DRY MATTER, ENERGY, AND NUTRIENT CONTENTS OF 8-YEAR-OLD STANDS OF EUCALYPTUS REGNANS, ACACIA DEALBATA, AND PINUS RADIATA IN NEW ZEALAND

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ABSTRACT

Acacia dealbata Link. and **Eucalyptus regnans** F. Muell. growing on a productive site contained 75% and 65% more dry matter in the above-ground parts of the trees than did an adjacent stand of **Pinus radiata** D. Don. The eucalypt and pine growth was close to that expected from more extensive studies in the same area.

The most striking difference among the stands was their nitrogen economy. To a depth of 40 cm but excluding roots in the soil, the **A. dealbata** contained over 60% more nitrogen than **P. radiata** and 40% more than the **E. regnans**. Using pine as a basis, **E. regnans** and **A. dealbata** had accumulated 77 and 277 kg N/ha/annum for 8 years.

Keywords: biomass; energy; nutrients; above-ground components; soil; nitrogen; **Eucalyptus regnans**; **Acacia dealbata**; **Pinus radiata**.

INTRODUCTION

The traditional objective of intensive forestry is to increase wood and fibre yields. Currently, energy shortages and the potential for using wood as an alternative or supplement to nonrenewable sources have combined to make intensive management of forest resources even more urgent. Yields can be increased by matching species to site and using genetically improved stock, site preparation, fertiliser, and weed and stocking control. Future productivity can be influenced by decisions, such as species selection, which may lead to changes in the physical or chemical site conditions. Inattention to any of these silvicultural choices can negate the benefits of the others. Proper species-site selection is initially the most important decision to be made for maximising future yields (Kellison *et al.* 1979). In New Zealand, *P. radiata* has been the major exotic species planted for wood and fibre production and has considerable potential as a source of energy. Dry matter production rates of 15 tonnes/ha/annum have been reported with rotations up to 29 years and thinning to a final-crop stocking of between 360 and 540 stems/ha (Madgwick *et al.* 1977; Webber & Madgwick 1983). With 6700 stems/ha and no thinning, a maximum mean annual increment of 21 dry tonnes/ha/annum occurred at age 10 years (Madgwick 1981a).

Eucalyptus regnans plantations in the central North Island have yielded 17 to 31 tonnes/ha/annum with 1000 or 2000 stems/ha and minimal levels of silviculture (Frederick *et al.* 1985). No data on yields at close spacing are available for *E. regnans* but may be inferred from *E. nitens* Maid. which has a similar early growth rate (Pederick 1979; Franklin 1980). *Eucalyptus nitens* growing at 6470 stems/ha produced 20 dry tonnes/ha/annum at age 4 (Madgwick *et al.* 1981) compared with 15 tonnes/ha/annum at 1675 stems/ha at age 5 years (Frederick *et al.* 1984).

Very few stands of *A. dealbata* exist in New Zealand and no dry matter production data are available. However, the species is an early fast grower, is an excellent pulping species, and is capable of fixing atmospheric nitrogen. Both private industry and the New Zealand Government have shown interest in its short fibre and its energy potential.

Dry matter production, nutrient content, and energy in trees and the nutrients in soils were compared for young *E. regnans, A. dealbata,* and *P. radiata* growing on a pumice soil in New Zealand's North Island.

MATERIALS AND METHODS

Sample Stands

Eight-year-old stands of *E. regnans, A. dealbata,* and *P. radiata* were located in close proximity to one another on lands of N.Z. Forest Products Ltd in the Pouakani North Block near Mangakino (38° 20'S, 175° 45'E). Prior to plantation establishment, the vegetation consisted of manuka (*Leptospermum scoparium* J.R. et G. Forst.), tussock (*Festuca novae-zelandiae* (Hack.) Ckn.), *Poa* spp., bracken fern (*Pteridium aquilinum* var. *esculentum* (Forst. f.) Kuhn.), and mixed herbaceous plants. Between November 1971 and May 1972 this vegetation was crushed and burned and the soils were double disced. The *A. dealbata* was established by seed which was sown in rows 3 m apart. One month after sowing, a 4 : 1 mixture of superphosphate : urea was applied at 224 kg/ha in a band close to the original drill lines. The eucalypts were planted at a stocking of 2150 stems/ha with seedlings which were of lower quality than operational planting stock (G. Fry, pers. comm.) and 60 g urea (46% N) was applied to each tree soon after planting. Urea was aerially applied at 250 kg/ha (115 kg N/ha) at the start of the second growing season. The pines were planted as 1/0 seedlings at 1775 stems/ha and received no fertiliser. Approximately one-half of the pines were low pruned at age 6 years. At the time of sampling (November 1980) *E. regnans* and *P. radiata* stockings were the same as at establishment and the *A. dealbata* had 2875 stems/ha in stems greater than 5.0 cm d.b.h.

