DRY MATTER, NITROGEN, AND PHOSPHORUS CONTENT OF LITTERFALL AND BRANCHFALL IN PINUS RADIATA AND EUCALYPTUS FORESTS

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ABSTRACT

The mass, nitrogen content, and phosphorus content of litterfall was estimated in five **Pinus radiata** D. Don and four **Eucalyptus** forests in Gippsland, Victoria. Litterfall in pines ranged from 258 to 386 g/m^2/year, and in eucalypts from 388 to 686 g/m^2/year. Dead foliage was the major component of litterfall in both forest types. Litterfall in eucalypts peaked in summer; in pines it peaked both in spring and in late summer to early autumn.

Concentrations of nitrogen and phosphorus in dead foliage varied markedly between seasons but were consistently lowest at times of peak fall of dead foliage. The nutrient content of litterfall in pines ranged from 1400 to 2400 mg N/m^2/year, and 97 to 230 mg P/m^2/year. In eucalypts, the corresponding ranges were 2100 to 4600 mg N/m^2/year and 94 to 200 mg P/m^2/year. In comparison with litterfall, branchfall returned only small amounts of nitrogen and phosphorus to the forest floor.

Concentrations of nitrogen in litterfall of pine and eucalypt forests were comparable; however, concentrations of phosphorus in pine litterfall were usually greater than those in eucalypt litterfall.

INTRODUCTION

The expansion of plantation forestry and increased use of fertilisers have prompted interest in the nutrition of both native and exotic forests, particularly at an ecosystem level. Litterfall is a major pathway for the biogeochemical (Switzer & Nelson 1972) cycle of nutrients in forests. There are few published studies of the transfer of nutrients by litterfall in *Pinus radiata* forests in Australia and New Zealand (e.g., Will 1959; Lamb & Florence 1975). However, for eucalypts there are data from some 23 natural forests in Australia (Baker & Attiwill 1981), mostly from recent work.

The aim of the present study was to measure the mass, nitrogen content, and phosphorus content of litterfall and branchfall in selected *P. radiata* and *Eucalyptus* forests in Gippsland, Victoria. *Eucalyptus* species were *E. regnans* F. Muell., *E. obliqua*

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L'Hérit., and *E. sieberi* L. Johnson. Five pine and four eucalypt stands growing on a range of sites were studied for 1 year to gain an appreciation of the variation between sites. Two pine-eucalypt pairs from high- and low-quality sites were studied for a further 2 years to assess annual variation in litterfall, and as part of a wider investigation of nutrient pools and transfers in these forests. The data in this paper are compared to those in other studies of litterfall in pines and eucalypts in Australia and New Zealand.

METHODS

Site Descriptions

The study area is in the central Gippsland region (146° 15'E, 38° 20'S) of Victoria, Australia. Within this region there are significant State and private reafforestation programmes on land cleared for pasture earlier in the century. Small areas of native vegetation remain. Annual rainfall is about 1000 mm with the maximum in winter-spring. On average there are at least 50 mm of rain in any month. Maximum summer temperature is about 40°C and maximum in winter about 20°C. Freezing conditions are rare.

Four pairs of 1000-m^2 sample plots were established to cover a range of site qualities in the study area. The plots (designated by the name of the dominant species and a Roman numeral) were on three recognised (Turvey & Poutsma 1980) soil types, viz Narracan clay-loam (*P. radiata* I, *E. regnans*; *P. radiata* II, *E. obliqua* I), Silver Creek loam (*P. radiata* III, *E. sieberi*), and Boolarra loam (*P. radiata* V, *E. obliqua* II). A ninth plot (*P. radiata* IV) was established to examine the "pasture effect" (Skinner & Attiwill 1981) by comparison with *P. radiata* II. However, it was determined later that *P. radiata* IV was at the boundary of three soil types and direct comparison was not valid. The Narracan clay-loam is a brown to dark brown gradational, well-structured soil (Brown podzolic soil, Stace *et al.* 1968). Silver Creek loam is a gradational, sometimes duplex, friable soil with a dark grey-brown loam surface horizon over a yellowish-brown, whole-coloured clay-loam. It is also a Brown podzolic soil. Boolarra loam has a duplex texture (structureless through the profile) with a dark-grey, fine sandy-loam resting on light-grey mottled clay. It is grouped with Stace's Grey podzolic soils.

Details of the sample plots are given in Table 1. In three of the four pairs of plots, older eucalypt stands were available for the study. However, on the highest quality sites in the study area there were no mature *E. regnans* forests remaining and therefore a relatively young plantation had to be used. *Pinus radiata* I–III were planted on abandoned farmland that had reverted to bracken and scrub, *P. radiata* IV on productive dairy pasture, and *P. radiata* V on an overmature eucalypt site. *Pinus radiata* I–IV had been variously thinned but in all plots the canopy had re-closed; *P. radiata* V was aerially topdressed with superphosphate (amount unknown) at 3 years of age. The two *E. obliqua* plots and *E. sieberi* were mature to overmature with closed canopy. In *E. regnans* natural thinning had occurred from the initial planting density of about 1400 stems/ha. There was minor past utilisation in *E. obliqua* II and *E. sieberi.*

In the pine plots, understorey vegetation was sparse but included both native species and agricultural weeds. In *P. radiata* V there was a significant amount of standing dead

TABLE 1—Site and stand details

Plot	Altitude (m)	Origin	Age* (years)	Live trees† (stems/ha)	Basal area† (m^2/ha)	Mean dominant height‡ (m)	Site index§ (m)
P. radiata I	160	planted 1960	18	870	38.2	28.5	29.5
P. radiata II	180	planted 1956	22	610	41.8	31.7	29.0
P. radiata III	240	planted 1958	20	560	41.1	29.2	28.3
P. radiata IV	180	planted 1956	22	500	36.1	29.8	27.3
P. radiata V	180	planted 1960	18	1400	43.6	25.5	26.2
E. obliqua I	280	natural	70–80	380	53.6	38.9	—
E. obliqua II	170	natural	80–90	650	48.3	25.1	—
E. regnans	160	planted 1959	19	560	41.3	38.4	38.4
E. sieberi	250	natural	60	1190	47.1	26.3	—

* At July 1978. For pines and **E. regnans**, age from planting (of 1-year-old nursery stock) is given. For naturally regenerated eucalypts, age is approximate.

