Biogeochemistry 4: 27–39 (1987)
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Fluxes of elements in rain passing through forest canopies in south-eastern Australia

T.G. BAKER* and P.M. ATTIWILL

School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia
* Present address: State Chemistry Laboratory, 5 Macarthur Street, East Melbourne, Victoria 3002, Australia

Key words: canopy interception, elemental fluxes, *Eucalyptus*, leaching, *Pinus radiata*, precipitation chemistry, throughfall, stemflow

Abstract. The elemental content of rainfall (bulk deposition), throughfall and stemflow was measured in *Pinus radiata* D. Don and *Eucalyptus* forests in Gippsland, Victoria. Accessions in rainfall ($mg\,m^{-2}\,year^{-1}$) averaged: organic-C 551, NO_3^--N 96, NH_4^+-N 62, total-N 303, K^+ 382, Na^+ 2250, Ca^{2+} 1170, and Mg^{2+} 678. The mean pH of rainfall was 5.9. Concentrations of all elements were greater in throughfall than in rainfall, and generally greater in stemflow than in throughfall. However, pH of pine throughfall was higher than that of rainfall, and pH of eucalypt throughfall was lower than that of rainfall. There was a net efflux of inorganic-N from pine crowns to rainfall, whilst in eucalypts there was generally net sorption of inorganic-N from rainfall. In both species organic-N was leached from the crowns and the net efflux of total-N from eucalypt crowns ($50\,mg\,m^{-2}\,year^{-1}$) averaged one-quarter of that in pines. Increases in the organic-C content of throughfall relative to rainfall in eucalypts were two to four times those in pines. Increases in the content of other elements in throughfall were comparable in pines and eucalypts and within the ranges K^+ 615–1360, Na^+ 480–1840, Ca^{2+} 123–780 and Mg^{2+} 253–993 $mg\,m^{-2}\,year^{-1}$. However, enrichment of Ca^{2+} may have been due to dust trapped in the canopies. Stemflow contributed significantly to the total amounts of elements reaching the forest floor in water.

Introduction

Elements are transferred from the atmosphere to forest ecosystems in wet and dry deposition (Miller and Miller, 1980), both of which have a component that can be attributed to impaction of particles on vegetation (Mayer and Ulrich, 1974). Elements collected in conventional, permanently open raingauges come from rain-out and wash-out from the atmosphere, sedimentation, and impaction of particles on the gauges (Miller and Miller, 1980); these sources together comprise bulk deposition (White and Turner, 1970). In forests, the amounts of elements in throughfall plus stemflow are usually greater than those in rainfall. The differences are due to many factors, including washing of impacted aerosols from plant surfaces and the net result of leaching and sorption.

There is relatively little work on the fluxes of elements, particularly N, in throughfall and stemflow in Australian forests. The aim of our study was to measure the accession of N and other selected elements in rainfall and to estimate the amounts cycled in throughfall and stemflow in *Pinus* *radiata* D. Don and *Eucalyptus* forests. Related studies on the cycling of elements in these forests include data on litterfall (Baker, 1983), litter decomposition (Baker and Attiwill, 1985a) and nutrient uptake (Baker and Attiwill, 1985b).

Materials and methods

The study area is in the central Gippsland region (146°15′E, 38°20′S) of Victoria, Australia. Mean annual rainfall is 1000 mm with a winter-spring maximum, and an average in every month of at least 50 mm. Maximum summer and winter temperatures are 40 °C and 20 °C respectively, and freezing conditions are rare. The sea is 40 km to the south.

Four pairs of *P. radiata* and *Eucalyptus* stands (matched by soil type) were chosen to represent a range of site qualities in the study area (Table 1, see Baker, 1983). The *P. radiata* and *E. regnans* F. Muell. stands were planted, and the *E. obliqua* L'Hérit. and *E. sieberi* L. Johnson stands were native. All stands were fully stocked, had uniform, closed canopies, and were within 3 km of a central location. Throughfall was measured during one year (August 1977 to July 1978) in the eight stands. Throughfall and stemflow were measured during a further year in *P. radiata* II and V and *E. obliqua* I and II. Rainfall was measured at five "open" sites in the first year and at three sites in the second year of the study. These sites were of similar altitude and were located as close as practicable (mostly within 300 m) to the stands. The sites were at least two tree heights distant from the surrounding forest and were cleared of all vertical obstructions higher than 45° from horizontal.