Field Procedures

Each stand was sampled at age 8 years for structure and stocking using a randomly located 20 × 20-m (0.04-ha) plot. In each plot, diameters were measured on all trees and either eight or nine sample trees were selected for detailed measurement and destructive sampling to give a stratified random sample based on diameter. Before felling, diameters outside bark (d.o.b.) were taken to the nearest 0.1 cm at ground level and at 0.1, 0.7, and 1.4 m high. Trees were felled, delimbed, and measured for total height and height to 5- and 10-cm d.o.b. points. Diameters were measured at quarter, half, and three-quarters total height and at 3- and 6-m points. Stems were cut into segments at each diameter point and weighed to the nearest 0.1 kg. Discs 10 cm thick were cut at each diameter measurement point and weighed fresh to the nearest 1 g, the bark was stripped, diameter inside bark (d.i.b.) was measured, and the wood and bark segments were bagged for transport to the laboratory for dry weight determination and nutrient analysis. Crowns were separated into dead branches, live branches, and foliated twigs and weighed fresh to the nearest 0.1 kg. A random sample of each category from each tree was selected by repeated mixing and quartering, weighed fresh to the nearest 1 g, and taken to the laboratory for dry weight determination and nutrient analysis.

The forest floor was sampled by removing all material from ten 0.25-m^2 quadrats randomly located in each stand. Soil samples were obtained from the 0–10, 10–20, and 20–40 cm depth in each stand using a 2.5-cm tube sampler. Three composite samples of nine cores each were taken from each study plot.

Ten randomly located 1 × 1-m litter traps with fibreglass screen bottoms were placed in each stand during late November 1980 and collections made at 4- to 6-week intervals for just over 2 years.

Laboratory Procedures

All tree samples were oven-dried at 70°C and weighed to obtain dry weight fractions and the ratios of stem wood and stem bark. After drying, foliated twigs were separated into leaves and twigs, redried, and weighed, and the ratios of the two components were determined. Stem wood and branch samples were chipped and all samples were ground to pass 2-mm- and 1-mm-mesh sieves for wood and foliage components respectively. Energy values were determined using bomb calorimetry (Lieth 1965). Chemical analyses were completed using standard Forest Research Institute (FRI) techniques (Nicholson 1984). Subsamples of tree material were digested using sulphuric acid and hydrogen peroxide in the presence of lithium sulphate and selenium. Nitrogen was determined by the indophenol-blue and phosphorus by the vanadomolybdate methods. Potassium, calcium, magnesium, manganese, zinc, and copper were determined by atomic absorption.

Forest floor samples were oven-dried at 70°C, weighed, ground to pass a 1-mm screen, and analysed using FRI methods (Nicholson 1984). Elements determined were nitrogen, phosphorus, potassium, calcium, and magnesium. An indication of organic material in the forest floor was obtained by weight loss on ignition at 500°C for 1 hour. Carbon percentage was estimated by a modified Walkley-Black chromic acid digestion. The pH of the forest floor was determined electrometrically using undried samples at a forest floor : water ratio of 1 : 4.

Mineral soil samples were air-dried and sieved to pass a 2-mm screen. Nitrogen was determined using Kjeldahl digestion; extractable phosphorus using the Bray-2 extraction; and exchangeable calcium, magnesium, and potassium by atomic absorption. Organic matter content was estimated by weight loss on ignition after 1 hour at 500°C. Soil pH was determined electrometrically using a soil : water ratio of 1.0 : 2.5 (Nicholson 1984).

Litterfall material was oven-dried at 70°C; it was separated into leaves, wood plus bark, reproductive parts, and miscellaneous, and weighed. Litterfall nutrient concentrations were determined by Analytical Services Limited. After wet digestion with nitric and perchloric acid, potassium and calcium were determined by flame emission; magnesium, manganese, zinc, and copper by atomic absorption; and phosphorus by colorimetry.

The weights and nutrient contents of the three stands were determined by the basal area ratio method (Madgwick 1981b) using the relationship:

$$\text{Estimated stand weight} = \frac{\text{sum of sample tree weights}}{\text{sum of sample tree basal area}} \cdot \text{stand basal area}$$

Tabulated litterfall data are based on the first 2 years of data only. Copper data for some components will have been affected by copper sprays used to control *Dothistroma pini* Hulbary in the *P. radiata* stand.

Reliability of Estimates

Accurate estimates of confidence intervals of stand weight are not possible to obtain using the sampling employed but simulated sampling of a known *P. radiata* stand suggests that stand estimates are likely to be within 15% of actual values (Madgwick 1981b). Confidence intervals for litterfall components vary among species and components but were less than 3% for foliage and 20% for woody material. Confidence intervals for litter layer dry weights were less than 9%.