† At July 1978. Basal area measured over-bark at a height of 1.3 m above-ground.

‡ At July 1979. Mean height of the 60 largest (d.b.h.o.b.) stems/ha.

§ Mean dominant height at 20 years of age (from seed). For **P. radiata,** general site index equation for Victoria used.

stems of *Acacia verniciflua* A. Cunn. *Eucalyptus obliqua* I and *E. regnans* were pure stands with dry- to wet-sclerophyll understorey species present. In *E. obliqua* I *A. verticillata* (L'Hérit.) Willd., *Cassinia aculeata* (Labill.) R. Br., *Pteridium esculentum* (Forst. f.) Nakai, and *Lepidosperma elatius* Labill. were prominent. In the *E. regnans* stand *A. dealbata* Link., *A. melanoxylon* R. Br., and *Pomaderris aspera* Sieber ex DC were also prominent. In the *E. sieberi* plot *E. obliqua* and *E. radiata* Sieber ex DC were present in the overstorey but contributed only 10% of the basal area; *A. mucronata* Willd. ex H. Wendl., *A. stricta* (Andr.) Willd., *A. verticillata,* and *A. verniciflua* dominated the understorey. In *E. obliqua* II, a few *E. radiata* and *E. baxteri* (Benth.) Maiden & Blakely trees were present. The understorey of this plot was dominated by *Gahnia radula* (R. Br.) Benth. and *Xanthorrhoea minor* R. Br.

Field Collections

Plant parts falling to the forest floor from living and dead vegetation were considered in two categories:

(1) Litterfall: All plant parts, but excluding woody material with a diameter greater than 20 mm;

(2) Branchfall: Wood and bark of branches with diameter greater than 20 mm. Female cones were included in branchfall.

Litterfall was divided into five components: (a) dead foliage – senescent eucalypt leaves or pine needles; (b) green foliage – green needles and leaves falling into litterfall traps were identifiable for at least 1 month; (c) reproductive structures – eucalypt buds and fruits, male cones and seeds of pines; (d) twigs and bark; (e) other species – all plant parts from species other than the tree species on the plot.

Five 1 × 1-m tray traps (sides 90 mm high, rim height 200 mm above ground, fine plastic mesh base) were used to sample litterfall in each of the nine plots. The statistical design was after Wilm (1946) with two of the five traps in "fixed" position and three "roving" throughout the period of the study. Litterfall was collected from the traps at approximately monthly intervals. At the beginning of each monthly sampling period the roving traps were moved to new randomly located positions selected from a 1 × 1-m grid over each plot. Litterfall was sampled for 12 months (August 1977 to July 1978) for *P. radiata* I, *P. radiata* III, *P. radiata* IV, *E. regnans,* and *E. sieberi.* For the other four plots (*P. radiata* II, *P. radiata* V, *E. obliqua* I, and *E. obliqua* II) litterfall was sampled for 36 months (August 1977 to July 1980).

Branchfall was sampled in five 5 × 5-m permanent subplots in each of eight plots (not in *P. radiata* I). Within each of these subplots all existing material with a diameter greater than 20 mm was tagged with yellow paint and thereafter new branchfall was collected at approximately yearly intervals. Branchfall was sampled for 1 year (winter 1977 to winter 1978) for *P. radiata* III, *P. radiata* IV, *E. regnans,* and *E. sieberi,* and for 3 years (winter 1977 to winter 1980) for *P. radiata* II, *P. radiata* V, *E. obliqua* I, and *E. obliqua* II.

Laboratory Analysis

Litterfall from each trap was sorted into the five components and, together with branchfall, dried at 80°C and weighed. For each plot for each month, chemical analysis of the first 24 months' collections of dead foliage was on a bulked sample from the five traps. For the last 12 months, however, dead foliage from each trap was analysed separately. For all other litterfall components, collections from the five traps on each plot were bulked for each 3 months (that is, seasonally) for chemical analysis. Dead foliage, green foliage, pine reproductive structures, and the "other species" component were subsampled and finely ground. Because of the heterogeneous nature of the woody material, samples were ground, mixed, and then subsampled. After wet ashing (H_2SO_4, H_2O_2 – Clarke & Jayman 1966) digests were analysed for nitrogen and phosphorus using a Technicon Auto Analyser II (Technicon Instruments 1977).

Statistical Analysis of Litterfall

The sampling design for litterfall was based on a system of "fixed" and "roving" traps, a method initially proposed for microclimatic variables such as throughfall (Wilm 1946). Using a random sample (roving traps) of litterfall for each sampling period, the total variance can be partitioned into that between time units and that within time units. By incorporation of one or more fixed traps into the design, an analysis of covariance enables prediction of the mean value for each sampling period with relatively high precision (compared to that obtained from five randomly located traps) for a small amount of extra work.

Litterfall masses for all components from all plots were initially analysed by the fixed and roving design of Wilm. From this analysis, the design was accepted or discarded depending upon the degree of correlation between observations taken at the fixed and roving positions. When the design was discarded, sample means and variances were calculated for each plot by assuming all five traps represented a random sample of litterfall for each sampling period. Amounts and standard errors over all sampling periods were then obtained by summation of means and variances. The amounts of nitrogen and phosphorus in litterfall components were calculated from the estimated or mean mass and the measured nutrient concentrations.

