UPTAKE AND ACCUMULATION OF NITROGEN IN PINUS RADIATA STANDS AS RELATED TO AGE AND THINNING

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ABSTRACT

Accumulation of nitrogen in above-ground components of **Pinus radiata** D. Don trees was measured annually in winter between ages 2 and 12 years, and stand estimates of above-ground current annual nitrogen uptake were derived. The trees, which were growing at Puruki in stands without known nitrogen or water limitations to growth, were subjected to different intensities of thinning commencing after age 6.

At age 2 the stands contained 20 kg N/ha in above-ground tree components, which increased to 600 kg/ha in the unthinned stand by age 12. In contrast, the heavily thinned stand contained only 200 kg N/ha in the live trees at age 12, but 500 kg N/ha had been deposited on the forest floor in two thinning steps. Nitrogen concentration (dry weight basis) averaged 1.6% in 1-year-old leaves, with no trend evident with stand age or thinning treatment. However, in 2-year-old leaves nitrogen decreased from 1.5% at stand age 2 to around 1.1% at stand age 5 and thereafter increased to 1.5%, a pattern evident in older leaves as well. Nitrogen in live branch wood and bark decreased from 0.3% and 1.1% respectively at age 2 to 0.15% and 0.65% by age 6, but remained more or less constant thereafter. Nitrogen in stem wood and bark decreased asymptotically from 0.26% and 1.0% respectively at age 2 to 0.10% and 0.46% by age 12. Stem nitrogen concentrations were not affected by thinning. Calculations of the current uptake of nitrogen by the leaf mass took account of (i) the nitrogen requirement for leaf growth (which peaked at 160 kg/ha/year at age 5–6), (ii) net nitrogen remobilisation from older leaves (which exported between 10% and 30% of their nitrogen, depending on current requirements for growth), and (iii) withdrawal of nitrogen from leaves immediately prior to abscission (estimated as 50% of the level in the retained cohort of leaves).

Initially the rate of nitrogen uptake above-ground increased with age from around 30 kg/ha/year at age 3 to 120 kg/ha/year at age 5. Thereafter, uptake decreased to around 90 kg/ha/year by age 12 regardless of thinning intensity, even though up to two-thirds of the stand basal area was removed at each thinning. On average 65%, 15%, and 20% of the above-ground nitrogen uptake was accounted for by leaf, branch, and stem components, respectively. With increasing stand age the percentage utilised in woody components increased slightly and leaf decreased slightly.

Keywords: nitrogen uptake; nitrogen content; nutrient translocation; thinning; **Pinus radiata**.

INTRODUCTION

Predicting the effects of management practices on long-term site productivity requires an understanding of factors controlling nutrient cycling (Kimmins & Scoullar 1984; Sands 1984). Even highly productive sites are subject to productivity declines (Messina *et al.* 1985; Dyck & Beets in press). Harvesting of *Pinus radiata* is projected to increase markedly from the mid-1990s in New Zealand. Endeavours to maintain or even increase site productivity in subsequent rotations should focus on factors controlling the established dynamics of nutrient cycling.

Various studies on accumulation and cycling of nutrients in *P. radiata* stands have been reported. These include information on the dry matter and nutrient content of the trees and litterfall collected from differently managed stands growing on relatively fertile (Madgwick 1985) and naturally infertile sites (Beets & Madgwick in press), forest floor dry matter and nutrient dynamics (Ballard & Will 1981; Carey *et al.* 1982; Will *et al.* 1983; Baker *et al.* 1986), and internal nutrient cycling (Fife & Nambiar 1984). The dynamics of nutrient cycling as affected by stand age and silvicultural treatment are still poorly understood, partly because long-term tree growth and nutrient cycling studies have not been made.

Objectives

This paper complements previous work on leaf area index and dry matter production and accumulation in *P. radiata* stands at Puruki (Beets & Pollock 1987). The concomitant uptake, accumulation, and loss of nitrogen, estimated annually between ages 2 and 12 in three stands subjected to contrasting thinning treatments and an unthinned stand at age 12, are now reported.

METHODS

Site Description and Stand Management

The forest was planted on volcanic ash soils previously under well-established pasture and converted to *P. radiata* in 1973. The area was first sprayed to kill the ryegrass/clover cover. A detailed description of Puruki soils, climate, forest establishment, and management has been given by Beets & Brownlie (1987). Stand management operations, including the timing and intensity of thinning and pruning, are outlined in Table 1. Assessment plots (between 30 and 50 plots), which are distributed randomly within the three Puruki subcatchments, Tahi, Rua, and Toru, provided data on stand basal

TABLE 1—Timing and intensity of the prescribed pruning and thinning operations in the three Puruki subcatchments until 1985. Stands were nominally planted at 2200 trees/ha in 1973

Subcatchment	Prune		First thinning		Second thinning	
	Date (mth/yr)	Height (m)	Date (mth/yr)	Stems/ha	Date (mth/yr)	Stems/ha
Tahi	3/79	2.2	5/79	550	8/83	137
Rua*	4/80	2.2	4/80	550	–	–
Toru	4/81	2.2	11/81	550	9/84	275

* A part of Rua (inviolate) was not pruned or thinned.

area, tree height, and biomass, including variability (Beets & Brownlie 1987). A large proportion of Toru was replanted in 1974 owing to poor establishment of the trees. Slash from thinnings and prunings was left on site.

Nitrogen Content

Between 15 and 21 sample trees were selected annually in winter (May through August) from 1975 to 1985, with a total of 174 trees being analysed for nutrient content (Table 2). The field and laboratory procedures for selecting and processing sample trees have been given by Beets & Pollock (1987). Oven-dry samples of 1-, 2-, and greater than 2-year-old leaves, branch wood, branch bark, dead branch matter, cones, stem wood, and stem bark from each tree were further processed as follows. Stem wood, branch wood, and dead branch samples were chipped, bark samples were crushed, and then ground to pass through a 2-mm sieve. Leaf samples were ground to pass through a 1-mm sieve. Live branches were not debarked in 1985. In 1979 crown components pruned from sample trees in February were processed as above and analysed separately.

TABLE 2—Number of sample trees harvested each year in the Puruki subcatchments, Tahi, Rua, and Toru. The unthinned inviolate area is within Rua

	Number of sample trees by year										
	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84	'85
Tahi	7	3	7	4	4	10	7	5	7	7	5
Rua	5	2	5	4	4	4	7	5	7	7	5
Toru	3	11	3	7	7	6	7	5	7	7	5
Inviolate	0	0	0	0	0	0	0	0	0	0	5
Total harvested	15	16	15	15	15	20	21	15	21	21	20

Chemical analyses were carried out by the Forest Research Institute Soils Laboratory in years 1975–78 and 1982–85. Samples were digested on a block digester with sulphuric acid and hydrogen peroxide in the presence of lithium sulphate and selenium catalyst. Nitrogen in the digest was determined colorimetrically using the indophenol blue method (Nicholson 1984). Analytical Services Limited analysed samples in 1979–81 using a Kjeldahl digestion with selenium catalyst, and nitrogen was determined colorimetrically. Nitrogen was expressed on an oven-dry weight basis for calculating nitrogen content. For leaves, nitrogen was also expressed on a leaf volume basis to examine nitrogen retranslocation.