Confidence intervals for mean stand values of nutrient concentration in tree components varied between 3% and 12%, being most variable for manganese and copper. Similar levels of variation were found for individual collections of leaf litterfall except for copper where values were 20% of plot means.

RESULTS

Stand Growth

Acacia dealbata had the highest basal area (47.9 m^2/ha) and the lowest average diameter (13.4 cm) (Table 1). *Pinus radiata* had the lowest stocking (1775 stems/ha), basal area (32.9 m^2/ha), and mean height, but the highest average diameter (14.7 cm). *Eucalyptus regnans* had the greatest average height and was nearly equal to the pine in average diameter. The *P. radiata* stand had a site index of 36 (height in metres at 20 years) according to the site index equations of Burkhart & Tennent (1977) and the *E. regnans* a site index of 40 (Campbell *et al.* 1979), both indicative of a good site for these two species.

TABLE 1—Stand characteristics, dry matter content, and litterfall in stands of **Acacia dealbata**, **Eucalyptus regnans**, and **Pinus radiata**

	A. dealbata	E. regnans	P. radiata
Stand characteristics			
Stocking (stems/ha)	2875	2150	1775
Basal area (m^2/ha)	47.9	39.1	32.9
Mean diameter (cm)	13.4	14.5	14.7
Average height (m)	15.6	17.6	12.3
Top height (m)	20.4	20.0	15.0
Volume under bark (m^3/ha)	367	307	175
Dry weight (tonnes/ha)			
Trees			
Leaves	6.4	8.7	9.2
Live branches	14.5	16.1	22.7
Dead branches	15.6	12.5	2.3
Fruits	0.0	0.0	1.0
Stem wood	129.5	122.0	61.2
Stem bark	15.6	12.3	7.4
Tree above-ground	181.6	171.6	103.8
Understorey	0.0	0.0	0.0
Litterfall			
Leaves	4.5	5.6	6.0
Wood and branches	2.5	2.5	< 0.1
Reproductive structures	< 0.1	< 0.1	0.2
Miscellaneous	< 0.1	0.0	0.0
Forest floor			
Dry matter	25.8	9.2	18.9
Loss on ignition	19.4	8.3	17.0
Mineral soil (0–40 cm)			
Loss on ignition	195.6	195.5	154.3

Tree Biomass

Acacia dealbata had the greatest weight of stem material and dead branches; *P. radiata* had the highest weight of live branches and leaves; *E. regnans* was intermediate in all categories. *Pinus radiata* contained about one-half the stem wood weight of the *A. dealbata* and *E. regnans*. The stem comprised 66% of the total above-ground dry weight for *P. radiata* compared to 78% and 80% for *E. regnans* and *A. dealbata*, respectively. Allowing for the pruning of *P. radiata*, total branch weight for all three species was similar. Leaf dry weight was lowest in the *A. dealbata* (6.4 tonnes/ha) and highest in the *P. radiata* (9.2 tonnes/ha).

Tree Nutrients

Unweighted average nutrient concentrations for the *P. radiata* components were comparable to averages for a *P. radiata* age series reported by Madgwick *et al.* (1977), and the stand appeared to be adequately supplied (Will 1978) with nitrogen, phosphorus, potassium, calcium, magnesium, manganese, and zinc (Table 2). There were high concentrations of copper in the *P. radiata* tissues which reflect past aerial spraying of copper sulphate for *Dothistroma pini* control.

Nutrient concentrations for the *E. regnans* were comparable to values for a 4- to 17-year age series in the same area (Frederick *et al.* 1985). Nutrient concentrations in *A. dealbata* were higher than those reported for *A. dealbata* foliage, stems, and branches in Australia (Feller 1980).

TABLE 2—Unweighted average nutrient concentrations in tissues of 8-year-old trees of **E. regnans**, **A. dealbata**, and **P. radiata**