RESULTS

Wilm Analysis of Litterfall

The nine Wilm regressions for dead foliage had high r^2 values; all were greater than 0.85, most were greater than 0.90. Similarly, r^2 values for the regressions for reproductive structures of pines were very high (>0.95). The Wilm technique and analysis for these components was successful because both dead foliage and reproductive structures of pines were finely divided, and thus spatial distribution of their fall approximated a continuous variate. In contrast, the fall of the remaining components – especially twigs and bark, and green foliage – was greatly influenced by storms and was consequently spatially heterogeneous. Only 20 of the remaining 31 Wilm regressions were significant and 16 of these had low (0.18 to 0.80) r^2 values. Furthermore, for these 16 regressions up to 6% of the data set had to be rejected to exclude extreme values which otherwise would have severely distorted the relationship shown by the majority of values. To maintain consistency in the calculation of litterfall for the remaining components and to avoid rejecting data representing relatively large amounts of litterfall the Wilm analysis was discarded for these components.

Mass of Litterfall

Litterfall in pines ranged from 258 to 386 g/m^2/year (Table 2). Over 3 years the within-plot range of annual litterfall was between 9% (*P. radiata* II) and 12% (*P. radiata* V) of the means. Litterfall in eucalypts ranged from 388 to 686 g/m^2/year (Table 2). Over 3 years the within-plot range of litterfall represented 6% and 3% respectively of the means for *E. obliqua* I and *E. obliqua* II. True means of litterfall were within 2–11% ($p < 0.05$) of the estimates for both pines and eucalypts, with pine litterfall generally estimated more precisely (<7%). True means of dead foliage for both pines and eucalypts and of reproductive structures for pines (estimated from Wilm regressions) were within 6% ($p < 0.05$) of estimates, while those of twigs and bark for eucalypts (estimated by summation of monthly means) were within 13–23%.

TABLE 2—Annual litterfall (g/m^2) in pines and eucalypts (standard error of mean given in brackets)

Plot	Litterfall component					Total
	Dead foliage	Green foliage	Reproductive structures	Twigs and bark	Other species	
P. radiata I	268.9	11.5	51.1	26.8	0.0	358.3
	(7.60)	(1.46)	(0.98)	(9.10)	(0.0)	(11.99)
P. radiata II*	284.1	12.9	58.1	16.6	14.2	385.9
	(2.06)	(1.46)	(0.52)	(4.24)	(2.33)	(5.48)
P. radiata III	192.2	4.8	54.3	6.8	0.1	258.2
	(3.53)	(0.35)	(0.88)	(2.42)	(0.12)	(4.39)
P. radiata IV	268.9	5.8	51.1	3.8	4.9	334.5
	(7.60)	(0.48)	(0.98)	(0.95)	(0.82)	(7.8)
P. radiata V*	304.3	16.4	44.8	8.8	0.9	375.2
	(2.35)	(2.22)	(0.73)	(1.99)	(0.66)	(3.92)
E. obliqua I*	246.3	20.4	55.1	191.6	4.9	518.3
	(1.41)	(1.40)	(2.96)	(12.22)	(2.39)	(12.95)
E. obliqua II*	242.9	16.4	13.7	115.1	0.3	388.4
	(2.09)	(1.50)	(0.94)	(6.51)	(0.18)	(7.06)
E. regnans	246.5	12.5	3.7	302.8	120.7	686.2
	(5.20)	(3.91)	(1.15)	(33.40)	(10.21)	(35.55)
E. sieberi	257.0	9.9	32.1	236.7	1.2	536.9
	(3.83)	(2.13)	(3.39)	(27.74)	(0.36)	(28.29)

* Mean of 3 years

The relative contribution of individual components to litterfall varied between pines and eucalypts. Dead foliage was the major component of litterfall in pines (74–81%) with reproductive structures next in importance (12–21%). Twigs and bark was only a minor component (<8%) of litterfall in pines whereas in eucalypts this component contributed from 29% to 44%. Dead foliage was usually the major component of litterfall in eucalypts, contributing from 36% to 63%. Understorey was rarely present in the pine plots and consequently other species litterfall was usually negligible. However, for *P. radiata* II and *P. radiata* IV, other species contributed 3.7% and 1.5% respectively, largely from litterfall blown into these plots from one or two *E. obliqua* trees nearby. In contrast, the considerable understorey development in *E. regnans* resulted in other species contributing 18% of litterfall. For the remaining three eucalypt plots, other species litterfall was negligible (<1%) but was under-estimated to an unknown extent because the litterfall traps were often higher than the ground vegetation.

The fall of dead foliage in eucalypts varied greatly between months, with peak fall during summer (e.g., *E. obliqua* I, Fig. 1). For the two eucalypt plots studied over 3 years the timing of the peak varied from December to January but was coincident for the two plots within each year. The fall of twigs and bark also tended to be greatest in summer but there was no seasonal trend for the other components. The relatively large amount of twigs and bark in June for *E. obliqua* I (Fig. 1) was due to a storm in June 1980. The confidence intervals for monthly totals of litterfall in *E. obliqua* I

