

NITROGEN AVAILABILITY AND COMPARISON TO UPTAKE IN TWO NEW ZEALAND PINUS RADIATA FORESTS

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ABSTRACT

Soil and forest floor net nitrogen mineralisation, and inorganic nitrogen in precipitation, throughfall, soil leachate, and streamwater, were measured; estimates of apparent plant nitrogen uptake derived from these data were compared to biomass estimates of nitrogen uptake for four *Pinus radiata* D. Don stands - a high- and a low-stocking density on a very fertile former pasture site, and a high- and a low-nutrition treatment on a low-fertility coastal sand site. Net nitrogen mineralisation rates for the four sites were 126, 90, 9, and 2 kg/ha/yr respectively. The annual rate for the low-nutrition treatment at the coastal sand site was lower than any previously reported for forests. Apparent nitrogen uptake from the forest floor and soil did not agree with biomass uptake estimates except at the highly stocked former pasture site. Differences in stocking did not have a significant effect on nitrogen mineralisation. At the coastal sand site, nitrogen mineralisation rates were significantly greater in the high-nutrition plots than the low-nutrition plots but were much lower than the rate required for current tree growth for both treatments. There are various possible reasons for the low measured nitrogen mineralisation rate.

Keywords: nitrogen; mineralisation; lysimeters; *Pinus radiata*.

INTRODUCTION

In many forest ecosystems production is limited by nitrogen (Cole 1981) and, for some sites, production has been shown to be highly correlated with soil nitrogen mineralisation (Pastor *et al.* 1984). Generally, most soil nitrogen occurs in organic form and low amounts exist in plant-available ionic forms, ammonium ($\text{NH}_4\text{-N}$) and nitrate ($\text{NO}_3\text{-N}$). Therefore, before the bulk of the soil nitrogen can be utilised, it must undergo microbial transformation to inorganic nitrogen, a process referred to as mineralisation. Simultaneously, microbial biomass utilises available nitrogen for its own development, a process known as immobilisation. Neither mineralisation nor immobilisation occur in isolation and the nitrogen made available for plant uptake is the net result of both processes, summarised as mineralisation-immobilisation turnover (MIT) or net mineralised nitrogen. It is MIT that largely regulates the supply of plant-available nitrogen and, thus, net primary production (NPP) (Jansson & Persson 1982).

An understanding of factors controlling net nitrogen mineralisation and an estimate of net mineralisation rates are required in some forest ecosystem models and for the prediction of the nutritional consequences of forest management practices (Kimmins

& Scoullar 1984). The objectives of the present study were (1) to measure nitrogen availability at two contrasting *P. radiata* forests, Puruki and Woodhill, (2) to compare nitrogen availability with nitrogen uptake for the two sites, and (3) to determine the influence of a change in tree stocking (i.e., stand density) and site fertility on net nitrogen mineralisation rates. Available nitrogen includes inorganic nitrogen present in the forest floor and soil, net nitrogen mineralised, and inorganic nitrogen added in precipitation.

METHODS

Location

Puruki is a 34-ha experimental catchment located on the central volcanic plateau of the North Island, New Zealand. The topography is moderately steep and annual precipitation is approximately 1500 mm. The soils are predominantly Oruanui silty sand formed from Taupo pumice, on older ash beds (Rijkse & Bell 1974). These have deep friable topsoils and loose coarse-textured subsoils. A more complete description of the site has been provided by Beets & Brownlie (1987).

The catchment was converted from native forest to pasture in the 1920s, allowed to revert to scrub, and reconverted to pasture in 1957. *Pinus radiata* was planted at 2000 stems/ha in 1973 and, beginning in 1979, the majority of the stand was thinned to 550 stems/ha. Nitrogen mineralisation was studied in the unthinned (P2000) and an adjacent thinned (P550) area. No understorey was present in the P2000 treatment and bracken (*Pteridium esculentum* (Forst. f.) Kuhn) was unevenly distributed in the P550 treatment. Accumulation and partitioning of dry matter at Puruki have been measured annually since 1974 (Beets & Pollock 1987). Fine and small root production was measured in 1985 and 1986 (Santantonio & Santantonio in press).