	N	P	K	Ca	Mg	Mn	Cu	Zn
	(%)					(ppm)		
A. dealbata								
Leaves	3.78	0.162	0.93	0.86	0.22	133	8.8	18.3
Twigs	1.84	0.102	1.05	0.56	0.15	48	7.1	21.0
Branches								
Live	1.03	0.049	0.69	0.36	0.11	35	4.6	14.6
Dead	0.74	0.020	0.18	0.49	0.12	35	6.5	23.7
Stem								
Bark	1.36	0.045	0.82	0.51	0.12	34	26.0	8.8
Wood	0.21	0.012	0.27	0.05	0.02	7	4.9	2.5
E. regnans								
Leaves	1.61	0.148	0.74	0.54	0.23	891	8.1	8.7
Twigs	0.59	0.081	0.64	0.76	0.15	467	9.4	12.0
Branches								
Live	0.23	0.057	0.32	0.25	0.08	307	3.4	6.3
Dead	0.21	0.016	0.05	0.54	0.09	512	4.4	8.5
Stem								
Bark	0.22	0.017	0.05	0.57	0.09	539	4.7	9.0
Wood	0.07	0.015	0.13	0.04	0.02	28	0.8	2.6
P. radiata								
Leaves	1.63	0.185	0.98	0.25	0.10	219	n.d.	44.6
Twigs	0.74	0.127	0.93	0.21	0.10	82	n.d.	38.7
Branches								
Live	0.25	0.039	0.36	0.26	0.07	84	18.7	27.5
Dead	0.29	0.031	0.16	0.32	0.11	149	37.9	46.7
Cones	1.04	0.176	0.71	0.03	0.08	27	11.2	31.9
Stem								
Bark	0.47	0.047	0.44	0.24	0.07	54	6.9	40.9
Wood	0.10	0.017	0.14	0.05	0.03	32	1.7	11.5

n.d. = not determined

Nitrogen concentrations for all components of *A. dealbata* were high compared to *P. radiata* or *E. regnans*. Copper and zinc concentrations in the *A. dealbata* stem components were very variable. *Eucalyptus regnans* was notable for high manganese and a tendency to low phosphorus and potassium concentrations compared with both *P. radiata* and *A. dealbata*. Foliage and bark calcium and magnesium tended to be highest for the two hardwoods which also had low zinc concentrations. Concentrations of other nutrients in the remaining components were comparable for all three species.

Total above-ground nutrient content in the three species reflected variations in weight and individual nutrient concentrations. *Acacia dealbata* contained about three times the amount of nitrogen and twice the potassium in either *P. radiata* or *E. regnans* (Table 3), and almost as much nitrogen in leaves and twigs as was in the entire

TABLE 3—Total nutrient content (kg/ha) of 8-year-old stands of **E. regnans**, **A. dealbata**, and **P. radiata**

	N	P	K	Ca	Mg	Mn	Cu	Zn
A. dealbata								
Leaves	227	9	52	56	14	0.9	0.05	0.12
Twigs	83	4	41	27	7	0.2	0.03	0.11
Branches								
Live	104	5	64	35	9	0.3	0.04	0.14
Dead	105	3	30	73	17	0.4	0.08	0.31
Stem								
Bark	209	7	121	86	15	0.5	0.21	0.10
Wood	279	15	330	57	24	0.9	0.47	0.20
Total	1006	43	638	334	86	3.3	0.88	0.97
E. regnans								
Leaves	141	14	64	54	19	8.1	0.07	0.08
Twigs	20	3	22	29	5	1.7	0.03	0.04
Branches								
Live	24	7	36	29	10	3.5	0.03	0.07
Dead	26	2	5	73	12	6.6	0.05	0.12
Stem								
Bark	37	6	68	146	22	8.7	0.03	0.06
Wood	91	19	170	46	22	3.4	0.11	0.30
Total	340	50	365	378	91	32.0	0.32	0.67
P. radiata								
Leaves	152	17	90	27	9	2.1	n.d.	0.43
Twigs	33	6	42	10	5	0.4	n.d.	0.18
Branches								
Live	45	7	65	46	13	1.4	0.32	0.49
Dead	6	1	4	8	2	0.4	0.09	0.11
Cones	9	2	5	<1	1	<0.1	0.01	0.03
Stem								
Bark	34	4	36	19	6	0.5	0.09	0.31
Wood	62	11	82	31	17	1.8	0.10	0.66
Total	342	48	323	141	53	6.5	0.83	2.20

n.d. = not determined

above-ground biomass of the other species. *Pinus radiata* had lower amounts of calcium and magnesium but higher amounts of zinc while *E. regnans* contained 5 to 10 times more manganese than the other two species.

Energy Values

Energy values were usually highest for foliage, especially in *E. regnans* which had higher foliar energy values than either *A. dealbata* or *P. radiata* (Table 4). Energy values for the woody tissues were similar within a species except for *E. regnans* bark which had significantly lower values than either stem wood or branches. While differences among species were numerically small, *P. radiata* had significantly higher energy values per unit mass for woody tissues than either hardwood.

Differences in the total energy content of the above-ground parts of the tree stands reflected differences in dry weight. Total energy content of the hardwoods was about 50% more than that of *P. radiata.* The hardwoods contained about twice as much energy in the stems as the pine.