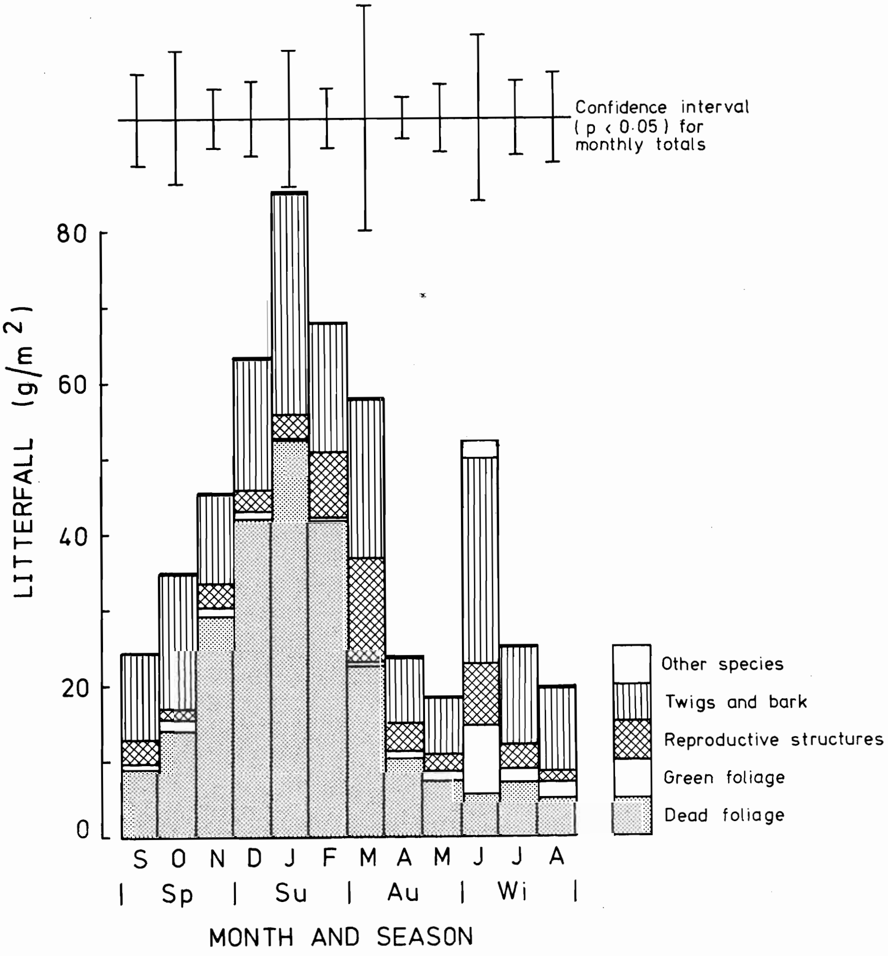

FIG. 1—Mean monthly distribution of litterfall for **E. obliqua** I.

(Fig. 1) are large because of high variability in the fall of twigs and bark. Litterfall in pines also varied greatly between months but with two major peaks (e.g., *P. radiata* II, Fig. 2). The peak in early spring was due to the fall of male cones after pollen-shed. The second peak, due to dead foliage, was broader than that observed for eucalypts and reached a maximum in late summer and early autumn. In *P. radiata* II and *P. radiata* V the peak for dead foliage was always in March. A decrease in April–May and subsequent increase in May–June (e.g., *P. radiata* II, Fig. 2) was consistent over the 3 years of the study. The other components for pines did not show any seasonal trend.

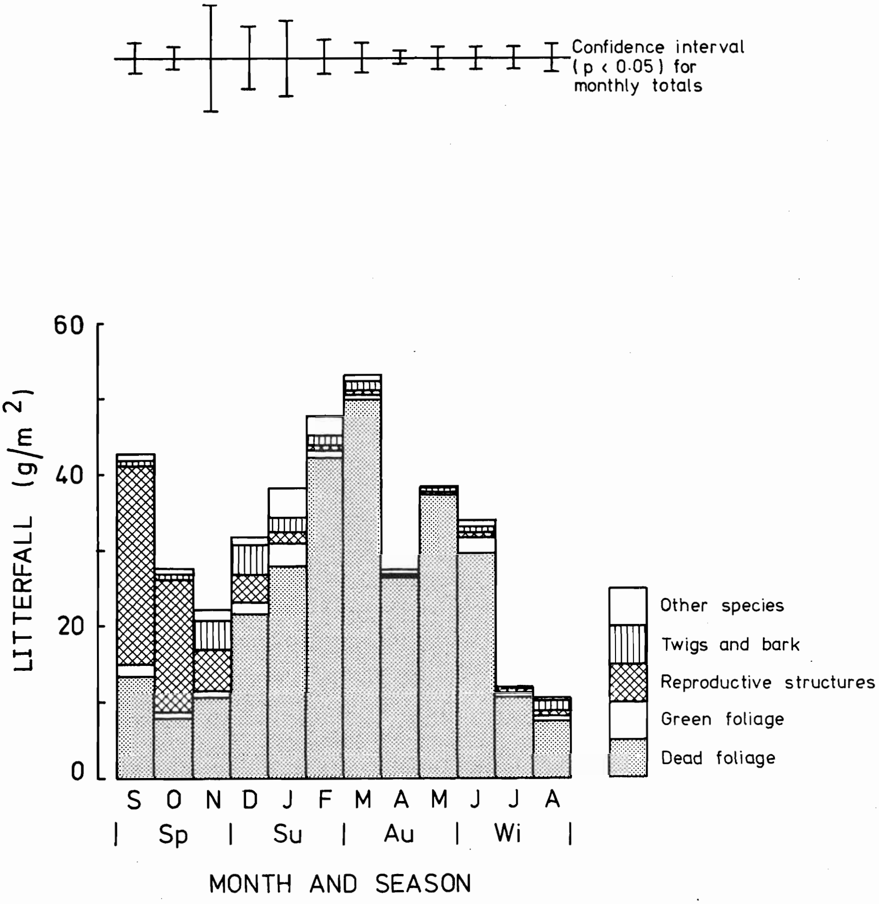

FIG. 2—Mean monthly distribution of litterfall for **P. radiata** II.

Nitrogen and Phosphorus Concentrations in Litterfall Components

For *P. radiata* II, *P. radiata* V, *E. obliqua* I, and *E. obliqua* II there were significant differences between the monthly concentrations of nitrogen and phosphorus in dead foliage (Fig. 3 and 4). The minimum monthly concentrations of nitrogen and phosphorus corresponded in time to the peak fall of dead foliage. Soil type (Narracan clay-loam or Boolarra loam) did not affect the concentration of nitrogen or phosphorus in dead foliage in the eucalypt stands but concentrations of both in dead foliage from *P. radiata* V (Boolarra loam) were significantly ($p < 0.001$) greater than for *P. radiata* II (Narracan clay-loam). Among the other litterfall components, only the concentration of nitrogen and phosphorus in reproductive structures from pines showed a seasonal trend with minima corresponding to the time of peak fall of this component. On average, the lowest concentrations of nitrogen and phosphorus were usually found in twigs and bark and the highest concentrations were found in green foliage (Table 3).

