NUTRIENT ACCUMULATION IN SECOND-ROTATION *PINUS RADIATA* AFTER HARVEST RESIDUE MANAGEMENT AND FERTILISER TREATMENT OF COASTAL SAND DUNES

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ABSTRACT

Nutrient accumulation and partitioning by second-rotation *Pinus radiata* D.Don and ecosystem recovery from intensive harvesting, residue management, and urea fertilisation were evaluated 5 years after trial establishment in a sand dune forest in New Zealand. Experimental treatments applied in a split-plot design included: whole-tree harvest and forest floor removal; whole-tree harvest; stem-only harvest; and stem-only harvest plus addition of extra slash. Urea was added quarterly to sub-plots at a rate of 200 kg N/ha each year. Forest floor removal substantially reduced stand productivity, and indicated the importance of organic matter as a store of nitrogen on the Pinaki sands. All stands without fertiliser continued to lose nitrogen over the 5-year period after trial establishment, and retained between 73% and 88% of the nitrogen left on site. Stands with fertiliser retained between 63% and 81% of the nitrogen added over the 5-year period. Slash increased ecosystem nitrogen retention. Stands treated with stem-only harvest plus extra slash and fertiliser accumulated nitrogen to pre-harvest ecosystem content, while those with other treatments did not. Urea additions amended productivity losses due to forest floor removal; however, fertiliser increased nutrient accumulation rates for elements not added to the site, and exacerbated reductions in nutrient availability caused by harvest treatments. Productivity to nutrient accumulation ratio (P/NA) of nitrogen was greater on the sand dune site (0.27 tonne/kg N) than observed at Purukohukohu Experimental Basin on a nitrogen-rich loamy pumice soil (0.16 tonne/kg N) in New Zealand. These differences suggest the need to revise critical levels for foliar nutrients based on site-specific P/NA values. Urea fertiliser generally increased P/NA for phosphorus and potassium, and reduced P/NA of nitrogen, calcium, magnesium. In stands with and without added fertiliser, P/NA for boron was lower in stands with slash retained than in stands with forest floor removal or whole-tree harvesting. In stands with forest floor removal, addition of urea increased the P/NA ratio for boron. We hypothesise that forest floor removal reduced the ability of the soil to satisfy tree demand for boron, especially for fast-growing fertiliser-treated trees.

Keywords: sand dune forestry; nutrient concentration; nutrient content; nutrient use efficiency; fertiliser; nitrogen; phosphorus; potassium; calcium; magnesium; boron; harvesting; residue management; productivity; *Pinus radiata*

INTRODUCTION

Losses of forest site productivity due to nutrient depletion caused by mechanical site disturbance and site preparation operations and harvest removals of merchantable biomass are expected to be greatest on sites with low fertility (Birk 1993; Crompton & Cole 1991). Furthermore, productivity declines due to nutrient depletion have been predicted to be exacerbated by silvicultural practices that increase stand nutrient demands and removal rates, such as fertiliser treatment of fast-growing species, shorter rotation lengths, commercial thinning, and intensified utilisation (Birk 1993; Webber 1978). However, detecting significant growth declines due to harvesting impacts has been hindered by the relatively low degree of experimental rigour of many trials (Burger & Powers 1991; Morris 1989). It has also been difficult to determine the threshold point between low and acceptable soil fertility levels for different combinations of species, sites, and harvest nutrient removal. Greater understanding of the relationship between total nutrient content and nutrient availability is required to develop management guidelines for residue retention on different sites.

A network of trials has been established across a range of soil types and climatic regimes in New Zealand to determine how second rotation productivity and nutrition of *Pinus radiata* are affected by various harvest residue management alternatives. These trials have been designed to determine the importance of different organic sources of nutrients for *P. radiata* nutrition and growth by experimentally removing tree boles, branches and foliage, forest floor materials, and at some sites the A-horizon. These treatments were selected because they manipulate the types of soil and site resources that are affected by harvesting operations, and can be managed through harvest planning. In addition, these materials contain organic sources of nutrients that differ in C/N ratio, nutrient concentration, and mineralisation potential. By alternatively retaining these materials, or removing them from the site, and by amending these removals with fertiliser, we can determine their relative contribution to total site nutrient content, nutrient availability, tree nutrition, and growth. This series of trials will be used to test hypotheses concerning the susceptibility of different soil types to productivity declines as a result of nutrient removal in harvesting.

A trial located on low fertility sand dunes was designed to determine the effects of harvest removals of organic matter and associated nutrients on second-rotation *P. radiata* productivity and nutrition. It was hypothesised that harvesting intensity would be negatively correlated with stand productivity in the following rotation, and that limited supplies of nitrogen would cause the negative correlation.

