DRY MATTER CONTENT AND NUTRIENT DISTRIBUTION IN AN AGE SERIES OF EUCALYPTUS REGNANS PLANTATIONS IN NEW ZEALAND

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ABSTRACT

Dry matter and nutrient content were determined for the above-ground vegetation, the forest floor, mineral soil, and litterfall in five plantations of **Eucalyptus regnans** F. Muell. ranging in age from 4 to 17 years. The stands had a site index of 42 m (based on an index age of 20). Crown component weights varied inversely with stocking. Tree foliage ranged between 6.2 and 15.5 tonnes/ha. Stem material increased with stand age to 410 tonnes/ha at 17 years. Mean annual increment of above-ground tree material ranged from 17 to 32 tonnes/ha and was highest in the 10-year-old stand. Understorey biomass was highly variable. The forest floor weighed 4.7 to 11.0 tonnes/ha. Leaf fall averaged 5.2 tonnes/ha/annum and was unrelated to stand age but varied significantly between years. Leaf fall had a summer maximum and winter minimum. Branch fall was erratic but was a minimum of 0.7 tonnes/ha/annum in the 4-year-old stand and a maximum of 4.9 tonnes/ha/annum in the 17-year-old stand.

Significant differences in foliar nutrient concentrations among stands were unrelated to stand age. Total nutrient content was closely related to stand dry weight. There were considerable variations in soil nutrient concentrations which were unrelated to stand age except for phosphorus in the surface soils, which decreased with age. The weight and nutrient content of the litterfall was high and that of the forest floor low, compared with published data on **Eucalyptus** species. This indicates a high rate of nutrient cycling in New Zealand's **E. regnans** plantations which also have a relatively high level of productivity.

Keywords: biomass; above-ground components; litter; nutrients; soil; energy; age; **Eucalyptus regnans**.

INTRODUCTION

Increasing scarcity and costs of renewable energy sources are fostering serious consideration of woody biomass as an alternative energy source in many parts of the world. The feasibility of using wood for energy is dependent upon numerous economic and biological factors, plus reliable estimates of dry matter and energy yields.

In New Zealand, *Pinus radiata* D. Don has been the major tree species considered for energy use. Average dry matter production rates of 14.4 tonnes/ha/annum have been reported at age 29 under conventional silvicultural regimes, with slightly lower yields between ages 4 and 8 years (Madgwick *et al.* 1977; Webber & Madgwick 1983). A close-spaced *P. radiata* stand near Rotorua with about 6700 stems/ha had a maximum mean annual increment of 21 dry tonnes/ha/annum at 10 years (Madgwick 1981a).

Fast-growing eucalypts may have potential for energy production, especially when grown under short-rotation intensive culture. *Eucalyptus regnans* is one of the most important and adaptable exotic species currently being planted in New Zealand (Wilcox 1979). Fast growth and relative frost tolerance have contributed to make it preferred for large-scale plantation culture (Rook *et al.* 1980). N.Z. Forest Products Ltd at Tokoroa currently has the largest *E. regnans* planting programme in New Zealand, with the objective of supplying short fibre for their pulping operation (Lembke 1977).

Production data for New Zealand-grown *E. regnans* are limited. At age 13 years, a 0.156-ha plot of *E. regnans* near Rotorua contained a stand volume of 307 m^3/ha and had a mean annual increment (MAI) of 23.6 m^3/ha/annum (Wilcox & Thulin 1979). This is equivalent to 175 tonnes/ha and an MAI of 13.5 tonnes/ha/annum in oven-dry stems. Preliminary volume measurements in several N.Z. Forest Products Ltd plantations at operational spacings have shown a range of yields from 144 m^3/ha at age 5 to 353 m^3/ha at age 10 (Poole 1979). An 8-year-old *E. regnans* plantation at 2150 stems/ha had an average above-ground yield of 21.5 tonnes/ha/annum, even though the planting stock for this plantation was below average (Frederick *et al.* 1981). There are no published yields for *E. regnans* at close spacing; however, *Eucalyptus nitens* Maid. and *E. fastigata* Deane & Maid. growing at 6470 stems/ha in Rotoehu State Forest yielded 20 and 15 tonnes/ha/annum, respectively, at age 4 (Madgwick *et al.* 1981).

Numerous studies of biomass and litterfall have been reported for a variety of *Eucalyptus* species. In Australia, most studies have been carried out in single stands of natural origin (Holland 1969; Cromer *et al.* 1975; Westman & Rogers 1977a, b; Hingston *et al.* 1979, 1981; Stewart *et al.* 1979; Feller 1980; Turner 1980). *Eucalyptus regnans* has been studied for biomass by Ashton (1976) and Feller (1980) and for litterfall by Ashton (1975), Feller (1980), and Baker (1983). *Eucalyptus obliqua* L'Herit. is a closely related species which tends to grow on drier sites and has a lower growth rate than *E. regnans* (Griffin & Eldridge 1980). When growing together, *E. regnans* and *E. obliqua* have similar diameter growth (West 1981). Natural stands of *E. obliqua* have been studied for biomass, litterfall, and nutrient cycling (Attiwill *et al.* 1978; Attiwill 1979; Baker 1983). Age series of young plantations have been studied in Australia (Bradstock 1981 for *E. grandis* Hill ex Maid.), Morocco (Knockaert 1981a for *E. camaldulensis* Dehn.), and India (Singh 1980 and 1982 for *E. tereticornis* Sm., and Negi *et al.* 1984 for *E. globulus* Labill.). We report similar data for an age series of *E. regnans* aged 4 to 17 years growing in the central North Island of New Zealand.