At each open site two raingauges (polyethylene funnels of diameter 115 mm) were mounted 1 m above the ground. Each gauge was surrounded by a baffle which included fine-wire spikes to deter birds. Gauges emptied through fine plastic mesh to polyethylene bottles which were coated with silver paint and completely enclosed by sun-shields. At one site, standard milled-edge raingauges were used to calibrate the funnel raingauges during the two years of the study. Rainfall was collected bi-monthly.

Three gauges of the same design used for rainfall were used to sample throughfall in a 0.1 ha sample plot in each stand. The sampling design was after Wilm (1946) with one gauge in a 'fixed' position and two gauges 'roving'. Analysis of covariance between roving (random sampling) and fixed gauges allowed the total variance of throughfall to be partitioned into that between sampling periods and that within sampling periods (spatial variation). Variation of the elemental content of throughfall was likewise analysed. By this method, a high precision of the estimates of annual totals can be achieved with relatively few gauges (Wilm, 1946). The gauges were mounted 0.6 m above the ground and the roving gauges were

Table 1. Description of trees at the study sites, July 1978

Stand	Age (years)	No. live trees (ha^{-1})	Basal area ($m^2 ha^{-1}$)	Dominant height (m)
P. radiata I	18	870	38	28
E. regnans	19	560	41	38
P. radiata II	22	610	42	31
E. obliqua I	70–80	380	54	38
P. radiata III	20	560	41	28
E. sieberi	60	1190	47	26
P. radiata V	18	1400	44	25
E. obliqua II	80–90	650	48	25

moved to new, randomly-located positions selected from a 1 m × 1 m grid over each plot at the beginning of each bi-monthly sampling period.

Stemflow was measured on eight trees in each of the two *P. radiata* stands and five trees in each *E. obliqua* stand. The trees were selected to span the diameter range within each 0.1 ha plot. Stemflow was collected with a spiral gutter nailed and sealed with bitumastic paint to each tree. The outside lip of the gutter was 50 mm from the outer bark to collect both stemflow and the major portion of stemdrip. Water from each tree was collected separately in a 55 l polyethylene bin. Any overflow from the bin was measured with a mechanical tipping-bucket; the design of the overflow outlet caused water to be taken from the centre of the full bin and ensured mixing of new inflow water with the water already collected. Less than 10% of the stemflow samples were from bins that had overflowed.

Since the chemical preservation of water samples in the field between collections may create difficulties for subsequent analysis, no preservatives were used in collection bottles and bins. Clean bottles were substituted at each collection and the bins were thoroughly rinsed. Algal growth was never observed. Concentrations of both NH_4^+–N and NO_3^-–N in the water samples averaged less than 0.2 $\mu g\, ml^{-1}$. Klingaman and Nelson (1976) showed that the concentration of NH_4^+–N in unpreserved water samples stored at 23 °C was constant for at least 1 week; at 4 °C the concentration was constant for up to 12 weeks. Their study included samples containing up to 10 $\mu g\, ml^{-1}$ NH_4^+–N. Over the period of our study the ratio of organic-N to inorganic-N in rainfall was 1:1 and the ratio of NO_3^-–N to NH_4^+–N was 1.5:1. In subsequent studies in south-eastern Australia (Adams and Attiwill, 1986) and in New Zealand (Baker et al., 1985) in which preservatives (H_2SO_4 and $HgCl_2$ respectively) were added to the rainwater collectors, almost identical ratios were measured. The storage time of samples in the field in our study varied from one to sixteen days, and assuming a random distribution of rainfall, the average storage time approximated one week. Mean monthly temperatures in the field during the study were in the range 10–20 °C. Thus both the evidence and the probability for major biological transformations of nitrogen in the unpreserved water samples are slight.

