ABOVE-GROUND DRY MATTER, ENERGY, AND NUTRIENT CONTENTS OF TREES IN AN AGE SERIES OF *PINUS RADIATA* PLANTATIONS

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ABSTRACT

Eight sample stands ranging in age from 2 to 22 years were studied to characterise dry matter, energy, and nutrient contents of the above-ground portion of intensively managed **Pinus radiata** D. Don plantations on a good site. Site index averaged 36 m at age 20. Dry matter content was closely comparable to similar data from Australia. Net dry matter production averaged 14.4 tonnes/ha/annum over the 22-year period; gross production was 22-25 tonnes/ha/annum during initial canopy closure and during canopy closure after heavy thinning. Stand nutrient contents were predominantly in the order N = K>Ca>Mg = P>Mn>Na>Zn. The high potassium content probably reflects the potassium-rich pumice soils on which the stands were growing. Compared with published results for a wide variety of pine species, these stands had high rates of dry matter accumulation and nutrient uptake. Nutrient content in relation to dry matter content was high for potassium, low for calcium, and intermediate for magnesium and manganese compared with other pines. Heavy thinning-to-waste with high pruning of remaining trees would have returned about 55% of the nutrients in the above-ground stand to the forest floor. The total amounts returned would have been similar to those resulting from harvesting of the 22-year-old stand. The total energy capture and the percentage of incoming radiation stored in woody tissue were high compared with published data for other forest types, even though the silvicultural practices employed were not designed to maximise energy capture.

INTRODUCTION

Information on nutrient and energy content of plantations is of increasing importance as a basis for understanding the ecological impact and economic limits of continuous forest production. Recent suggestions that forests can supply a renewable source of energy (Szego *et al.*, 1972; Troughton, 1976) heighten the need for data. Temporary sample plots covering an age series of stands have been used as a traditional method of studying the volume growth of forests. More recently, following the lead of Ovington (1957a), this method has been used to study dry matter production and nutrient uptake. Use of temporary sample plots in this way assumes that all sites studied are uniform throughout the age range. Such plots can give reasonable estimates of standing crop but

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estimates of periodic annual increment are not reliable (Spurr, 1952). Thus the data from such studies may be used to indicate general trends only.

In New Zealand, Orman and Will (1960), Will (1964; 1966; 1968), and Gadgil (1976) have provided a number of estimates of dry matter production and nutrient content of *Pinus radiata* D. Don stands. In Australia, Forrest and Ovington (1970) have studied dry matter of *P. radiata* plantations up to age 12 years, with additional data provided in papers by Stephens and Bond (1957), Waring (1969; 1974), Siemon (1973), and Williams (1976). Data for one plantation are also available from Italy (Giulimondi and Duranti, 1975). The dry matter production and concurrent nutrient uptake of New Zealand *P. radiata* are of particular interest as the more productive sites carry some of the fastest-growing temperate conifer forests in the world.

The purposes of the study reported here were to:

(1) Determine the dry matter, energy, and nutrient content of an age series of *P. radiata* plantations on a high quality site;

(2) Compare the results with comparable data from Australian plantations;

(3) Place *P. radiata* dry matter production and nutrition in the perspective of pine as a genus.

MATERIALS AND METHODS

Sample Stands

A series of eight plots, all within 9 km of each other, was selected in *Pinus radiata* plantations in the north-eastern corner of Kaingaroa Forest (38° 18'S, 176° 44'E). The average annual rainfall (1941-1970) for this area is between 1425 mm (Kopuriki, immediately south-east) and 1549 mm (Kaingaroa Forest Headquarters, to the south-west). The latter station has a mean annual temperature of 10.7°C, with a seasonal range from 5.4°C in July to 15.8°C in February, and an average of 107 ground frosts per annum. The sampled stands ranged in age from 2 to 22 years, and were growing on 75 to 100 cm of Tarawera scoria and Kaharoa ash, overlying older and more consolidated volcanic ash showers. These are classified as Matahina gravels or Matahina hill soils, with a site index of about 36 m at age 20 years (C. J. Goulding, unpubl.). Sample plots and stands chosen reflected as closely as possible the then current management practice of planting 2500 stems/ha, with live-crown pruning of selected crop trees to a height of 6 m followed by thinning to 540 stems/ha at about age 8 years, when the trees were 12 m tall. It was impossible to find stands over 10 years old which had received this treatment; thus, the 17-year-old plot had been thinned to 860 stems/ha, and the 22-year-old plot had been thinned at age 9 years. The 8-year-old stand had a low stocking (Beekhuis, 1966) and additional data on the effects of thinning and pruning, collected later, are included in the Appendix.

Field Procedures

In each plantation a previously established sample plot of 0.1 acres (approximately 0.04 ha) was selected and all the trees were measured for height and diameter. In the 8-year-old stand, which had been marked for thinning, a note was kept of trees to be removed. Sample trees covering the size range within each plot were felled. Seven trees were taken in unthinned plots and five trees in thinned plots. Sampling extended from June to September 1971. The crown of each sample tree was divided into zones representing the year in which the branches were initiated. For each zone all first- and second-order branches were separated according to the age of needles which they bore, and each subdivision was weighed. Large subsamples were then separated into needles and woody material prior to being weighed after drying at 60°C. Ratios of dry weight of needles and woody material to fresh weight were used to obtain estimates of total dry weight of each component for each zone of the crown. All cones within the crown were combined before drying and weighing. Male strobili were present on only the 22-year-old stand at the time of sampling.

Stems were divided into sections and total fresh weight was determined prior to sampling for moisture content. Within the live crown each section comprised an annual height increment; below the lowest live branch, sections consisted of 2-metre lengths. Discs were cut from the end of each segment and at breast height for detailed study. Before drying, the discs were separated into wood and bark.

Laboratory Procedures

In order to reduce the numbers of samples to be analysed, material was combined to provide one representative sample for each category of material for each tree. The categories chosen were needles by age class, live branches, dead branches, cones, strobili, stem bark, and stem wood. Canopy material was combined according to the relative proportion of material in each crown layer. Stem material was combined according to the relative weight of each segment of the stem. Woody material was chipped before grinding in a stainless-steel Wiley Mill, and needle material was ground directly. After drying, samples were ground to pass through a 1-mm round-holed sieve.

Nitrogen was determined by a semi-micro-Kjeldahl procedure using a selenium catalyst (Bremner, 1960). The ammonium N in the diluted digest was determined colorimetrically by an automated adaptation of the indophenol blue method.

Phosphorus and cations (Na, K, Ca, Mg, Zn, and Mn) were determined after dry-ashing at 480°C. Test solutions were prepared from a dilute hydrochloric acid extract of the ash after preliminary removal of silica by a process involving dehydration. Phosphorus was determined colorimetrically by an automated adaptation of the vanadomolybdophosphoric acid yellow method described by Jackson (1958). Cations were determined by atomic absorption spectrophotometry. For Ca and Mg, strontium chloride was added to the solutions as a releasing agent (at a concentration of 1500 ppm of Sr^{2+}) to prevent interference from aluminium and phosphate.

All samples were analysed in duplicate. Analyses were repeated where the difference between duplicates relative to their mean values exceeded 6% for N, 4% for P, 8% for K and Mg, 10% for Ca, and 14% for Zn. The variations in precision between elements reflect the known variation in analytical procedures (Madgwick, 1970b).

Energy content was determined for ground samples using an adiabatic calorimeter (Lieth, 1965) and expressed on a dry weight basis. When the quantity of sample material was limited, the highest priority was given to nitrogen determinations and lowest to caloric value.