MATERIALS AND METHODS

Sample Stands

All sample stands were located on lands of N.Z. Forest Products Ltd near Mangakino, central North Island (38° 20′ S, 175° 45′ E). Stands were aged 4, 7, 10, 13, and 17 years and had different stand histories (Table 1). These sample stands were typical of operational plantings by N.Z. Forest Products Ltd on well-drained soils and had received no post-planting treatments other than fertiliser. The soil under the 4-, 7-, and 13-year-old stands was identified (N. Kennedy, DSIR Soils Bureau, pers. comm.) as Taupo sandy loam composed of Taupo pumice plus older tephras, and that under the 10- and 17-year-old stands as Ngakuru sandy loam composed of fine tephra (Vucetich & Wells 1978).

TABLE 1—Stand history of an age series of **Eucalyptus regnans** plantations

	Stand age (years)				
	4	7	10	13	17
Planting date	5–6, 1976	6–7, 1973	9, 1970	1967	1963
Density (stems/ha)	1400	1575	1400	1250	1680
Former vegetation	**P. radiata**	Manuka scrub	Lucerne	**P. radiata**	Manuka scrub
Site preparation	Clear cut Windrowed Slash burn Herbicide	Crushed Burnt Disced	Herbicide	Clear cut Burnt	Burnt Cleared Ploughed
Fertiliser					
At planting/tree	56 g	60 g	56 g	56 g	None
Type	Urea	Urea	Mixed*	Mixed*	
Post-planting/ha	250 kg	None	250 kg	250 kg	None
Year	1977		1972	1972	
Type	Urea		Urea	Urea	

* Mixed = 2 : 1 mixture of blood and bone plus superphosphate.

Field Procedures

Each stand was sampled for structure and stocking using a randomly located 20 × 20-m (0.04-ha) plot. In each plot, diameters of all trees were measured and seven to 10 sample trees were selected for detailed measurement and destructive sampling. The felled trees were a stratified random sample based on the diameter distribution present. The trees felled in each stand gave approximately a 12% sample by number of stems. Before felling, diameters outside bark (d.o.b.) were taken to the nearest 0.1 cm at ground level and at 0.1 m and 1.4 m heights.

During November 1980 to February 1981 trees were felled, delimbed, and measured for total height and height to 5- and 10-cm d.o.b. points; d.o.b. was also measured at quarter, half, and three-quarters total height. Stems were cut at each height and diameter measurement point and each segment was weighed. Discs 10 cm thick were cut from each diameter measurement point and weighed, and the bark was stripped. Diameter inside bark was measured and both wood and bark fractions were bagged for transport to the laboratory. Crowns were separated into dead branches, foliated twigs, and live branches. Live branches were further subdivided into branch wood greater or less than 5 cm d.o.b. However, the quantity of material over 5 cm was so small that only combined branch and twig weights are reported. All crown components were weighed fresh, and random samples were taken and weighed prior to bagging for transport to the laboratory. Total weights were obtained to the nearest 100 g and sample weights to the nearest 1 g.

Understorey vegetation was sampled using four, randomly located 2 × 3-m plots in each stand. All vegetation in each plot was clipped at ground level and separated into woody material, foliated twigs of woody plants, ferns, and herbs. Each category in each plot was weighed fresh to the nearest 1 g and entire samples or subsamples (depending on quantity) were taken for determining dry matter content.

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

Litterfall was measured for 2 years after trees were sampled. Ten 1.0-m^2 traps with fibreglass screen bottoms were located at random within each plot and collected every 4 to 6 weeks.

Laboratory Procedures

Tree, understorey, and forest floor samples were oven-dried at 70°C and weighed to obtain dry matter fraction. After drying, foliated twigs of trees were separated into leaves, twigs, and reproductive structures; they were then redried and weighed to obtain ratios of the three components. Litterfall was separated into leaves, wood plus bark, reproductive parts, and miscellaneous material. Dry weight data are reported for each component. The weights of reproductive and miscellaneous material were negligible and are combined with the woody component for reporting nutrient contents. Stem wood and branch samples were chipped. All samples were ground prior to chemical analysis. Sieve sizes were 2 mm for woody components and 1 mm for foliage and forest floor samples.

Tree, understorey, and forest floor material was analysed for nutrient concentrations using standard FRI methods (Nicholson 1984). Subsamples 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 vanado-molybdate methods. Potassium, calcium, magnesium, manganese, zinc, and copper were determined by atomic absorption. Calorific values were determined using an adiabatic bomb calorimeter (Lieth 1965).

The nutrient content of each tree was obtained by multiplying component weight and nutrient concentration. Stand dry weight and nutrient contents were obtained by the basal area ratio method (Madgwick 1981b) using the relationship:

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

Data for each stand were kept separate to yield independent estimates. This method has been shown to yield more consistent estimates of component weight than log-log regression techniques which were also calculated (Madgwick 1983).

Litterfall samples were analysed by Analytical Services Limited. Nitrogen was determined from Kjeldahl digestion. 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.

Soil samples were air dried, sieved to pass a 2-mm screen, and analysed using standard FRI methods (Nicholson 1984). Total nitrogen content of the mineral soil was determined by Kjeldahl digestion, available phosphorus by the Bray No. 2 extraction, and exchangeable calcium, magnesium, and potassium after leaching with neutral normal ammonium acetate. Carbon in the forest floor was estimated by a modified Walkley-Black chromic acid digestion. The pH of fresh forest floor material and air-dried mineral soils were determined electrometrically using a ratio of soil to water of 1 : 4 and 1.0 : 2.5 respectively. Loss on ignition was obtained after heating at 500°C for 1 hour.

Reliability of Estimates

The restricted number of sample trees per stand precluded accurate estimates of confidence intervals for stand weight using the basal area ratio method (Madgwick 1981b). Simulated sampling of stands where the weights of all trees were measured indicated that the intensity of sampling used should give estimates within 15% of actual values at the 95% confidence level. Such intervals were also suggested by estimates from log-log regressions of weight on d.b.h. though such estimates are known to be unreliable (Madgwick & Satoo 1975).

