. Differences for all tests were considered to be significant at the 0.05 level.

Results

Initial characteristics of experimental logs

Physical characteristics

Physically, the six species were similar to each other (Table 2). Densities of the large logs of the six species varied little, from 0.4 g·cm^{-3} for *E. calophylla* to 0.5 g·cm^{-3}

[2] Simpson, L. 1985. Acid-catalysed hydrolysis of wood polysaccharides with HCl gas. B.Sc. Honours thesis, Department of Chemistry, Murdoch University, Perth, Western Australia.

Table 2. Initial physical and chemical characteristics of experimental woody debris.

Characteristic	*Allocasuarina fraseriana*	*Banksia grandis*	*Eucalyptus calophylla*	*Eucalyptus diversicolor*	*Eucalyptus marginata*	*Pinus pinaster*
Wood density ($g \cdot cm^{-3}$)*	0.44±0.00	0.49±0.00	0.40±0.01	0.47±0.01	0.50±0.00	0.43±0.01†
Bark fraction (%)						
Small wood	37.8±2.6*b*	35.9±1.2*b*	35.6±4.2*b*	24.8±1.5*c*	49.3±3.6*a*	17.8±1.7*c*
Large wood	23.2±1.6*a*	25.2±1.3*a*	25.8±1.9*a*	22.1±1.1*a*	21.3±1.3*a*	27.3±3.5*a*
Wood fraction (%)						
Small wood	62.2±2.6*b*	64.1±1.2*b*	64.4±4.2*b*	75.2±1.5*a*	50.7±3.6*c*	82.2±1.7*a*
Large wood	76.8±1.6*a*	74.8±1.3*a*	74.2±1.9*a*	77.9±1.1*a*	78.7±1.3*a*	72.7±3.5*a*
Extractives (%)‡						
Cold water						
Small bark	9.8±0.5*b*	10.3±1.6*b*	4.3±3.7*b*	10.7±1.4*b*	5.5±0.6*b*	17.7±0.2*a*
Large bark	7.0±1.5*a*	6.9±0.7*a*	5.3±0.6*a*	8.9±1.2*a*	7.6±1.2*a*	6.4±1.2*a*
Small wood	8.0±0.1*a*	7.4±0.2*a*	1.7±0.5*d*	3.5±0.6*c*	3.7±0.1*c*	5.7±0.4*b*
Large wood	6.6±0.8*ab*	6.4±0.2*ab*	2.7±1.2*c*	8.9±1.0*a*	5.9±0.7*b*	8.2±0.9*ab*
0.1 M NaOH						
Small bark	20.7±0.4*c*	21.3±1.8*c*	24.0±0.0*c*	29.4±0.0*b*	19.9±2.1*c*	42.8±0.1*a*
Large bark	21.0±1.0*bc*	15.3±1.1*d*	19.0±0.8*cd*	32.6±0.0*a*	25.4±1.2*b*	23.9±2.8*b*
Small wood	13.0±0.3*b*	15.5±0.6*a*	11.0±0.5*b*	11.3±0.5*b*	10.6±0.2*b*	10.6±1.0*b*
Large wood	22.9±0.9*a*	13.3±0.7*bc*	10.8±1.4*c*	18.4±3.2*ab*	16.3±1.8*b*	14.1±1.6*bc*
Nitrogen ($mg \cdot g^{-1}$)						
Small bark	4.89±0.32*a*	2.46±0.31*b*	2.50±0.32*b*	1.59±0.38*b*	1.86±0.43*b*	1.74±0.20*b*
Large bark	3.90±0.15*a*	0.85±0.06*e*	2.00±0.12*b*	1.54±0.07*c*	1.41±0.17*cd*	1.15±0.08*de*
Small wood	2.03±0.27*a*	0.84±0.08*c*	1.33±0.16*b*	0.86±0.06*c*	1.25±0.15*bc*	0.37±0.06*d*
Large wood	2.21±0.34*a*	0.49±0.05*b*	0.88±0.06*b*	0.70±0.11*c*	0.58±0.04*b*	0.54±0.04*b*
Phosphorus ($mg \cdot g^{-1}$)						
Small bark	0.09±0.01*c*	0.13±0.02*bc*	0.31±0.06*a*	0.11±0.01*bc*	0.26±0.09*ab*	0.14±0.02*bc*
Large bark	0.06±0.00*b*	0.05±0.00*b*	0.18±0.04*a*	0.11±0.00*ab*	0.15±0.06*ab*	0.06±0.01*b*
Small wood	0.03±0.01*b*	0.09±0.04*b*	0.25±0.07*a*	0.06±0.01*b*	0.14±0.04*b*	0.04±0.01*b*
Large wood	0.05±0.01*a*	0.05±0.01*a*	0.13±0.06*a*	0.07±0.03*a*	0.08±0.03*a*	0.06±0.01*a*
Potassium ($mg \cdot g^{-1}$)						
Small bark	5.18±1.38*a*	3.33±0.30*ab*	2.37±0.11*bc*	3.64±0.60*ab*	2.42±0.48*bc*	0.48±0.07*d*
Large bark	2.97±0.44*a*	1.40±0.23*bc*	3.36±0.43*a*	3.12±0.41*a*	1.65±0.72*b*	0.16±0.04*d*
Small wood	2.25±0.42*a*	2.12±0.17*ab*	1.18±0.20*c*	1.35±0.10*c*	1.49±0.16*bc*	0.27±0.06*d*
Large wood	1.94±0.75*ab*	1.08±0.07*bc*	2.16±0.24*a*	1.00±0.27*bc*	0.69±0.12*c*	0.46±0.09*c*
Calcium ($mg \cdot g^{-1}$)						
Small bark	12.36±1.87*a*	1.70±0.11*c*	8.70±2.12*ab*	8.00±1.84*ab*	3.94±0.93*bc*	11.30±2.21*a*
Large bark	19.23±1.56*a*	1.44±0.24*de*	8.41±1.87*b*	9.29±0.57*b*	0.81±0.36*e*	4.92±0.61*cd*
Small wood	1.41±0.23*b*	0.84±0.10*b*	1.69±0.45*a*	0.98±0.21*b*	1.05±0.31*b*	0.74±0.03*b*
Large wood	1.10±0.23*ab*	0.57±0.04*bc*	1.63±0.32*a*	1.09±0.29*a*	0.27±0.03*c*	0.92±0.09*ab*
Magnesium ($mg \cdot g^{-1}$)						
Small bark	1.71±0.25*bc*	1.78±0.15*bc*	2.47±0.39*bc*	2.92±0.39*a*	1.40±0.34*c*	2.03±0.06*b*
Large bark	1.00±0.08*c*	1.99±0.22*b*	2.42±0.36*a*	2.52±0.33*a*	0.53±0.15*c*	0.50±0.04*c*
Small wood	0.45±0.09*c*	0.31±0.03*c*	1.00±0.17*a*	0.45±0.06*c*	0.51±0.17*c*	0.82±0.10*b*
Large wood	1.02±0.27*a*	0.34±0.02*a*	0.99±0.17*a*	0.71±0.29*a*	0.24±0.02*a*	0.62±0.07*a*