The nitrogen content in the above-ground components of individual trees was calculated by multiplying the oven-dry weight of each tree component by its nitrogen concentration (wt basis). The nitrogen content in the above-ground components of the stands was estimated from the sample tree and plot assessment data using the basal area ratio method (Madgwick 1981). Separate ratios were calculated for each sub-catchment and year to avoid possible bias associated with ratios based on the combined data.

Stand Nitrogen Uptake Above-ground

Stem, branch, and cone nitrogen uptake were calculated as the increase in the nitrogen content of the component per hectare between successive years, including mortality losses. As thinning prevented most branch and tree mortality, uptake in thinned stands was associated mainly with living components. Leaf nitrogen uptake was calculated as the weight of nitrogen per hectare in 1-year-old leaves (that is, the nitrogen requirement for new leaf growth) minus nitrogen which had been retranslocated from leaves older than 1 year. Retranslocation was, in turn, estimated as the nitrogen content per hectare of each cohort of leaves in year t minus the amount of this nitrogen which could be accounted for in (i) attached leaves in year t + 1, and (ii) abscissed leaves assuming these had a nitrogen content equal to 50% of their attached counterparts. No adjustments were made for nitrogen losses due to leaf consumption and canopy leaching, and foliar uptake of nitrogen from atmospheric sources was assumed to be zero (Dyck *et al.* 1987). Leaf density changes were ignored when calculating losses associated with litterfall. Leaf retention was assumed to be 3 years at maximum; most leaves had a life span of 2 years or less (Beets & Pollock 1987).

Because annual biomass estimates were not made in the inviolate plots, nitrogen uptake for the 1984–85 increment period had to be estimated using a different method. The nitrogen concentrations in stem wood and bark at ages 11 and 12 were estimated using the equations:

$$\text{Stem wood nitrogen concentration} = 0.313_e{}^{-0.104\,\text{Age}} \qquad (r^2 = 0.99)$$

$$\text{Stem bark nitrogen concentration} = 1.1673_e{}^{-0.0849\,\text{Age}} \qquad (r^2 = 0.99)$$

These exponential functions, which were fitted using nonlinear least squares regression to the data given later in this paper, describe the decrease in stem nitrogen concentration up to age 12. The estimated nitrogen concentrations were then applied to the dry matter data measured in 1985 and estimated in 1984 (Beets & Pollock 1987); nitrogen uptake was then calculated by the difference in nitrogen content between years. Nitrogen uptake into branches was obtained as for stems; however, the nitrogen concentration used at age 11 was that measured at age 12. Nitrogen uptake into leaves was calculated as described for leaves already, but making the additional assumption that the pattern of distribution of leaf dry matter and nitrogen between age-classes in 1984 was the same as that measured in 1985.

These uptake calculations gave the nitrogen requirements of above-ground tree components that had to be met by root uptake.

RESULTS

Component Nitrogen Concentrations

The weighted mean nitrogen concentration of 1-year-old leaves was almost constant at 1.6% for all stands regardless of tree age and thinning. Mean foliar nitrogen concentration decreased as leaves aged on the trees (Fig. 1), especially in cohorts produced when the stands were younger (Fig. 2a). Withdrawal of nitrogen from the leaves is confounded by concomitant increases in leaf density (Beets & Lane 1987) in Fig. 2a. Leaf nitrogen content was therefore expressed on a leaf volume basis (Fig. 2b); trends are due to net retranslocation of nitrogen. The downward trends are steepest between stand ages 3 to 5 years (1976–78) during which time net withdrawal averaged 32%. From age 6 (1979 onwards) withdrawal declined to 10%, on average. Leaf nitrogen concentration on a volume basis is more variable in 1-year-old leaves than corresponding data expressed on a dry weight basis, and shows a tendency to increase with stand age.

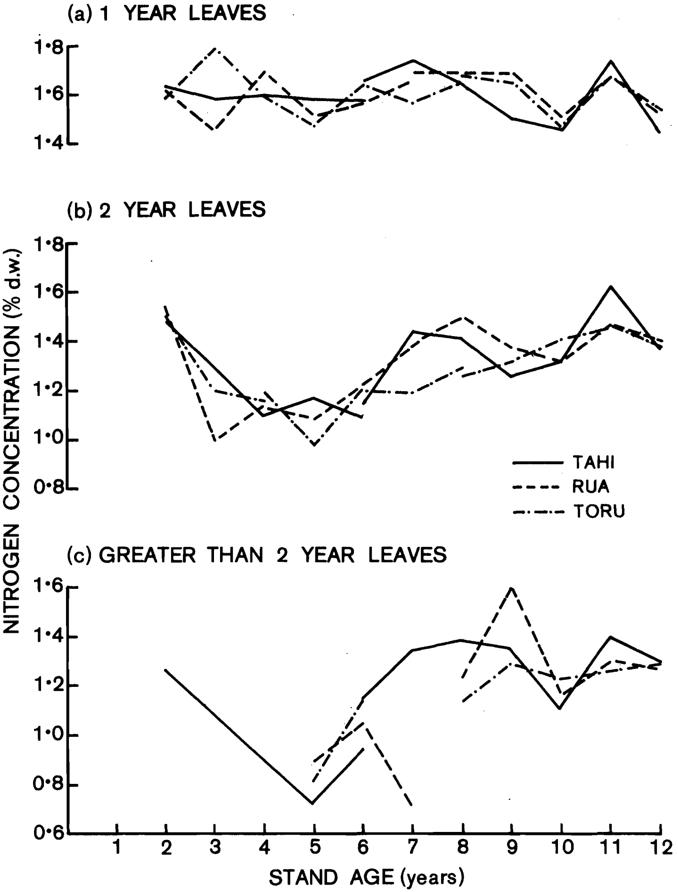
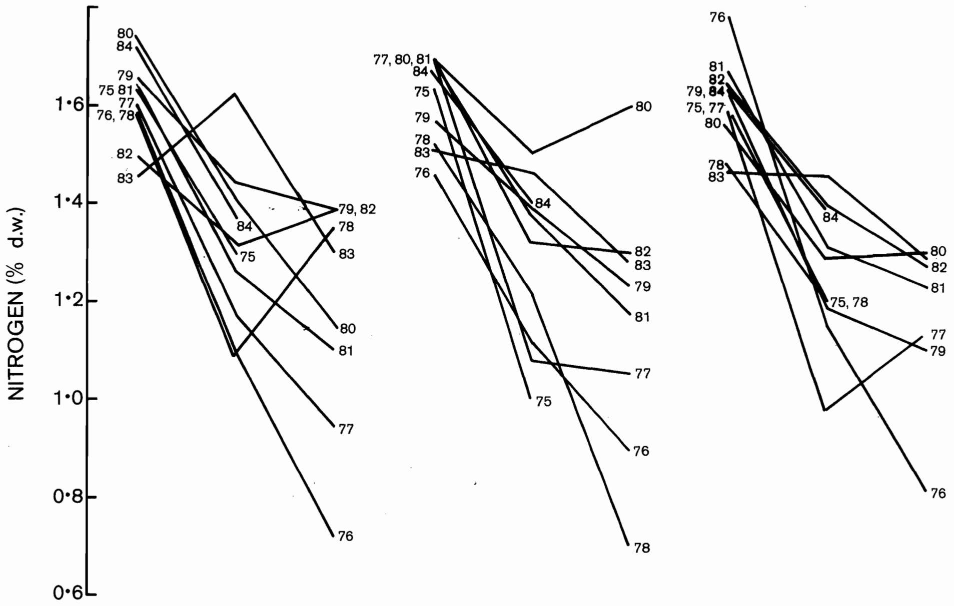