Confidence intervals for stand nutrient concentrations in foliage and litterfall varied among elements but all except foliar manganese were less than 10% of stand mean values. Variability of litterfall weights was higher for branches (with 2-year totals estimated within plus or minus 10%) than for foliage (where estimates were within 2%).

RESULTS

Stand Growth

Current stocking ranged from 2050 stems/ha in the 4-year-old stand to between 1075 and 1300 stems/ha for stands 10 years and older (Table 2). The current stocking of the 4- and 7-year-old stands was above the nominal planting rate because of the development of double stems at or near ground level. Natural mortality had occurred in the 10- and 17-year-old stands. Average heights ranged from 11.6 to 29.5 m in the 4- and 17-year-old stands, respectively (Table 2).

Trees

Total dry weight of foliage ranged between 6.2 and 15.5 tonnes/ha, and that of live branches between 10.7 and 28.5 tonnes for the 4- and 10-year-old stands respectively (Table 2). For both foliage and branches weight was inversely correlated with stocking. Since stocking was highest in the younger stands it was not possible to separate aging and stocking effects. Dead branch material was lowest in the 4-year-old stand but remained around a mean value of 12 tonnes/ha thereafter. The dry weight of stem

TABLE 2—Stand characteristics and dry matter content of an age series of **Eucalyptus regnans** plantations

	Stand age (years)				
	4	7	10	13	17
Stand characteristics					
Stocking (stems/ha)	2050	1850	1075	1300	1250
Basal area (m^2/ha)	19.3	45.7	58.5	53.9	65.0
Mean diameter (cm)	10.5	17.1	25.0	21.6	24.1
Average height (m)	11.6	19.5	22.7	23.8	29.5
Top height (m)	14.5	22.2	26.3	30.7	37.2
Volume under bark (m^3/ha)	103	371	537	542	854
Dry weight (tonnes/ha)					
Trees					
Leaves	6.2	10.5	15.5	14.9	11.5
Live branches	10.7	17.1	28.5	21.4	27.9
Dead branches	4.2	12.8	13.0	10.0	11.2
Fruits	0.0	0.0	0.1	0.1	0.1
Stem wood	42.2	142.7	242.9	228.2	381.8
Stem bark	5.3	15.0	19.1	19.8	27.9
Tree above-ground	68.5	198.0	319.1	294.4	460.4
Understorey					
Woody	0.1	4.7	0.0	32.0	2.0
Foliated twigs	0.5	0.9	0.0	1.7	0.6
Ferns	1.6	< 0.1	0.0	3.7	3.1
Herbaceous	0.3	0.2	0.0	0.0	< 0.1
Annual litterfall					
Leaves Year 1	5.6	5.6	6.3	5.0	6.2
Year 2	4.2	4.1	5.2	4.4	5.1
Woody material	0.7	2.2	2.5	2.3	4.9
Reproductive parts	< 0.1	< 0.1	0.1	< 0.1	< 0.1
Miscellaneous	< 0.1	< 0.1	0.0	0.1	< 0.1
Forest floor					
Dry matter	4.9	5.0	7.8	4.7	11.0
Loss on ignition	4.4	4.5	7.0	4.2	10.1
Mineral soil (0–40 cm)					
Loss on ignition	240	227	277	285	198

wood plus bark (Ws) increased with stand basal area (BA) and average height (Ht). The ratio of Ws to the product of BA and Ht ranged between 0.18 and 0.21 among the stands, with a mean of 0.20.

Total above-ground dry matter production was related to average stand basal area, diameter, and height (Table 2). The 10-year-old stand had the greatest mean, annual, dry matter increment at 32 tonnes/ha/annum and also the lowest stocking while the 4-year-old stand had produced about 17 tonnes/ha/annum. With increasing age, stands generally had a decreasing fraction of their above-ground biomass in leaves and branches.

Bark comprised over 11% by weight of the 4-year-old stems but had decreased to under 7% by age 17 years. Likewise, live and dead branches comprised a major portion of woody material in the younger stands. This trend was reversed in older stands because of branch death and natural pruning and increasing stem dry matter accumulation. Thus with increasing age, the proportion of stem wood plus bark in woody material increased from 69% to over 88% between the 4- and 17-year-old stands respectively.

Analysis of variance of foliar nutrient concentrations with estimation of Least Significant Difference indicated significant differences among stands for nitrogen, magnesium, copper, and manganese but with no discernible trends associated with stand age (Table 3).

TABLE 3—Foliar nutrient concentrations of an age series of **Eucalyptus regnans** plantations*

Age (yr)	N	P	K	Ca	Mg	Mn	Cu	Zn
	(%)						(ppm)	
4	1.79a	0.151a	0.66a	0.56a	0.198ab	0.120a	6.0a	10.5a
7	1.64b	0.106b	0.67a	0.66a	0.249c	0.058bc	5.4a	10.2a
10	1.79a	0.124ab	0.69a	0.59a	0.187a	0.031c	4.6a	11.1a
13	1.52c	0.130ab	0.70a	0.61a	0.240bc	0.095ab	8.9b	9.6a
17	1.61bc	0.135ab	0.73a	0.60a	0.253c	0.102ab	6.3a	11.0a

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

Total nutrient contents in the crown components were closely related to dry matter amounts so the weight of foliage nutrients tended to decrease in the following order 10-, 13-, 17-, 7-, and 4-year-old stands (Table 4). Stem nutrient contents increased from the 4- to 7-year-old stands and were usually greater in the older stands. Among the older stands there was no consistent relationship in spite of the much higher total wood weight in the 17-year-old stand.

The relative proportions of total nutrient content in leaves, live branches, stem wood, and stem bark varied markedly among the elements (Table 4). Thus nitrogen amounts were usually highest in leaves, potassium in stem wood, and calcium and magnesium in stem bark.