TABLE 4—Average calorific value and energy content of 8-year-old stands of **A. dealbata**, **E. regnans**, and **P. radiata**

	A. dealbata		E. regnans		P. radiata	
	kJ/g	10^{12}J/ha	kJ/g	10^{12}J/ha	kJ/g	10^{12}J/ha
Leaves	21.8	1.4	24.4	2.1	21.2	1.9
Live branches	19.3	2.8	19.4	3.1	20.1	4.6
Dead branches	19.8	3.1	19.4	2.4	21.5	0.5
Fruits	—	0.0	—	0.0	20.0	0.1
Stem wood	19.3	25.0	19.4	23.6	20.4	12.5
Stem bark	19.9	3.1	17.6	2.2	20.4	1.5
Tree above-ground	—	35.4	—	33.5	—	21.1

Soils

The weight of the forest floor ranged from 9 tonnes/ha under *E. regnans* to 26 tonnes/ha under *A. dealbata* (Table 1). Differences in total nutrient content tended to reflect differences in dry weight (Table 5). Thus, the forest floor under *E. regnans* contained less of each of the macronutrients than that under either *P. radiata* or *A. dealbata.* For instance, the forest floor under *A. dealbata* had three times the dry weight but over six times the nitrogen of that under *E. regnans.* The pine forest floor had twice the weight of the eucalypt but contained three times as much nitrogen.

The pH of the mineral soil was lowest under the eucalypt and highest under the pine but only in the surface 10 cm were these differences significant (Table 6). Nitrogen concentration in the surface 20 cm of mineral soil increased in order *P. radiata* < *E. regnans* < *A. dealbata.* Although some statistically significant differences occurred

TABLE 5—Ecosystem nutrient pools in 8-year-old stands of **A. dealbata**, **E. regnans**, and **P. radiata**. Mineral soil values are total nitrogen, Bray No. 2 phosphorus, and exchangeable potassium, calcium, and magnesium (kg/ha)

	N	P	K	Ca	Mg
A. dealbata					
Trees (above-ground)	1006	43	638	334	86
Forest floor	560	12	27	275	34
Mineral soil (0–40 cm)	3969	33	269	660	124
E. regnans					
Trees (above-ground)	340	50	365	378	91
Forest floor	87	7	9	104	10
Mineral soil (0–40 cm)	3507	44	377	594	117
P. radiata					
Trees (above-ground)	342	48	323	141	53
Forest floor	271	16	30	121	25
Mineral soil (0–40 cm)	2718	29	353	628	104

among plots for phosphorus and exchangeable nutrients, no consistent patterns were observed. The nutrient pool of Bray-extractable phosphorus and exchangeable potassium, calcium, and magnesium in the soils was broadly similar for the three species (Table 5). Total nitrogen in the surface mineral soil was highest under *A. dealbata* and lowest under *P. radiata*.

Litterfall

Annual litterfall ranged between 6.2 tonnes/ha for *P. radiata* and 8.1 tonnes/ha for *E. regnans* (Table 1). Branch fall was negligible for pine but amounted to about one-third of the total litterfall for the two hardwoods. For the first 2 years of observation little reproductive material fell in any stand (Table 1) but at the beginning of the third year 670 kg seeds and seed pods per hectare fell in the *A. dealbata* stand (Fig. 1). Both *A. dealbata* and *E. regnans* litterfall followed a seasonal pattern with distinct summer maxima primarily due to fluctuating leaf fall (Fig. 1). Litterfall in *P. radiata* was more erratic but was higher in the summer half year than in the winter. Leaves contained the majority of nutrients returned to the forest floor in litterfall (Table 7). Woody material in *A. dealbata* and *E. regnans* and reproductive structures in *P. radiata* returned appreciable amounts of nutrients but other components contained only negligible quantities. The difference in total nutrient content of litterfall among species was greater than that in weight. Thus, nitrogen in *A. dealbata* litterfall was more than twice that in the other two stands. Calcium and magnesium in the hardwoods were more than twice that in pine, while pine litterfall contained relatively large amounts of potassium and phosphorus.

TABLE 6—Soil characteristics under 8-year-old stands of **A. dealbata**, **E. regnans**, and **P. radiata***