Water samples were measured immediately after collection for pH, filtered, measured for absorbance at 275 nm, acidified with H_2SO_4 and stored at 4 °C. Samples were then analysed for NO_2^- + NO_3^- (hereafter referred to as NO_3^-), NH_4^+, total-N, K^+, Na^+, Ca^{2+} and Mg^{2+}. Stemflow was not analysed for NO_3^- or NH_4^+ because of interferences in the methods due to high colour or high organic matter concentrations in the samples. Linear regressions between the concentrations of Walkley-Black organic-C in water and absorbance at 275 nm (prior to acidification) were developed. The relationship for rainfall, throughfall and pine stemflow (r^2 = 0.98) was significantly different ($p < 0.01$) from that for eucalypt stemflow (r^2 = 0.98). The respective slopes of the relationships were 13.6 and 11.8 $\mu g\,ml^{-1}$ of oxidizable-C per unit absorbance. NO_3^- and NH_4^+ were determined by automated colorimetric analysis, and total-N was measured by quantitative recovery of NO_3^- with a reduced-Fe pretreatment followed by Kjeldahl digestion (Nelson and Sommers, 1975). K^+ and Na^+ were determined by emission photometry and Ca^{2+} and Mg^{2+} by atomic absorption spectrophotometry (in the presence of La^{3+}). Fouled samples were obvious either from the presence of bird droppings on the funnels or from extraordinarily high concentrations of NH_4^+ and total-N and were rejected.

Results

Rainfall, throughfall and stemflow

Analyses of variance demonstrated that there were ($p < 0.05$) differences in rainfall and element content between sampling periods, and except for total-N, that there were significant yearly differences between some sites in at least one of the two years. However, differences between sites were minor; the coefficient of variation for rainfall was 6%, and for element content ranged from 4% to 15% but was typically less than 10%. Because rainfall and element content from each year of the study were comparable (within 10% of the mean) average values are presented here (Table 2). Rainfall increased with altitude and varied widely between sampling periods, from almost zero to 160 mm. The seasonal distribution of rainfall was, however, relatively even ranging from 200 mm in summer to 250 mm in spring.

The Wilm technique proved particularly suitable for the analysis of throughfall and elemental content; more than 80% of the ninety analyses of covariance (all significant $p < 0.001$) had coefficients of determination greater than 0.7, and only one had a value less than 0.4. Thus the confidence limits ($p < 0.05$) of the annual totals of throughfall and element content in each plot were typically less than 5% of the mean. As for

Table 2. Amount, pH and elemental content of rainfall (bulk deposition), throughfall and stemflow for *P. radiata* and *Eucalyptus* forests

Site/stand (altitude, m)		Amount (mm)	pH	Org-C	NO_3^-–N	NH_4^+–N	Total-N	K^+	Na^+	Ca^{2+}	Mg^{2+}
				($mg\,m^{-2}\,year^{-1}$)							
Site A (160)	Rainfall	942	5.9	577	93	54	292	386	2420	1150	707
P. radiata I	Throughfall	552	6.0	1180	125	106	417	1460	2900	1390	1080
E. regnans	Throughfall	678	5.4	1770	70	99	383	1750	2890	1580	960
Site B (180)	Rainfall[a]	892	6.0	521	86	59	295	378	2160	1190	674
P. radiata II	Throughfall[a]	448	6.2	1190	213	108	531	1180	4000	1970	1670
	Stemflow	52	5.0	462	ND	ND	40	165	583	173	205
Site B' (280)	Rainfall[a]	1028	5.9	581	93	67	305	397	2310	1100	667
E. obliqua I	Throughfall[a]	740	4.8	2990	79	54	357	1480	3620	2060	1660
	Stemflow	3.5	3.3	210	ND	ND	8.3	18	65	34	27
Site C (250)	Rainfall	980	6.0	564	113	76	325	396	2220	1440	787
P. radiata III	Throughfall	605	6.0	1200	187	125	539	1360	3920	2220	1680
E. sieberi	Throughfall	670	5.5	2010	112	70	347	950	3230	1920	1370
Site D (180)	Rainfall[a]	902	5.8	511	94	55	300	355	2150	977	554
P. radiata V	Throughfall[a]	542	6.0	1250	107	124	445	1190	2920	1100	1050
	Stemflow	57	4.9	497	ND	ND	41	176	506	144	173
E. obliqua II	Throughfall[a]	671	4.7	2180	74	57	329	970	2900	1140	910
	Stemflow	6.4	3.3	379	ND	ND	14	41	123	63	48