Note: Means ± SE are based on five samples unless noted otherwise. Samples among species (i.e., by row) followed by different letters are significantly different by analysis of variance and Fisher's protected least significant difference test.

*Large logs only, including bark.

†Number of samples = 20.

‡Number of samples = 3.

for *E. marginata*. The fraction of bark of large logs was more or less the same for all species at approximately 21–27% of the log mass. However, the fraction of bark of small logs was generally more variable among species (18–49%) and larger than that for large logs with the exception of pine. The relatively large mass of bark (and presumably thickness) of these species is indicative of their tolerance to fire.

Extractives

Concentrations of cold-water extractives of bark and wood components from the small and large logs provided some

indication of the potential for wet season leaching (Table 2). The water soluble components in bark and wood tissue for all species were generally near or below the 10% that has been reported elsewhere for *E. diversicolor* twig material (O'Connell 1988). None of the species appeared remarkable with respect to cold-water extractives in comparison with the others, although *E. diversicolor* was mostly high and *E. calophylla* was consistently the lowest.

Concentrations of extractives soluble in 0.1 M NaOH (polyphenolic substances) were variable and high, ranging from 11 to 33%, with bark tending to have higher concentrations than wood (Table 2). Polyphenolic concentrations were particularly high in *E. marginata* and *E. diversicolor* and are in general agreement with those obtained by others (Iiyama and Wallis 1988; L. Simpson, unpublished data (see footnote 2)).

Nutrient elements

Clear species differences in initial concentrations of nutrients existed between size of logs and between bark and wood (Table 2). Concentrations of all nutrients were higher in bark than in wood and tended to be higher in small bark and wood than in large bark and wood. Values for all elements for the small wood and bark of eucalypt species are comparable to those reported for the same species by others (Hingston et al. 1979, 1989; Bell and Ward 1984; O'Connell 1988).

Significantly higher nitrogen concentrations in all components of *A. fraseriana* were obtained (Table 2), reflecting the influence of the symbiotic nitrogen-fixing *Frankia* sp. Concentrations of nitrogen in most components of the other five species were not significantly different from each other.

Phosphorus concentrations were high in all components of *E. calophylla* and most components of *E. marginata* and *E. diversicolor* (Table 2). The ability of eucalypts to sequester phosphorus was previously noted (Glossop et al. 1980). Unlike nitrogen, *A. fraseriana* generally had the lowest phosphorus concentrations in all components.

The angiosperms generally had initial potassium concentrations similar to each other in most components and were significantly higher than for *P. pinaster* except in the large wood. In contrast, concentrations of calcium were generally much higher in bark than in wood for all species with the exception of *B. grandis* and *E. marginata*. Magnesium had a tendency to show a pattern of distribution similar to calcium, with highest concentration in small and large bark.

Changes in moisture content

The moisture content of the experimental logs fluctuated according to time of collection, study site, and species. The moisture content of large logs collected from Dwellingup and Gnangara was highest after the first 6 months in the field, following the first wet season, but subsequent collections were drier at about 25% (Fig. 1). The same pattern was found for the small logs for these two sites, with moisture content ranging from 40 to 80% at the end of the first wet season and less than 10% at subsequent collection dates (data not shown). At Manjimup, the wettest site, moisture content for most species (except *A. fraseriana*) was, in general, markedly higher in the large logs of the last collection (Fig. 1). The same pattern was found for small logs, with moisture content up to 150% at the last collection date.

In summary, large logs had higher moisture content than small logs at all sites, and the experimental logs retained moisture the longest at the Manjimup site, followed generally by Dwellingup, and then Gnangara. However, the moisture content for *A. fraseriana*, *E. calophylla*, and *E. diversicolor* after 5 years of field exposure was somewhat higher at Gnangara than at Dwellingup. The moisture content for the three sites, in general, appeared to follow the expected trend: the clear-cut site at Gnangara would be the driest; the central-zone selectively cut site at Dwellingup intermediate; and the southerly Manjimup site with its closed canopy was the site with the wettest conditions for decomposition.