	Species		
	A. dealbata	**E. regnans**	**P. radiata**
Forest floor			
pH	5.6	4.8	5.4
C/N	18a	46b	29c
Mineral soil (0–10 cm)			
pH	5.45a	5.23b	6.01c
Total N (%)	0.40a	0.32b	0.23c
Bray-2 P (ppm)	15.2a	12.9a	14.5a
Exchangeable cations (m.e. %)			
K	0.51a	0.29b	0.51a
Ca	4.0a	1.8a	3.9a
Mg	1.2a	0.6b	1.0ab
Mineral soil (10–20 cm)			
pH	5.20ab	5.77a	5.93b
Total N (%)	0.23a	0.17ab	0.13b
Bray-2 P (ppm)	10.5ab	14.8a	9.7b
Exchangeable cations (m.e. %)			
K	0.29a	0.31a	0.42b
Ca	1.5a	2.1a	1.4a
Mg	0.5a	0.6a	0.4a
Mineral soil (20–40 cm)			
pH	5.99a	5.80b	5.99a
Total N (%)	0.09a	0.07a	0.09a
Bray-2 P (ppm)	19.8a	20.5a	15.3a
Exchangeable cations (m.e. %)			
K	0.29a	0.49b	0.37c
Ca	0.7a	0.5a	0.6a
Mg	0.3a	0.2a	0.2a

* Numbers in any row followed by the same letter are not significantly different at the 5% level based on Least Significant Difference.

TABLE 7—The nutrient content (kg/ha) of the major components of the annual litterfall in stands of **E. regnans**, **A. dealbata**, and **P. radiata** between ages 8 and 10 years

	N	P	K	Ca	Mg	Mn	Cu	Zn
A. dealbata								
Leaves	105	2.6	14.6	44	9.4	0.66	0.05	0.06
Woody	34	0.7	7.2	18	4.7	0.17	0.03	0.08
E. regnans								
Leaves	51	3.5	11.2	48	9.8	4.1	0.04	0.05
Woody	10	0.6	2.4	16	3.0	1.0	0.02	0.03
P. radiata								
Leaves	66	6.0	24.0	23	6.2	1.4	0.39	0.31
Cones	2	0.1	0.5	< 1	0.2	< 0.1	< 0.01	0.01

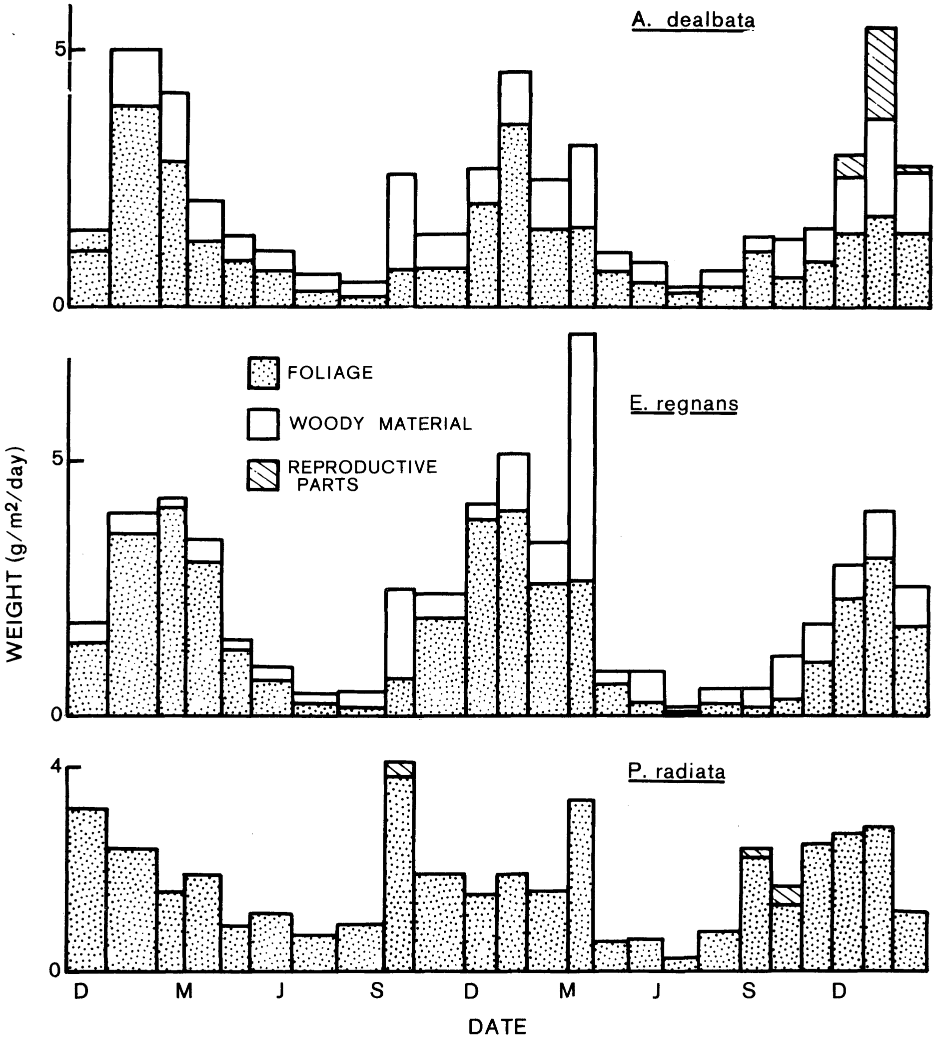

FIG. 1—Average daily litterfall in three 8-year-old forest stands.