FIG. 1—Nitrogen concentration in different age-classes of live foliage v. stand age.

Both in branches and in stems, bark and wood nitrogen concentrations (dry weight basis) decreased by a factor of 2 to 3, as stand age increased. In branches (Fig. 3) most of the decrease occurred by age 6, but in stems (Fig. 4) the nitrogen concentration decreased throughout the study period. The nitrogen percentage of bark was five times higher than wood (Fig. 3, 4); however, wood plus bark combined had only double the nitrogen concentration of wood alone. Because thinning prevented most branch mortality at the base of the crown, the dead branch matter consisted mainly of dead twigs from within the live crown; these tended to have a higher nitrogen concentration than live branches (Fig. 3).

(a) EXPRESSED ON A LEAF DRY WEIGHT BASIS



(b) EXPRESSED ON A LEAF VOLUME BASIS

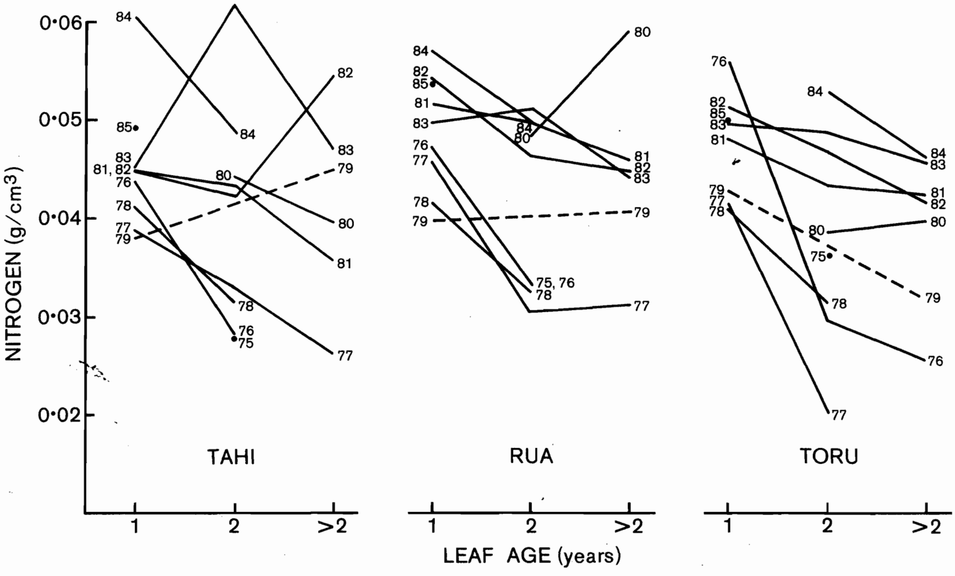
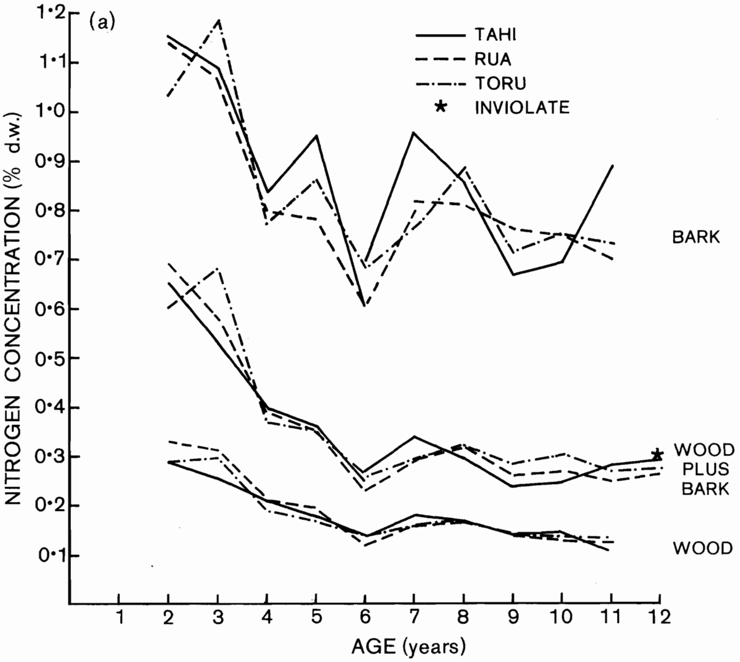


FIG. 2—Leaf nitrogen concentration v. leaf age for cohorts of leaves initiated in the year shown (dashed line = missing data).



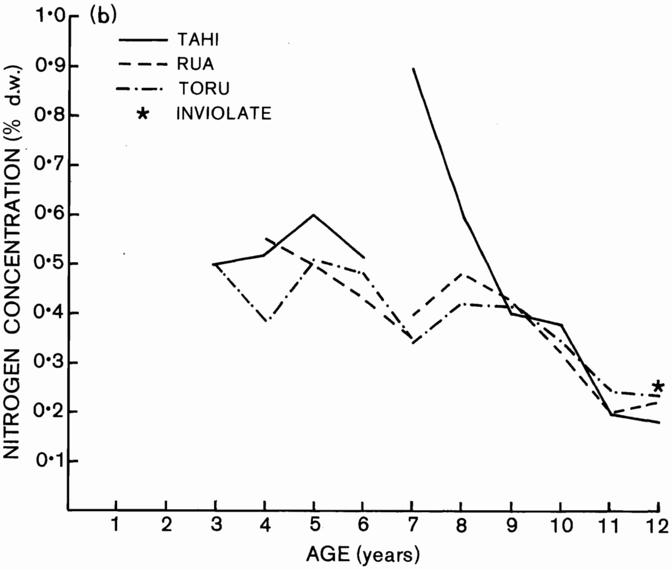


FIG. 3—Nitrogen concentration (a) in live branch components **v.** stand age, and (b) in dead branch matter **v.** stand age.

