

Research Article

Leaf Litter Decomposition and Nutrient Dynamics in Woodland and Wetland Conditions along a Forest to Wetland Hillslope

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Leaf litters of jarrah (*Eucalyptus marginata* Donn ex Sm.) and banksia (*Banksia menziesii* R. Br.) were decomposed at woodland and wetland conditions for two years to test site influence on the rates of decomposition. Weight loss was rapid in early rains but slowed substantially in the following months, resulting in 2/3 to 1/2 weights remaining after two years of field exposure. Litter weight loss was well described by a two-substrate quality decay model ($R^2 = 0.97 - 0.99$), and the half-lives were 2.6–3.2 weeks (labile fraction) and 6.4–6.9 years (recalcitrant fraction) for jarrah, and 1.0–1.7 weeks (labile) and 6.6–9.9 years (recalcitrant) for banksia. The nutrient mobility was $K \approx Mg \approx S > Ca > P$, and the losses of K, Mg and S were correlated with the weight loss of litter ($R^2 = 0.77 - 0.94$, $P < 0.03$). P mass increased by 129% in jarrah litter and 174% in banksia litter in the woodland site, suggesting woodland with tree cover provided a better habitat for microbial biomass than non-inundated wetland, hence a notable P conservation in the decomposing litter.

1. Introduction

Plant litter from fringing vegetation is a primary energy and nutrient source for wetland ecosystems [1–3]. Terrestrial litter also serves as a nutrient source for downstream waters via direct litterfall, transport of litter, or litter-derived nutrients via wind or runoff and by seepage [1, 4, 5]. Nutrient turnover from plant litter usually proceeds in two phases, an initial rapid phase via leaching, followed by structural disintegration and decomposition, primarily due to fungal and bacterial activity [2, 6]. Processes such as animal grazing and mesofauna activities may contribute to the decomposition, but studies showed the role of mesofauna in mineralisation of nutrients to be small [7, 8]. Apart from its time dependency, litter decomposition behaviour is controlled by litter structure and its chemical composition [9–11] and site microclimate conditions, especially those associated with microbial abundance and activity [12, 13].

Wetlands of the Swan Coastal Plain, south-western Australia, usually have catchments with significant areas of vegetation cover, primarily woodland and native forest. The most notable environmental factors operating on a wetland catchment are probably those associated with seasonal

drying and reflooding in the wetland itself, and the shift from wet (low lying) to comparatively dry upland conditions as one approaches the elevated forested area. Previous studies suggest that seasonal inundation may accelerate litter decomposition and nutrient release [14–16]. It is however not known how terrestrial litter would decompose in response to the “dry” to “wet” site conditions encountered along the catchment transect. Such information is critical not only to understanding catchment litter turnover but also for understanding the role of litter as a nutrient source for downstream waters.

This paper reports the results from a litter decomposition study in a small woodland catchment under a Mediterranean-type climate and seasonal rainfall. It forms part of an integrated study of the role of catchment litter in wetland P cycling. Results about litter leaching, soil microbial activity, soil nutrient dynamics, and P loading to the wetland during refilling have been previously reported [17–21]. In this study, leaf litter from *Eucalyptus marginata* and *Banksia menziesii*, growing in the woodland catchment, was exposed to contrasting sites on a dry to wet transect. An upland (woodland) site was used to represent the terrestrial condition and the wetland site to represent conditions along

the fringing area of the seasonal wetland. Weight loss and nutrient dynamics were studied over a two-year period, and data fitted by a double exponential decay model and assessed for rate of decomposition and nutrient mobility in relation to species difference, litter quality, and site conditions.

2. Materials and Methods

2.1. Meteorological Conditions. The region experiences a Mediterranean climate, with hot dry summers and wet, mild winters. The mean daily maximum temperature ranges from 17°C in July to 30°C in January and February. Of an average annual rainfall of about 800 mm, 90% falls in cool months from May to October, resulting in seasonal refilling and flooding of many wetlands that are otherwise dry. The wet season is followed by a period of almost no rain from November until April of the following year. Potential evaporation is high during dry months and low in wet months.