TABLE 4—The nutrient content of an age series of **Eucalyptus regnans** plantations*

	Stand age (yr)				
	4	7	10	13	17
Nitrogen (kg/ha)					
Trees					
Leaves	108.8	164.3	270.4	227.6	182.4
Live branches	39.3	46.7	92.0	56.5	78.7
Dead branches	9.0	21.7	28.5	21.2	18.5
Fruits	0.0	0.0	1.3	0.5	0.9
Stem wood	41.5	113.1	236.1	156.1	208.7
Stem bark	20.6	46.0	63.7	57.1	67.2
Understorey					
Woody	0.1	19.2	0.0	108.4	7.1
Foliated twigs	5.0	15.9	0.0	34.8	7.9
Ferns	19.6	0.5	0.0	38.1	37.1
Herbaceous	3.5	2.2	0.0	0.0	0.3
Annual litterfall					
Leaves	42.7	43.8	46.3	35.2	49.7
Other	3.4	6.9	10.8	8.2	15.7
Forest Floor	51.0	51.1	80.1	46.8	82.7
Soil	4363	4454	6097	6017	3666
Phosphorus (kg/ha)					
Trees					
Leaves	7.8	11.2	20.0	19.4	16.1
Live branches	5.5	7.2	14.4	7.9	11.7
Dead branches	0.4	1.4	2.4	1.5	1.0
Fruits	0.0	0.0	0.2	0.1	0.1
Stem wood	6.6	15.8	32.0	18.0	36.2
Stem bark	2.1	6.7	9.7	6.6	11.3
Understorey					
Woody	0.1	2.4	0.0	12.8	0.9
Foliated twigs	0.6	1.2	0.0	2.9	0.7
Ferns	3.1	0.1	0.0	3.2	4.3
Herbaceous	0.8	0.2	0.0	0.0	0.1
Annual litterfall					
Leaves	3.1	3.0	3.2	1.6	3.5
Other	0.2	0.3	0.6	0.4	1.0
Forest floor	3.9	3.8	7.2	3.5	7.1
Soil	44	34	23	30	10

TABLE 4—(Contd) The nutrient content of an age series of **Eucalyptus regnans** plantations

	Stand age (yr)				
	4	7	10	13	17
Potassium (kg/ha)					
Trees					
Leaves	40.1	64.6	97.6	100.4	76.1
Live branches	41.5	52.8	92.6	73.1	79.0
Dead branches	3.7	5.8	8.9	5.3	7.8
Fruits	0.0	0.0	1.3	0.5	0.9
Stem wood	66.1	173.9	277.4	241.5	214.8
Stem bark	28.4	91.8	129.9	126.1	147.5
Understorey					
Woody	0.2	39.4	0.0	239.6	13.9
Foliated twigs	3.9	10.2	0.0	39.2	8.5
Ferns	21.4	0.5	0.0	52.4	46.9
Herbaceous	6.8	1.3	0.0	0.0	0.5
Annual litterfall					
Leaves	9.8	9.0	12.1	8.0	9.2
Other	0.9	1.2	2.7	1.4	2.9
Forest floor	5.5	6.4	8.9	7.4	10.6
Soil	418	375	219	539	392
Calcium (kg/ha)					
Trees					
Leaves	36.7	73.6	92.5	92.6	56.6
Live branches	56.1	75.1	124.7	90.8	109.2
Dead branches	31.2	52.3	75.7	49.5	33.8
Fruits	0.0	0.0	0.3	0.2	0.4
Stem wood	19.2	52.2	103.4	81.6	106.9
Stem bark	75.4	135.9	265.2	207.3	267.7
Understorey					
Woody	0.1	11.7	0.0	127.0	7.4
Foliated twigs	3.7	10.9	0.0	23.9	9.6
Ferns	3.4	0.1	0.0	13.1	10.1
Herbaceous	2.8	1.3	0.0	0.0	0.1
Annual litterfall					
Leaves	47.8	44.9	57.7	40.5	36.1
Other	4.2	15.0	20.1	14.4	24.2
Forest floor	76.2	57.5	120.7	48.5	75.8
Soil	959	1308	945	2691	786

TABLE 4—(Contd) The nutrient content of an age series of **Eucalyptus regnans** plantations

	Stand age (yr)				
	4	7	10	13	17
Magnesium (kg/ha)					
Trees					
Leaves	12.2	27.4	29.4	33.5	27.0
Live branches	12.1	20.6	27.6	21.4	28.8
Dead branches	5.2	12.8	12.3	11.1	7.9
Fruits	0.0	0.0	0.1	0.1	0.2
Stem wood	9.3	23.9	34.0	32.3	37.2
Stem bark	12.4	29.4	37.1	37.3	48.9
Understorey					
Woody	< 0.1	4.3	0.0	25.0	1.6
Foliated twigs	0.8	4.2	0.0	6.9	3.1
Ferns	2.5	0.1	0.0	6.4	6.7
Herbaceous	0.8	0.5	0.0	0.0	0.1
Annual litterfall					
Leaves	8.2	8.4	10.4	9.0	9.3
Other	0.9	0.3	3.4	2.8	5.1
Forest floor	7.2	7.1	10.8	8.0	12.5
Soil	193	223	102	580	197
Manganese (kg/ha)					
Trees					
Leaves	7.3	5.8	4.9	11.1	9.6
Live branches	5.4	3.6	4.7	7.2	16.1
Dead branches	1.8	4.4	1.3	3.3	3.4
Fruits	0.0	0.0	< 0.1	< 0.1	0.1
Stem wood	1.5	2.0	2.5	5.3	8.5
Stem bark	4.2	4.7	2.1	6.6	10.3
Understorey					
Woody	< 0.1	0.2	0.0	1.4	0.1
Foliated twigs	0.1	0.2	0.0	0.3	0.1
Ferns	0.2	< 0.1	0.0	1.0	0.6
Herbaceous	< 0.1	< 0.1	0.0	0.0	< 0.1
Annual litterfall					
Leaves	4.5	2.4	2.0	3.0	4.1
Other	0.3	0.8	0.3	0.6	1.8
Forest floor	n.d.	n.d.	n.d.	n.d.	n.d.
Soil	n.d.	n.d.	n.d.	n.d.	n.d.