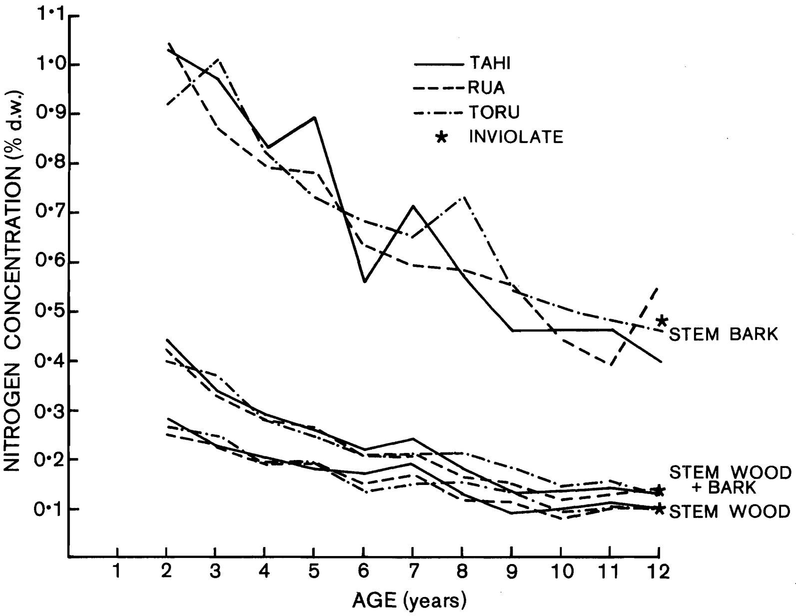


FIG. 4—Nitrogen concentration in stem components v. stand age.

Nitrogen Accumulation Over Time

Tree nitrogen content above-ground (Fig. 5) and by tree component (Table 3) was influenced by the need to replant in Toru, and by stand age, thinning and sampling variability. At age 2 years between 8 and 24 kg N/ha were contained in above-ground components. By age 12 this had increased in the unthinned (inviolate) stand to 561 kg/ha. In contrast, the twice-thinned Tahi stand contained only 214 kg N/ha at age 12, but was accumulating nitrogen rapidly. The standard error of the dry matter estimates increased with increasing stand age (Beets & Pollock 1987). Most variability in nutrient contents is associated with variability in the dry weight estimates (Levett *et al.* 1985).

The proportion of the above-ground nitrogen distributed in stems increased with stand age, but also seemed to depend on thinning (Fig. 5). Thus, while the canopy was open, more nitrogen accumulated in crowns than in stems, countering the effects of pruning which removed the lower portion of the tree crowns. This pattern reversed after canopy closure. Hence, on a stand basis, thinning was associated with a reduction not only in the above-ground nitrogen content per hectare in live trees but also in the proportion of nitrogen in the stems of the remaining trees.

Current Annual Nitrogen Uptake

Current annual uptake of nitrogen above-ground peaked at ages 4–5 (Fig. 6) and corresponded with more-intense nitrogen withdrawal from the older leaf age-classes (Fig. 2b). The rate of uptake increased steeply from about 30 kg/ha/year at age 3 to

PERCENTAGE NITROGEN IN STEM

TAHI	13	18	15	16	17/25	29	24	23	25/25	29	27
RUA	14	15	16	18	16	29/35	28	27	27	29	31
TORU	14	18	16	17	16	25	30/37	31	26	26/26	29
INVIOLATE											38

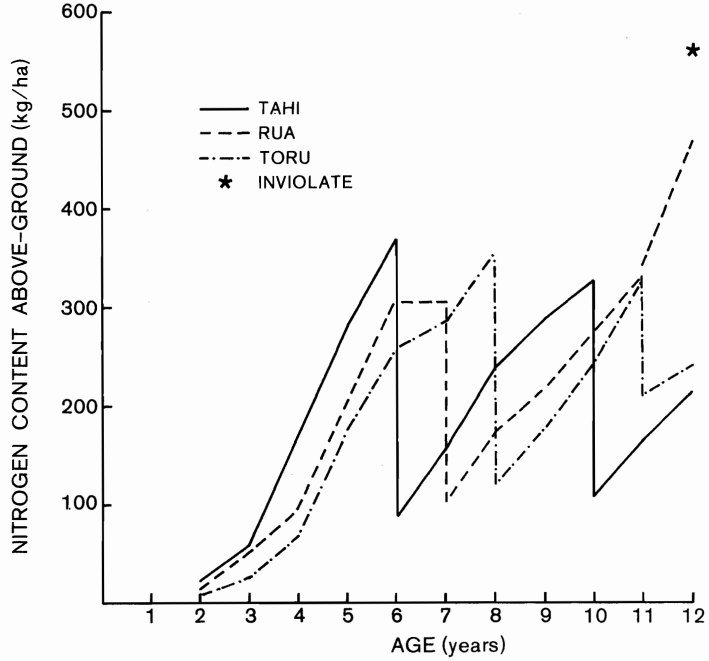


FIG. 5—Nitrogen accumulation by above-ground live tree components of **Pinus radiata** stands in different subcatchments at Puruki.

120 kg/ha/year at age 5; thereafter it tended to decrease and by age 12 had declined to around 90 kg/ha/year. The peaks and troughs in Fig. 6 are not consistently associated with thinning operations. Sampling variability increased with age; the high uptake shown for Rua at age 12 appeared to be an over-estimate as uptake decreased to 55 kg/ha in the following year (P. N. Beets, unpubl. data). The over-all decrease in current annual uptake of nitrogen after age 5 (with 14 of the 18 estimates less than 90 kg/ha/year) occurred in both thinned and unthinned stands, even though up to two-thirds of the stand basal area was removed at each thinning.

Of the current annual uptake of nitrogen above-ground in successive years, on average about 65%, 15%, and 20% was accounted for by leaf, branch, and stem uptake, respectively (Fig. 7). These percentages varied only slightly over time, but showed a trend for the relative contribution to above-ground uptake by the leaves to decrease with stand age as those for branches and stems increased.