Woodhill Forest is located 50 km north-west of Auckland on recently stabilised coastal sands. Topography is rolling sand dunes, and rainfall averages 1100 mm per year. The sands are recently deposited from the Tasman Sea and, under the influence of vegetation, weather to Pinaki sands (Cox 1977). The nitrogen content of the sand is very low (Gadgil *et al.* 1984) and forest management relies on tree lupin (*Lupinus arboreus* Sims.), a nitrogen-fixer, to supply nitrogen.

Five hectares of Cpt 138 at Woodhill Forest have been the site of a long-term trial established in 1968 to investigate the importance of soil moisture and soil fertility on the early growth of *P. radiata* planted on coastal sands (Jackson *et al.* 1983). Above-ground dry matter and nutrient content of the trees have been measured periodically (Beets & Madgwick in press) as have the distribution and cycling of nutrients (Baker *et al.* 1986). In the present study, nitrogen mineralisation was measured in the lupin plus fertiliser (LF) high-nutrition treatment and in the lupin excluded (LE) low-nutrition treatment. Tree stocking was 2224 stems/ha and, at the time of the study, no understorey was present in either treatment. Nitrogen input by fertiliser and lupins to the LF treatment ended approximately 7 and 12 years respectively prior to this study, by which time approximately 900 kg N/ha had been applied in fertiliser, and a considerable, but undetermined amount had been supplied by lupin (Gadgil *et al.* 1984). Standing crops of fine roots have recently been measured for both treatments (D. Santantonio, unpubl. data).

Forest Floor and Soil Analyses

At Puruki, forest floor and soils were sampled at 2-m intervals along two 20-m transects in each treatment at the following depths: forest floor, 0–10 cm, and 10–20 cm. Forest floor samples including thinning slash (present in P550 only), and L and F layers were taken using a 0.25-m² frame. No H layer was present. Soils were sampled with a Hoffer soil tube. Ten samples from each depth were collected per transect and all samples were then oven dried for weight determination and subsequently bulked to four samples per depth per transect for analysis by standard Forest Research Institute methods (Nicholson 1984). Forest floor samples were analysed for loss on ignition (to correct for soil content) and nitrogen, and soil samples were analysed for total nitrogen, carbon, and pH. Volumetric cores were collected for bulk density determination using 10 cores per transect at each depth. The soils at the Woodhill site had been sampled previously (Baker *et al.* 1986).

Nitrogen Mineralisation

Net nitrogen mineralisation was measured by an *in situ* core incubation method previously used by Rapp *et al.* (1979) and similar to the buried polyethylene bag technique (Lennon *et al.* 1985; Pastor *et al.* 1984) except that there is less soil disturbance using cores. A detailed description of methodology has been given by Raison *et al.* (1987).

At Puruki, the field study ran from April 1985 to June 1986. The forest floor was incubated in 15-cm-long, 200-mm-diameter, PVC tubes installed by cutting around the base of the tube while pushing it through the forest floor and into the mineral soil. Soil was incubated in 50-mm-diameter PVC tubes sharpened at one end and forced into the soil. The tops of the tubes were covered with thin polyethylene to exclude rain water but allow gaseous exchange. Forest floor and soil incubation tubes were inserted at 2-m intervals along two transects in each of the stocking treatments as follows: five at forest floor, 10 at 0–10 cm, and 10 at 10–20 cm. Starting in May 1985 (i.e., the second collection) five tubes were also inserted at the 20–40 cm depth. The same number (i.e., five, 10, 10, and five) of initial samples were collected at the start of each incubation period. Tubes were left in the ground for 4 weeks except from May to September (winter) 1985 when the incubation period was extended to 6 weeks. The tubes were shifted 3 m laterally after each collection.

Initial and incubated forest floor and soil samples were taken to the laboratory where they were bulked as follows: forest floor and 20–40 cm – no bulking; 0–10 and 10–20 cm – 10 bulked to five. The samples were thoroughly mixed and subsamples extracted for 24 hours with 2 N KCl (Vitousek & Matson 1985). Extracts were analysed for ammonium and nitrate (G. M. Nicholson unpubl. data). Soil moisture content was determined from weight differences after drying subsamples at 100°C for more than 48 hours.