TABLE 4—(Contd) The nutrient content of an age series of **Eucalyptus regnans** plantations

	Stand age (yr)				
	4	7	10	13	17
Copper (g/ha)					
Trees					
Leaves	39	55	58	123	72
Live branches	40	54	65	106	132
Dead branches	12	31	22	79	33
Fruits	0	0	1	<1	1
Stem wood	65	184	280	248	209
Stem bark	22	38	34	57	52
Understorey					
Woody	<1	25	0	179	5
Foliated twigs	4	12	0	19	3
Ferns	17	<1	0	72	23
Herbaceous	3	2	0	0	<1
Annual litterfall					
Leaves	22	28	27	20	28
Other	4	13	14	22	33
Forest floor	n.d.	n.d.	n.d.	n.d.	n.d.
Soil	n.d.	n.d.	n.d.	n.d.	n.d.
Zinc (g/ha)					
Trees					
Leaves	63	106	173	140	130
Live branches	154	179	409	156	268
Dead branches	59	156	176	88	64
Fruits	0	0	1	<1	1
Stem wood	469	1250	1352	1046	503
Stem bark	32	63	89	85	125
Understorey					
Woody	2	55	0	457	20
Foliated twigs	13	27	0	66	22
Ferns	33	1	0	69	56
Herbaceous	17	5	0	0	<1
Annual litterfall					
Leaves	66	58	50	49	66
Other	11	39	35	29	6
Forest floor	n.d.	n.d.	n.d.	n.d.	n.d.
Soil	n.d.	n.d.	n.d.	n.d.	n.d.

* Soil values are total nitrogen, Bray No. 2 phosphorus, and exchangeable potassium, calcium, and magnesium.
n.d. = not determined.

Calorific values varied from 18.0 kJ/g for stem bark to 23.3 kJ/g for foliage on trees at least 7 years old (Table 5). The foliage of the 4-year-old trees had a statistically significant ($p < 0.01$) lower value than that of older trees. No other age effect was statistically significant at the 5% level. Total energy content of the trees (above-ground) may be obtained by multiplying weight data in Table 2 by the corresponding calorific values in Table 5.

TABLE 5—Mean calorific values and standard deviation for individual samples for components of **E. regnans** trees based on oven-dry weight

Component	Energy value (kJ/g)	
	Mean	S.D.
Foliage		
4-year-old stand	22.5	0.26
Other stands	23.3	0.30
Live branches	19.5	0.31
Dead branches	19.4	0.20
Stem wood	19.5	0.33
Stem bark	18.0	0.38

Understorey

The amount of understorey biomass was highly variable among stands, reflecting differences in site, stand age, overstorey stocking, and past history (Table 2). Generally, understorey biomass increased with age but as a result of grazing there was no measurable understorey vegetation in the 10-year-old stand. The greatest accumulation occurred in the 13-year-old stand which also had the highest ratio of understorey to overstorey biomass. There were considerable differences among the four categories of understorey vegetation (Table 2). Native woody species and ferns generally increased with stand age while herbaceous species declined.

The total nutrient content of the understorey reflected the variability in dry weight among stands. The relative importance of the understorey as a pool of nutrients varied among stands and elements. Thus in the 13-year-old stand, which had the greatest understorey mass, there was 60% as much potassium in the understorey as in the overstorey whereas for nitrogen the value was only 35%.

Forest Floor

The weight of the forest floor ranged from 4.7 to 11.0 tonnes/ha with no clear trend with age (Table 2). Levels of macronutrients were usually greater in the forest floor than in litterfall except for potassium (Table 4).

Soil

Considerable variation was evident in the concentration of all soil nutrients examined except for phosphorus which decreased in the surface 20 cm of the mineral soil with increasing stand age (Table 6). Phosphorus availability was unrelated to other soil properties such as acidity, cation levels, or organic matter content. There were significant differences among stands in nutrient concentrations at the 20–40 cm depth which presumably reflect real differences in site rather than differential effects of the vegetation.

TABLE 6—Soil characteristics of an age series of **Eucalyptus regnans** plantations*

	Stand age (yr)				
	4	7	10	13	17
Forest floor					
pH	5.1	5.7	5.5	5.3	5.2
C/N	38 a	38 a	38 a	41 a	56 b
Mineral soil 0–20 cm					
pH	5.6 a	5.9 b	5.5 a	5.6 a	5.6 a
Total N (%)	0.28a	0.31a	0.41a	0.34a	0.27a
Bray-2 P (ppm)	28 a	21 ab	19 ab	17 ab	7 b
Exchangeable cations (m.e. %)					
K	0.41b	0.44b	0.24a	0.61c	0.54bc
Ca	3.5 a	5.5 ab	3.1 a	9.4 b	3.4 a
Mg	1.1 a	1.4 a	0.5 a	3.1 b	1.4 a
Mineral soil 20–40 cm					
pH	5.7 a	6.1 b	5.7 a	5.9 b	5.7 a
Total N (%)	0.11a	0.15a	0.17a	0.17a	0.14a
Bray-2 P (ppm)	11.1 a	13.4 a	3.4 b	9.0 a	3.5 b
Exchangeable cations (m.e. %)					
K	0.49b	0.47b	0.26a	0.57b	0.54b
Ca	0.9 a	1.4 a	1.3 a	2.9 b	1.1 a
Mg	0.4 a	0.5 a	0.3 a	1.3 b	0.5 a

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

Litterfall

Average leaf fall for the 2-year study period ranged between 4.7 and 5.7 tonnes/ha/annum with no trend with stand age (Table 2). Leaf fall varied markedly between the 2 years being approximately 25% higher in the first year than the second. Leaf fall was highest in summer (Fig. 1). Woody litterfall occurred sporadically throughout the year (Fig. 1) and increased with stand age from 0.7 to 4.9 tonnes/ha/annum.