[a] Mean for two years
ND = Not determined

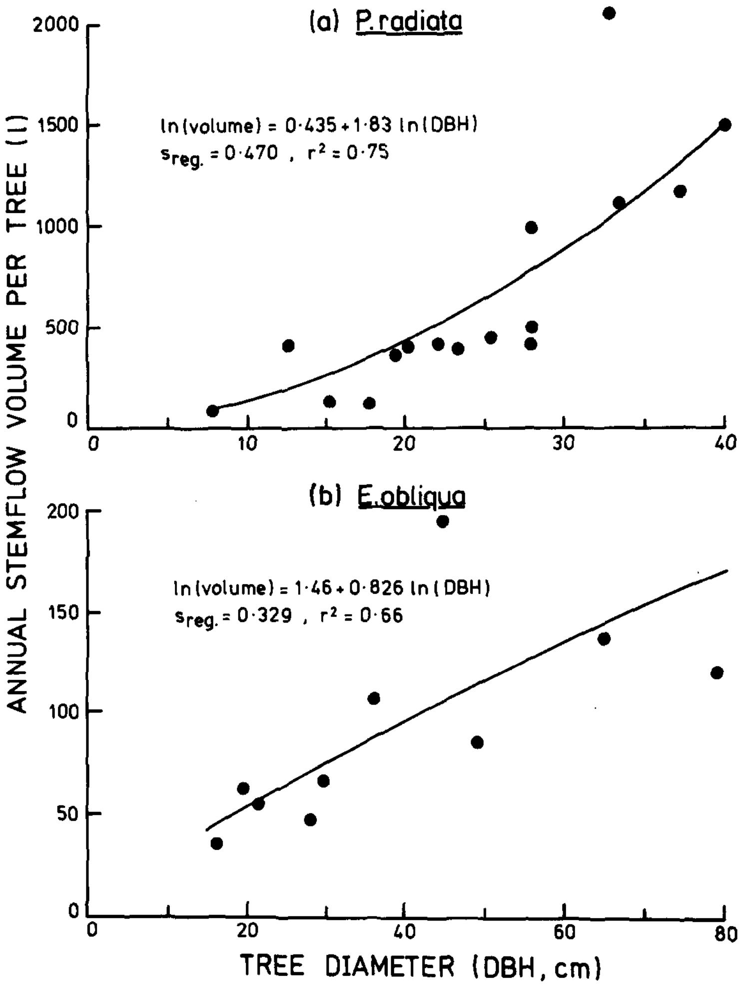

Figure 1. Relationships between the annual volume of stemflow per tree and tree diameter for forests of *Pinus radiata* and *Eucalyptus obliqua* ($s_{reg.}$ is the standard error of the regression and r^2 is the coefficient of determination).

rainfall, there was little difference in throughfall between years, and means are presented here (Table 2).

Stemflow was sampled with the intention of calculating multiple regressions of stemflow volume per tree (and elemental content) with tree diameter at breast height (DBH) and rainfall for individual sampling-periods. These regressions were to be used to estimate stemflow contributions on an areal basis. However, the data were too variable and therefore log–log regressions between the annual volume of stemflow (and elemental content) per tree and DBH for each species were calculated assuming that there would be an analogous relationship to the allometric model for

Table 3. Concentrations ($\mu g\, ml^{-1}$) of elements in annual rainfall, throughfall and stemflow

Element	Rainfall	Throughfall		Stemflow[a]	
		P. radiata	*Eucalyptus*	*P. radiata*	*E. obliqua*
Organic-C	0.58	2.0–2.7	2.6–4.0	8.8	60
NO_3^--N	0.10	0.20–0.48	0.10–0.17	ND	ND
NH_4^+-N	0.065	0.19–0.24	0.07–0.15	ND	ND
Total-N	0.32	0.76–1.19	0.48–0.57	0.74	2.3
K^+	0.40	2.2–2.6	1.4–2.6	3.1	5.8
Na^+	2.4	5.3–8.9	4.3–4.9	10	19
Ca^{2+}	1.2	2.0–4.4	1.7–2.9	2.9	9.8
Mg^{2+}	0.71	1.9–3.7	1.4–2.2	3.5	7.6