Mass loss

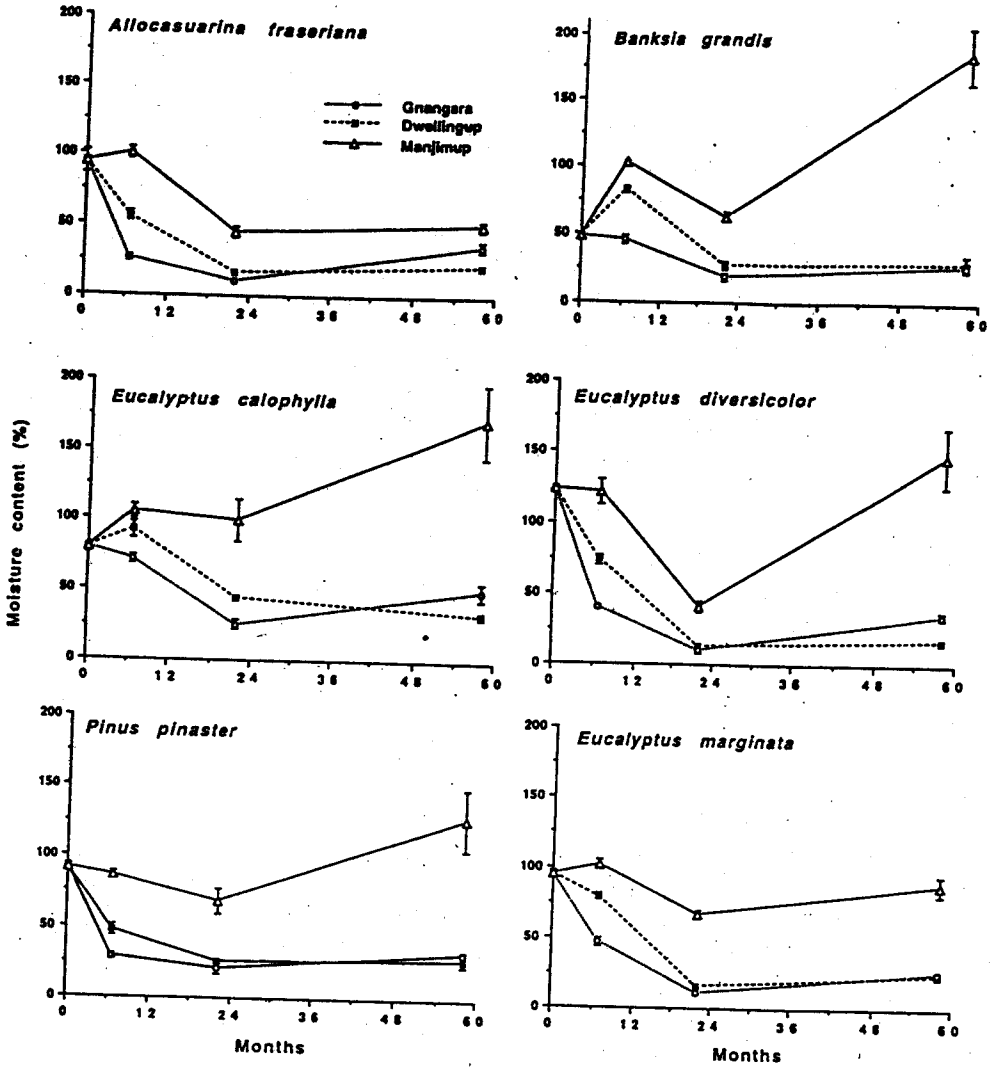
Significant main effects were observed in mass loss depending on site, species, component, and time (Table 3). Overall, after about 5 years in the field, about 60% of the original mass of woody debris of Western Australian species remained, with significant differences among sites (Table 3; Fig. 2*a*). At the end of the study, mass loss was slightly larger at Manjimup and slightly smaller at Gnangara. Significant time by site interaction effects were noted, with mass loss in earlier sampling times being greatest at Dwellingup than at either Manjimup or Gnangara.

Mass loss over time differed significantly by species (Table 3; Fig. 2*b*). *Pinus pinaster* lost the least amount of mass over the course of the study, 75% of initial mass remaining, compared with *E. calophylla* that lost the most amount of mass, 30% of the initial amount remaining (Fig. 2*b*). Mass loss for *P. pinaster* and *E. marginata* was uniformly slow throughout the total period of study. *Eucalyptus diversicolor* lost mass slowly at first, but more rapid mass loss occurred between the 2- and 5-year collections. In contrast, mass loss in *A. fraseriana* and *Banksia grandis* were rapid at first but slowed markedly after the initial collection. Rate of mass loss in *E. calophylla* was generally constant throughout the study period. Although differences in mass loss between large and small logs were significant (Table 3), differences were only apparent for the final collection (Fig. 2*c*).

In addition to significant main effects, all interactions terms for mass loss were also significant ($p < 0.001$ for all possible interactions; data not shown). Examination of these interactive terms provided further insights on decomposition in Western Australian forests. For example, although mass loss of all logs grouped was largest at Manjimup, mass loss of small logs of *A. fraseriana*, *B. grandis*, and *E. diversicolor* was largest at Dwellingup (species × component × site interaction). Large logs of *E. calophylla* and *E. marginata* had more mass remaining at Dwellingup at the end of the study than at Gnangara (species × site interaction). Mass loss of small logs was highest for *E. marginata* at Gnangara at all collection dates (species × site).

The bark fractions of the experimental logs changed markedly in some species over time but not in others. For

Fig. 1. Mean moisture content (±1 SE) of large experimental logs of six species from three Western Australian productive forests.



example, for all the species in decreasing order of mass loss, *E. calophylla*, *E. diversicolor*, *B. grandis*, *A. fraseriana*, *E. marginata*, and *P. pinaster*, the average percentages of the bark fraction at the final to the initial collection (for all sites and size classes combined) were 80, 66, 113, 68, 63, and 87%, respectively. The relatively high percentages for several species indicate that mass loss in bark was not markedly faster than in the wood. The increase in the bark fraction at the final collection for *Banksia* suggests that mass loss of wood of this species was faster than the bark.