2.2. Study Area. Soils in the Swan Coastal Plain are built up by the accumulation of marine, Aeolian, and alluvial sediments and most are severely leached, infertile, and typically contain low P and organic matter [22]. Freshwater wetlands in the region are generally P limited in relation to the algal growth. Due to the poor soil P content in the region, P accumulation in wetlands has been largely attributed to human activities such as agriculture and urbanisation during the last few decades [23].

Thomsons Lake is a freshwater wetland, one of a chain of wetlands in interdunal depressions between the Bassendean and Spearwood Sand Dune systems of the Swan Coastal Plain. The lake is about 20 km from Perth and 5 km from the ocean and is surrounded by jarrah-banksia woodland catchments (Figure 1). It is highly seasonal, with the highest water level recorded at 15.51 m AHD (Australian Height Datum) and a minimum of 10.75 m [24]. The lake has often dried in summer in recent years and was dry at the beginning of this study, with most of the lakebed exposed and cracked. Surface soils on the study catchment are generally loamy sand in texture with various amounts of organic debris. The lakebed was black and oozy, composed of peaty sand with small amounts of plant debris near the surface.

2.3. Litter and Soil Collection. Litter was collected from the southern catchment before the onset of the wet season. Litterfall from jarrah (*Eucalyptus marginata* Donn ex Sm.) and banksia (*Banksia menziesii* R. Br.), common overstorey species in the region, were collected by litter trays randomly deployed on the study catchment. Leaf litter was hand sorted, thoroughly mixed, and air-dried. A portion of leaf litter was oven dried (70°C), ground to about 50 µm, and stored in a desiccator at room temperature for nutrient analysis. Litterbags were made by weighing 10 g dry weight of leaf litter into each 20 × 20 cm nylon mesh bag (2 mm mesh size). These were placed at two sites in Thomsons Lake: one at the fringing area of the lake bed (wetland), in an open area ca 10 m from the *Baumea articulata* dominated margin,

the other in an upland of the wooded southern catchment (Figure 1). The upland site was about 200 m uphill from the wetland site, and the surface litter was removed before the deployment. Surface soils (0–5 cm) were collected from the two sites by manual coring on 22 February before the onset of the wet season. Three cores were collected from a 4 m² area from each site. Samples were then air-dried and sieved (1 mm) for further analysis.

A total of 96 litterbags, comprising 48 jarrah and 48 banksia, were deployed in triplicate at the two sites. Litterbags were placed in three randomly selected quadrats (2 × 2 m each) on the upland (woodland) site, and in three random quadrats (2 × 2 m each) at the wetland site. This resulted in 8 litterbags of jarrah and 8 litterbags of banksia in each quadrat, randomly pinned to the woodland floor from which fresh litter had been removed. A nylon line connected each litterbag for easy collection. The layout and number of litterbags allowed for the comparison between the two sites (woodland and wetland), with the retrieval of 3 bags of each species at a sampling time from each site, after 6, 11, 19, 28, 39, 52, 67, and 105 weeks from setup. On each occasion, soil particles attached to the residue litter were removed using a soft brush, and the leaf litter was then dried in an air circulation oven (70°C) to constant weight. The leaf litter before exposure and after retrieval on weeks 6, 11, 19, 28, and 39 (spanning the wet winter till the next dry summer) were analysed from nutrients (K, Ca, Mg, S, and P) after milling to about 50 µm.

2.4. Model Fitting and Statistical Analysis. The double exponential decay model based on two substrate-quality fractions [25–27] was used to fit the decomposition data over the study period. The model is in the form

$$Wt = Ae^{-k_1t} + (1 - A)e^{-k_2t}, \quad (1)$$

where Wt is the percentage of weight remaining of litter at time t . A is the portion of labile material relative to the total mass, and $1 - A$ is the ratio of recalcitrant materials to the total mass, k_1 is the decomposition rate constant for the labile fraction, k_2 is the decomposition rate constant for the recalcitrant fraction, t is the time elapsed from the commencement of decomposition (days).