Net nitrogen mineralisation was determined by multiplying measured changes (final – initial) in ammonium plus nitrate concentrations by forest floor or soil layer weight. Concentration data for each incubation period were subjected to analysis of variance.

A similar procedure was used at Woodhill except that the experiment ran from May 1985 to May 1986 and only the forest floor and 0–10 cm soil were studied. (Deeper soil had very low organic matter and nitrogen content (Baker *et al.* 1986).) Sampling occurred every 6 weeks and, because of delays in returning to the laboratory, the soils were bulked and potassium chloride was added in the field. Despite the coarse texture of the soil, there was never any problem recovering all of the soil in the tube. Also, no roots were found to have grown into the soil in the tubes during the incubation period.

Throughfall, Precipitation, and Temperature

At Puruki, throughfall was collected in five 108-mm-diameter funnels, located 1 m above ground and 4 m apart on the two initial 20-m transects in each treatment. Collectors were preloaded with mercuric chloride to prevent microbial activity. Throughfall was measured and collected every 2 weeks if sufficient rain had occurred, and was bulked to one sample per transect per collection. Precipitation was collected in a pasture adjacent to the forested catchment. Samples were stored at 4°C until analysed for ammonium and nitrate (Nicholson 1984). Data of Baker *et al.* (1985) were used for precipitation and throughfall at Woodhill.

At both sites, the temperature of the forest floor and each soil depth, excluding 20–40 cm, was recorded at the time of each collection at each sampling location (i.e., 10 measurements per depth per treatment per collection). Effort was made to measure temperatures as quickly as possible to reduce variation caused by diurnal temperature fluctuation.

Soil Leachate and Streamwater Loss

To monitor soil leachate nitrogen concentrations, five pairs of porous cup suction lysimeters (Dyck *et al.* 1983) were installed (one at a depth of 25 cm and one at 60 cm) at 2-m intervals along the two initial transects in each treatment (i.e., 20 lysimeters/treatment). Streamwater was collected using a flow-proportional sampler (Quality Environment Ltd) installed at the weir at the base of the catchment. Lysimeter and streamwater samples were collected every 2 weeks and analysed for ammonium and nitrate (Nicholson 1984). Estimates of leaching nitrogen losses were made by multiplying average monthly lysimeter concentrations by a drainage value calculated from streamflow measured at the weir. The same drainage value was used for both treatments because, although annual throughfall volume was 11% lower for the P2000 treatment, a corresponding increase in stemflow owing to higher stocking would have compensated for this (P. D. Hodgkiss, unpubl. data).

Lysimeters were not installed at Woodhill as Baker *et al.* (1986) had previously found that virtually no nitrogen leaching was occurring at this site.

RESULTS

Forest Floor and Soil Analyses

The forest floor and soil at Puruki contained far greater amounts of organic matter and nitrogen than at Woodhill (Table 1). There were no differences in soil properties between treatments. At Puruki, however, the lower stocking (P550) had slightly lower

TABLE 1—Site characteristics

	Puruki		Woodhill	
	P2000	P550	LF	LE
Tree age (years)	12	12	17	17
Stocking (nominal) (stems/ha)	2000	550	2224	2224
Stemwood production (t/ha/yr)	24.0	19.4	18.1	8.1
Foliage production (t/ha/yr)	7.0	6.4	5.7	2.8
Current foliage N (%)	1.73	1.61	1.09	0.80
Forest floor				
Weight (t/ha)	24.9	24.6*	14.9	6.7
N (kg/ha)	455	373	210	57
C/N	26	32	36	61
Soil (0–10 cm)				
Bulk density (g/cm ³)	0.589	0.586	1.34	1.40
pH	5.0	5.4	5.6	5.6
N (%)	0.504	0.532	0.030	0.012
C (%)	8.870	7.898	0.485	0.303
C/N	17.6	14.8	16.2	25.3

* Includes thinning slash.