Calculations

The nutrient and energy contents of each sample tree were obtained by multiplying the oven-dry weight by the relevant concentration. Regressions were calculated relating logarithm component dry weight and nutrient content to logarithm height for 2- and 4-year-old stands and logarithm height × $(\text{diameter})^2$ for older stands. Total dry weight and energy content of stand components were found by applying these regressions to the unsampled trees after correction for bias due to logarithmic transformation (Finney, 1941). This method is known to give reasonably close estimates of dry weight and overestimates of error terms (Madgwick and Satoo, 1976). In the present study 95% confidence intervals in unthinned stands were about ± 20% and in thinned stands ± 40% of estimated totals, respectively. Separate estimates were made for the 8-year-old stand (a) in its unthinned condition and (b) assuming that the stand had been thinned and crop trees pruned to a height of 6 m.

Net annual values of biomass increase, nutrient uptake, and energy capture of the above-ground stands were calculated using the formula

$$\frac{W_2 - W_1}{t_2 - t_1}$$

where W_i is the weight, nutrient, or energy content of the stands at age t_i years. Gross annual values of biomass increase (net production), nutrient uptake and capture were more difficult to estimate owing to loss of material through death and to changes in chemical composition with time. However, from ages 4 to 8 years such losses would have been minimal, and gross annual values were obtained from the annual increment in stems, branches, and cones using the formula given above, plus the average annual production of needles. For those nutrient elements which were found to increase in concentration with needle age (calcium, sodium, manganese, and zinc) the relevant additional nutrient uptake was accounted for by multiplying the average quantity of 2- and 3-year-old needles by the average increase in nutrient concentration. No account was taken of possible translocation of nutrients back into the branches from ageing or dying needles. Roots were not measured, so that values of biomass increase and nutrient uptake are all underestimates of stand values.

RESULTS

Stand Growth

Stand mean height ranged from 1 m at age 2 years to 31 m at age 22. The young stands tended to be on or above the site index 36 curve and the 17- and 22-year-old stands were below the curve (Fig. 1). Basal area increased to 29 m²/ha before thinning at age 8. Thinning would have removed about half the basal area (Table 1). The basal area of the oldest stand was 54 m²/ha.

Tree Biomass

Total above-ground dry matter content was closely related to height and basal area (Table 1). The total weight of 1-year-old needles reached a maximum between ages 4 and 8 when intermingling of branches was present. Thinning and pruning at age 8 would have removed about 55% of the 1-year-old foliage which then built up almost to a secondary maximum in 2 years. The impact was more severe on older needles since all the lower live branches were pruned and the only 3-year-old needles left on the trees were stem needles. Estimates of needle retention based on closed stands with stable canopies indicate higher variability and lower average retention in younger

(6- and 8-year) than in older (17- and 22-year) stands. This difference could reflect the relatively greater susceptibility of young *P. radiata* stands to infection by *Dothistroma pini* Hulbary in New Zealand. However, needle retention has also been found to increase with tree age in *Pinus virginiana* Mill. (Madgwick *et al.*, 1977), and with thinning in *Pinus ponderosa* Laws (Wollum and Schubert, 1975).

Canopy structure is illustrated in Fig. 2. Maximum foliage production and maximum foliage and branch weights occurred in the second yearly growth zone from the tree apex in stands up to age 6. The weights of foliage and branches per zone were much higher than they were later in the rotation. In older stands canopies were deeper and maximum foliage production occurred in the fourth annual growth zone or below; maximum foliage and branch weights both occurred lower in the canopy. These distri-

TABLE 1—The stocking, basal area, average height, and oven-dry weights of components of an age series of radiata pine plots in Kaingaroa Forest. (n.d. not determined; * present in smaller quantities than units tabulated)

	Age (years)								
	2	4	6	8 (unthinned)	8 (thinned)	9	10	17	22
Stems/ha	2496	2347	2224	1507	544	544	544	855	544
BA m²/ha	0.0	7.4	20.1	29.4	14.0	12.3	20.8	51.3	53.9
Height (m)	1.05	3.91	7.12	10.98	11.71	17.00	16.71	26.08	30.74
Dry weights and standard deviation (tonnes/ha)									
Stem wood	0.17	7.19	22.64	45.99	25.89	29.07	49.59	214.83	243.50
	0.02	0.72	2.54	6.05	4.40	6.51	11.09	17.91	50.05
Stem bark	0.06	1.27	2.92	5.26	2.89	3.60	4.78	21.86	27.36
	0.01	0.13	0.32	0.67	0.48	0.79	1.04	1.77	5.69
Live branches	0.12	6.56	14.97	23.79	4.78	5.53	11.38	22.04	27.36
	0.01	0.63	1.48	3.10	0.79	1.18	2.57	1.96	5.72
Dead branches	0.00	*	0.33	1.58	0.00	*	0.05	9.08	4.66
	0.00	*	0.03	n.d.	0.00	n.d.	0.01	0.81	0.86
Strobili	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	0.53
	—	—	—	—	—	—	—	—	0.16
Cones	0.00	0.00	0.00	0.09	0.08	0.60	0.21	5.02	3.21
	0.00	0.00	0.00	n.d.	n.d.	0.12	n.d.	n.d.	n.d.
1-year needles	0.29	5.38	7.97	5.44	2.48	3.03	4.73	4.94	4.02
	0.03	0.53	0.82	0.68	0.39	0.67	1.03	0.46	0.81
2-year needles	0.07	1.49	3.44	0.34	0.03	0.37	1.07	4.01	3.07
	0.01	0.14	0.33	n.d.	0.01	0.00	n.d.	0.37	0.64
3-year needles	0.00	0.25	0.12	0.14	*	0.00	0.05	1.81	1.91
	0.00	0.02	n.d.	n.d.	n.d.	0.00	n.d.	0.16	0.40
4-year needles	0.00	0.03	0.02	0.00	0.00	*	*	0.06	0.26
	0.00	n.d.	n.d.	0.00	0.00	n.d.	n.d.	n.d.	0.06
	0.00	n.d.	n.d.	0.00	0.00	n.d.	n.d.	n.d.	0.06
5-year needles	0.00	0.00	0.00	0.00	0.00	*	0.00	*	0.01
	0.00	0.00	0.00	0.00	0.00	n.d.	0.00	n.d.	*

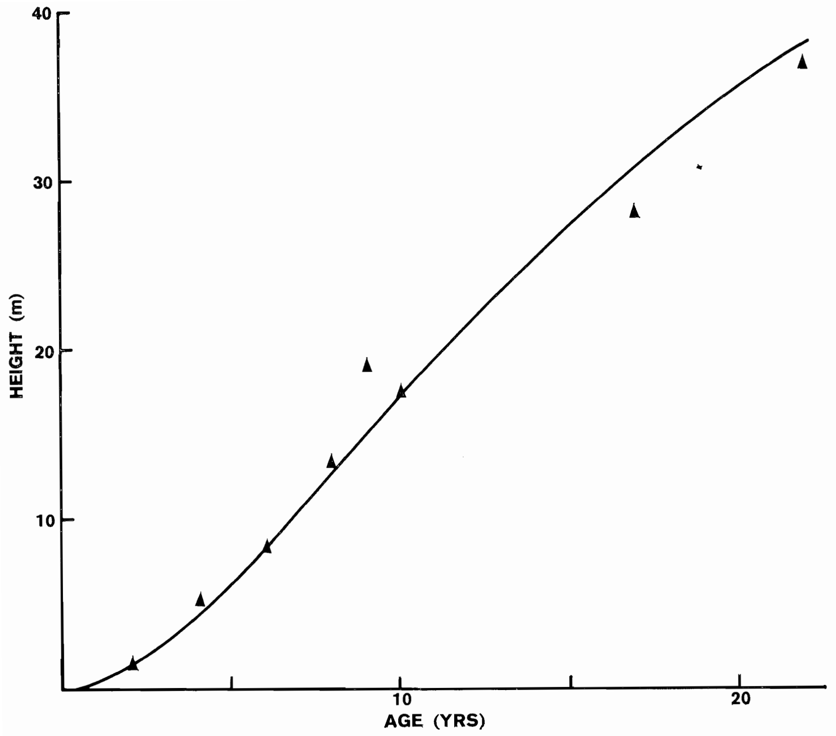

FIG. 1 (above)—Mean top height of sample plots compared with the predicted height growth curve for a plantation with a site index of 36 m at age 20 years.