The model parameters, A , k_1 , and k_2 , were estimated by nonlinear regression fitting to the data using the SPSS statistics package. The goodness of fit (correlation between actual and estimated weight loss over time) was calculated as $R^2 = 1 - \text{residual sum squares/corrected sum squares}$. Half-life values of litter decomposition were calculated from the Olson equation $t_{(1/2)} = 0.693/k$ [28]. Single factor ANOVA, based on the means of triplicates, was used to assess the effects of site or species on decomposition and nutrient loss over the study period. To account for statistically significant differences, F and P values are presented in parentheses with between- and within-group degrees of freedom presented as a subscript of F .

2.5. Chemical Analysis. Soil water content, pH, organic carbon, and Colwell K were measured using the methods

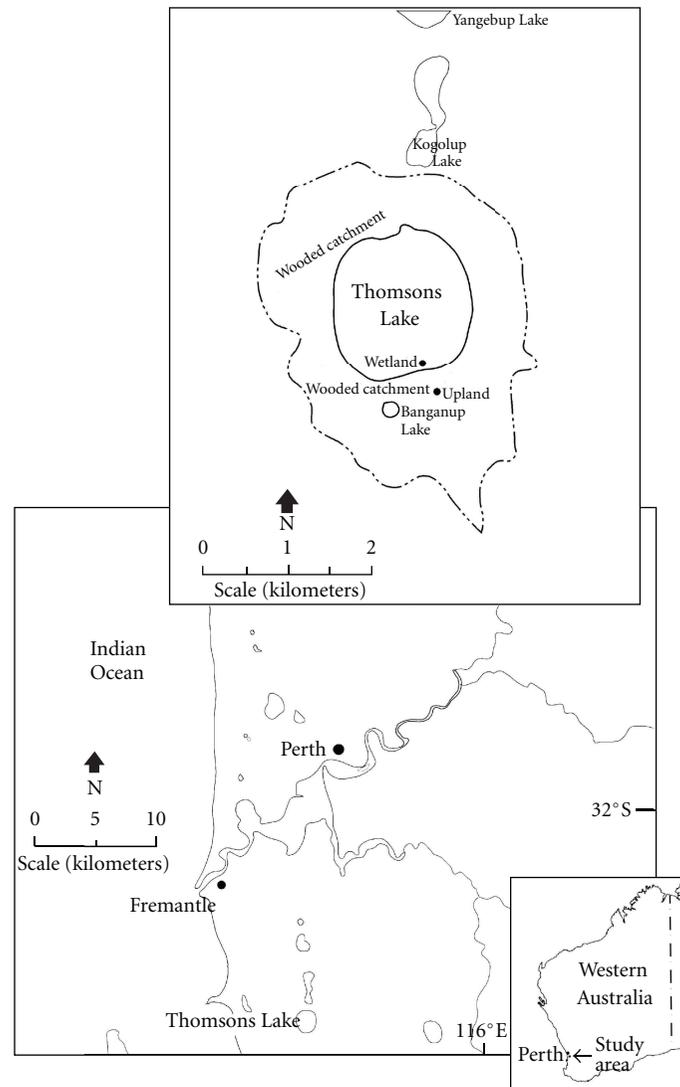


FIGURE 1: The study sites and the location of Thomsons Lake.

of Rayment and Higginson [29]. Organic carbon was determined by H_2SO_4 and dichromate oxidation and Colwell K was extracted by 0.5 M NaHCO_3 (pH 8.5) for 16 h, at a soil water ratio of 1:100. Extractable ammonium- and nitrate-N were measured simultaneously in 1 M KCl extracts using a Lachat Flow Injection Analyser. Extractable S was measured by ICP after extracting soil at 40°C for 3 hours with 0.25 M KCl [30]. Anion exchange membrane extractable P (AEM-P) was measured by shaking 1 g soil with an AEM strip (2 × 2 cm) in 50 mL distilled water (16 hours). Retained P was eluted in 0.1 N H_2SO_4 , and measured by molybdenum-blue spectrophotometry [18, 31]. Total P was measured by molybdenum-blue spectrophotometry after perchloric acid digestion. Plant elemental analysis was carried out on milled samples using inductively coupled plasma spectrometry after HNO_3 digestion. Reference plant materials with known nutrient compositions were used for analytical quality control.