DISCUSSION

The site index of the eucalypt stand was slightly less than that of stands in an age series of *E. regnans* plantations in the same area (Frederick *et al.* 1985). Stand foliage, branch, and stem weights were all slightly less than expected from the *E. regnans* age series. Energy values were higher than those reported for *E. tereticornis* Sm. (Singh 1980), *E. fastigata* Deane & Maid. and *E. nitens* (Madgwick *et al.* 1981), and *E. camaldulensis* Dehn. (Tischler & Karschon 1983). Annual litterfall and its seasonal distribution as well as the weight and nutrient content of the forest floor were similar to that of the other *E. regnans* stands.

The site index of the *P. radiata* stand was similar to that of the age series studied by Madgwick *et al.* (1977). Foliage and branch weights were close to those expected from stand stocking. Energy values were slightly above those reported previously for *P. radiata* growing in the central North Island (Madgwick *et al.* 1977). The weight of the litterfall was greater than that reported in the literature (Pawsey 1959; Will 1959; Versfeld 1981; Cromer *et al.* 1984). Needle production has been shown to change with stand age, and leaf litterfall weight was slightly above annual needle production reported for 8-year-old *P. radiata* plantations (Madgwick *et al.* 1977). Needle fall also varies from year to year (Versfeld 1981) and is affected by moisture supply (Cromer *et al.* 1984). The forest floor was comparable to that expected at age 18–20 years (Carey *et al.* 1982) in the same general geographic area.

Comparable New Zealand data are not available for *A. dealbata.* Japanese 4- and 5-year-old stands all had lower foliage and branch weights per hectare than our stand (Fujimori & Yamamoto 1967 and Ando & Takeuchi 1973, as reported by Cannell 1982). Other species of *Acacia* have been reported to have higher foliage weights (Tadaki 1965; Milton & Siegfried 1981). Net annual above-ground production of dense natural regeneration of *A. dealbata* in Australia rose rapidly over the first 3 years to a value of 9.6 tonnes/ha/annum (Adams & Attiwill 1984) but no details of distribution within above-ground components were reported.

The hardwood stands contained above-ground about 70% more total dry matter and energy than the pine and twice the stem amounts. Some differences among the three stands are attributable to differences in stocking. Thus, increasing the stocking of the *P. radiata* stand to that of the *A. dealbata* would be expected to decrease branch weight, leave foliage weight unaffected, but increase the weight of stems (Madgwick *et al.* 1977; Madgwick 1981a). Comparisons among the species need to take intc account the seed origin of the *A. dealbata* compared with the planted origin of the other two stands. However, of more importance is the nature of the stands relative to typical conditions for the species in the area. In this regard the *E. regnans* and *P. radiata* stands were representative of many plantations in the central North Island (Madgwick *et al.* 1977; Frederick *et al.* 1985).

The most striking difference among the stands was in their nitrogen economy. The above-ground vegetation and the soil to a depth of 40 cm in the *A. dealbata* stand contained over 60% more nitrogen than the *P. radiata* and 40% more than the *E. regnans.* Nitrogen cycling through litterfall was more than twice as large in *A. dealbata* than in either of the other species. The absolute level of nitrogen within the ecosystem before stand establishment is unknown but McIntosh (1980) reported a significant decrease in soil nitrogen 45 years after the conversion of manuka scrub to *P. radiata.* This decrease was restricted to the top few centimetres of the soil and no estimate of total loss was given. For our stands, net annual accumulation of nitrogen in the *E. regnans* stand was 70 kg/ha and in the *A. dealbata* 280 kg/ha. Hamilton (1965) also found that conversion of dry sclerophyll eucalypt stands to *P. radiata* resulted in a lower soil nitrogen content. In a wet sclerophyll stand nitrogen levels were similar under both pine and eucalypt. How much of the difference in nitrogen between the eucalypt and the pine stands was due to differences in nitrogen retention as opposed to nonsymbiotic nitrogen fixation in the forest floor and rhizosphere is unknown.