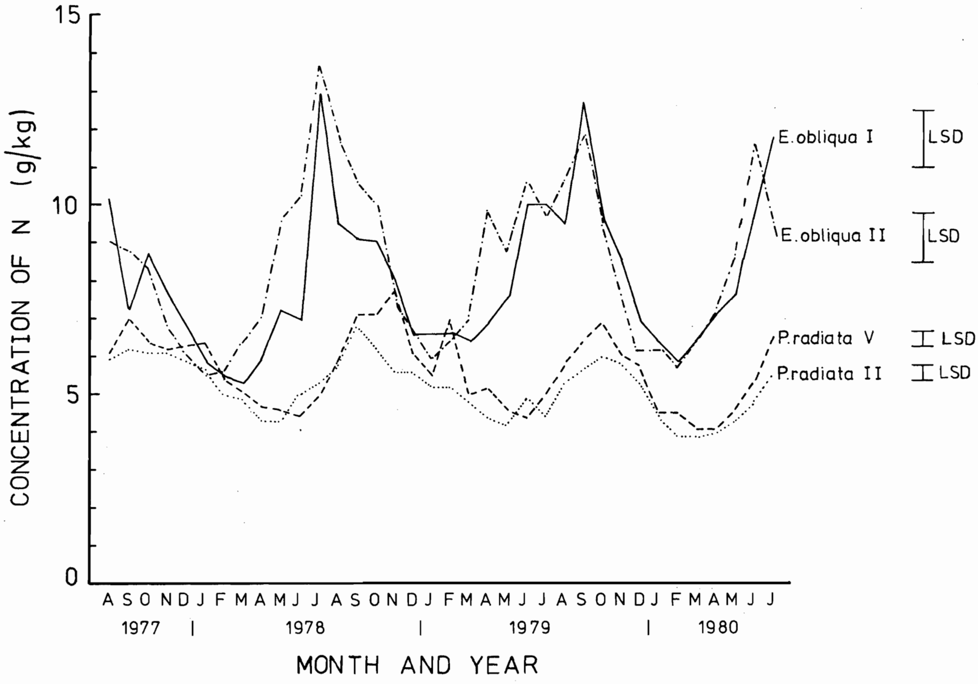

FIG. 3—Monthly variation of the concentration of nitrogen in dead foliage from **P. radiata** II, **P. radiata** V, **E. obliqua** I, and **E. obliqua** II. Least significant differences between months (LSD, $p < 0.05$) are given for each plot.

Nitrogen and Phosphorus Contents of Litterfall

The nitrogen and phosphorus content of litterfall from pines and eucalypts is given in Tables 4 and 5. Generally, the relative contributions of components to the total followed that for mass of litterfall. In the *E. regnans* plot, however, other species contributed 37% of the nitrogen content and 32% of the phosphorus content of litterfall but only 18% of the mass. In the other eucalypt plots and in the pine plots the other species contribution was small. Although concentrations of nitrogen and phosphorus in dead foliage from both pines and eucalypts were lowest at the time of peak fall, the increase in the amount of dead foliage outweighed the decrease in concentration. Consequently, nitrogen content, phosphorus content, and amount of dead foliage all peaked simultaneously in summer for eucalypts and late summer to early autumn for pines.