TABLE 3—Nitrogen content of above-ground components of *Pinus radiata* stands in three subcatchments at Puruki

Sub-catchment	Age (years)	Stand nitrogen (kg/ha)										
		Stem wood	Stem bark	Dead branch	Branch wood	Branch bark	Leaves >2 yr	Leaves 2 yr	Leaves 1 yr	Leaves immature	Cones	Tree total
Tahi	2	1.51	1.55	0.00	0.75	2.18	0.38	2.22	8.20	3.65	3.42	23.86
	3	5.85	4.29	0.05	3.02	5.97	0.00	3.09	31.62	2.04	1.84	57.77
	4	14.70	10.39	0.31	10.48	17.11	0.00	10.89	106.91	0.08	0.00	170.87
	5	26.95	17.95	0.18	18.76	31.78	0.22	36.07	148.10	0.47	0.47	280.95
	6	41.64	21.30	1.13	21.46	31.42	25.96	65.88	158.78	0.00	0.00	367.58
	T6	14.72	7.53	0.00	4.67	7.44	2.65	6.93	46.01	0.00	0.00	89.95
	7	31.17	14.10	0.45	11.35	15.29	0.27	15.46	62.83	2.27	2.40	155.59
	8	37.92	19.48	0.72	19.49	24.55	2.64	32.93	99.25	0.66	0.61	238.24
	9	43.09	23.12	1.95	24.20	27.22	4.84	51.41	106.35	2.34	3.35	287.86
	10	52.75	27.96	5.66	37.14	41.88	3.40	60.43	95.39	0.00	2.91	327.52
	T10	17.52	9.29	1.88	12.34	13.91	1.13	20.07	31.69	0.00	0.97	108.80
	11	33.62	13.94	0.81	12.33	28.86	7.93	22.58	42.60	0.00	1.27	163.93
	12	39.31	18.16	1.48	54.11*	0.00	5.98	23.29	69.58	0.00	2.05	213.97
Rua	2	0.84	0.94	0.00	0.36	1.03	0.07	1.08	3.90	2.50	2.37	13.09
	3	4.54	3.06	0.05	3.03	5.86	0.00	0.30	28.64	2.65	2.62	50.74
	4	8.85	6.12	0.11	4.84	7.93	0.00	5.80	60.70	0.00	0.00	94.34
	5	22.59	13.34	0.25	12.25	18.68	1.71	23.03	101.72	0.04	0.04	204.66
	6	32.08	17.01	1.49	19.54	26.16	18.64	68.38	122.36	0.00	0.00	305.67
	7	63.10	25.12	8.20	20.41	27.34	0.14	45.19	109.39	2.39	4.98	306.26
	T7	26.50	10.55	0.68	6.83	9.00	0.04	14.06	35.44	0.80	1.89	105.79
	8	31.95	15.82	2.05	12.08	17.55	0.49	13.20	77.33	1.15	1.64	173.24
	9	38.37	20.67	5.32	13.09	18.91	0.32	12.95	106.50	0.64	1.15	217.93
	10	46.49	26.31	4.99	22.10	36.36	0.35	41.50	91.58	0.00	1.28	270.97
	11	68.51	29.55	6.75	29.72	40.23	25.03	56.46	73.70	0.00	3.13	333.05
	†11	70.72	30.50	6.96	30.67	41.52	25.84	58.28	76.07	0.00	3.23	343.79
	12	93.75	50.77	6.59	117.67*	0.00	38.61	53.03	97.67	0.00	6.60	464.69
Toru	2	0.57	0.55	0.00	0.29	0.73	0.06	0.60	3.19	1.11	1.05	8.15
	3	2.73	2.23	0.05	1.23	3.68	0.00	0.24	16.25	0.97	0.97	28.33
	4	6.13	4.29	0.14	3.09	5.58	0.00	1.79	45.75	0.39	0.00	67.17
	5	19.16	9.99	0.36	10.03	17.62	0.65	29.48	86.80	0.03	0.03	174.15
	6	25.15	17.06	2.84	15.47	22.41	0.45	37.53	139.38	0.00	0.00	260.28
	7	44.47	24.93	11.80	18.00	25.19	0.04	35.70	114.72	3.84	3.43	283.10
	8	71.23	35.18	11.40	25.83	39.59	1.54	29.74	134.68	2.05	2.59	353.82
	T8	30.25	15.58	2.18	7.13	11.29	0.57	8.19	48.70	0.66	0.00	124.55
	9	34.36	19.38	2.71	10.59	17.32	0.63	19.63	69.79	0.32	0.33	175.07
	10	37.09	24.37	2.51	13.85	28.76	2.79	45.25	85.99	0.00	0.18	240.78
	11	59.09	27.70	6.00	19.91	32.41	14.43	68.36	99.51	0.00	0.71	328.13
	T11	38.21	17.92	3.88	12.88	20.96	9.33	44.21	64.35	0.00	0.46	212.20
	12	45.71	22.98	3.20	42.45*	0.00	16.13	36.27	71.16	0.00	0.64	238.54
Inviolate‡	12	141.25	71.23	54.04	89.75*	0.00	28.66	61.01	111.56	0.00	3.11	560.60

T After thinning.

* At age 12 branch wood includes bark.

† Assessment plots increased from seven to 10 in Rua.

‡ Located within the Rua subcatchment.

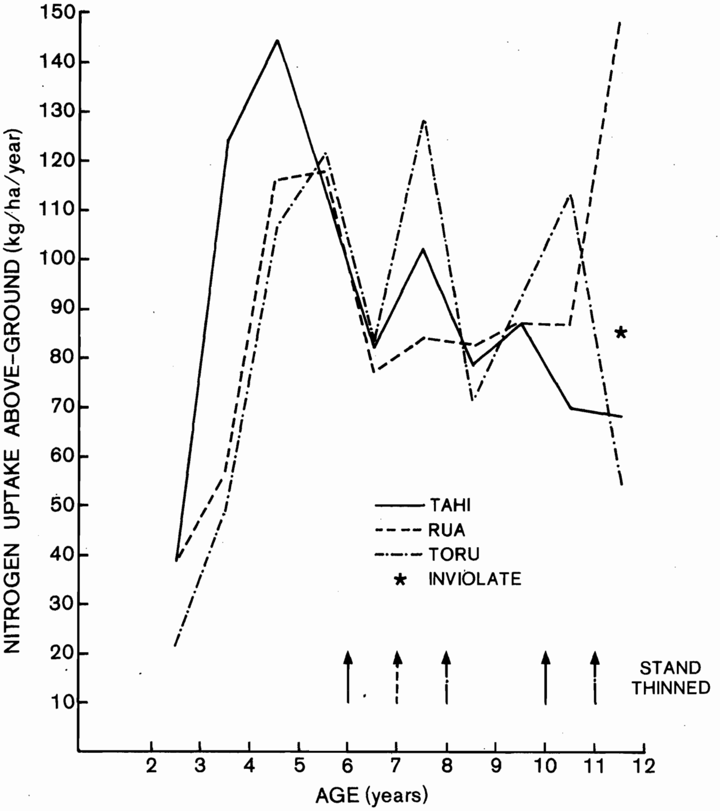


FIG. 6—Nitrogen uptake by above-ground tree components of **Pinus radiata** stands in different subcatchments at Puruki.