SOURCES

Puruki: stem and foliage production (Beets & Pollock 1987), foliar N (P. Beets unpubl. data);
Woodhill: stem and foliage production (Beets & Madgwick in press), foliar N, forest floor and soil values
(Baker *et al.* 1986).

nitrogen concentration in the forest floor than the denser stand (P2000) and a similar trend occurred with foliar nitrogen levels. At Woodhill, the lupin plus fertiliser (LF) treatment had double the mass of forest floor with nearly four times the nitrogen content, and much greater soil nitrogen and carbon levels than the lupin excluded (LE) treatment.

Mineralised Nitrogen

The pool of inorganic nitrogen (ammonium and nitrate) was considerably greater at Puruki than at Woodhill (Table 2) and varied seasonally at both sites (Fig. 1). Highest levels occurred in April and May at Puruki and in January at Woodhill.

There were no significant differences in inorganic nitrogen concentrations between treatments at Puruki; however, there were significant differences in nitrate levels between the two transects in the P550 treatment. Transect 1 had consistently and usually significantly lower nitrate levels than Transect 2. The main visible difference between the transects was a greater amount of bracken in the understorey in Transect 1. Bracken is reported to produce allelopathic chemicals that appear to reduce the vigour of potential competitors (Page 1986) and it may be that bracken is capable of suppressing nitrifying

TABLE 2—Mean forest floor and soil inorganic nitrogen pools and annual net nitrogen mineralisation for *Pinus radiata* sites

	Puruki		Woodhill	
	P2000	P550	LF	LE
Inorganic nitrogen (kg/ha)				
Forest floor	1.4	1.0	0.2	0.1
0-10 cm	3.9	3.0	0.7	0.4
10-20 cm	3.6	2.1	na	na
20-40 cm	6.7	3.1	na	na
Total	15.5	9.2	0.9	0.5
Net nitrogen mineralisation (kg/ha/yr)				
Forest floor	10.5	6.2	1.1	0.2
0-10 cm	74.6	47.3	8.3	1.4
10-20 cm	23.5	18.0	na	na
20-40 cm	17.1	18.0	na	na
Total	125.7	89.5	9.4	1.6
Nitrification (% mineralisation)				
	81	77	0	0

na = no analyses for these depths.

organisms. At Woodhill, for most of the year inorganic nitrogen was only in ammonium form and was significantly greater in the LF treatment than in the LE treatment. Inorganic nitrogen concentrations at Puruki decreased significantly with depth; however, because of the greater weight of the soil, the amount of inorganic nitrogen contained in the soil was much greater than in the forest floor (Table 2). In contrast to Puruki, inorganic nitrogen concentrations at Woodhill were significantly lower in the forest floor than in the soil.

Standard errors for ammonium were generally less than 10% of the mean for Woodhill, and less than 20% for Puruki. At Puruki, the standard error for nitrate was somewhat higher than for ammonium.

Net nitrogen mineralisation was very much greater at Puruki than at Woodhill and for both sites significantly lower in the forest floor than in the mineral soil. Annual net nitrogen mineralisation rates for each depth are shown in Table 2. Nitrification, the biochemical oxidation of ammonium to nitrate, was a high proportion of mineralisation at Puruki but negligible at Woodhill. Stocking did not have a significant effect on mineralisation at Puruki, although the rates for the P2000 treatment tended to be consistently higher than for the P550 treatment. Net nitrogen mineralisation in the mineral soil decreased with depth but the annual rate was still considerable at the lowest depth measured (Table 2). It should be noted that the rate for the 20–40 cm depth is for twice as much soil as for the other soil depths (Fig. 2).

At Woodhill, net nitrogen mineralisation was significantly greater in the lupin plus fertiliser (LF) treatment than where lupin had been excluded (LE) and the rate was