3. Results

Soils in the woodland site were infertile especially in relation to phosphorus, while the wetland site had relatively higher nutrient levels (Table 1). The weight loss of the litter bags was initially rapid in response to seasonal rainfall, but gradually slowed, especially after the first 7 weeks (Figure 2). Jarrah leaves lost weight faster than banksia in both wetland and woodland sites ($F_{1,16} = 4.18$ and 7.18, $P = 0.05$ and 0.02), resulting in 14.6 and 15.6% (based on Figure 2 data) more loss over the 2-year period. There was higher weight loss at the woodland site than the wetland site (jarrah $F_{1,16} = 14.4$, $P = 0.002$; and banksia $F_{1,16} = 203$, $P < 0.001$, ANOVA). The two substrate-quality model [25] well described the decomposition behaviour of jarrah and banksia leaf litters under both site conditions and explained 97–99% of variance for the weight loss (Table 2). Both of the labile and recalcitrant fractions of litter were lost

TABLE 1: Properties of surface soils (0–5 cm) at the two sites before the onset of the rainy season. The nutrient concentrations are all in mg kg^{-1} .

	Organic C%	H ₂ O%	pH	Extractable S	Colwell K	NO ₃ -N	NH ₄ -N	Total P	AEM-P*
Woodland	2.2	0.8	5.6	27	27	3	24	154	11
Wetland	6.2	11.9	5.1	1268	525	85	34	1007	1

*AEM-P: anion exchange membrane extractable P.

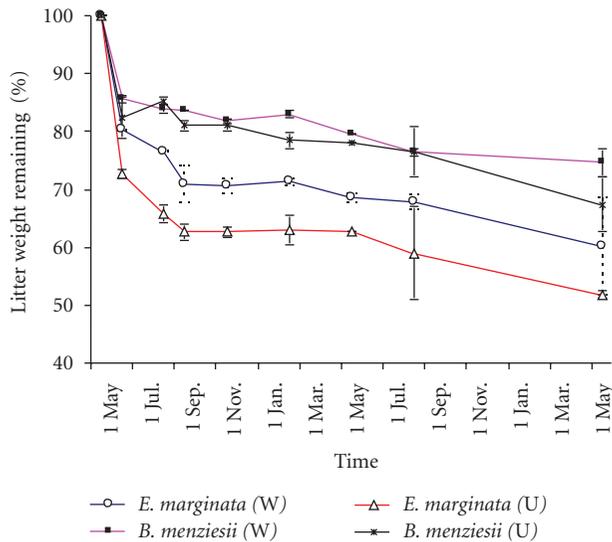


FIGURE 2: Dry weight remaining (of initial weight, mean \pm SE) from leaf litter of jarrah (*E. marginata*) and banksia (*B. menziesii*), decomposing at the upland/woodland site (U) and nonflooded wetland site (W) over two years.

more rapidly in the upland woodland site than in the wetland site, based on the model estimation.

The nutrient content of the initial litter in mesh bags was in the order $\text{Ca} > \text{Mg} > \text{S}, \text{K} > \text{P}$, and this order remained the same during the field exposure (Figure 3). Jarrah litter generally maintained higher mass of Mg, K, and S than did banksia (t -test, $P = 0.002$ – 0.05), irrespective of site conditions ($F_{1,10} = 0.62$ – 2.86 , $P = 0.12$ – 0.45). There was no between-litter difference in Ca content at both sites ($F_{1,10} = 0.27$ – 2.53 , $P = 0.14$ – 0.62).

Nutrient release was faster in the early phase of the field exposure except for P (Figure 3). The loss of Ca appeared to be stabilised after 11 weeks (May–July) in the middle of the wet season, followed by an increase in Ca mass in the litterbags (Figure 3). The concentrations of K, Mg, and S in the decomposing litter declined with the weight loss of litter, but Ca concentrations ended higher (Figure 4). The mass loss of K, Mg and S was correlated with weight loss of the leaves ($R^2 = 0.77$ – 0.94 , $P < 0.03$ – 0.001). There were close correlations between the mass losses of K, Mg, and S during decomposition ($R^2 = 0.72$ – 0.94 , $P = 0.03$ – 0.001).