Using least squares regression analysis, we found that the exponential model generally fit the data on percent mass remaining over time better than the linear model, as indicated by the coefficients of determination (Table 4). Decomposition coefficients ranged from 0.049 year^{-1} for *P. pinaster*, the slowest decomposer, to 0.215 year^{-1} for *E. calophylla*, the fastest decomposer. These k's translate into half-lives of about 3 to 14 years (Table 4). Laboratory tests to measure decay resistance of wood found that *E. marginata* was considerably more decay resistant than either *E. diversicolor* or *E. calophylla* (Da Costa 1979), a trend that was confirmed by the results of our study (Table 4).

Changes in nutrient concentration and content

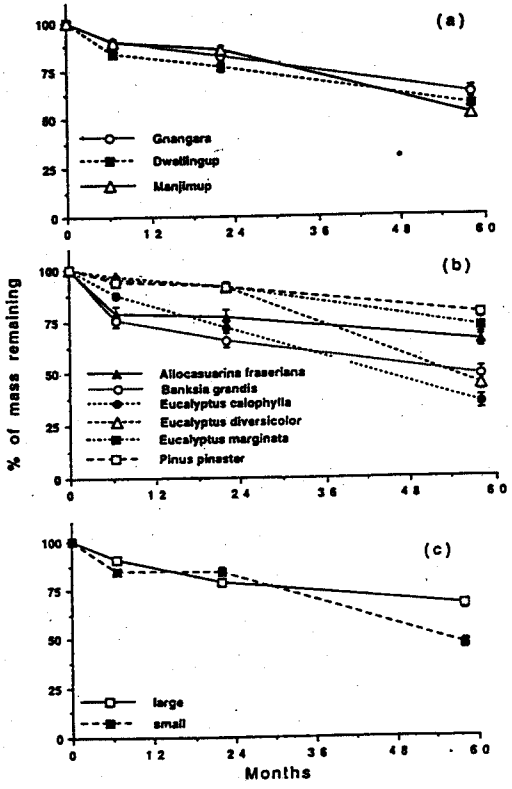
Concentration

Significant increases in nitrogen concentration in the experimental logs over time were recorded at all sites for all

Table 3. *F*-statistic and probability of significant difference by analysis of variance for the main effects on mass loss and nutrient elements in decomposing experimental logs in Western Australian production forests.

	Species		Site		Component		Time	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Mass loss	30.95	<0.000	12.49	<0.000	15.01	<0.000	638.19	<0.000
Nitrogen	4.15	<0.001	8.02	<0.000	5.24	<0:001	69.61	<0.000
Phosphorus	11.92	<0.000	1.75	0.176	5.29	0.001	8.18	0.004
Potassium	14.39	<0.000	0.34	0.714	0.85	0.470	57.53	<0.000
Calcium	3.89	0.002	0.41	0.665	2.99	0.031	27.68	<0.000
Magnesium	1.98	0.082	0.70	0.497	6.95	<0.000	4.98	0.026

Fig. 2. Mean percent (±1 SE) of original mass remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.



species and for all components (Table 3; Fig. 3). Increases in nitrogen were less obvious at Gnangara compared with the logs at Dwellingup and Manjimup (Fig. 3*a*). Species differences were marked, with percent increases in *E. diversicolor* being more than double those in the logs of *A. fraseriana* (Fig. 3*b*). Increases in nitrogen concentration were higher in small log components than in large log components

Table 4. Decomposition coefficients (k), half-life, and coefficients of determination (r^2) for the exponential decomposition model of fraction of mass remaining (y) and time (x) for experimental logs from Western Australian production forests.

	k (year^{-1})	Half-life (years)	
Gnangara	0.091	7.6	0.99
Dwellingup	0.110	6.3	0.96
Manjimup	0.132	5.3	0.96
Allocasuarina fraseriana	0.072	9.6	0.77
Banksia grandis	0.133	5.2	0.90
Eucalyptus calophylla	0.215	3.2	0.99
Eucalyptus diversicolor	0.174	4.0	0.93
Eucalyptus marginata	0.067	10.3	0.98
Pinus pinaster	0.049	14.1	0.97
Large logs	0.078	8.9	0.94
Small logs	0.148	4.7	0.94

(Fig. 3*c*). However, there were no differences in concentrations between the bark and wood components at the final collection for either size class of wood. The pattern of increase in nitrogen concentrations by site and by component generally follows the pattern of mass loss (Figs. 2*a* and 2*c*).

Phosphorus concentration in the experimental logs was not significantly different among sites, although increases were apparent at all study sites (Table 3; Fig. 4*a*). Significant differences in phosphorus concentration were recorded among species, wood component, and time (Table 3). Species that were low initially in phosphorus, e.g., *A. fraseriana*, *B. grandis*, and *E. diversicolor*, showed marked increases in phosphorus concentration, while *E. calophylla* and *E. marginata*, the species with the highest concentrations of phosphorus initially, showed indications of phosphorus loss by the last collection (Fig. 4*b*). Phosphorus concentrations in small log components and large bark showed increases, but they remained constant in large wood (Fig. 4*c*).

Significant losses of potassium were recorded in all sites, in all species (except *P. pinaster*), and in all wood

Fig. 3. Mean percent (±1 SE) of original nitrogen concentration remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.