[a] Unweighted mean for two plots
ND = Not determined

canopy mass (or surface area) and DBH. Stemflow volume per tree was 6 to 16 times greater for *P. radiata* than *E. obliqua* over the DBH range 15 to 40 cm (Figure 1). This difference reflects both the greater interception of rainfall by, and the less absorbent bark of *P. radiata*. Annual stemflow and nutrient content for each plot were calculated by summing for all trees the estimated values (from DBH) using the above relationships ($r^2 = 0.65$ to 0.93, $p < 0.01$) and correcting for bias due to logarithmic transformation. By this calculation, stemflow was approximately ten times greater in *P. radiata* than in *E. obliqua* (Table 2).

Concentrations of all elements were greater in throughfall than in rainfall (Table 3). Concentrations in stemflow were usually greater than those in throughfall, with eucalypt stemflow having markedly greater concentrations than pine stemflow (Table 3). Assuming that stemflow water initially had the same composition as throughfall, a comparison of concentrations in throughfall and stemflow indicated that stembark contributed 70% and 95% of the organic-C in stemflow in *P. radiata* and *E. obliqua*.

Interception, and the change in elemental content of rainfall passing through the canopy

Throughfall was greater in eucalypts (68% to 75% of rainfall) than in pines (50% to 62% of rainfall). Stemflow averaged 6% of rainfall in *P. radiata* but less than 1% of rainfall in *E. obliqua*.

The increase of organic-C in throughfall relative to rainfall was two to three times greater in eucalypt forests than in pine forests (Table 4); however there were similar increases of organic-N, indicating differences in the nature of the organic matter (Table 4). Assuming that pH can be used to estimate hydrogen ion concentrations, there was a net efflux of H^+ from eucalypt crowns to rainfall. The efflux from *E. obliqua* was approximately ten times that from *E. regnans* or *E. sieberi* (Table 2). In contrast there was less H^+ in pine throughfall than in rainfall.

Table 4. Ranges of the differences between the element contents of throughfall and rainfall ($mg\,m^{-2}\,year^{-1}$)

Element	*P. radiata*	*Eucalyptus*
Organic-C	603–739	1190–2410
NO_3^--N	13–127	$^-$23–$^-$1[a]
NH_4^+-N	49–69	$^-$13–45
Total-N	125–236	22–91
K^+	802–1070	615–1360
Na^+	480–1840	470–1310
Ca^{2+}	123–780	163–960
Mg^{2+}	373–996	253–993

[a] Negative values indicate net sorption.

The inorganic-N content of throughfall under pines was greater than that in rainfall (Table 4). In contrast, there was generally less inorganic-N (particularly NO_3^-) in eucalypt throughfall than in rainfall; the comparatively large increase of NH_4^+ in *E. regnans* throughfall (Table 2) was probably due to the effects of a tall, well-developed and N-rich understorey (Baker 1983). The ratio of inorganic-N to organic-N in throughfall increased in pines (mean = 1.3) and decreased in eucalypts (mean = 0.9) relative to that in rainfall (mean = 1.1). The net efflux of total-N from eucalypt crowns averaged 50 $mg\,m^{-2}\,year^{-1}$ and was about one-quarter that from pine crowns. Increases in the metal cations in throughfall relative to rainfall were comparable in pines and eucalypts; there was however considerable variation within species (Table 4).

Discussion

With the exception of Adams and Attiwill (1986) no Australian study gives data for all major dissolved forms of nitrogen in rainfall. In the present study, half of the total-N in rainfall was inorganic (Table 2) which is within the range (20 to 70%) reported by Adams and Attiwill (1986) and in overseas studies (Parker, 1983). Total-N inputs in rainfall in Australia, with the exception of 6000 $mg\,m^{-2}\,year^{-1}$ reported by Westman (1978), are low relative to world data (Table 5). Furthermore, the pH of rainfall (Table 2) indicated no 'acid-rain' effect even though the study area is less than 20 km south-west of Morwell and Yallourn which are in the centre of the industrialized (including coal-fired power stations) Latrobe Valley.