Accumulation of P in the decomposing litter typically occurred after 3 months in the field (late September onwards), when rainfall was less intense than in previous months and the temperature was higher. Compared with the

initial P, there was a 129% increase in P mass in jarrah litter and 174% in banksia litter, in the woodland site (Table 3). In the wetland site, however, there was less change of P in the litter during field exposure (Table 3; Figure 5).

4. Discussion

4.1. The Predicted Leaf Decomposition Rate. There were few previous studies on the decomposition of jarrah and banksia leaf litter in the region. Jarrah (*E. marginata*) leaf litter was reported to have a half-life of 260–340 days in stream conditions [32] and to be more resistant than the river red gum (*Eucalyptus camaldulensis*) in the floodplain forest [16]. The half-life of the labile fraction for the leaf litter studied here was 2.6–3.2 weeks (*E. marginata*) and 1.0–1.7 weeks (*B. menziesii*) in two site conditions. The recalcitrant fraction had a much longer half-life, ranging between 6.4–6.9 years (jarrah) and 6.6–9.9 years (banksia). These parameters are comparable with those reported by O’Connell and Mendham [33] in a recent study on decomposition (2 mm mesh) of *E. marginata* leaf litter, in a location ca. 30 km east from our study site. Using the same decay model, they predicted the half-life of the leaf litter to be 5 weeks (labile fraction) and 5 years (recalcitrant fraction). Fertilizer application in that study was found to increase the amounts of litterfall and nutrient content of litter but did not alter decomposition parameters.

4.2. Mobility of Nutrients. The structural intactness of the leaves over the period of field exposure and the linear correlation between nutrient loss (mass) and litter weight loss appear to suggest that the release of K, Mg, and S was largely associated with the leachable and labile components. The elemental weight loss of K, Mg, and S (mean $53.5 \pm 2.5\%$ of initial mass) in our study was more rapid than the weight loss of the litter (mean $26.1 \pm 4.3\%$ of initial weight), suggesting that the leachable and labile materials had higher K, Mg, and S content per unit mass, and/or the recalcitrant fractions released nutrients before their main structures were decomposed. Since K, Mg, S behaved in a similar manner ($R^2 = 0.84$ – 0.98 , and $P < 0.05$ – 0.001) and had similar cumulative percentage losses in this study, we conclude that the mobility of these elements in the leaf litter was in the order $\text{K} \approx \text{Mg} \approx \text{S} > \text{Ca} > \text{P}$.

Calcium has been found to have lower mobility than K and Mg, but it is more mobile than the macronutrients N and P [34]. Increased Ca was commonly observed during litter decomposition [35]. In this study, Ca leaching loss (Ca mass) occurred mainly over the first 6–11 weeks when rainfall was intense (Figure 3). The increased Ca in litter

TABLE 2: Parameters estimated by the two-substrate quality decay model*, describing litter weight remaining as functions of the duration of field decomposition. $t_1(1/2)$ and $t_2(1/2)$ are half-lives for the labile and recalcitrant fractions.

Litter species	Site	A (%)	k_1 year ⁻¹	k_2 year ⁻¹	$t_1(1/2)$ week	$t_2(1/2)$ week	R^2
<i>E. marginata</i>	woodland	33.10	13.8	0.11	2.6	334	0.99
<i>E. marginata</i>	wetland	24.67	11.4	0.10	3.2	360	0.99
<i>B. menziesii</i>	woodland	14.57	34.7	0.11	1.0	344	0.97
<i>B. menziesii</i>	wetland	14.54	21.5	0.07	1.7	515	0.98

*See Section 2 for model details.