Acacia species are known to enhance soil nitrogen. Langkamp *et al.* (1982) found that a very young stand of *A. holosericea* A. Cunn. ex G. Don on mine spoil fixed 6.4 kg N/ha/annum. Orchard & Darby (1956) reported a 200 kg/ha/annum increase in nitrogen under *A. mearnsii* De Wild. in the surface 23 cm of soil over a 30-year period compared with the neighbouring veld. Turvey *et al.* (1983) estimated an annual addition of 32 kg N/ha/annum in the surface 5 cm of soil under *A. verniciflua* A. Cunn. at 4000 stems/ha. Adams & Attiwill (1984) gave a tentative, conservative estimate of 15–20 kg/ha/annum in stands regenerating after fire. Mean rates of accumulation will be time dependent as stands and soils come into equilibrium, and no estimate of ultimate level of nitrogen accumulation is possible. These results are in marked contrast to those of Venkataramanan *et al.* (1983) who compared litterfall and soil conditions under *Eucalyptus globulus* Labill. and *A. mearnsii.* In their study litterfall was only 1.9 and 1.0 tonnes/ha/annum, respectively, in 12-year-old plantations at about 2500 stems/ha. The total nutrient content of the litterfall was consequently small. Their *E. globulus* litterfall contained more nitrogen, phosphorus, and potassium and much more calcium and magnesium than *A. mearnsii* litterfall. Both species increased soil nitrogen, potassium, and calcium. After 12 years of afforestation soil nitrogen to a depth of 15 cm under the two species was similar.

Nutrient cycling of other elements through the litterfall showed marked differences among elements and species. Higher amounts of phosphorus, potassium, copper, and zinc and lower amounts of calcium and magnesium cycle under the pine compared with the two hardwood species. Manganese in *E. regnans* litterfall was much higher than for either *A. dealbata* or *P. radiata.* Attiwill (1981) characterised nutrient cycling behaviour of different nutrients by comparing ratios derived from green foliage and foliage litterfall nutrient concentrations. Such ratios may be calculated from our data but as they are affected by changes in nutrient concentrations of green foliage with time and by foliage longevity we feel they are inapplicable to our study.

Similarly, the ratios of inputs in litterfall to contents of the forest floor showed marked differences among species and nutrients. Dry weight of litterfall and of the forest floor were of the same order of magnitude under *E. regnans* suggesting that an equilibrium in forest floor weight may have been attained under this species. For both *A. dealbata* and *P. radiata* the ratio of weights of forest floor to litterfall was around 3. Assuming a simple model of litter decay (Olson 1963), it is probable that the forest floor under both species would continue to increase. Ratios of litterfall input to forest floor contents of nitrogen, phosphorus, calcium, and magnesium were comparable to those for dry weight. However, with potassium the equivalent ratios were about 0.65 for *E. regnans* and 1.25 for the other two species, indicating much more rapid potassium cycling in the forest floor for all species and a faster cycling of nutrients through the *E. regnans* litter pathway than that in either *A. dealbata* or *P. radiata.*

Nutrient demands on the site by the three species will depend on rotation length, harvesting intensity, and the nutrient concerned (Madgwick *et al.* 1977; Crane & Raison 1980; Frederick *et al.* 1985). At the present stage of development the removal of nitrogen per tonne of stem (wood + bark) would be almost 50% higher for *P. radiata* and over 250% greater for *A. dealbata* than for *E. regnans.* Harvesting all above-ground material would approximately double the removal of nitrogen per tonne of dry matter. For phosphorus, removal of only stem would reduce the relative difference among species considerably with the heaviest demand (*P. radiata)* being only 40% above the lowest demand (*A. dealbata*). Total removal would increase the demand from between 50% for *E. regnans* to 100% for *P. radiata.* As stands mature, the relative nutrient demands per tonne of harvested material for all species would decline. These estimates may be compared with those of Crane & Raison (1980) who concluded that with stands older than about 7 years, three to five times more phosphorus would be removed by harvesting a unit weight of *P. radiata* stem wood plus bark as opposed to *E. delegatensis* R.T. Bak.

The high removal of nitrogen in the crop of *A. dealbata* would be more than offset by the additional nitrogen added to the soil and the forest floor through fixation. With other elements we need to know more about the effects of species on the site before the long-term effects of growing and harvesting forests can be assessed.

New Zealand is developing a forest resource based primarily on *P. radiata* far beyond the country's needs for timber. The long-term impact of such a programme on site productivity is unclear but it is known that lack of nitrogen limits growth on many sites (Will *et al.* 1981). Our results demonstrate that the use of a nitrogen-fixing tree such as *A. dealbata* could yield considerable amounts of wood and improve soil nitrogen status. In its native habitat *A. dealbata* frequently occurs as an understorey species in eucalypt forests. In New Zealand it warrants consideration for planting in a rotation with pine crops or as a component in mixed stands. Both *A. dealbata* and *E. regnans* have excellent pulping qualities (Batchelor *et al.* 1970) and are capable of capturing significant quantities of solar energy. Along with *P. radiata* they could provide versatile sources of energy or raw material.

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