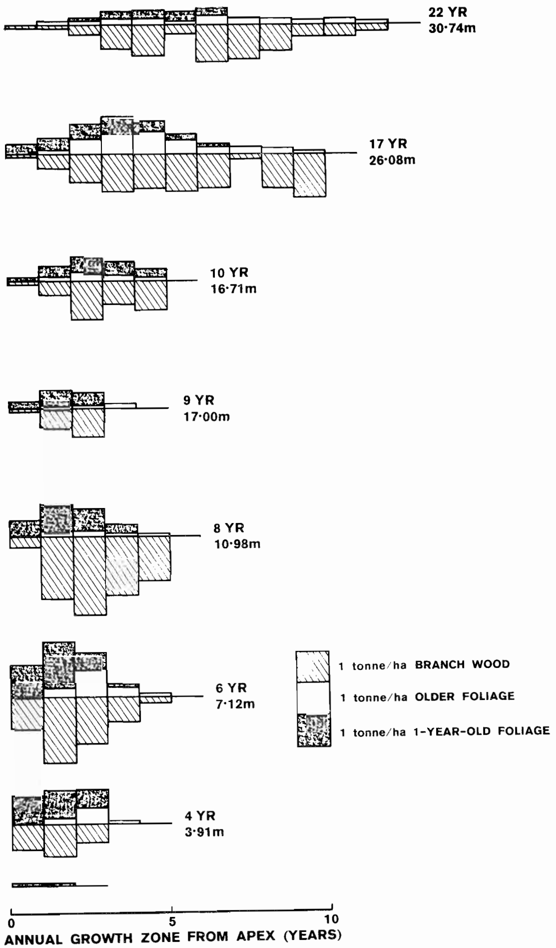

FIG. 2 (right)—The distribution of foliage and branches by annual height increments of radiata pine stands.

butional changes reflect the transition from a shallow canopy comprising many intensely competing individuals to a less competitive distribution of similar foliage mass over fewer (and taller) trees.

Bark comprised almost 25% by weight of the 2-year-old stems but by age 6 had decreased to 10% (Table 1). Similarly, branch material comprised a major proportion of woody material in the 2-year-old stand but the combined effects of branch death and natural and artificial pruning reduced branches to about 10% of the above-ground woody material at age 22. The heavy pruning and thinning treatment would have transferred over 80% of the branch material produced by age 8 to the forest floor.

Net above-ground dry matter increment was 14.4 tonnes/ha/annum over the first 22 years after planting. Gross annual increment was 21.7 tonnes/ha between ages 4 and 8 and at least 24.6 tonnes/ha between ages 10 and 22.

Comparison with Australian Data

Compared with the data of Forrest and Ovington (1970) the Kaingaroa stands had slightly better growth, particularly between ages 2 and 4, so that the size and weight of the 6-year-old Kaingaroa stand were very close to the values for the 7-year-old stand in Tumut, Australia. Part of the higher rate of dry matter increment in New Zealand was due to a 50% higher stocking at planting. It is interesting that the 9-year-old Australian stand had a lower foliage weight than the corresponding 7-year-old stand, paralleling the change found in New Zealand between ages 6 and 8. In order to compare the two sets of data they have been plotted together in Fig. 3 and 4. Also included are earlier data from New Zealand (Will, 1964; 1966), Australia (Ovington *et al.,* 1967; Waring, 1969; 1974; Siemon, 1973; Williams, 1976), and Italy (Giulimondi and Duranti, 1975). For relationships between stocking and canopy weight (Figs. 3 and 5), only stands with closed canopy have been plotted. The data also exclude cases where live branch pruning might have affected the current foliage biomass. Foliage weight increases with stocking up to 400 stems/ha, but above this level appears to be independent of stocking and averages about 10 tonnes/ha. Branch biomass is more variable, partly due to variations in pruning. It increases with stand age and decreases with increased stocking. Stem biomass is directly related to stand basal area times mean height. The age series studied by Forrest and Ovington (1970) had a gross annual production of 23.4 tonnes/ha between ages 5 and 7, a value closely comparable with the Kaingaroa stands between ages 4 and 8.

Nutrient Concentrations

Nutrient concentrations within 1-year-old needles (Table 2) suggest that the stands were adequately supplied with nitrogen, phosphorus, potassium, calcium, magnesium, manganese, and zinc (Ballard, 1977).

Nutrient concentrations in stem and branch materials tended to decrease with tree age (Fig. 6) except for calcium and manganese.

The changes in nutrient concentration with needle age were examined by considering only those trees on which both ages of tissue occurred (Table 3). Changes followed the expected patterns with nitrogen and potassium decreasing, and calcium, sodium, manganese, and zinc increasing with needle age. Magnesium and phosphorus showed no

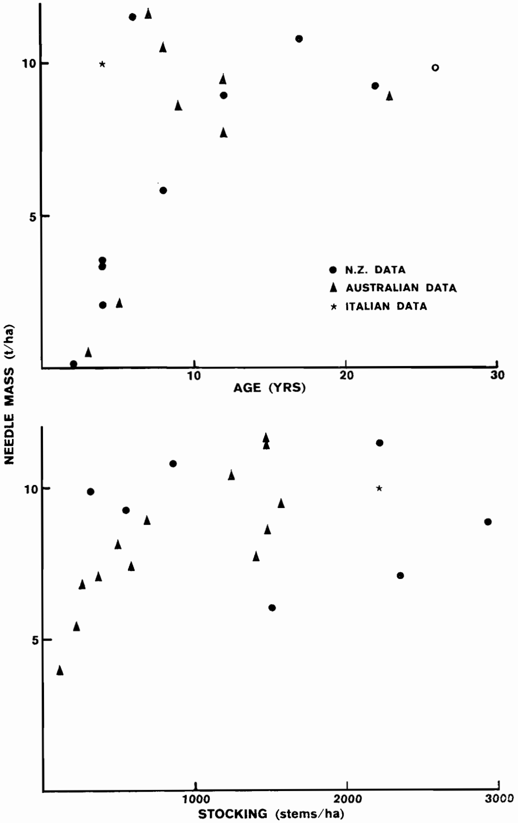

FIG. 3—Total weight of needles on radiata pine stands related to (a) age and (b) stocking. (Siemon's thinned stands excluded from (a). Stands less than 6 years old or green-pruned excluded from (b)).