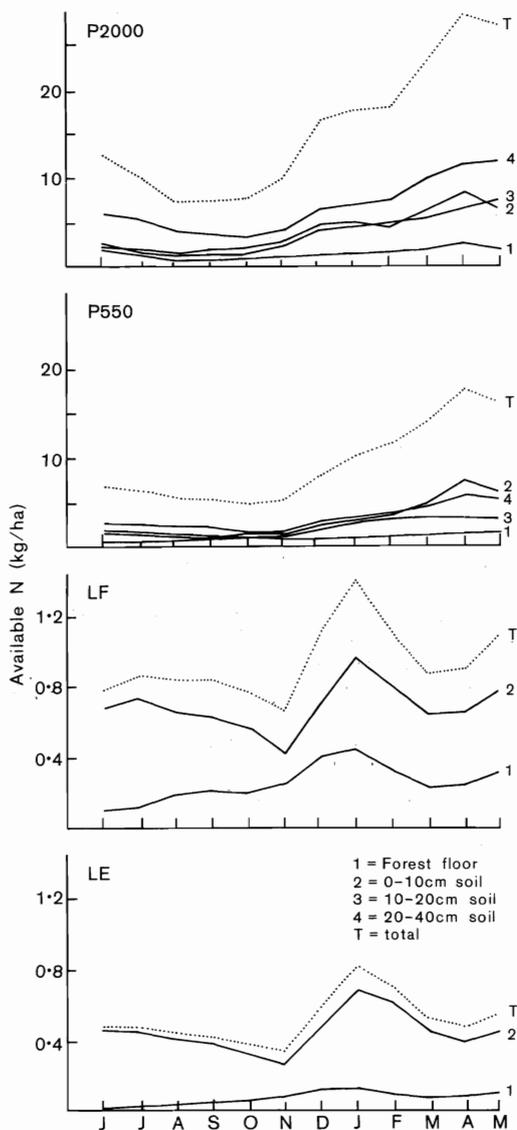


FIG. 1.—Inorganic nitrogen content of forest floor and soil for P2000, P550, LF, and LE treatments (1 = forest floor, 2 = 0-10 cm, 3 = 10-20 cm, 4 = 20-40 cm soil depth, T = total).

highest in the mineral soil. In October, and again in February and March, immobilisation exceeded mineralisation in the LE plots, resulting in negative net mineralisation for these periods (Fig. 2). Standard errors were sometimes greater than 40% of the mean daily mineralisation rate in the forest floor, but were generally less than 30% for the mineral soil depths.

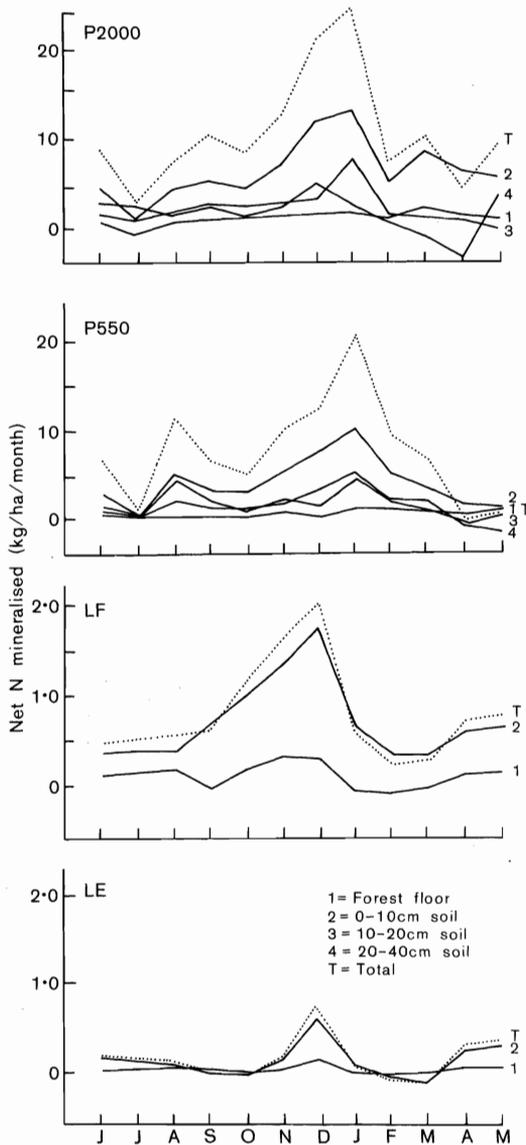


FIG. 2—Net nitrogen mineralisation in forest floor and soil for P2000, P550, LF, and LE treatments (1 = forest floor, 2 = 0-10 cm, 3 = 10-20 cm, 4 = 20-40 cm soil depth, T = total).