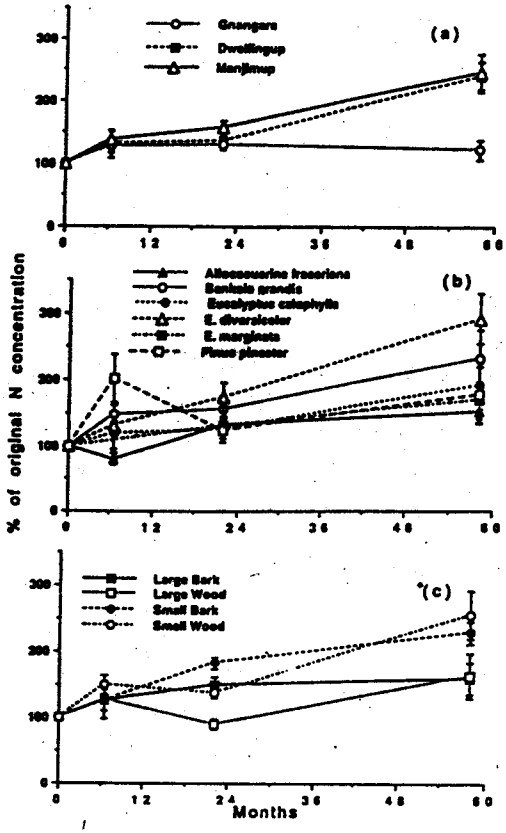
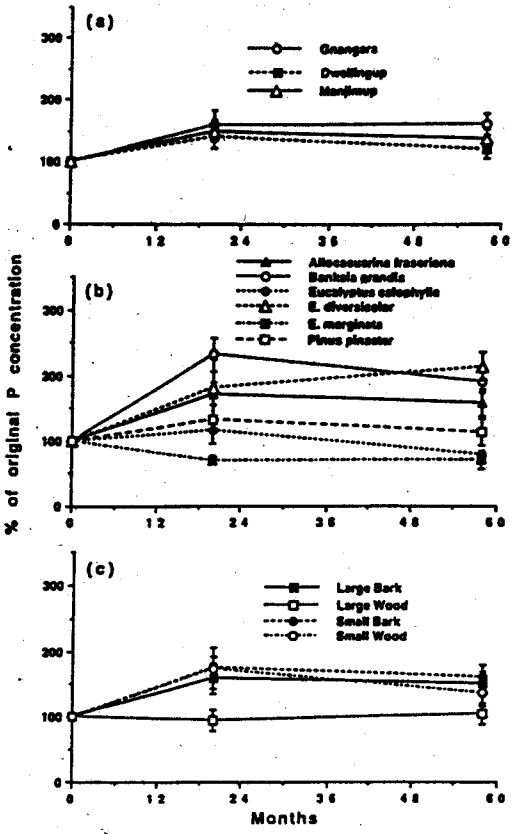


Fig. 4. Mean percent (±1 SE) of original phosphorus concentration remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.



components over the 5 years of exposure, but no significant differences were recorded among sites or components (Table 3; Fig. 5) The potassium concentrations of *P. pinaster* were extremely low initially (Table 2), which may partially explain the lack of any further concentration changes.

In contrast with potassium, calcium is quite immobile and not readily leached from plant tissues. As with the other elements, concentrations of calcium increased in all sites, species, and wood components (Table 3; Fig. 6). Differences in calcium among sites however, were not significant. Magnesium concentrations varied little over time and showed no significant differences among species or sites (Table 3; Fig. 7). Differences were significant by components, with small wood having the lowest concentration.

Content

Comparisons of nutrient content of the experimental logs among sites indicated that only nitrogen was immobilized, and then only in the moister Dwellingup and Manjimup sites (Fig. 8*a*). Generally, losses in the contents of other nutrient from the logs were in the order P ≈ Ca < Mg < K.

Species comparisons indicated that all species immobilized nitrogen (Fig. 8*b*). In contrast, only some immobilized phosphorus and calcium. For example, *A. fraseriana*, *B. grandis*, and *E. diversicolor* had up to 180% of the original content of phosphorus after 5 years in the field. All the eucalypt species had higher quantities of calcium in the logs at the end of the study than initially. All species lost potassium and magnesium. Potassium losses were particularly large, except in *P. pinaster*, the species with the lowest original levels of this nutrient. By components, immobilization of nitrogen was apparent in small bark and small wood, and immobilization of calcium apparent in small wood (Fig. 8*c*).

Changes in concentration of extractives

After 5 years in the field, the mean concentration of cold-water extractives in large bark of all species at all sites significantly decreased by between one-third to two-thirds of the initial value (except *E. diversicolor*) (Table 5). For large wood, cold-water extractives changed little over time by site. Like cold-water extractives, NaOH extractives in large bark generally showed significant decreases in all species for all sites. Large wood showed generally none

Fig. 5. Mean percent (±1 SE) of original potassium concentration remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.

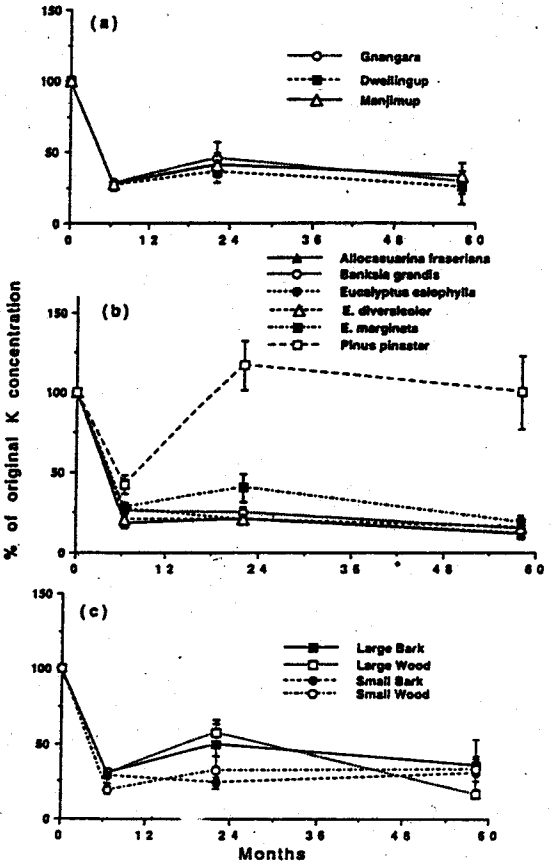
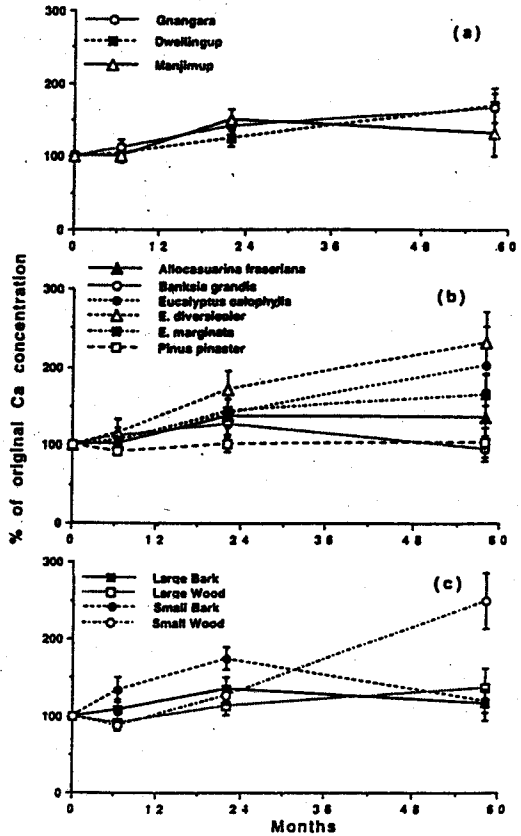