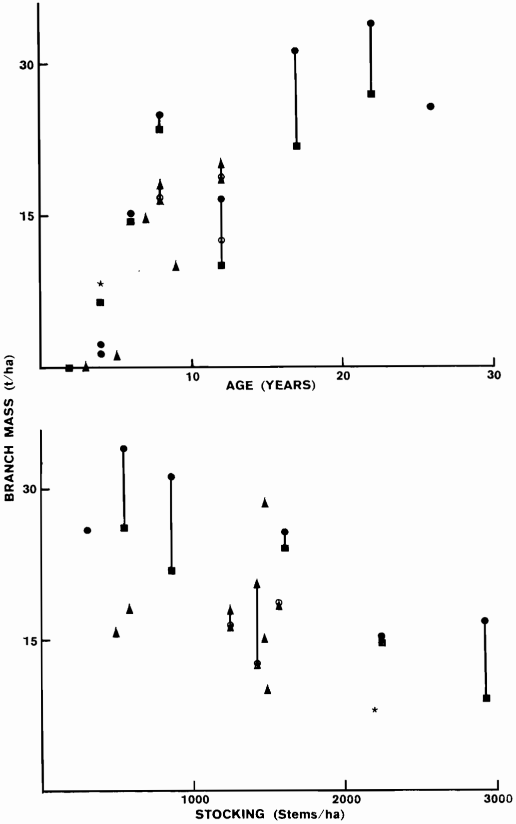

FIG. 4—Total (circles) and live (squares) branch biomass on radiata pine stands related to age and stocking. Notes as Fig. 3.

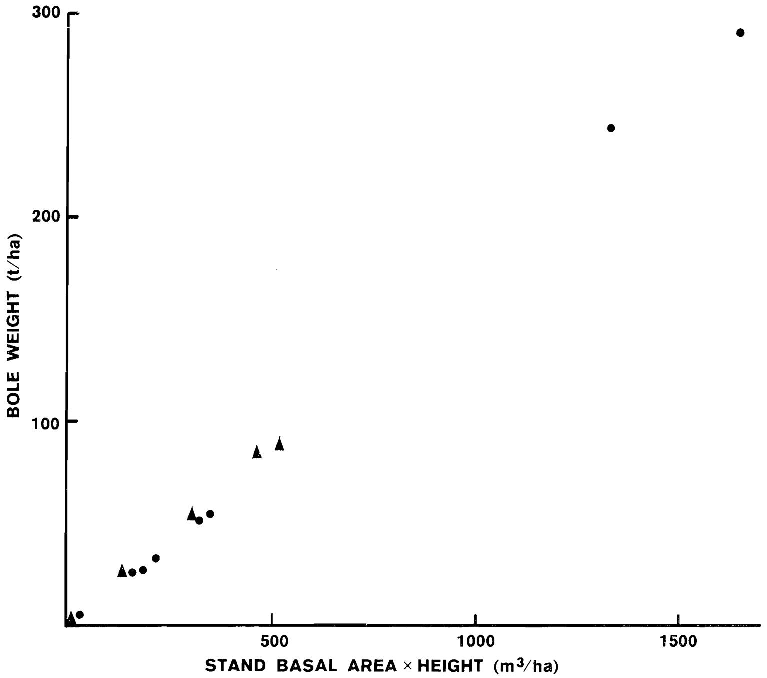

FIG. 5—Bole dry weight in relation to (stand basal area) × height for N.Z. (circles) and Australian (triangles) radiata pine stands.

TABLE 2—Average nutrient concentrations in 1-year needles, cones, and strobili based on 48, 14, and 5 observations, respectively

Element	Needles		Cones		Strobili	
	Conc.	s.d.	Conc.	s.d.	Conc.	s.d.
N %	1.50	0.17	0.47	0.52	1.41	0.24
P %	0.17	0.03	0.07	0.02	0.21	0.02
K %	0.83	0.14	0.16	0.07	0.94	0.14
Mg %	0.13	0.02	0.036	0.007	0.11	0.02
Ca %	0.27	0.08	0.022	0.004	0.05	0.01
Na ppm	61	34	41	9	36	2
Mn ppm	204	145	11.1	2.3	43	5
Zn ppm	50	16	11.8	2.5	41	6

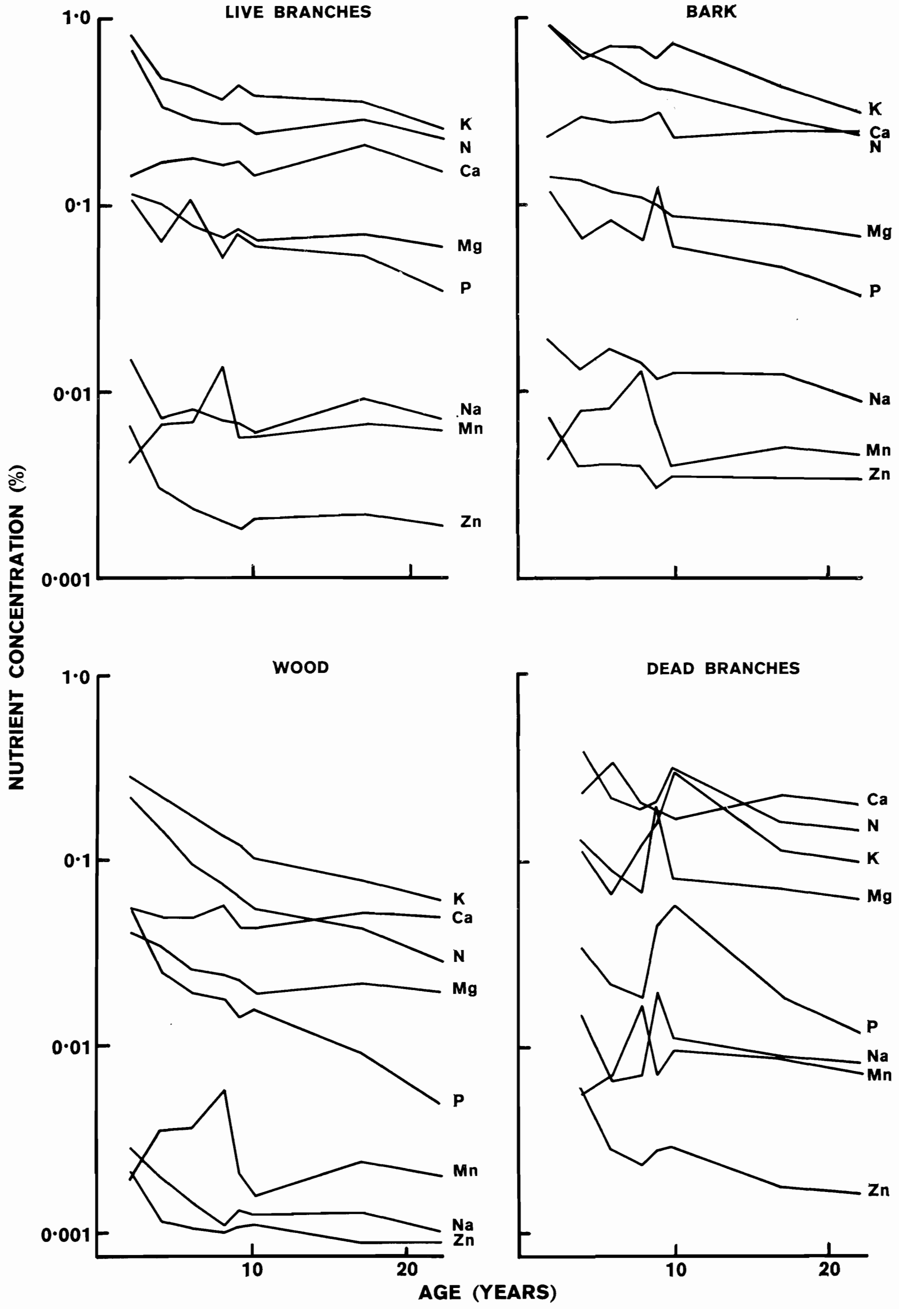

FIG. 6—The relationship between tree age and nutrient concentrations in live branches, dead branches, stemwood and stembark.