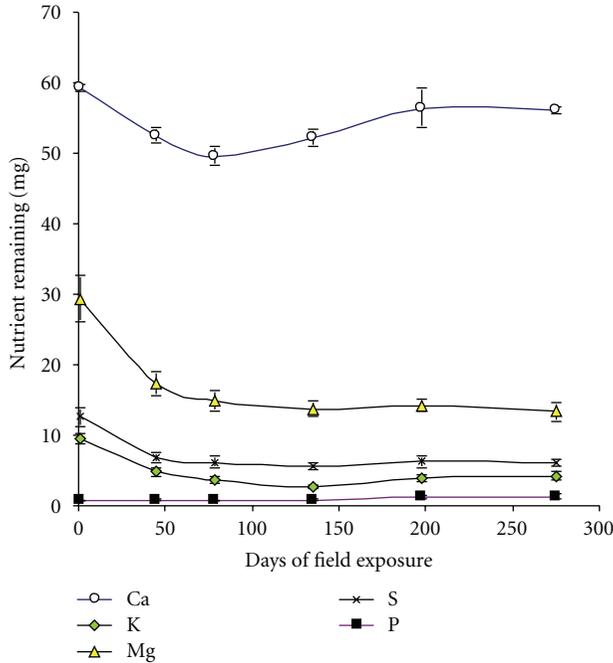


FIGURE 3: Elemental weight remaining (mean \pm SE) from the leaf litters decomposing during the field exposure, averaged for the two site conditions.

was found during the warmer and drier months. Retention or accumulation of Ca in litter has been attributed to the formation of calcium oxalate by certain fungi [36], and Reddell and Malajczuk [37] demonstrated the abundant accumulation of calcium oxalate on the surface of the ectomycorrhizal hyphae associated with jarrah forest.

Fluctuation in P concentrations but a net trend towards P accumulation has often been observed in litter decomposition studies [38–40]. O’Connell [26] and O’Connell and Mendham [33], when studying leaf litter decomposition in karri (*Eucalyptus diversicolor* F. Muell.) and jarrah forests of south-Western Australia, attributed the increased nutrients (N, P) in decaying litter to external soil sources sequestered via fungal and bacterial activities. We report here an increase of 1.3–1.7 times in P mass from leaf litter under woodland conditions (Table 3; Figure 5), which may be attributable to microbial immobilisation. Typical soil microbial biomass may have a C/N/P ratio of 60/7/1 [41], while for averaged plant litter from local wetland catchments this ratio is estimated to be 845 : 17 : 1 [17]. Thus, litter has a shortage of

N and P relative to C supply for microbial cell construction under growth conditions. The oversupply of C and limited P availability means that microbial immobilisation may dominate over mineralisation, resulting in higher P storage in microbial biomass [42]. In a parallel study on this transect, we found that soil microbial activity was associated with soil organic matter near the surface, and an overall increase in microbial biomass P (from $7.5 \mu\text{g g}^{-1}$ to $21.6 \mu\text{g g}^{-1}$ soil) over the wet season [18]. Rainfall-induced leaching and lower winter temperature (June–Sep) in the wet season appear to have limited effects of microbial immobilisation so no significant accumulation of P was evident over that period. The accumulation of P in leaf litter was evident only in later months when the likelihood of rain leaching was minimal and the higher temperature together with adequate soil moisture appeared to have revived microbial activity (Figure 5).

The litter P appears to be relatively immobile during the wet season, but this appears to be the net result of the dynamic exchange between litter and soil. The initial P leaching loss may be compensated by subsequent P sorption on soil colloidal surfaces or by microbial immobilisation. Reddell and Malajczuk [37] reported that litter on the jarrah forest floor was the main host for the formation of the white and brown ectomycorrhizae and removal of the litter layer by prescribed burning reduced these ectomycorrhizae by 90%. The microbial retention of P would depend on habitat litter and soil conditions, and be related to the nutrient availability and C/N/P ratio, and the microclimate (temperature and moisture) on the forest floor. Moreover, the accumulation of P in decomposing litter does not appear to be a short-term process; the increased P in litter has been reported to continue for 9 years in a jarrah forest site after P fertilisation, and a four-fold increase of P was found in litter decomposing for 5 years [33].