Calculated mean monthly soil temperatures for all soil depths at Puruki were very similar to values from continuous recording at the Puruki meteorological station (R. Brownlie, unpubl. data). Soil temperatures and soil moisture contents for the 0-10 cm depth for Puruki and Woodhill are shown in Fig. 3. The mean soil temperature at this depth during the study period was 5.6°C higher at Woodhill than at Puruki. Soil

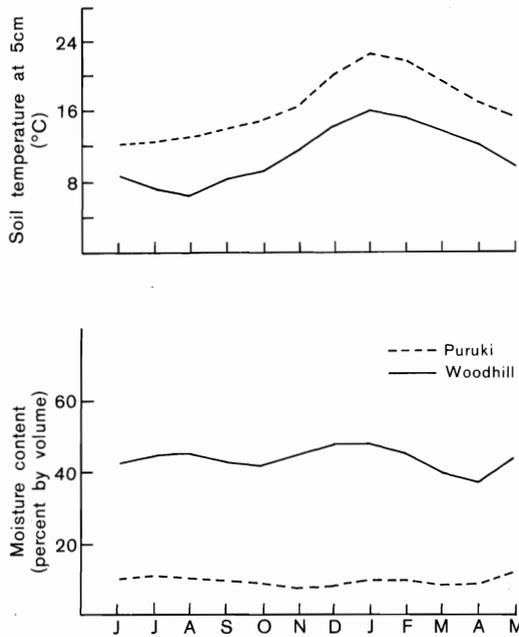


FIG. 3—Monthly temperature and moisture content of 0–10 cm soil depth for Puruki and Woodhill sites.

moisture showed only small fluctuations at both sites and, primarily because of the coarse texture of the coastal sands, was considerably lower at Woodhill.

Net nitrogen mineralisation at the 0–10 cm depth was highly correlated with soil temperature and moisture ($r^2 = 0.92$, $p < 0.001$) for P2000 and somewhat less so for the P550 treatment ($r^2 = 0.74$, $p < 0.001$). There was no correlation between nitrogen mineralisation and soil temperature and moisture for the Woodhill treatments.

Inputs and Outputs

Inorganic nitrogen in throughfall at Puruki was 7.1 and 5.3 kg/ha/yr for the 2000 and 550 stems/ha treatments respectively. Precipitation input was 6.4 kg/ha/yr (Table 3). Reasons for differences in throughfall nitrogen between treatments are not known but it may be because the denser stand (P2000) trapped more inorganic nitrogen in aerosols than the open stand (P550). The P550 treatment also had lower foliar nitrogen levels than the P2000 treatment and may have absorbed more atmospheric input of nitrogen. At Woodhill, Baker *et al.* (1985) reported equal amounts of inorganic nitrogen in throughfall as in precipitation (Table 3). The tree canopy absorbed a small amount of nitrate from precipitation and trapped a similar amount of ammonium in aerosols which was subsequently washed to the forest floor in throughfall (Baker *et al.* 1985).

Approximately 13 (P2000) and 5 (P550) kg N/ha/yr leached through the soil at Puruki, almost entirely as nitrate (Table 3). Streamwater inorganic nitrogen loss

measured at the base of the catchment was < 1 kg/ha for the sampling period (Table 3).

Nitrate is removed from drainage water before it leaves the catchment (Table 3), and this may be because of denitrification in the riparian zone soils because nitrate concentrations are reduced from an average of 1.33 mg/l in soil leachate to 0.6 mg/l (Cooper 1986) in spring water. However, denitrification in the surface soils of the study plots was unlikely to be very high as the *in situ* core technique allowed moisture to drain from the incubated soil and the soil was not saturated at any collection.

TABLE 3—Inorganic nitrogen inputs and outputs for *Pinus radiata* sites (kg/ha/yr) ,

	Puruki		Woodhill	
	P2000	P550	LF	LE
Precipitation	6.4	6.4	1.7	1.7
Throughfall	7.1	5.3	1.7	1.7
Soil leaching (@ 60 cm)	12.8	4.9	0	0
Streamwater loss	0.7	0.7	0	0

SOURCE: Woodhill: Baker *et al.* (1985, 1986).