TABLE 3—Change in nutrient concentration with needle age, based on those trees for which both ages of needles were analysed

Element		1-2 yr	2-3 yr	3-4 yr	4-5 yr
N	Number	48	37	24	8
	Average %	—0.3042	—0.1811	—0.1075	0.1025
	s.d.	0.1426	0.0831	0.0838	0.3333
P	Number	48	35	21	5
	Average %	—0.0192	—0.0069	0.0138	0.0016
	s.d.	0.0334	0.0306	0.0288	0.0139
K	Number	48	35	21	5
	Average %	—0.0567	—0.0428	—0.0058	—0.0477
	s.d.	0.1341	0.1024	0.0746	0.0270
Mg	Number	48	35	21	5
	Average %	—0.0029	0.0064	0.0130	—0.0060
	s.d.	0.0265	0.0211	0.0214	0.0084
Ca	Number	48	35	21	5
	Average %	0.1747	0.0842	0.0708	0.0444
	s.d.	0.0842	0.0720	0.1156	0.0332
Na	Number	48	35	21	5
	Average ppm	59.6	52.7	113.3	2.0
	s.d.	54.5	46.2	118.6	45.7
Mn	Number	48	35	21	5
	Average ppm	101.4	43.0	51.3	26.7
	s.d.	115.1	98.3	116.5	38.8
Zn	Number	48	35	21	5
	Average ppm	8.7	9.9	13.4	9.3
	s.d.	13.4	12.7	17.8	2.6
Caloric value	Number	40	29	12	3
	Av. kcal/g	0.0567	—0.0801	—0.0253	0.0005
	s.d.	0.0482	0.0577	0.0585	0.0234

consistent trend. The relative concentrations in component parts of the tree similarly reflected well-known patterns, with levels usually decreasing in the order: foliage, stem bark, live branches, stem wood.

Nutrient Content

The total nutrient content of the above-ground portions of the stands closely reflects changes in dry matter content (cf. Table 1 and Fig. 7). The same broad pattern of net nutrient uptake held for all elements because the variation in stand dry weight with age was much greater than the variation in concentration of any one nutrient. Although there was a 100-fold difference in nutrient concentration between the most and least abundant of the nutrients determined, these differences affected the level of total content rather than the pattern of nutrient content in relation to stand age. The total content of nutrients in the above-ground portion of the stands was predominantly in the order N = K; Ca; Mg = P; Mn; Na; Zn. The potassium contents were relatively high compared with published data (Rodin and Bazilevich, 1967), reflecting the potassium-rich soils on which the stands were growing.

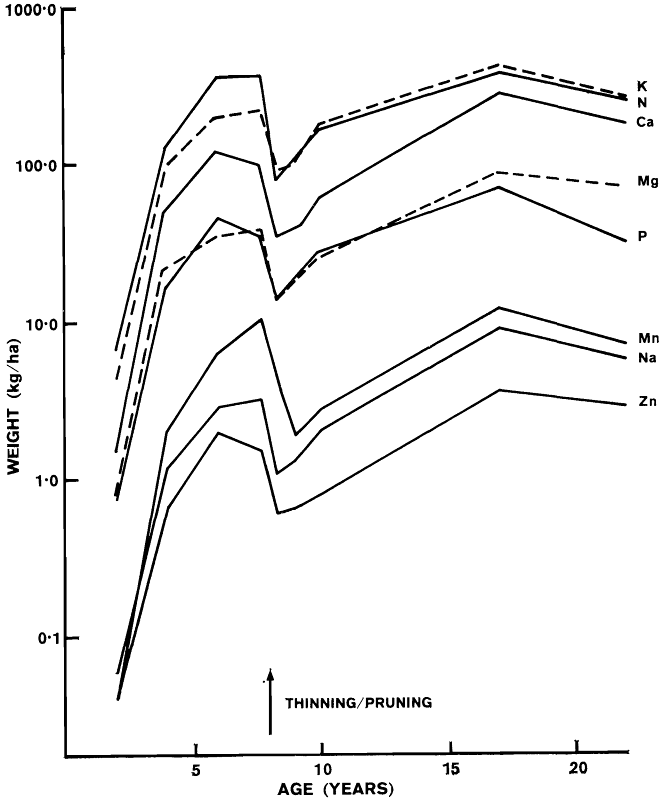

FIG. 7—The nutrient content of trees in an age series of radiata pine plantations.

In young stands, total nutrient weight increased relatively more rapidly than total dry weight. This is a result of the large contribution of canopy weight to stand dry weight and the high nutrient concentrations of the canopy components.

In the 22-year-old stand, stem wood comprised 77% of the above-ground dry matter but contained only about 20% of the nitrogen and phosphorus, 40% of the potassium, and 50% of the magnesium, calcium, manganese, and zinc (Fig. 8). At the other extreme, needles comprised only 3% of the dry weight but contained 10% of the calcium and zinc, 15-20% of the potassium, magnesium, and manganese, and 35% of the nitrogen and phosphorus. During the life of the stand any variable which affects total needle mass, such as stand closure, will have a relatively larger effect on both nitrogen and phosphorus contents of the stand. Any variable which affects total stem mass, such as stand density in closed stands, will have a relatively larger effect on the content of elements such as magnesium and calcium. However, these effects of stand structure on the nutrient content of the stands will be smaller than effects of stand age.

Nutrient Demand as a Function of Time

There was a relatively low nutrient demand on site resources during the first 2 years after establishment. Between the second and fourth years net nutrient uptake attained a high level (Table 4). At this stage, the stand is closing canopy rapidly, with a con-

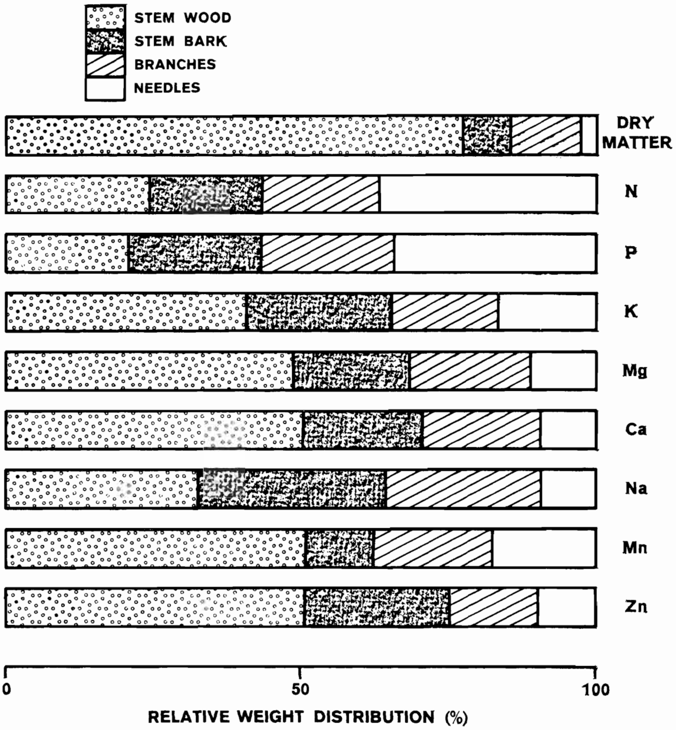

FIG. 8—The relative distribution of dry matter and eight nutrients in the main above-ground components of a 22-year-old radiata pine stand.