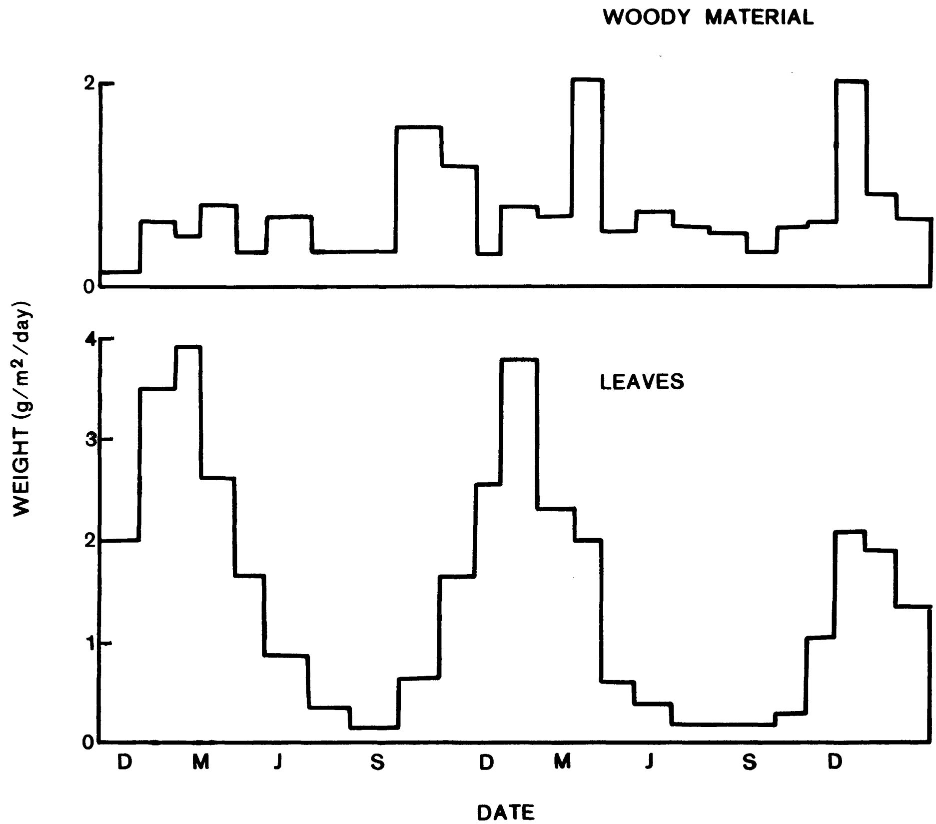

FIG. 1—Average daily litterfall based on five plantations of **E. regnans** ranging from 4 to 17 years old.

Leaves contained the major portion of all nutrients except copper returned to the soil in litterfall (Table 4). However, the relative importance of leaves and woody material varied greatly among nutrients with woody material being of relatively greater importance for calcium, copper, and zinc than for other elements. There were also marked differences in the ratios of weights of nutrients in leaf fall and in the leaves on the trees, ranging from potassium (8–24%) to calcium (44–130%).

Nitrogen, phosphorus, and zinc concentrations in the leaf fall were at a maximum and manganese at a minimum during times of low litterfall (Fig. 2). Seasonal fluctuations in other nutrient concentrations were less consistent. Thus, potassium was at a maximum during the second and third summers but showed no peak in the first summer of observation.

DISCUSSION

The relatively recent development of *E. regnans* plantation silviculture in New Zealand and the changes in practices with time precluded the selection of a set of sample plots with uniform site characteristics and past treatment. Previous land use,