4.3. Influence of Site Conditions. The site conditions are clearly different in terms of the probability of flooding in wet seasons. The woodland site was under canopy cover, and was well shaded at most times, while the wetland site was open and more exposed to solar radiation and evaporation. There was a significant drought in the region prior to this study, and the lake was dried in the early phase of this study as it had been in the dry seasons of recent years. Although the lake refilled during the wet season (July–September), the wetland site (at the margin of the lake) was nonflooded over the whole period. This appeared to be the major difference compared to previously reported decomposition behaviours in wetland

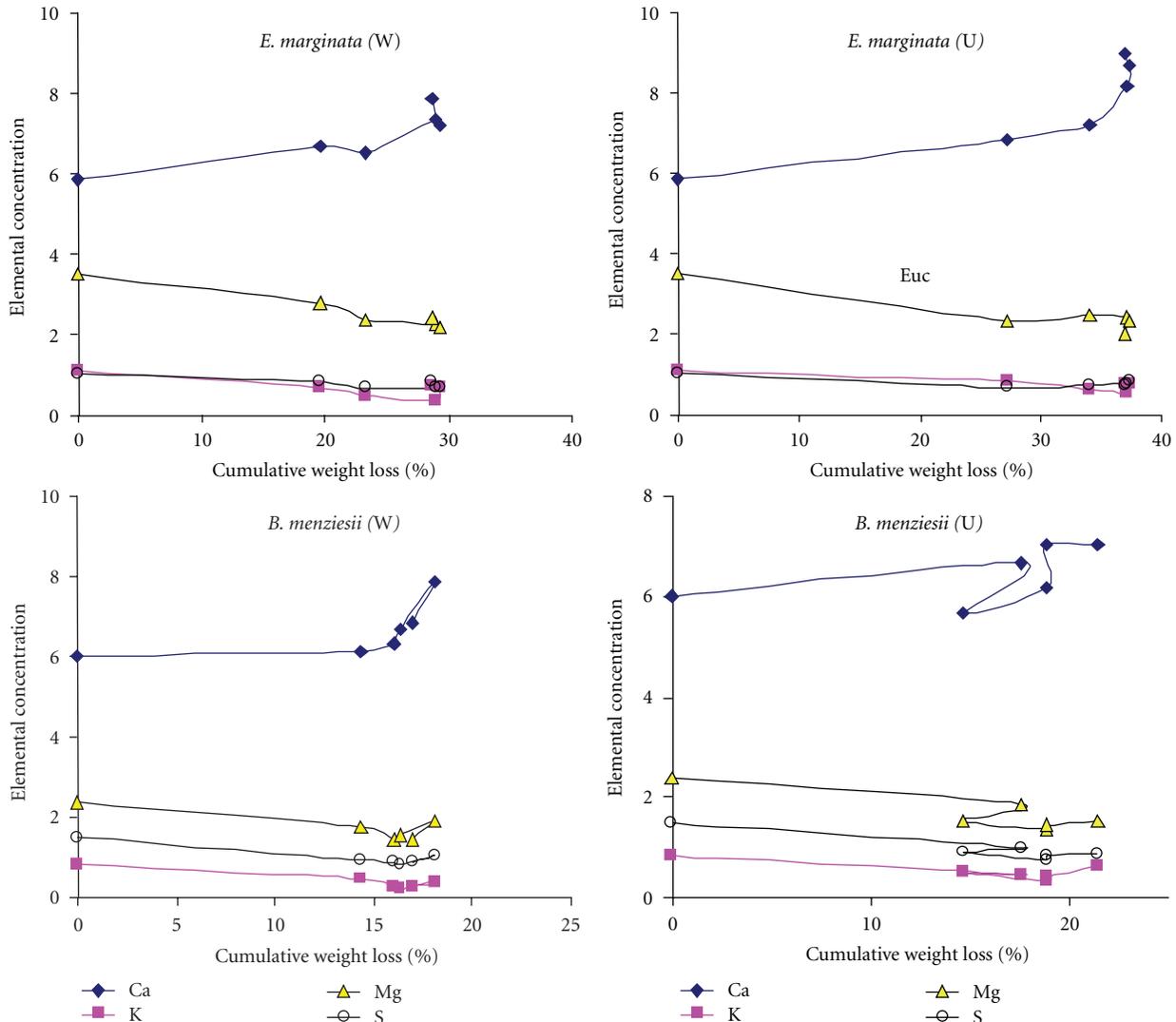


FIGURE 4: Changes in total P mass (mg) during decomposition at the upland/woodland (U) and wetland (W) sites. See Table 3 for total loss or accumulation.