Fig. 6. Mean percent (±1 SE) of original calcium concentration remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.



to little change after 5 years. Change in both extractives was not different among sites.

Discussion

Decomposition includes leaching, microbial mineralization, and fragmentation. As most woods are high in polymeric material and low in soluble substrates (Harmon et al. 1986), there is an expectation of slow rates of mass loss and mineralization of nutrients from woody material compared with leaf litter components. As microbes convert complex polymers into simpler soluble materials, leaching may increase. Slow rates of change are also, in part, due to the low surface area to volume ratios typical of woody debris, which reduce leaching losses and invasion by microbiota relative to that found in leaf litter. However, fragmentation may increase the importance of mineralization and leaching in decomposition of woody debris because of its effect on the surface area to volume ratios.

The estimates of decomposition coefficients (k) from our study (0.049–0.215 year^{-1}) are generally within the range of those reported for wood of similar size class as ours for other temperate hardwood species (0.02–0.5 year^{-1}; Harmon et al. 1986; MacMillan 1988) and tropical hardwood species (0.006–0.13 year^{-1}; Brown 1987). Decomposition coefficients for similar diameter woody debris for northern conifer species are smaller than the values we obtained (0.011–0.033 year^{-1}; Harmon et al. 1986). However, these comparisons are somewhat misleading because most of the other studies estimated k from differences in wood density of fresh samples of wood and the density of woody debris after some known time period in the field. This approach measures loss in mass by leaching and microbial activity mostly; it generally does not account for fragmentation losses (Harmon et al. 1986). Thus, the k's from these other studies are probably underestimated. This suggests, therefore, that the decomposition rates for the species used in our study are probably low in comparison with other hardwood species.

Effects of climate on wood decomposition

Although mass losses were greatest in the wettest site (Manjimup) and least in the driest site (Gnangara), the

Fig. 7. Mean percent (±1 SE) of original magnesium concentration remaining of experimental logs by (*a*) site, (*b*) species, and (*c*) component.

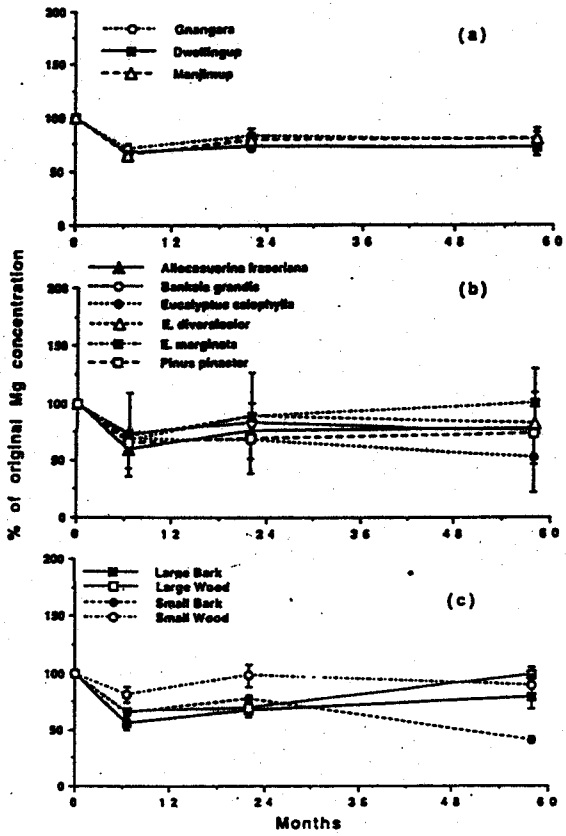
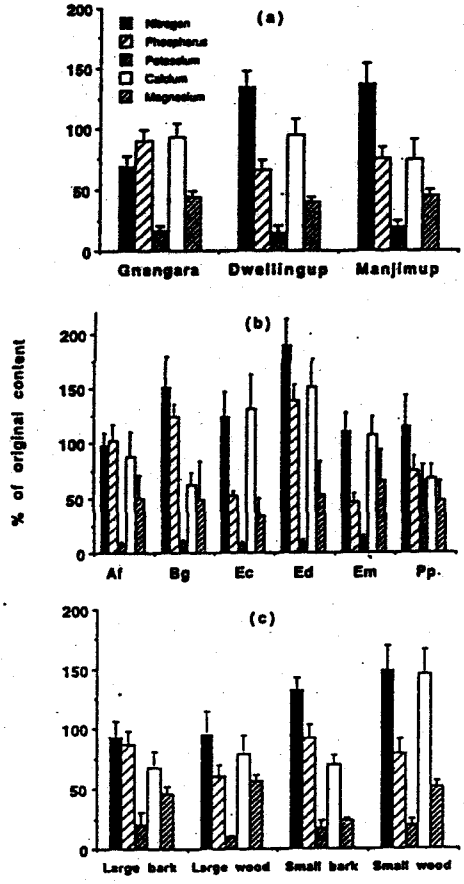