There are numerous estimates of the metal cation content of rainfall with two Australian studies (Hutton and Leslie, 1958; Hingston and Gailitis, 1976) of the geographic variation of the accession of salt in Australia. Accessions of K^+, Na^+, Ca^{2+} and Mg^{2+} in the present study (Table 2) are within the ranges for Australian and world data (Parker, 1983) but such comparison means little without reference to the source of these elements. Inputs of K^+ and Na^+ are comparable to inputs reported

Table 5. Nitrogen content of rainfall for selected studies

	NO_3^--N	NH_4^+-N	Total-N
	($mg\,m^{-2}\,year^{-1}$)		
Present study	96	62	303
Australian data[a]	17–105	0–230	77–570
World data[b]	4–471	0–2200	60–2500

[a] Adams and Attiwill (1986), Drover and Barrett-Lennard (1956), Feller (1981a), Flinn et al. (1979), Probert (1976), Turner and Lambert (1983), Wetselaar and Hutton (1963).
[b] Parker (1983).

for sites in Victoria at similar distances from the sea; however, inputs of Ca^{2+} and Mg^{2+} are relatively high (Ca^{2+}: 80–1490 $mg\,m^{-2}\,year^{-1}$, Mg^{2+}: 60–900 $mg\,m^{-2}\,year^{-1}$) and are at the upper end of the range for world data (Parker, 1983). The high inputs of Ca^{2+} may be due to dust (e.g., Tamm and Troedsson, 1955) because all the raingauge sites were within 50 m of unsealed roads.

In some environments, washing of impacted aerosols can be the major component of increases in Na^+, Ca^{2+} and Mg^{2+} in throughfall relative to rainfall (e.g., Miller et al., 1976; Baker et al., 1985; also the review by Parker, 1983). Tree crowns also capture dust (e.g., Lindberg and Lovett, 1985), and in the present study the increases of Ca^{2+} in throughfall were typically higher than expected due to leaching from crowns. On the other hand, ratios of Na^+ to K^+, Ca^{2+} and Mg^{2+} are always less in throughfall than in rainfall and are evidence of leaching (Attiwill, 1966). Parker (1983) suggests that leaching contributes at least 85% of the net increase of C and K^+ in throughfall and more than 60% of N. For other elements, the proportion attributed to leaching is highly variable and in most studies it is not possible to distinguish between leaching from plant tissue and the wash-down of impacted aerosols. Leaching dominates the total above-ground movement of K^+ from plant to soil but is a minor component for N (e.g., Attiwill, 1980; Baker et al., 1985; Adams and Attiwill, 1986; also the review by Parker, 1983). Litterfall-N in the present study ranged from 1400 to 4600 $mg\,m^{-2}\,year^{-1}$ (Baker, 1983) compared with a maximum 20 to 280 $mg\,m^{-2}\,year^{-1}$ leached from the trees (Tables 2 and 4).

Table 6. Accession of N, K, Ca and Mg in rainfall and removals in stems by harvesting over one rotation

Stand	Rotation length (years)		N	K	Ca	Mg
			($g\,m^{-2}$)			
P. radiata	20	removal[a]	12	14	10	5
		accession	6	8	23	14
E. obliqua	50	removal[a]	23	14	16	8
		accession	15	19	59	34

[a] Includes stemwood and stembark. Averages from Attiwill (1980), Stewart et al. (1981) and Baker and Attiwill (1985b).

Since the water which is measured as stemflow was initially channelled through the canopy, net leaching of elements from the canopy will be underestimated if stemflow is not measured. This underestimate is 10% in pines and less than 1% in eucalypts, the same proportions as stemflow is to throughfall (Table 2). However, total movement from plant to soil may be seriously underestimated if stemflow is not measured. This degree of underestimation in pines is as much as 40% of C, 22% of total-N and 54% of Ca, and in eucalypts as much as 18% of C, 33% of total-N and 27% of Ca (Table 2).