Apparent Nitrogen Uptake

Nitrogen uptake can be estimated by measuring the fluxes into and out of the available nitrogen pool (Nadelhoffer *et al.* 1985) using the equation:

$$Nu = Nm + Np - Nl - Ns$$

where Nu = apparent nitrogen uptake, or inorganic nitrogen flux from available nitrogen pool to vegetation

Nm = net nitrogen mineralised in forest floor and soil

Np = inorganic nitrogen in precipitation

Nl = nitrogen leached below effective rooting depth

Ns = increment in inorganic soil nitrogen during study period

In our study, throughfall nitrogen was used for input instead of precipitation nitrogen (Nadelhoffer *et al.* 1985); we feel it is a more reliable indicator of inorganic nitrogen reaching the forest floor as inorganic nitrogen trapped by the tree crown is included (Baker *et al.* 1985). Nm included forest floor data as well as data for the 0–40 cm (Puruki) and 0–10 cm (Woodhill) soil layer.

$$Nu = Nm + Ntf - Nl - Ns$$

where Nm = net nitrogen mineralised in forest floor and soil

Ntf = nitrogen in throughfall.

Apparent nitrogen uptake by *P. radiata* ranged from 3 to 109 kg/ha/yr (Table 4). Over the year, inorganic nitrogen in the soil and forest floor at Puruki increased by 11 and 6 kg/ha for P2000 and P550 respectively and there was virtually no change at the Woodhill sites. For both Puruki sites, net nitrogen mineralisation exceeded apparent nitrogen uptake because leaching losses plus increases in soil inorganic nitrogen during the year were greater than nitrogen additions in throughfall.

Plant nitrogen uptake for the Puruki sites (Table 4) was calculated from annual above-ground biomass measurements and coarse root estimates (Beets & Pollock 1987) and fine root production values measured for P550 in 1984–85 (Santantonio & Santantonio in press). For the Woodhill sites (Table 4) plant nitrogen uptake was estimated from above-ground biomass and litterfall measurements (Baker *et al.* 1986) plus estimates of nitrogen stored in woody roots and nitrogen used for fine root production. The equations of Jackson & Chittenden (1981) were used with LF and LE stemwood nitrogen concentrations to estimate nitrogen stored in woody roots (11 and 0 kg/ha, respectively). Measured fine root production for Puruki (Santantonio & Santantonio in press) was used with LF and LE fine root nitrogen concentrations (D. Santantonio and W. J. Dyck, unpubl. data) to estimate nitrogen used for fine root production (13.2 and 8.8 kg/ha, respectively).

As can be seen from Table 4, nitrogen made available from mineralisation should be approximately 119, 132, 52, and 20 kg/ha/yr for P2000, P550, LF, and LE treatments respectively. Values from the *in situ* core technique were 8%, 36%, 79%, and 85% lower for the respective treatments.

TABLE 4—Plant nitrogen uptake and apparent nitrogen uptake for *Pinus radiata* sites (kg/ha/yr)

	Puruki		Woodhill	
	P2000	P550	LF	LE
Plant nitrogen uptake	119	132	52	20
Apparent nitrogen uptake*	109	84	11	3

* Apparent Nu = Nm + Ntf–Nl–Ns (see text)

SOURCES

Puruki: Beets & Pollock (1987), P. Beets unpubl. data, Santantonio & Santantonio (in press), D. Santantonio & W. Dyck (unpubl. data);
Woodhill: Baker *et al.* (1986), Jackson & Chittenden (1981), D. Santantonio & W. Dyck (unpubl. data).

DISCUSSION

Annual net nitrogen mineralisation rates at Puruki are at the high end of the range of values reported for 13 forest ecosystems in the north-eastern United States (Aber *et al.* 1985) and five in Europe (Alexander 1983) while those for the Woodhill lupin exclusion (LE) treatment are lower than any previously reported for forests.