Although thinning did not seem to influence nitrogen uptake into above-ground components on an area basis, in the recently thinned stands both the nitrogen used in leaf growth and that recycled internally from aging and dying leaves decreased compared to unthinned stands (Fig. 8). The same trend is likely to occur for stems and branches. The net effect determines the amount of current annual uptake of nitrogen into above-ground components on an area basis. If the current annual uptake value (Fig. 6) is divided by the corresponding stocking (Table 4), it can be seen that mean nitrogen uptake per tree increased immediately after each thinning to a higher plateau level dependent on stocking.

The quantity of leaf nitrogen retranslocated annually peaked between ages 6 and 7, 1 year after nitrogen requirements for new leaf growth peaked (Fig. 8). Between 60 and 80 kg N/ha/year were retranslocated at that time. The secondary peaks in requirements and retranslocation, recorded 4 years after a thinning (Fig. 8), were smaller and decreased with stand age. By age 12 only about 40 kg leaf N/ha was retranslocated annually (Fig. 8).

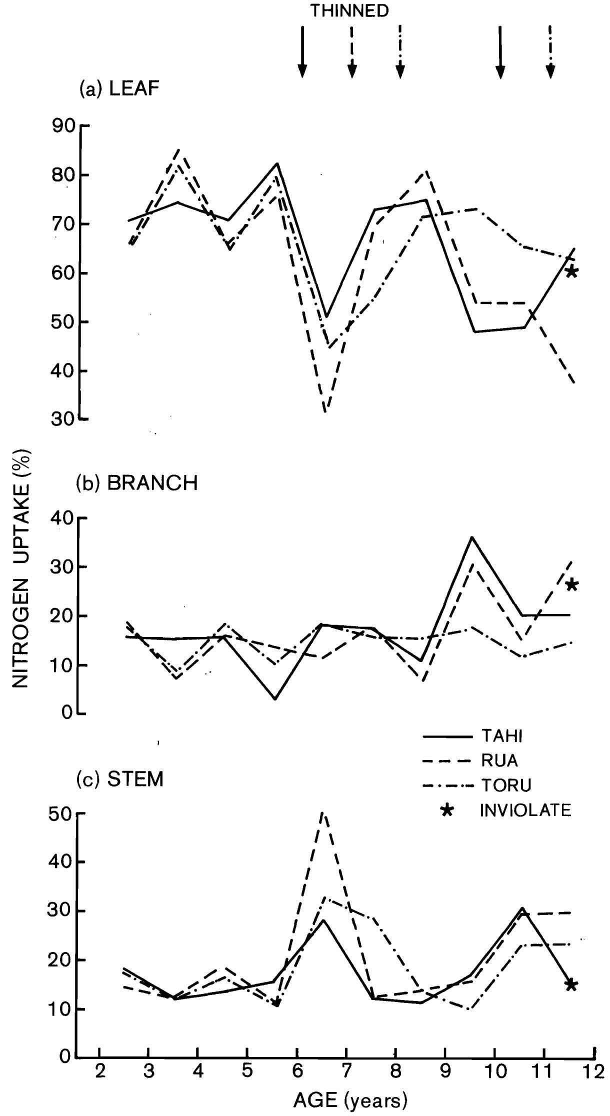


FIG. 7—Percentage of current annual nitrogen uptake above-ground due to leaf, branch, and stem uptake.

Cumulative Nitrogen Uptake and its Disposition

Although the cumulative amount of nitrogen taken up into above-ground tree components between ages 2 and 12 years was similar for the different stands, it was distributed very differently at age 12, depending on the particular thinning regime (Table 5). Cumulative uptake was around 900 kg/ha, though slightly less in Toru, which had to be replanted because of tree establishment problems. If we assume nitrogen

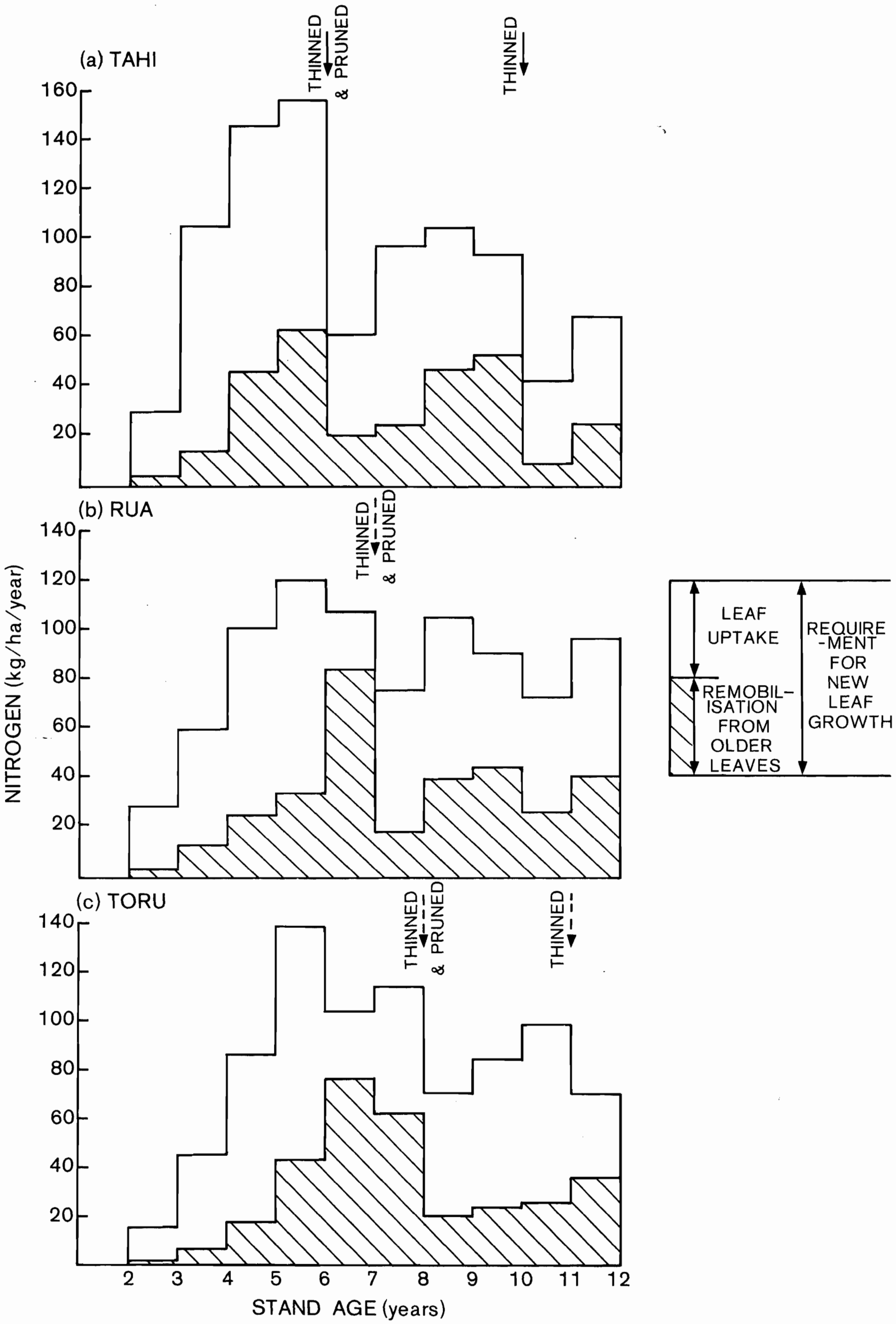


FIG. 8—Amount of nitrogen required annually for leaf growth and how this was met through remobilisation from older leaves and uptake for Tahi, Rua, and Toru stands.