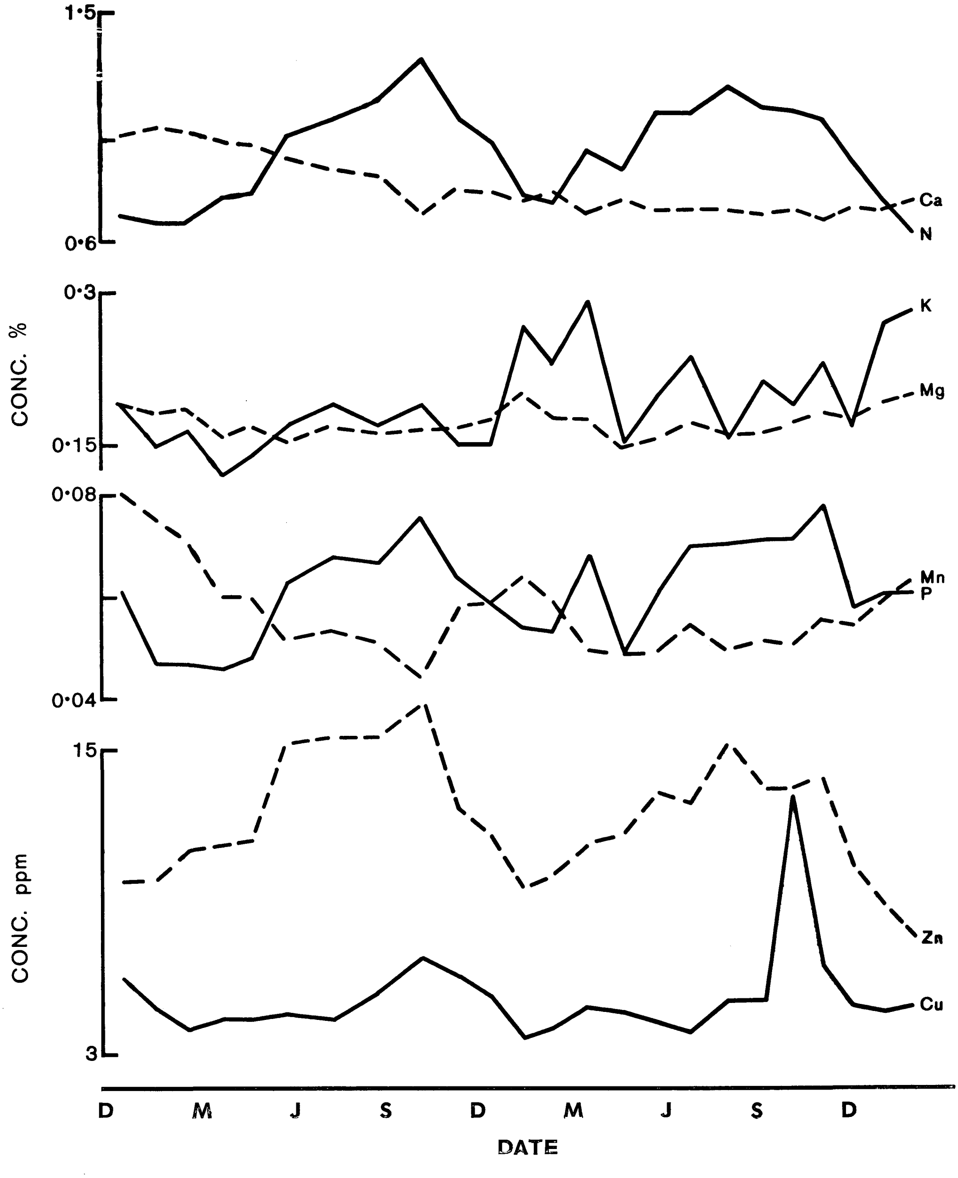

FIG. 2—Seasonal variation in the concentrations of nutrients within leaf fall of **E. regnans** based on five plantations ranging in age from 4 to 17 years old.

planting density, and fertiliser treatment varied among sites. The most notable effect of these differences was in the 10-year-old stand for which the previous lucerne crop and subsequent grazing had resulted in a high nitrogen status and a lack of understorey. The 13-year-old stand was notable for its high rate of litter decomposition and nutrient incorporation in the surface soil. In spite of such variation there was a close similarity among sites in terms of productive capacity as measured by site index. Temporary sample plots are suitable for estimating mean annual increment and for determining approximate nutrient demands on the site but should not be used to estimate current annual increment.

Relating the results of our study to data from natural stands of *E. regnans* or its related species *E. obliqua* is difficult. Although little difference in growth between plantations and natural stands has been observed (Borough *et al.* 1978) our stands are younger than most natural stands studied for biomass (Ashton 1976; Attiwill 1979; Feller 1980) or litterfall (Ashton 1975; Attiwill *et al.* 1978; Feller 1980; Baker 1983). Griffin *et al.* (1982) and Wilcox (1982) found that growth of *E. regnans* was related to seed source. Seed collected in the area of our sample stands performed well in provenance trials and it is likely that our stands were grown from stock genetically suited to the planting site (Wilcox 1982).

Opie *et al.* (1978) found that stand productivity in 11-year-old stands of *E. regnans* in Australia was affected by spacing, with the standing volume of stems at 5627 stems/ha almost 50% greater than that at 1617 stems/ha. However, our 10-year-old stand had a higher basal area and a greater height than any spacing reported by Opie *et al.* (1978). Our 13-year-old stand contained a greater biomass than the more open stand of similar age reported by Wilcox & Thulin (1979). Based on Reineke's index of stocking for natural stands of *E. regnans* (Dahl 1940; Ashton 1976) our stands achieved full stocking by age 10 years. Numbers of stems per hectare were lower than the average for natural stands at all ages (Ashton 1976). It is likely that our production data fall below the potential of the species under closer spacing, especially at young ages.

Eucalyptus regnans is expected to grow faster than its close relative *E. obliqua* (Griffin & Eldridge 1980). Our three oldest stands had basal areas comparable to, or exceeding, those of *E. regnans* or *E. obliqua* for which dry matter data are available (Attiwill 1979; Feller 1980; Baker 1983). Growth in height, basal area, and volume was comparable to *E. grandis* and *E. globulus* on good sites in Uganda and the Transvaal (FAO 1979) with MAI reaching over 50 m^3/ha/annum and high compared with Australian data (Borough *et al.* 1978). The site index of the 10- to 17-year-old stands averaged at least 40 m at 20 years according to the height curves of Webb (1965) and the growth model of Campbell *et al.* (1979). Basal area in the stands was larger than that predicted from Campbell's model. Mean annual increment of dry matter was approximately double that of an age series of *E. grandis* plantations in Australia (Bradstock 1981) and exceeded values for *P. radiata* grown in New Zealand even when the latter were planted at relatively high stocking (Madgwick *et al. 1977;* Madgwick 1981a).

The leaf biomass on our stands was negatively correlated with stocking. Stands older than 10 years had higher foliage amounts than those reported for a range of *Eucalyptus* species in Australian studies (Ashton 1976; Attiwill 1979; Harrington 1979; Hingston *et al.* 1979, 1981; Stewart *et al.* 1979; Feller 1980; Bradstock 1981; Cromer & Williams 1982) or for young plantations in India, Morocco, or New Zealand (Knockaert 1981a; Madgwick *et al.* 1981; Frederick *et al.* 1984; Negi *et al.* 1984). The foliage mass also exceeded values for *P. radiata* plantations in New Zealand (Madgwick *et al.* 1977) except when planted at close spacing (Madgwick 1981a).