TABLE 4—Net and gross uptake of nutrients and their return to the soil as thinnings for selected periods of stand growth

	N	P	K	Mg	Ca	Na	Mn	Zn
Net annual uptake 0-22 years (kg/ha)	13	1.5	13	3.5	8.9	0.3	0.3	0.15
Net annual uptake 2-4 years (kg/ha)	62	7.9	49	10.5	24.4	0.6	1.0	0.32
Net annual uptake 8-10 years (kg/ha)	43	7.4	44	5.9	13.9	0.5	—0.4	0.32
Gross annual uptake 4-8 years (kg/ha)	106	13.8	77	13.8	39.5	1.0	3.7	0.5
Nutrients returned at thinning (%)	61	60	58	62	65	66	65	59
Nutrients returned at thinning in relation to amounts returned by harvesting at age 22 (%)	88	118	142	114	126	106	269	126

comitant increase in the quantity of nutrients being returned to the forest floor in litter. Towards the end of this phase net annual uptake decreases as a steady-state nutrient cycle develops under closed canopy conditions. Between ages 6 and 8 most net nutrient uptake is incorporated in branches and stems.

The scheduled thinning and pruning at age 8 would have had a dramatic effect on nutrient distribution in the ecosystem, returning about 58-66% of the elements studied to the forest floor. The total quantity of nutrients returned in this thinning is of the same order of magnitude as that which would be returned had the 22-year-old stand been harvested by clearfelling (Table 4).

As the stand begins to reclose canopy after thinning and pruning, net uptake of nutrients is high, but 2 years after thinning the total values of nutrients in the stand had not regained the levels attained before thinning. Once the canopy has regained a stable condition, net nutrient uptake drops relatively rapidly to a point where net uptake again represents nutrient added to the tree stems only.

Estimates of gross nutrient uptake are harder to obtain since effects of tissue ageing and death must be considered. The values presented in Table 4 were calculated for the period from age 4 to age 8 years when branch loss through death was negligible.

Energy Values

The caloric values of the various tissues were all slightly lower than those for a wide variety of other pine species (Ovington, 1961; Minderman, 1967; Madgwick, 1970a; Wiegert and Monk, 1972; Howard, 1973; Nemeth, 1973) (Table 5). Season of sampling has been shown to affect caloric values of branches and current needles (Madgwick, 1970a, Philpot and Mutch, 1971) but these effects are small and the observed lower values in *P. radiata* are probably real. Reproducibility of caloric values is much higher than for nutrient concentrations.

Gross energy capture of the above-ground tree biomass between ages 4 and 8 amounted to 1026 gram calories/cm^2/annum. Compared with incident radiation estimated for Rotorua (de Lisle, 1966) this respresents an efficiency of capture of 0.79%. Energy captured and stored in woody tissue based on a total 22 years' growth was about 479 calories/cm^2/annum. This value is higher than for 17 of the 19 temperate forest stands tabulated by Jordan (1971). Making assumptions similar to Jordan's, and expressing efficiency on the photosynthetically active portion of incoming radiation, the above estimate of the rate of net photosynthesis is equivalent to percentage yields of 0.79 which, according to Jordan's summary, is close to the average for temperate forests.

DISCUSSION

Over the past 20 years numerous papers have been published on pine forest biomass. Only for *Pinus densiflora* Sieb. et Zucc. has the large body of knowledge accumulated on a single species from a wide variety of sites been summarised (Satoo, 1968). In that analysis of 67 *P. densiflora* stands, Satoo concluded that foliage mass was independent of stand age from 4 to 46 years in closed stands. Only in open stands was foliage mass related to stocking. The effects of site on leaf mass were not clear, though it is known from fertiliser experiments with *Pinus resinosa* Ait. (Madgwick *et al.,* 1970; Leaf *et al.,*

TABLE 5—Caloric values (kcal/g o.d.)

Tissue	No. of samples	Average	Standard deviation
1-year needles	48	4.84	0.07
2-year needles	40	4.90	0.09
3-year needles	29	4.81	0.11
4-year needles	14	4.86	0.14
5-year needles	3	4.97	0.01
Strobili	5	5.03	0.04
Cones	14	4.77	0.05
Live branches	45	4.66	0.06
Dead branches	23	4.69	0.09
Bole bark	40	4.71	0.13
Bole wood	29	4.53	0.06

1975), *Pinus elliottii* Engelm. and *Pinus taeda* L. (White and Pritchett, 1970), *P. radiata* (Waring, 1974), and *Pinus nigra* Arnold (Miller and Miller, 1976) that increased foliage biomass is associated with growth response to fertilisation. The data for *P. radiata,* although limited, fit the patterns described for *P. densiflora,* but total weight of foliage tends to be higher for *P. radiata* than *P. densiflora.* In *P. densiflora,* branch mass increased with stand age and decreased with increased stocking. *Pinus radiata* shows similar trends.

Compared with data drawn worldwide from almost 250 stands of 16 other pine species, *P. radiata* in Australia and New Zealand has one of the fastest rates of dry matter accumulation (Fig. 9). Only a stand of *Pinus caribaea* Morelet in Nigeria (Egunjobi, 1975) and some of the stands of *P. elliottii* in Florida, United States (White and Pritchett, 1970) had a higher biomass for their age than did *P. radiata* on these Kaingaroa sites. This high rate of dry matter accumulation by *P. radiata* is not solely due to an ability to carry a heavy foliage mass, since 5 of the 17 species summarised in Table 6, exceed *P. radiata* in maximum foliage mass. Only *Pinus banksiana* Lamb., *P. ponderosa, Pinus strobus* L., and *P. virginiana* have recorded maxima well below the values for *P. radiata* stands. Very limited data are available for some of these species. Branch weights in *P. radiata* stands include some of the highest values recorded for pines, but branches form a relatively small percentage of the total above-ground mass in the older, heavier stands. From this it may be concluded that *P. radiata* canopies are relatively efficient producers of bole material. This efficiency is attributable to a high rate of assimilation per unit of foliage per annum which probably results from the prolonged season of photosynthetic activity in a favourable climate.