TABLE 4—Current annual nitrogen uptake (kg) per tree in relation to tree stocking changes following thinning in the Tahi, Rua and Toru subcatchments. The unthinned inviolate stand is in Rua.

	Tahi		Rua		Toru		Inviolate	
Stand age (yrs)	Stems/ha	Uptake	Stems/ha	Uptake	Stems/ha	Uptake	Stems/ha	Uptake
2–3	1970	20	1843	22	2133	10	1975	–
3–4	1960	63	1843	31	2092	23	1935	–
4–5	1960	73	1843	63	1969	54	1930	–
5–6	1950	59	1843	64	1969	62	1930	–
6–7	495*	166	1843	42	1962	42	1910	–
7–8	495	206	550*	153	1962	66	1905	–
8–9	495	160	550	150	561*	127	1875	–
9–10	495	176	550	158	549	155	1750	–
10–11	159*	440	550	158	540	208	1645	–
11–12	156	437	577*	258	292*	188	1610	53

* Assessment area increased by increasing the size or number of plots.

TABLE 5—Nitrogen cumulative uptake above-ground between stand ages 2 to 12 years and its disposition amongst live and dead tree components in each of the Puruki stands

Sub-catchment	Stand nitrogen (kg/ha)					
	Uptake* Age 2–12	In live trees		Total thinnings	Natural† mortality	Error‡
		Age 2	Age 12			
	A	B	C	D	E	F
Tahi	910	24	214	496	220	4
Rua	897	13	465	200	255	–10
Toru	834	8	239	345	256	2
Inviolate§	904	19	561	0	362	0

* $A = (C - B \pm F) + D + E$.

† Includes leaves, branches, and stems.

‡ Error (F) is due to assessment plot area increase over time and is calculated as the residual of the other terms, all of which are known.

§ Uptake and live trees at age 2 estimated as average of Tahi and Rua.

uptake in the inviolate stand was the average of Tahi and Rua uptakes (which seems reasonable because thinning did not influence uptake), 60% of the cumulative uptake had accumulated in live tree components at age 12 and the remainder was lost through natural mortality – mostly in leaf litter. In contrast, only 21% of the nitrogen taken up over the 10-year study period by the trees in Tahi was still present in live tree components at age 12. At Tahi, the amount of nitrogen deposited on the forest floor in thinning operations was more than double that lost through natural mortality.

DISCUSSION

The distribution of nitrogen among the main live and dead above-ground tree components was markedly affected by thinning and also varied with stand age. This confirmed results from previous *P. radiata* studies which highlighted the major influence of management factors (Madgwick *et al.* 1977; Madgwick 1985; Beets & Madgwick in press). The thinning intensities used at Puruki were severe, with up to two-thirds of the nitrogen contained in above-ground tree components deposited on the forest floor at each thinning. This nitrogen, together with that associated with natural mortality, could become available for tree uptake again later as all thinnings were left on the forest floor. Mineralisation of nitrogen in forest floor leaf litter and soil organic matter at Puruki has been reported by Dyck *et al.* (1987); however, no information is available on the fate of nitrogen in coarse thinning slash.

The uptake estimates developed using Puruki data are based on nitrogen accumulated in stands remeasured annually and include adjustments for mortality of leaves, branches, and stems. Uptake estimates for *P. radiata* given by Madgwick *et al.* (1977) are not comparable to ours because (i) their estimates were based on nitrogen accumulated in components of live trees only, and (ii) sample trees of varying ages were located in different stands. Net nitrogen accumulation rate rather than total accumulation and uptake rate was obtained in their study.

Internal redistribution of nitrogen, both from existing leaves as they age and from senescing leaves, is an important aspect of the nitrogen dynamics of trees. Fife & Nambiar (1984) demonstrated the importance of seasonal retranslocation in and out of attached leaves of all ages, this movement serving to buffer the nitrogen supply through root uptake depending on the seasonal nitrogen demands for growth. However, these workers did not examine nitrogen withdrawal at abscission. At Puruki net retranslocation out of leaves provided around 30–40 kg/ha/year of the current annual nitrogen requirements in closed stands at age 12, and more so earlier on (Fig. 8). Withdrawal of nitrogen was reflected in the measured gradual decline in leaf nitrogen concentration with age, and the assumed marked decline (50%) immediately prior to abscission. The intensity of nitrogen withdrawal from attached leaves as these aged on the trees (Fig. 2b) was most pronounced prior to stand age 6, when the tree surface roots would still have been competing with those of dense grass, fern, and other herb growth. Weed growth decreased as the tree canopy closed at about age 6 but recurred after thinning. After age 6 the intensity of nitrogen withdrawal from leaves retained on the tree decreased and the nitrogen status (leaf volume basis) of all the leaves improved, irrespective of thinning (Fig. 2b). Whether the withdrawal of nitrogen from leaves undergoing abscission remained constant at 50% of their retained counterpart values throughout the study is uncertain, given the above changes over time. If so, over-all withdrawal would average 65% and 55% prior to and after age 6, respectively.

The assumption of 50% withdrawal of leaf nitrogen immediately prior to abscission is based on live and dead foliage nitrogen concentrations in *P. radiata* stands at relatively fertile sites (Madgwick 1985), and more recent data from the inherently infertile Woodhill Forest which is established on sand dunes – all stands were over 6 years of age. Nitrogen concentrations, averaged over all age-classes of live foliage, ranged between 1.2% and 1.5% (dw) which can be compared to litterfall nitrogen which averaged 0.6% (Madgwick 1985). At Woodhill, the addition of fertiliser in conjunction with lupin doubled *P. radiata* stem growth but nitrogen withdrawal, calculated as litterfall nitrogen concentration relative to nitrogen concentration in 1-year-old foliage, averaged 50% in all treatments, regardless of the nitrogen status of the trees (Baker *et al.* 1986). However, relatively more nitrogen was withdrawn gradually as the leaves aged in the most fertile lupin plus fertiliser (LF) treatment (22%) compared to 14% in the control (C), but relatively less at the time of leaf abscission (39% in the LF compared to 43% in the C), based on tree data given by Beets & Madgwick (in press). Comparing live and dead leaf nitrogen concentrations provides a reasonable indication of nitrogen withdrawal (van den Driessche 1984).