The high leaf mass on our *E. regnans* stands was associated with annual litterfall which was above average compared with a range of *Eucalyptus* species summarised by Bevege (1978) and by Baker (1983), and with *Eucalyptus* plantations in India and Morocco (Knockaert 1981b; George 1982). Our leaf fall was considerably greater than that reported for natural stands of *E. regnans* by Ashton (1975) and Baker (1983), and for *E. obliqua* by Attiiwill *et al.* (1978) and Baker (1983). Leaf fall varied significantly between the 2 years studied, which agrees with the results of Ashton (1975) in natural stands of *E. regnans* and with observations in other *Eucalyptus* species (McColl 1966; Lee & Correll 1978). In the year after tree biomass sampling, leaf fall ranged from 90% of the estimated standing crop of leaves in the 4-year-old stand to 34% in the 13-year-old stand. This compares with a value of 20–30% estimated from the *E. obliqua* data of Attiwill *et al.* (1978) and Attiwill (1979). In our stands the changing composition of the litterfall reflected an increase in absolute amounts of branchfall with stand age since variations in total leaf fall were within about 12% of the over-all mean. The low foliage fraction found by Attiwill *et al.* (1978) is partly explained by their relatively low absolute leaf fall values.

The seasonality of leaf fall is well documented in *Eucalyptus* species (Wallace & Hatch 1952; McColl 1966; Webb *et al.* 1969; Ashton 1975; Rogers & Westman 1977; Less & Correll 1978; Birk 1979a; Knockaert 1981b; Baker 1983; Zohar 1984; Lamb 1985; Pook 1985). In the Southern Hemisphere, peak leaf fall can occur as early as October (*E. maculata* Hook. – Pook 1985) or as late as March (*E. botryoides* Sm. – Lamb 1985) but more usually occurs during summer months unless the normal pattern is disturbed by severe drought (Pook 1985). The winter maxima in nitrogen and phosphorus concentrations have also been found by Lee & Correll (1978) and Baker (1983). Lee & Correll (1978) also reported seasonality in nutrient concentrations for the other elements we examined but the results of the two studies are inconsistent – partly because our data showed different relationships among years.

The accumulated forest floor in our stands was less than reported for a range of *Eucalyptus* stands (Bevege 1978; Knockaert 1981b; Lamb 1985) and indicates a high rate of decomposition under the conditions studied in New Zealand. The variability of litterfall from year to year (cf. Lamb 1985) emphasises one of the problems of estimating litter decomposition rates from litterfall and the weight of accumulated litter in the forest floor. Bevege (1978) found decomposition coefficients (k) of 0.10 to 0.85 based on seven studies of Australian *Eucalyptus* stands using the simple exponential model of Olson (1963). Lamb (1985) found annual litter decomposition rates of 20–30% per annum in two *Eucalyptus* stands in New South Wales. In our stands, annual litterfall exceeded the weight of accumulated litter layers. Under these conditions, estimating k values from litterfall and accumulated litter is unsatisfactory as seasonal patterns of litterfall and the relative contributions of different litter types become important in determining the weight of the surface forest floor during the year (Ashton 1975; Birk 1979b; Birk & Simpson 1980; Richards 1981). The fragmented "frayed" appearance of the leaf material in the F-layer, and the general lack of a distinct humus horizon suggest a strong influence of soil fauna on organic matter turnover in our stands. In Australia, Wood (1974) found that, under suitable soil moisture and temperature conditions, faunal feeding caused over one-half of the weight loss of eucalypt leaves in the forest floor. In his stands, total weight loss of *E. delegatensis*

R.T. Bak. leaves ranged from 72% to 97% after 12 months. The optimal conditions reported in the Australian study would be expected to be drier than those found in our New Zealand sites and the light, friable, pumice soil beneath our stands would improve aeration and favour the development of an active faunal population.

Over the 17-year period of afforestation with *E. regnans* total litterfall would be appreciable compared with the amount of organic matter in the top 40 cm of soil. However, there was no apparent trend in total soil organic matter with stand age.

Compared with the natural stands of *E. regnans* reported by Ashton (1976) and Feller (1980) which were about 27 and 39 years old, respectively, our plantations had accumulated more nitrogen and phosphorus in the trees by age 7 years. However, even at age 17 years the New Zealand plantations contained only a fraction of the potassium, calcium, and magnesium in the standing trees of the natural stand examined by Feller (1980). The differences in the results between the Australian and New Zealand studies reflect both the lower foliage weight but higher amount of stem material in the stands studied by Ashton and Feller, and the higher nitrogen and phosphorus concentrations and lower potassium concentrations in our material. Feller (1980) tabulated the range of nutrient concentrations found in a number of Australian studies. Even given the wide range of species and sites represented, very large differences between maximum and minimum values were found for most components. Our 10-year-old stand contained more nitrogen, phosphorus, potassium, magnesium, and zinc than estimated for 10-year-old plantations of six species under Australian conditions (Wise & Pitman 1981). This could be due to the manner in which the Australian data were estimated but also reflects the differences in estimated dry matter content of the trees which were two to three times higher for our 10-year-old plantation.

Litterfall in our plantations contained quantities of nitrogen, phosphorus, potassium, and calcium which are at the upper end of the range found in a survey of Australian eucalypt data (Bevege 1978) and in more recent studies (Attiwill *et al.* 1978; Lee & Correll 1978; George 1982; Baker 1983; Venkataramanan *et al.* 1983; O'Connell 1985). On the other hand, the total nutrient content of the accumulated forest floor in our plantations was at the lower end of the range summarised by Bevege (1978) and reported in later work (O'Connell *et al.* 1978; Hingston *et al.* 1979, 1981; Feller 1980; Turner 1980; Knockaert 1981b). Thus the rates of cycling of nutrients both through the tree-litterfall pathway and through litter decomposition are higher under the highly productive New Zealand plantations than both the natural Australian eucalypt forests and the plantations in drier climates.

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