Fig. 8. Mean percent (±1 SE) of original content of nutrient elements remaining at the end of 5 years by (*a*) site, (*b*) species (Af, *Allocasuarina fraseriana*; Bg, *Banksia grandis*; Ec, *Eucalyptus calophylla*; Ed, *Eucalyptus diversicolor*; Em, *Eucalyptus marginata*; Pp, *Pinus pinaster*), and (*c*) component.



differences were relatively small (Fig. 2*a*). In the Mediterranean climate of Western Australia, decomposition may be driven by more than just precipitation and moisture availability, with temperature being another variable to consider. Temperature and moisture conditions and their influence on decomposition rates are often difficult to separate. Swift et al. (1979), in a review of the literature, found that consistent differences in decomposition rates persisted between litters of different species regardless of climatic conditions and concluded that substrate quality must be the prime determinant of decomposition. Bunnell et al. (1977) and Mikola (1960), however, claimed that conditions of temperature and moisture were the dominant controlling factors for litter decay. These authors were mainly concerned with decomposition of leaf litter that has physical characteristics markedly different from woody debris (e.g., surface area to volume ratios, chemical characteristics, etc.).

The main effects of climate on decomposition processes of woody debris appear to be threefold: (*i*) its influence on the moisture content of the logs and the corresponding effect on microbial activity, (*ii*) its influence on the temperature of the logs and corresponding effect on microbial activity, and (*iii*) its influence on leaching rates. Small differences in mass loss among the sites are probably caused by the fact that each site had different climatic variables limiting decomposition at different times of the year. All sites have sufficient moisture during the winter wet months, but temperature regimes vary. The winter temperature regimes for the sites are warmest at Gnangara, coolest at Manjimup, and Dwellingup is in between. For example, the Gnangara site was generally warmer than the other two sites not only because it is further north and at a lower elevation (Table 1) but also because there was no canopy and the logs would warm quickly on sunny winter days. Microbial activity and thus mass loss would be largest for logs at this site during the winter months. However, in the dry summer months, the moisture content of logs is likely the limiting factor for decomposition (Fig. 1). In large logs at Gnangara and Dwellingup, the moisture content

Table 5. Mean (%, ± 1 SE) concentrations of cold water and 0.1 M NaOH soluble extractives for the initial and final (5 years in field) samples of large bark and large wood from the three study sites.

	Initial	Final		
		Gnangara	Dwellingup	Manjimup
Cold Water				
Large bark				
Allocasuarina fraseriana	7.0±1.5*a*	4.1±0.5*b*	4.1±0.5*b*	4.1±0.3*b*
Banksia grandis	6.9±0.7*a*	2.1±0.4*b*	2.7±0.2*b*	2.9±0.9*b*
Eucalyptus calophylla	5.3±0.6*a*	3.3±0.6*b*	3.6±0.1*b*	2.8±0.5*b*
E. diversicolor	8.9±1.2*a*	7.5±1.3*a*	4.9±0.1*a*	8.0±0.7*a*
E. marginata	7.6±1.2*a*	3.9±0.6*b*	3.4±0.4*b*	4.0±0.4*b*
Pinus pinaster	6.4±1.2*a*	4.2±0.4*b*	4.4±0.4*b*	3.7±0.1*b*
Large wood				
Allocasuarina fraseriana	6.6±0.8*a*	4.6±0.1*b*	5.1±0.3*ab*	4.2±0.1*b*
Banksia grandis	6.4±0.2*a*	4.6±0.7*a*	4.6±0.3*a*	6.5±1.3*a*
Eucalyptus calophylla	2.6±1.2*b*	5.0±0.5*a*	6.2±0.1*a*	4.0±0.4*ab*
E. diversicolor	8.9±1.0*a*	5.4±1.0*b*	4.7±0.6*b*	6.6±0.8*ab*
E. marginata	5.9±0.7*a*	3.5±0.0*b*	3.6±0.2*b*	5.0±0.1*ab*
Pinus pinaster	8.2±0.9*a*	4.6±0.4*a*	7.4±0.8*a*	5.8±1.2*a*
NaOH				
Large bark				
Allocasuarina fraseriana	21.0±1.0*a*	14.7±0.8*b*	13.0±1.4*bc*	10.6±0.9*c*
Banksia grandis	15.3±1.1*a*	9.9±0.4*c*	6.7±0.8*d*	12.3±0.3*b*
Eucalyptus calophylla	19.0±0.8*a*	20.0±0.9*a*	15.0±2.3*ab*	13.3±0.2*b*
E. diversicolor	32.6±0.0*a*	23.6±0.6*b*	22.2±2.1*bc*	16.6±2.7*c*
E. marginata	25.4±1.2*a*	10.7±0.5*b*	22.2±2.1*a*	13.3±1.3*b*
Pinus pinaster	23.9±2.8*a*	10.4±1.0*b*	13.5±1.7*b*	11.4±2.3*b*
Large wood				
Allocasuarina fraseriana	23.0±0.9*a*	12.3±1.8*c*	16.2±0.4*b*	11.4±0.4*c*
Banksia grandis	13.3±0.7*a*	18.2±2.4*a*	16.2±2.2*a*	15.8±3.9*a*
Eucalyptus calophylla	10.8±1.4*a*	14.2±1.8*a*	14.5±0.5*a*	9.6±1.4*a*
E. diversicolor	18.4±3.2*a*	18.9±2.3*a*	10.4±1.0*b*	15.0±0.7*b*
E. marginata	16.3±1.8*a*	10.4±0.9*b*	10.4±1.0*b*	13.6±0.4*ab*
Pinus pinaster	14.1±1.6*ab*	4.6±1.0*c*	16.3±2.3*a*	9.7±1.1*bc*