Data on nutrient uptake by pine stands are fewer than data on dry matter content. Since rates of dry matter accumulation in *P. radiata* stands are relatively high compared with other pines, it is not surprising that rates of net nutrient accumulation also tend

TABIE 6—Maximum needle and branch biomass for pine species

Species	Needles		Branches		References searched
	No. of stands	Mass (t/ha)	No. of stands	Mass (t/ha)	
P. banksiana	7	5.8	4	8.7	Adams, 1928; Hansen, 1937.
P. caribaea	1	11.5	1	9.4	Egunjobi, 1975.
P. contorta	6	17.4	3	23.5	Johnstone, 1971; Moir and Francis, 1972.
P. densiflora	67	9.7	67	27.0	Satoo, 1968.
P. elliottii	9	11.1	9	10.1	White and Pritchett, 1970; McKee and Shoulders, 1974.
P. nigra	11	18.1	11	38.3	Ovington, 1957a; Wright and Will, 1958; Lamberts, 1962; Minderman, 1967; Miller and Miller, 1976.
P. palustris	3	9.2	0	—	Wiegert and Monk, 1972.
P. pinaster	4	24.4	4	25.4	Keay and Turton, 1970; Turton and Keay, 1970.
P. ponderosa	1	6.8	1	30.0	Whittaker and Niering, 1975 .
P. pumila	4	25.3	4	63.9	Shidei, 1963.
P. radiata	20	15.4	17	34.0	Orman and Will, 1960; Will, 1964; Ovington **et al.**, 1968; Forrest and Ovington, 1970; Siemon, 1973; Waring, 1974; Giulimondi and Duranti, 1975; Gadgil, 1976; Williams, 1976; Present paper.
P. resinosa	70	24.7	38	30.8	Heiberg **et al.**, 1959; Jurgensen and Leaf, 1965; Singer and Hutnik, 1966; Stiell, 1966; Madgwick **et al.**, 1970; Wittwer **et al.**, 1975.
P. sylvestris	58	13.3	48	33.9	Ovington, 1957a; Wright and Will, 1958; Ovington and Madgwick, 1959; Manakov, 1961; Mälkönen, 1974; Myakushko, 1974.
P. strobus	1	2.7	1	6.8	Swank and Schreuder, 1974.
P. taeda	28	13.9	28	29.1	Akai **et al.**, 1968; 1972; Smith **et al.**, 1963; White and Pritchett, 1970; Ralston, 1973; Baker **et al.**, 1974; Wells and Jorgensen, 1975.
P. thunbergii	6	13.8	6	15.9	Ando, 1965.
P. virginiana	13	7.5	13	25.8	Madgwick, 1968; 1971; unpublished data.

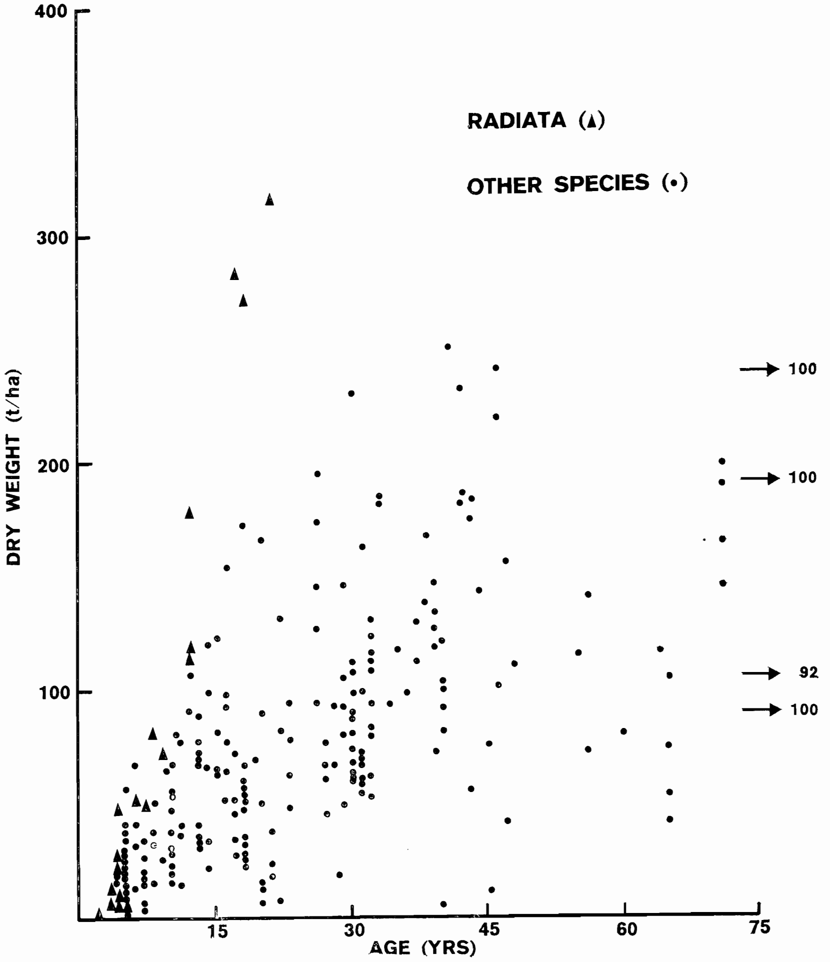

FIG. 9—Dry weight of above-ground stands of radiata pine and other pines as related to stand age.

to be higher, as illustrated for nitrogen data from 170 stands of 12 species (Fig. 10). However, plotting nutrient content against total biomass indicates that there is a broadly similar relationship for pines in general. Nitrogen data are illustrated in Fig. 10.

To investigate these relationships further, regressions were calculated of the form:

$$\log_e (\text{nutrient content}) = a + b.\log_e (\text{dry weight}) + \sum_{i=1}^{n} c_i X_i$$

where n is the number of pine species other than *P. radiata* and the X_i are dummy variables having the value 1 for the species in question and 0 for all other species. (Only those species represented by more than three plots were included). This type of analysis yields a series of values of c_i which can be considered as measures of the