Considering the possible measurement errors involved, the *in situ* core method provided apparently reasonable data for actual net nitrogen mineralisation for the unthinned Puruki stand (P2000), but not for the other sites (Table 4). Baker *et al.* (1986) calculated that, for Woodhill, internal nitrogen redistribution plus precipitation nitrogen inputs accounted for 60% and 32% of the above-ground annual nitrogen demand for the LE and LF treatments respectively, the remainder presumably being derived from mineralisation of forest floor material and soil organic matter (not measured in their study). Despite high productivity and the addition of approximately 900 kg N/ha in

fertiliser alone, the LF treatment was still very deficient in nitrogen for tree growth (current foliage N 1.09%), and measured net nitrogen mineralisation was 79% lower than that apparently required for actual above-ground production.

Mycorrhizal roots of *P. radiata* have been shown to reduce forest floor decomposition rates (Gadgil & Gadgil 1971, 1975, 1978); however, the exact mechanism has not been determined (Gadgil & Gadgil 1978). Alexander (1983) speculated that it was because of the competitive advantage of the mycorrhizal fungi over decomposer organisms in obtaining available nitrogen. The advantage exists because mycorrhizal roots, the hyphae of which effectively exploit decomposing organic matter so that they are at the site of nitrogen release, obtain their energy from simple carbohydrates from the host tree, whereas saprophytic soil organisms must obtain their energy from recalcitrant organic matter (Alexander 1983). This is especially important where the C/N ratio is high and competition for available nitrogen is strong.

One possible reason why the *in situ* incubation technique under-estimated net nitrogen mineralisation at both Woodhill and Puruki is because, in the undisturbed forest floor and soil (i.e., outside the tubes), *P. radiata* roots are able to outcompete decomposer organisms for inorganic nitrogen. Severing roots eliminates tree uptake and allows decomposers to immobilise inorganic nitrogen into microbial biomass. Thus, immobilisation is much greater inside than outside the tubes and actual uptake is under-estimated. Net nitrogen mineralisation is likely to be most under-estimated for sites with a high C/N ratio because of the high immobilisation capacity of these sites (Vitousek *et al.* 1982). In our study the percentage that net nitrogen mineralisation under-estimated biomass nitrogen followed the trend for forest floor C/N ratios (i.e., LE > LF > P550 > P2000) which indicates the relative quality of organic matter available for decomposition.

Puruki is a very fertile site, with high levels of soil inorganic nitrogen and high concentrations of nitrogen in soil water, and thus nitrogen would not be expected to limit tree growth. However, Cooper (1986) has shown that since planting, nitrification has been reduced at Puruki and that nitrifiers are limited by ammonium supply, apparently associated with the presence of live *P. radiata* roots. Our data suggest that this may be because mycorrhizal competition for ammonium limits supplies for nitrifiers (Vitousek *et al.* 1982; Alexander 1983). Thinning (trees were left on site) increased the C/N ratio of the forest floor (P550) and increased the immobilisation capacity of the site, and may explain why measured net nitrogen mineralisation and nitrification in the thinned stand was lower than in the unthinned stand (P2000).

It is also possible that nitrogen mineralisation is occurring below 40 cm at Puruki and below 10 cm at Woodhill. However, at the Woodhill sites it is unlikely that nitrogen mineralisation at soil depths greater than 10 cm could account for the total shortfall because the organic matter (and nitrogen) content of the soil below 10 cm is very low.

Severed roots will immobilise or release inorganic nitrogen with time, and may affect net nitrogen mineralisation during the 4- to 6-week incubation period used in this study. However, Raison *et al.* (1987) found that, comparing different incubation lengths, there was a smooth pattern of inorganic nitrogen accumulation, suggesting that decomposition of the severed roots did not have any significant effect on net nitrogen

mineralisation. It is more likely, as discussed above, that previously dead and decomposing organic matter would have a greater immobilising effect once the mycorrhizal influence of live *P. radiata* roots was removed. This is supported by a recent laboratory study which showed that when soil from the LF and LE sites was incubated in the laboratory with and without fine roots there was no significant increase in net nitrogen mineralisation resulting from root removal, and in fact the LF soil showed a significant ($p < 0.01$) decrease (20%) in nitrogen mineralisation (C. A. Mees & P. D. Hodgkiss, unpubl. data).

In conclusion, the *in situ* core technique appears to under-estimate net nitrogen mineralisation in *P. radiata* forests, especially in slowly mineralising soils. The influence of mycorrhizal roots on nitrogen mineralisation requires further investigation.

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