Withdrawal of nitrogen is better calculated from the change in leaf nitrogen content expressed on either a leaf number or a leaf volume basis. Wells & Metz (1963) compared the nitrogen content per needle of yellow and green fascicles of the same age in *P. taeda* L. and calculated that 50% of the nitrogen, phosphorus, and potassium was translocated out of the leaves prior to abscission. Likewise, we estimated nitrogen withdrawal at Puruki (P. N. Beets unpubl. data) by selecting paired fascicles (one green, the other yellow and still fully turgid) from throughout the crowns of 12 clonal trees during July 1987. Six trees (three clones × two replicate trees) were located in Tahi (at 160 stems/ha), the other six in Rua (at 550 stems/ha). Fascicle fresh volume, oven-dry weight, and nitrogen content were measured using methods described by Beets & Pollock (1987). Senescing leaves had a significantly lower nitrogen concentration (dry weight basis) and dry weight than their green counterparts, and nitrogen withdrawal (reduction in nitrogen concentration expressed on a leaf volume basis, assuming that nitrogen concentration of matching green fascicle is the correct initial value for the yellow fascicle) was significantly different between subcatchments (Table 6). The 50% withdrawal assumption seems reasonable while the stands were recovering from the effects of thinning, but may be too high for the fully closed Rua stands growing with an ample supply of soil nitrogen. Leaf litterfall collected monthly in litter traps during 1984–85 had 0.7% and 0.9% N in Tahi and Rua, respectively (D. Santantonio, unpubl. data), while our mass balance estimates for the corresponding period, with the 50% retranslocation assumption, gave 0.8% and 0.7% N in leaf litter for Tahi and Rua respectively. These data also suggest that nitrogen withdrawal was slightly less in Rua for that period. These discrepancies due to assumptions are small, especially when viewed in relation to sampling variability.

TABLE 6—Nitrogen concentration and density of green and yellow *P. radiata* leaves sampled from throughout the crown of 12 trees, with calculated nitrogen and dry matter withdrawal values immediately prior to leaf abscission in the Tahi (open) and Rua (closed canopy) subcatchments at Puruki

Subcatchment	Variable	Green	Yellow	Withdrawal† (%)
Tahi	Nitrogen (% dw)	1.41	0.79	48*
	Density (g/cc)	0.37	0.35	6.5
Rua	Nitrogen (% dw)	1.33	0.92	35*
	Density (g/cc)	0.37	0.35	6.7

* Significantly different at 5% probability level.

† In Tahi withdrawal (%) = [(1.41 x 0.37) – (0.79 x 0.35)] / (1.41 x 0.37)
Dry matter withdrawal (%) = (0.37 – 0.35) x 100 / 0.37.

Current annual uptake of nitrogen into above-ground tree components reflects (i) annual dry matter growth above-ground, (ii) partitioning of growth to leaves, branches, stems, and cones, (iii) component nitrogen concentrations (weight basis), and (iv) nitrogen remobilisation. Compared to nitrogen concentrations, which are nearly constant for leaves, dry matter growth and partitioning are more variable over time (Beets & Pollock 1987). Furthermore, retranslocation after age 6 decreases over time (Fig. 8). Hence, the dynamics of nitrogen uptake reflect the (initially) rapid increase in leaf mass followed by the progressive decrease in partitioning of growth to leaves over time.

Thinning did not switch the dry matter partitioning strategy back to a more juvenile growth pattern (Beets & Pollock 1987) and, consequently, the nitrogen uptake pattern did not revert to an earlier stage. A secondary nitrogen uptake peak hypothesised by Miller (1981) and Turner & Lambert (1986) was not evident at Puruki (Fig. 6). Stands in which a positive growth response to nitrogen fertiliser occurs soon after thinning (Hunter *et al.* 1985), but not otherwise, may do so because nitrogen supply to the trees is reduced in some way by the thinning operation. Such a reduction could be due to increased competition from weeds and temporary immobilisation of nitrogen by the thinning waste (Dyck *et al.* 1987). The relationship between thinning and other aspects of nutrient cycling is generally poorly understood (Nambiar *et al.* 1984).

Interestingly, a marked and immediate increase in nitrogen uptake on a mean tree basis occurred at Puruki after thinning. Extensive grafting of *P. radiata* root systems, previously reported by Will (1966), was evident at Puruki from the large number of tree stumps which remained alive. Thus, an immediate increase in per tree uptake after thinning would not be unexpected, but translocation across root-grafts does not seem to have been examined quantitatively (van den Driessche 1984). The relationship between above-ground dry matter production and nitrogen uptake varied with tree age but not with stocking as discussed by Beets & Pollock (1987).

The Puruki data will be useful for predicting likely nitrogen demands for maximum growth. Nitrogen supply from the soil, on an annual basis, could not have limited tree growth even in the heavily thinned Tahi stand. The foliar nitrogen concentration measured after the main period of seasonal growth (February–March) decreased in Tahi compared to the unthinned and lightly thinned stands (Beets & Brownlie 1987), and nitrogen withdrawal from senescent leaves increased while the canopy was open (Table 5), presumably in response to increased weed competition and temporary immobilisation of nitrogen in thinning slash. At age 12 at least as much weed growth occurred in Tahi as at any other time, with 164 kg N/ha in understorey vegetation in 1978 (Beets & Brownlie 1987), and some adaptation by the trees to the reduced supply of nitrogen from the soil was evident. Nevertheless, the rapid net nitrogen mineralisation rates and the high nitrate concentrations in ground water measured at Puruki (Dyck *et al.* 1987) indicate that nitrogen supply exceeded requirements for maximum growth of the trees and the understorey vegetation; addition of further nitrogen (for example, in fertiliser) may increase nitrogen concentrations in the tree components but will more surely accentuate leaching problems.

CONCLUSIONS AND IMPLICATIONS

Annual amounts of nitrogen taken up into above-ground components of *Pinus radiata* increased markedly during the years prior to canopy closure which occurred at age 6 and then slowly decreased, irrespective of the thinning intensities studied.

More rapid development of leaf mass in young stands was associated with high nitrogen uptake rates and a greater internal redistribution of nitrogen. A progressive reduction in the proportion of dry matter growth partitioned to leaves with increasing stand age decreased nitrogen uptake after canopy closure, and prevented thinned stands from reverting to their juvenile high peak uptake levels.

After thinning, factors such as increased weed competition and temporary immobilisation of nitrogen by thinning wastes could reduce nitrogen supply to the trees. Such supply factors, may underlie the response of some recently thinned stands in Kaingaroa Forest to fertiliser additions.

A growth response to fertiliser is highly unlikely at Puruki because nitrogen supply is adequate to meet the demands of the trees, the understorey vegetation, and, presumably, the decomposer organisms.

Under conditions of ample nitrogen supply, thinning did not affect cumulative nitrogen uptake by the trees over a 10-year period, but did markedly alter the distribution of nitrogen in various live and dead organic matter pools.

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