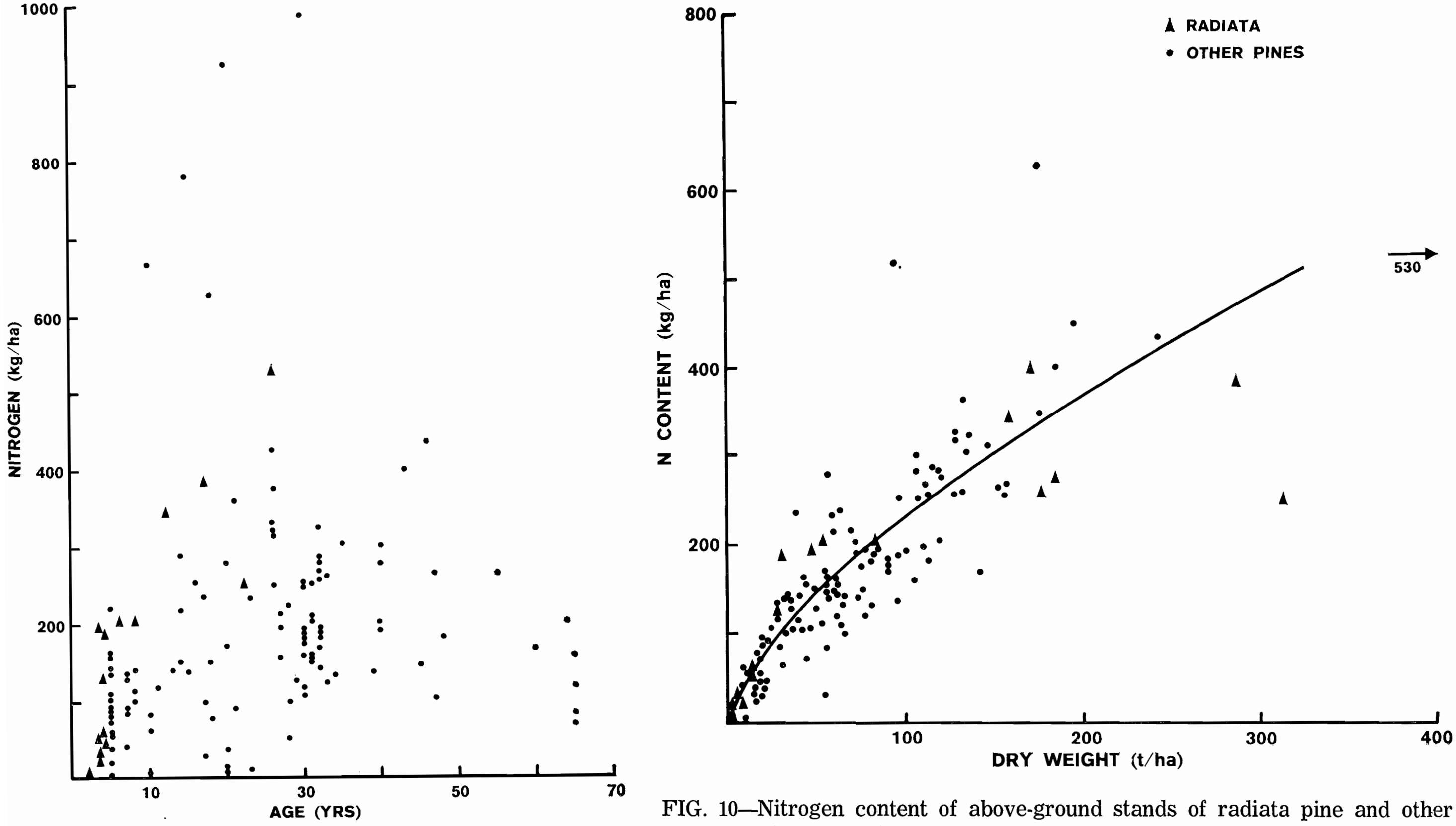

FIG. 10—Nitrogen content of above-ground stands of radiata pine and other pines as related to stand age (left) and to dry weight (right).

differences between the relationship of nutrient to dry matter contents of stands of other species compared with *P. radiata.* The results are summarised in Table 7.

A significant positive coefficient suggests that a species has a relatively higher nutrient content per unit of dry weight than does *P. radiata* while a negative coefficient suggests a relatively lower content. Coefficients which do not differ significantly from zero suggest that the relationship for the nutrient is the same for the species in question

TABLE 7—Results of multiple regression analysis relating $\log_e$ nutrient weight (kg/ha) to $\log_e$ dry weight (t/ha) and dummy variables for pine species (Significance of regression coefficients: *5%, **1%, ***0.1%)

Independent variable	N	P	K	Ca	Mg	Mn	Zn
P. banksiana[1]	—0.34**	—0.61***	—1.01***	0.03	—0.89***	—0.11	—
P. densiflora[2]	0.02	0.38	—0.33	1.18*	0.93	—	—
P. elliottii[3]	0.02	0.05	—0.68***	0.19	0.02	—1.27***	—0.60
P. nigra[4]	0.47***	0.05	—0.35	0.18	—0.57*	—	—
P. pinaster[5]	—0.40	—0.75**	—0.64*	1.00***	0.76**	—	—
P. resinosa[6]	0.04	0.02	—1.09***	1.05***	—0.57**	1.57***	0.82
P. sylvestris[7]	0.06	—0.04	—0.48	0.25	—0.31	—	—
P. taeda[8]	—0.08	—0.07	—0.76***	0.21	—0.13	—1.63***	—0.52
P. virginiana[9]	—	—0.79***	—0.60***	0.50	—0.06	1.16***	0.66
Log_e (weight)	0.65***	0.63***	0.69***	0.72***	0.76***	0.23***	0.52
Constant	2.47	0.39	2.06	1.30	0.38	0.73	—2.10
Error mean square	0.14	0.22	0.20	0.19	0.20	0.16	0.50
Number of observations	171	156	148	141	133	31	28

References searched

[1] Adams, 1928; Morrison, 1973; Foster and Morrison, 1976.

[2] Tsutsumi, 1962.

[3] White and Pritchett, 1970; McKee and Shoulders, 1974.

[4] Ovington, 1957b; Wright and Will, 1958; Lamberts, 1962.

[5] Keay and Turton, 1970; Turton and Keay, 1970.

[6] Heiberg **et al.**, 1959; Madgwick, 1962; White, 1964; Xydias, 1964; Jurgensen and Leaf, 1965; Wittwer **et al.**, 1975.

[7] Ovington, 1957b, 1959; Wright and Will, 1958; Neumann, 1966; Heinsdorf, 1967; Mälkönen, 1974.

[8] Smith **et al.**, 1963; Akai **et al.**, 1968, 1972; White and Pritchett, 1970; Switzer and Nelson, 1972; Baker **et al.**, 1974; Wells and Jorgensen, 1975.

[9] Madgwick, 1970b.

and for *P. radiata.* Thus *P. radiata* stands contain relatively larger amounts of potassium (all species coefficients negative), lesser amounts of calcium (a preponderance of positive coefficients), and intermediate amounts of magnesium and manganese. Such conclusions must be tempered by a knowledge that the data for nutrient uptake are often from a limited range of sites. Adam's (1928) plots of *P. banksiana* had an average nitrogen content 71% above predicted values and Morrison's (1973) data for the same species had average contents 16% below predicted values. Differences in stand structure would also be expected to influence the results. Similarly, the stands of *P. nigra* studied by Lamberts (1962) and one stand from Ovington (1957b) had exceptionally high contents of nitrogen for their age compared with other *P. nigra* reported in the literature (Ovington, 1957b; Wright and Will, 1958). In Fig. 10 (left) these exceptional stands constitute almost all the points plotted above and to the left of the values indicated for *P. radiata.* The *P. radiata* stands reported in this paper were on pumice soils rich in potassium. Thus the apparent species effects may really be due to different cultural environments.

Recently there has been increasing interest in the feasibility of using plants as a renewable source of energy in New Zealand (Troughton, 1976). High rates of energy capture per unit of crop area are necessary, to offset the costs of transporting the raw material to a conversion plant; these costs escalate greatly as haulage distances increase (Troughton and Cave, 1976). The *P. radiata* stands studied had a high rate of net energy capture, suggesting that this could be a candidate species for use as a source of energy in New Zealand. Further study with a view to maximising potential energy yields would appear warranted.

High nutrient uptake and the drastic effects of very heavy thinning and clearfelling on the nutrient distribution within stands emphasise the need for current research on the ecological impact of forest management. Should *P. radiata* forests also become an economic, renewable source of energy, or whole tree utilisation become the vogue, the results reported here could provide a basis for estimating nutrient drain on forest sites, and for better management of the energy-capturing process.

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APPENDIX

In the original study it was not possible to find an 8-year-old stand in the same locality and with a stocking commensurate with the other unthinned stands sampled. In view of this situation, and consequent criticism by a reviewer, additional data were collected in May 1977 from a stand (now 8 years old) within one of the original compartments studied 6 years earlier. The results are presented in Appendix Table 1.

These new data agree well with our earlier findings. Live branch mass was lower, as might be expected with higher stocking (Fig. 4 of the paper). Total foliage mass was almost identical with the earlier data (Table 1 of the paper). Predicted residual stand values are lower than in the original study because the residual crop trees in the more heavily stocked stand were smaller than the comparable stems in the stand with lower stocking. The fraction of the above-ground stand returned to the forest floor by thinning and high pruning would have been 60%, which agrees closely with the value of 55% found in the main study.

APPENDIX TABLE 1—Stocking and oven-dry weight for an 8-year-old stand sampled in May 1977

	Unthinned	Thinned
Stems/ha	2220	544
BA m^2/ha	23.1	9.6
Height (m)	10.36	11.83
Dry Weights (tonnes/ha)		
Stem wood	37.05	16.61
Stem bark	4.43	1.95
Live branches	10.53	2.73
Dead branches	0.78	0.01
1-year needles	5.13	1.90
2-year needles	0.89	0.20