conditions, which typically involve a period of inundation and faster decomposition than in noninundated conditions [14, 16, 43]. Overall, our results suggest that the shaded and protected forest sites can provide a better microclimate and microbial habitat for litter decomposition, compared to the exposed fringing wetland area. In the absence of flooding, factors such as microbial habitat condition and species difference (e.g., *E. marginata* versus *B. menziesii*) may then become primarily important in determining litter decomposition behaviour.

5. Conclusion

Decomposing leaf litter from jarrah and banksia generally followed a two-substrate quality decay model, involving rapid weight loss in the early phase followed by orders of magnitude slowing of the rate for recalcitrant materials. The order for mobility of litter nutrients can be expressed as

TABLE 3: The loss (%) of nutrients (Ca, Mg, K, S, and P) from litter at the two site conditions compared with the litter weight loss (%) over the first 275 days from wet winter (May) to next summer (February). Negative values indicate an accumulation of the nutrient.

	<i>E. marginata</i>		<i>B. menziesii</i>	
	Wetland	Woodland	Wetland	Woodland
Litter	28.7	37	17	21.5
Ca	4.3	2.8	5.5	8.4
Mg	50.4	64.3	50.3	50.2
K	51.0	55.7	74.3	40.3
S	44.8	55.3	51.5	54.1
P	4.4	-129.0	-15.1	-174.8

$K \approx Mg \approx S > Ca > P$. There were generally three patterns of nutrient dynamics: (1) K, Mg, and S behaved similarly,

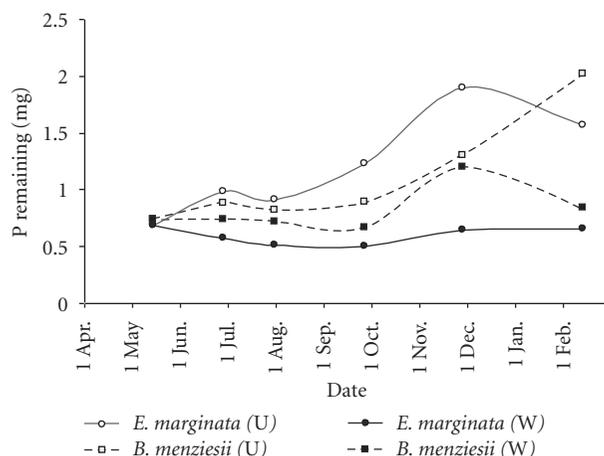


FIGURE 5: The relationship between the cumulative weight loss of leaf litter and the corresponding concentration of K, Mg, Ca, and S (mg g^{-1}) at the upland/woodland site (U) and nonflooded wetland (W) site.

and the release typically flattened out between 6–11 weeks from the commencement of the wet season; (2) Ca was released rapidly for 6–11 weeks, followed by an apparent increase in Ca mass, but overall no net accumulation; (3) net accumulation of P occurred in woodland conditions for both types of leaf litter. Overall, the between-litter difference in weight loss was evident during the 2-year field exposure, while the site influence on litter decomposition and nutrient dynamics was subtle and was not interpreted by its position in the upland-wetland transect, or its physical distance to the wetland. In a drought year when the area fringing wetland was free of temporary inundation, litter processing can be less efficient compared with the upland woodland site under tree canopy cover.

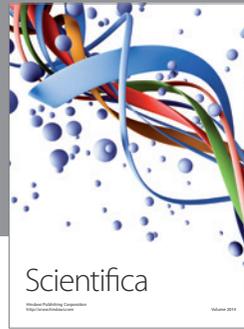
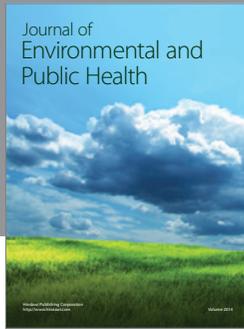
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