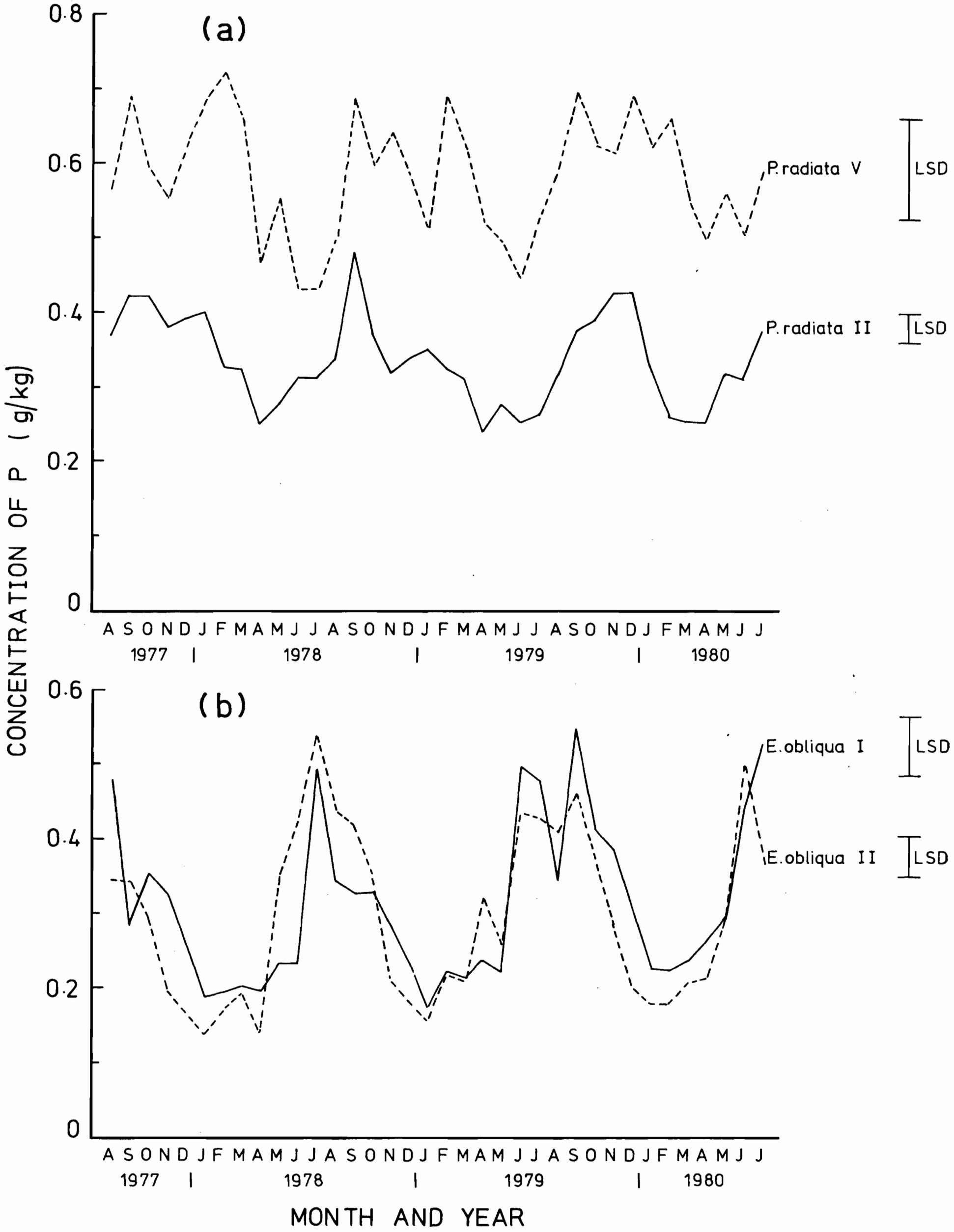

FIG. 4—Monthly variation of the concentration of phosphorus in dead foliage from (a) **P. radiata** II and **P. radiata** V, and (b) **E. obliqua** I and **E. obliqua** II. Least significant differences between months (LSD, $p < 0.05$) are given for each plot.

TABLE 3—Concentrations of nitrogen and phosphorus (g/kg) in components of annual litterfall from pines and eucalypts

Component	Pines (five plots)		Eucalypts (four plots)	
	Mean	Range	Mean	Range
Nitrogen				
Dead foliage	5.8	4.8 - 7.0	6.9	5.3 - 7.7
Green foliage	13.8	12.7 -15.7	11.7	10.0 -13.8
Reproductive structures	6.5	6.2 - 6.8	6.0	3.9 - 5.7
Twigs and bark	5.4	3.1 - 7.4	3.0	2.3 - 3.7
Other species	9.0	4.8 -17.4	9.6	5.4 -14.3
Total	6.1	5.4 - 7.1	5.7	4.0 - 6.8
Phosphorus				
Dead foliage	0.38	0.23- 0.58	0.25	0.20- 0.32
Green foliage	1.05	0.79- 1.34	0.64	0.59- 0.70
Reproductive structures	0.59	0.51- 0.65	0.42	0.36- 0.49
Twigs and bark	0.46	0.34- 0.69	0.18	0.16- 0.23
Other species	0.32	0.16- 0.46	0.38	0.22- 0.54
Total	0.43	0.29- 0.62	0.26	0.20- 0.29

TABLE 4—Nitrogen content of annual litterfall (mg/m^2) in pines and eucalypts

Plot	Litterfall component					Total
	Dead foliage	Green foliage	Reproductive structures	Twigs and bark	Other species	
P. radiata I	1810	158	348	84	0	2400
P. radiata II*	1371	167	375	65	101	2079
P. radiata III	981	61	338	36	1	1417
P. radiata IV	1890	91	338	28	32	2379
P. radiata V*	1618	224	279	62	16	2199
E. obliqua I*	1766	239	267	714	32	3018
E. obliqua II*	1749	186	78	398	1	2412
E. regnans	1907	172	21	806	1729	4635
E. sieberi	1359	99	125	541	14	2138

* Mean of 3 years

Branchfall

Branchfall in both pines and eucalypts was highly variable but was usually greatest in eucalypts (Table 6). The standard errors for branchfall in both pines and eucalypts were particularly high, and consequently so for the nitrogen and phosphorus contents

TABLE 5—Phosphorus content of annual litterfall (mg/m²) in pines and eucalypts

Plot	Litterfall component					Total
	Dead foliage	Green foliage	Reproductive structures	Twigs and bark	Other species	
P. radiata I	92.6	10.4	26.0	9.9	0.0	138.9
P. radiata II*	90.0	13.9	37.9	5.7	5.8	153.3
P. radiata III	80.9	5.5	32.3	3.3	0.0	122.0
P. radiata IV	63.0	4.6	27.2	1.5	1.3	97.6
P. radiata V*	175.6	22.0	29.1	6.1	0.4	233.2
E. obliqua I*	66.3	13.5	22.2	43.1	1.7	146.8
E. obliqua II*	57.0	9.6	5.7	21.2	0.1	93.6
E. regnans	77.7	8.8	1.8	47.3	65.1	200.7
E. sieberi	50.9	6.2	11.5	39.3	0.5	108.4

* Mean of 3 years

(Table 6), reflecting large spatial variability in the fall of branches. Branchfall contained 6% or less of the nitrogen and phosphorus content of litterfall plus branchfall, but contributed a higher proportion (up to 14%) of the combined mass.

TABLE 6—Mass, nitrogen content, and phosphorus content of annual branchfall in pines and eucalypts (standard error of mean given in brackets)

Plot	Mass (g/m²)	N-content (mg/m²)	P-content (mg/m²)
P. radiata II*	5.3 (0.7)	6.4 (0.4)	0.76 (0.11)
P. radiata III	56 (55)	57 (56)	8.2 (8.1)
P. radiata IV	10 (8)	12 (6)	1.1 (0.6)
P. radiata V*	6.2 (2.2)	17 (7)	1.0 (0.3)
E. obliqua I*	38 (15)	37 (14)	2.0 (0.8)
E. obliqua II*	11 (5)	10 (4)	0.61 (0.27)
E. regnans	74 (27)	92 (29)	6.9 (3.1)
E. sieberi	65 (27)	31 (11)	4.5 (1.7)

* Mean of 3 years

DISCUSSION

Litterfall in pine stands (258 to 386 g/m²/year) in this study is on the low side of the range (370 to 720 g/m²/year) reported for pines in Australia and New Zealand (Pawsey 1959; Will 1959; Spain 1973; Florence & Lamb 1974; Levett 1978). However, the *P. radiata* forests in the present study are generally younger than the other pine forests for which data are available (Fig. 5); in those studies litterfall increased with stand age, much of the increase due to components other than needles (Fig. 5). For closed-canopy stands of *P. radiata* in Australia and New Zealand, observed needle-litterfall ranges between 200 and 400 g/m²/year.