Accessions of elements in rainfall were similar at all sites (Table 2), and the leaching of the metal cations in throughfall was similar for both pine and eucalypt canopies (Table 4). However, changes in forms of N, in pH and in organic-C in throughfall and stemflow relative to rainfall depended markedly on species (Tables 2, 3 and 4). In particular, the observations of net sorption of inorganic-N from rainfall by eucalypt crowns and of net leaching of inorganic-N from pine crowns (Table 4), represent a real difference between the two canopies since methodology and sampling were constant over all sites. Net sorption of NO_3^-, NH_4^+ and total-N by tree crowns has been commonly reported (Parker, 1983) but because individual components of the crown behave differently with respect to sorption or efflux (Reiners and Olson, 1984) interpretation of bulk throughfall is difficult. Miller and Miller (1980) observed that differential sorption of NH_4^+ by crowns of N-deficient trees and trees receiving N-fertiliser was associated with reverse fluxes of hydrogen-ion. Similarly, leaching of NH_4^+ from pine crowns in the present study may be associated with sorption of H^+ from rainfall. However, changes in the pH of eucalypt throughfall relative to rainfall were not consistently related to NH_4^+ fluxes; these changes are discussed later. Net sorption of NO_3^- from rainfall by eucalypt crowns was consistent in the present study, and distinguished eucalypts from pines (Table 4). However, sorption of NO_3^- by eucalypts is not universal since Adams and Attiwill (1986) observed leaching of NO_3^- from crowns in seven eucalypt stands.

The pH of pine throughfall was higher than that of rainfall, whilst eucalypt throughfall had a lower pH than rainfall (Table 2). This observation is the opposite of that asserted by Parker (1983) for conifer and hardwood forests remote from acid rain, but may be related to the varying concentrations of organic matter (including organic acids) in water. For example, organic-C leached from eucalypt crowns averaged 2.5 times that from pines (Table 2), and the lower pH of eucalypt stemflow corresponded to organic-C concentrations about seven times that of pine stemflow (Table 2). The lower pH of throughfall in *E. obliqua* than in the other eucalypts may also be related to organic matter (Table 2). *E. obliqua* has a fibrous water-absorbent bark continuous to the branch tips, whereas the bark of branches of *E. regnans* and *E. sieberi* is smooth and watershedding. It is therefore probable that leaching of branch-bark of *E. obliqua* contributed significantly to the organic-C content (including organic acids) of throughfall.

On average, interception of rainfall in *P. radiata* plantations (37% — Baker et al., 1985; Baker et al., 1986; Feller, 1981b; Smith, 1974; Will, 1959) is greater than that for other forest types (world conifers — 27%, world hardwoods — 20%, Parker, 1983) and is almost twice that in *Eucalyptus* (21% — Attiwill, 1966; Calvo de Anta et al., 1979; Feller, 1981b; Guthrie et al., 1978; Prebble and Stirk, 1980; Smith, 1974). Interception by eucalypts (typically evergreen) is comparable with that for world hardwoods but the data for hardwoods are biased towards deciduous forests. However, *Eucalyptus* leaves are pendulous and interception per unit of leaf area would be expected to be less than that for species with horizontally oriented leaves. In the present study there was no correlation between interception and basal area or tree density within pines or eucalypts as a group. Whilst interception may be influenced by the clear differences in canopy architecture between *P. radiata* and eucalypts, it is more likely related to foliage mass; the mass of *P. radiata* foliage (average 1.4 $kg\,m^{-2}$) was twice that of *E. obliqua* (0.7 $kg\,m^{-2}$) (Baker and Attiwill, 1985b). The interception of up to 50% of rainfall by *P. radiata* and the resultant low average moisture content of litter is an important factor limiting rates of litter decomposition (Baker and Attiwill, 1985a), particularly in those plantations established in low rainfall (600–700 mm) areas.

Accessions of nutrients to forests balance to varying extents the losses due to harvesting or other management practices (Wells and Jorgenson, 1979). In calculating nutrient budgets it is necessary to consider all inputs and outputs, but it is apparent in the present study that the accession of nutrients in rainfall over one rotation can be significant (Table 6). There is clearly a net gain of Ca and Mg during one rotation and the manager need not normally be concerned with these elements. N in rainfall, however, replaces at a maximum only 50% to 65% of removals and to maintain productivity in the long-term, inputs through fertilisers or by biological N_2-fixation will be required.

Acknowledgements

The studies presented in this paper were supported by a Commonwealth Forestry Postgraduate Research Award and University of Melbourne Caroline Kay Scholarship in Botany. We gratefully acknowledge the co-operation of A.P.M. Forests Pty. Ltd. for providing the field sites.

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