Note: Values followed by different letters within a species are different by analysis of variance and Fisher's protected least significant difference test.

in midsummer, when temperatures are warmer, was close to the minimum for microbial activity (30–100% of dry weight; Kaarik 1974; Flanagan and Bunnell 1976; Griffin 1977), and mass loss would be small. At Manjimup, the relatively high moisture content of the logs well into the summer coupled with warm temperatures would result in a larger mass loss during this time of the year.

Effects of substrate quality on wood decomposition

We demonstrated that initial substrate quality differed among species and components, with bark generally having higher nutrient and extractive concentrations than wood (Table 2). We also demonstrated that mass loss was significantly different among species. The six species could be divided into two groups: relatively fast decomposers, i.e., *E. calophylla*, *E. diversicolor*, and *Banksia grandis*, and the relatively slow decomposers, i.e., *A. fraseriana*, *E. marginata*, and *P. pinaster*. Initial nitrogen concentrations, as well as lignin, in wood were purported to influence its rate of decomposition (Melillo et al. 1982; Harmon et al. 1986). Results from our study do not support this trend. For example, one of the slowest decomposers, *A. fraseriana*, had the highest nitrogen concentrations in all components (Table 2). However, *E. calophylla*, the fastest decomposer, had the next highest nitrogen concentrations in all components. No general pattern between decomposition and nitrogen concentration was exhibited by the other species.

Trends in mass loss over the course of the experiment did not seem to be explained by the initial concentrations of the other elements. However, concentrations of phosphorus were the highest in *E. calophylla* and *E. diversicolor*, the two species showing the greatest mass loss, and lowest in *P. pinaster* and *A. fraseriana*, two of the three slowest decomposers.

Polyphenolic substances in wood can influence decomposition rates because many of these substances are toxic to fungi and invertebrates (Bultman and Southwell 1976; Findlay 1985). However, the role of extractives in influencing decomposition rates of wood is complex (Scheffer and Cowling 1966; Harmon et al. 1986) because not all extractives inhibit microbial activity and their concentrations change over time. The extractives of interest here are mostly those soluble in NaOH, or the polyphenolics. Once again, there appeared to be no trend between concentrations of NaOH extractives and rates of mass loss (Table 2 and Fig. 2). Furthermore, the highest initial extractive concentrations were found in the bark of all species, the component that exhibited the greatest changes in nutrients (Figs. 3–8), and in most cases mass loss (see above). Furthermore, all extractives in small and large bark generally decreased by the end of the study period; however, the amount of decrease was not related to the rate of mass loss of the species.

Clearly, concentrations of polyphenolic substances alone do not explain differences in decomposition rates. Extractives that inhibit decay are often in small concentrations in the wood (Scheffer and Cowling 1966). We suspect that particular extractives are responsible for the slow rate of decomposition of the slower decomposers, but until further work on identifying the likely candidate(s) is accomplished, we cannot be certain at this time.

Effects of size class on wood decomposition

Many studies of wood decomposition found an inverse relationship between decomposition rate and diameter of debris (Harris et al. 1972; Gosz et al. 1973; Fogel and Cromack 1977; Lambert et al. 1980; Abbott and Crossley 1982; Foster and Lang 1982). However, there were others in which this trend was not clear (Graham 1982; Harmon 1982; MacMillan 1988). Efforts to explain the relationship (or lack of) between decomposition and size have not been very successful (Harmon et al. 1986). Results from our study support the inverse correlation between decomposition and size (Figs. 2*c*, 8*c*). We believe that the differences in decomposition rates between small and large logs is caused by a combination of the wetting–drying regimes (large logs are moister for a longer time than small logs), different nutrient concentrations (small logs are more nutrient rich than large logs), and surface area to volume considerations (larger surface area to volume ratios in small logs than large logs).

Role of woody debris in forests of Western Australia

The relatively slow rates of wood decomposition, even for small diameter branches, that we found in this study for important forest species of Western Australia suggest the relatively low importance of this resource as a supply of nutrients to the ecosystem. The actual role of woody debris in nutrient cycling depends, of course, of the input rate as well, which at this time has not been measured for these forests in Western Australia. The slow rates of decomposition, however, suggest that woody debris may be important to other biogeochemical cycles such as carbon. The slow decomposition rates mean that woody debris serves as a carbon sink for up to many decades.

Another potentially significant role of large woody debris in these Western Australian forests is that it maintains a favorable moisture balance well into the dry season, providing a refuge for the decomposer community and extending its activity for a longer time period. Thus the presence of large, moist logs has the potential to enhance and (or) maintain biodiversity of organisms associated with the decomposer food web in these forests when other organisms become dormant in the extended dry season.

Fires are an important factor in the natural forests of Western Australia and are important for nutrient cycling (Raison 1980; Bell et al. 1989). In fact, controlled burning is used extensively in the management of these forests, mainly to reduce fuel loads and also to control a root pathogen (*Phytophthora cinnamomi*) in the *E. marginata* forest. In the natural forests, fire has a relatively long return interval of >20 years for the *E. marginata* forest and >50 years for the *E. diversicolor* forest (Bell et al. 1989). Therefore, larger woody debris in these forests is likely to have sufficient moisture content at these return intervals that it will not readily burn and will still serve as a pool or sink of nutrient and carbon, and in the dry season, a potential moisture pool for fine roots as well as a refuge for the decomposer community.

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