The literature on litterfall in eucalypt stands is extensive (*see* Fig. 6, sources). Litterfall ranges from 150 to 1000 g/m²/year, with drier low-productivity forests (e.g., *E. socialis* F. Muell. ex Miq.) at the lower end and wet sclerophyll forest (e.g., *E. regnans,*

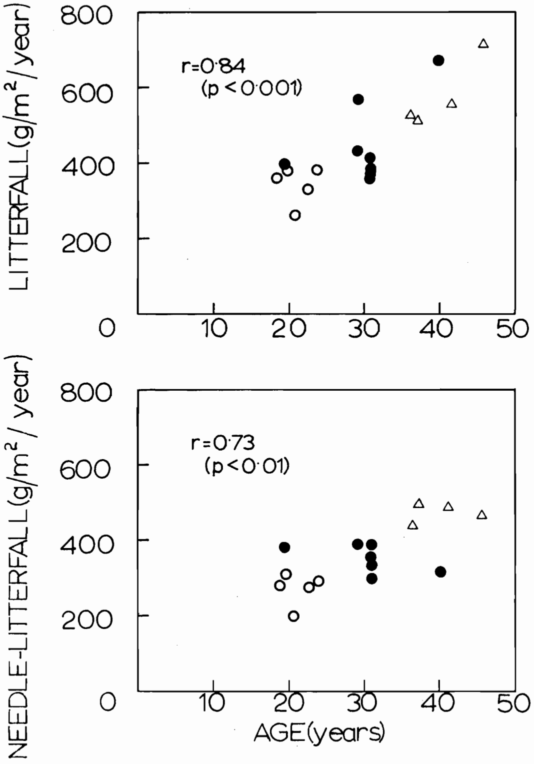

FIG. 5—Correlation of litterfall and needle litterfall with age (from seed) for closed-canopy pine forests in Australia and New Zealand. Symbols: **P. radiata**, ○ This study, ● Other studies; Other pines △. (Data from Lamb & Florence 1975; Levett 1978; Pawsey 1959; Spain 1973; Will 1959).

E. diversicolor F. Muell.) at the higher end (Fig. 6). In the present study, litterfall in *E. obliqua* and *E. sieberi* (388 to 537 g/m^2/year) is typical for dry sclerophyll forest and that in *E. regnans* (686 g/m^2/year) typical for young, wet sclerophyll forest. These values are similar to mean litterfall (550 g/m^2/year) for warm temperate forests of this latitude (Bray & Gorham 1964).

The proportions of dead foliage in litterfall in this study accord with those reported for pines (e.g., Will 1959; Spain 1973) and eucalypts (e.g., Hatch 1955; Ashton 1975). The marked seasonal variations in litterfall are typical of those reported from previous studies in pines (e.g., Will 1959; Pawsey 1959) and eucalypts (e.g., Attiwill *et al.* 1978).

Seasonal variations in concentrations of nitrogen and phosphorus in litterfall have been noted for pines (Lamb & Florence 1975) and for eucalypts (Lee & Correll 1978; Attiwill *et al.* 1978). Minima of concentrations of both nitrogen and phosphorus in dead foliage in the present study are associated with the peak litterfall probably because at this time the bulk of the dead foliage is material from which nitrogen and phosphorus have been biochemically (Switzer & Nelson 1972) withdrawn. At other times of the year a considerable proportion of what looks like dead foliage may be only partly aged, having been blown prematurely from the crown by strong winds. Furthermore, withdrawal of nitrogen and phosphorus may not be as active as during the periods of peak fall and, consequently, winter concentrations in dead foliage from eucalypts in the present study approach those in green foliage. For pines, however, winter concentrations

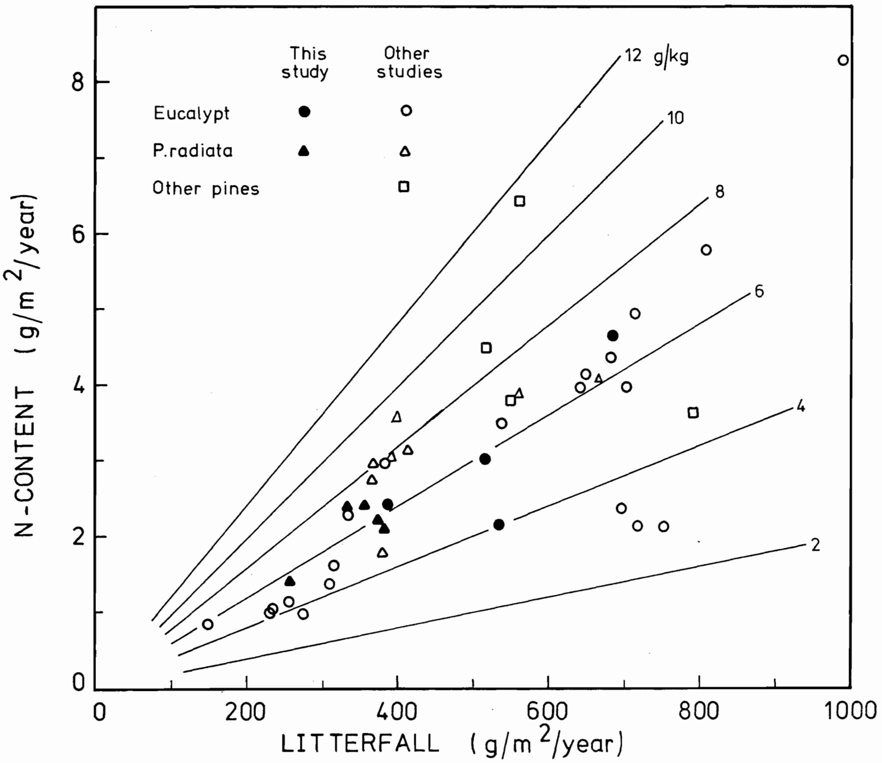

FIG. 6—Nitrogen content of litterfall and amount of litterfall for selected eucalypt and pine forests in Australia and New Zealand. The lines within the graph describe the nitrogen concentration (g/kg) (Data from Ashton 1975; Burrows 1976; Bevege 1978; Connell **et al.** 1981; Florence 1961; Hatch 1955; Lamb & Florence 1975; Lee & Correll 1978; Levett 1978; O'Connell 1981; O'Connell **et al.** 1979; Richards & Charley 1977; Rogers & Westman 1977; Spain 1973; Turner & Lambert 1981; Webb **et al.** 1969; Will 1959).

are only about half those in green foliage. The significantly greater concentration of phosphorus in dead foliage in *P. radiata* V than in *P. radiata* II (and indeed the other three pine plots) may have resulted from the early application of superphosphate.

The concentration of nitrogen in litterfall from both pines and eucalypts in Australia and New Zealand generally falls between 4 and 8 g/kg with little apparent difference between the two over the range of total litterfall (Fig. 6). Three *E. pilularis* Sm. forests (Florence 1961) with low concentrations of nitrogen in litterfall, and a *P. ponderosa* C. Lawson forest (Spain 1973) with a high concentration of nitrogen in litterfall are notable exceptions. *Eucalyptus sieberi* also had a relatively low concentration of nitrogen in litterfall compared to the other eucalypts in this study. The concentration of phosphorus in eucalypt litterfall is usually less than 0.3 g/kg (Fig. 7) – a value for *E. delegatensis* R.T. Bak. of 0.54 g/kg (Connell *et al.* 1981) being the major exception – and contrasts with that for pines (usually >0.3 g/kg, Fig. 7) over the range of litterfall. While the observed concentrations of phosphorus in litterfall from most *P. radiata* forests in Australia range between 0.3 and 0.5 g/kg, the concentrations in litterfall in New Zealand (Will 1959; Levett 1978) are at least 0.5 g/kg. The concentrations of phosphorus in litterfall in *P. radiata* V (with superphosphate applied) and in *P. lambertiana* Dougl. and *P. ponderosa* (Spain 1973) are similar to the *P. radiata* forests in New Zealand. There are insufficient data from the studies in Fig. 6 and 7 to interpret in any detail (for example, with respect to available soil nutrients) the differences in nitrogen

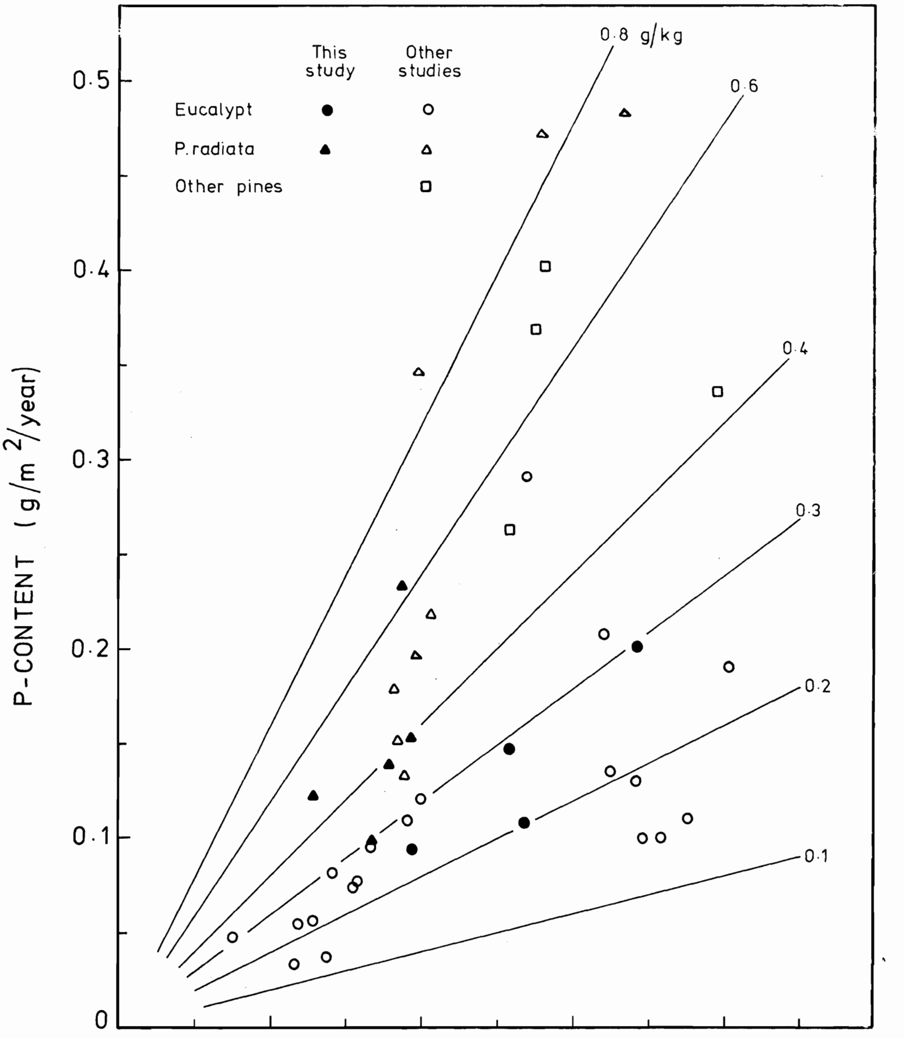

FIG. 7—Phosphorus content of litterfall and amount of litterfall for selected eucalypt and pine forests in Australia and New Zealand. The lines within the graph describe the phosphorus concentration (g/kg) (Sources of data as for Fig. 6, and Attiwill 1964).

and phosphorus concentrations in litterfall. Broadly, however, the differences in concentration of phosphorus in litterfall between pines and eucalypts, and between *P. radiata* in Australia and *P. radiata* in New Zealand, are because of the lower absolute requirement of eucalypts for phosphorus than Northern Hemisphere tree species (Attiwill 1981) and the characteristic low total-phosphorus content of many Australian soils (Wild 1958).

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