The objectives of this paper are to examine how harvest removals of organic matter affected accumulation and partitioning of nitrogen, phosphorus, potassium, calcium, magnesium, and boron by *P. radiata* at plantation age 5 years, and to evaluate changes in ecosystem nutrient contents over the 5-year period after trial establishment. We consider the implications of these results for understanding nutrient use efficiency (NUE) and nutrition management of *P. radiata*, and for ecosystem recovery from harvesting removals of nutrients.

METHODS

Study Area

The study area was located in Woodhill Forest, a 9000-ha plantation of *P. radiata* established on sand dunes along the west coast of the North Island, New Zealand (37°15′S, 174°25´E) to stabilise shifting sands. Woodhill Forest has a mild, maritime climate, with 30-year average February temperature of 19°C, average July temperature of 10°C, and average annual precipitation of 1330 mm (NZ Meteorological Service unpubl. data).

The soils at the study site were derived from sand dune materials. The typical profile of these Pinaki sands consists of an O-horizon over a deep, uniform, sandy C-horizon. Forest establishment of coastal sand dunes historically required stabilisation by marram grass (*Ammophila arenaria* (L.) Link) and nitrogen addition by lupin (*Lupinus arboreus* Sims). The lupin and marram grass system is capable of fixing at least 160 kg N/ha annually (Gadgil 1971), and the sand dune ecosystem could have contained about 1600 kg N/ha when the first rotation of *P. radiata* was planted (Gadgil 1979). Nitrogen accumulation by the first rotation of *P. radiata* in Woodhill Forest has been described by Beets & Madgwick (1988) and Dyck *et al.* (1988).

Experimental Treatments

The trial was established in 1986 on a site occupied by a 42-year-old, first-rotation stand of *P. radiata* that was established in 1944. Preharvest conditions were described by Dyck *et al.* (1991). The stand was harvested in April-May 1986 and harvest treatments have been described in detail by Smith *et al.* (1994). A split-plot randomised block design was used to establish four harvesting and site preparation treatments replicated in three blocks, with and without additions of urea-nitrogen in split-plots, giving 24 sub-plots. The main treatments were:

FF	Whole-tree harvest and forest floor removed
WT	Whole-tree (above-ground) harvest
SS	Stem-only harvest (single layer of harvest slash)
DS	Stem-only harvest plus slash (double layer of slash).

These experimental harvesting treatments were applied as uniformly as possible to two adjacent 30 × 30 m subplots within each block. Machine compaction of subplots was minimised by winching logs with skidders from corridors between plots.

Urea-nitrogen was hand applied to one of the adjacent subplots in each block at quarterly intervals at a rate of 50 kg N/ha to give:

FF+N	Whole-tree harvest (above-ground) and forest floor removed plus 200 kg N/ha•year
WT+N	Whole-tree harvest plus 200 kg N/ha•year
SS+N	Stem-only harvest (single layer of harvest slash) plus 200 kg N/ha•year
DS+N	Stem-only harvest plus slash (double layer of slash) plus 200 kg N/ha•year.

The urea-nitrogen additions—900 kg N/ha total between September 1986 and January 1991—were designed to maintain adequate nutrition on the nitrogen-deficient sands. No other nutrients were added during the first 5 years of the trial.

Measurements were restricted to the central 20 × 20 m of each subplot.

Pinus radiata bare-root seedlings (1/0) were hand planted in July 1986 at a 2 × 2 m spacing (2500 stems/ha). Weed competition was virtually eliminated manually and with herbicides throughout the trial. Additional details of trial installation have been presented by Dyck *et al.* (1991).

Ecosystem Biomass and Nutrients

Above-ground tree components

Estimates of above-ground biomass at age 5 years were made in April 1991 for eight tree components, including 1-year foliage, ≥2 year foliage, dead foliage, live and dead branches, cones, stem bark and wood, using methods described by Smith *et al.* (1994). Average total height for the treatments 5 years after establishment ranged from 6.22 to 6.97 m, and average quadratic diameter at breast height (dbh) ranged from 8.6 to 10.9 cm (Smith *et al.* 1994).

Nutrient estimates were based on samples collected from each component of five trees from each subplot, thus 120 trees total. The nutrient concentrations of cones were not determined. Tree component samples were analysed to determine the total concentration of nitrogen, phosphorus, potassium, calcium, magnesium, and boron using methods described by Nicholson (1984). Amounts of each nutrient contained in the above-ground tree components (kg/ha) were estimated from the product of average component nutrient concentration (mg/kg) and average component stand weight (tonnes/ha) (Smith *et al.* 1994) for the respective subplots. Subplot stocking was standardised to 2500 stems/ha for stand level estimates of nutrient contents. Thus, stocking levels for the treatments were adjusted by the following factors: FF (1.10); WT (1.08); SS (1.09); DS (1.14); FF+N (1.12); WT+N (1.10); SS+N (1.14); DS+N (1.29). As a result, stand nutrient contents should be interpreted as reflecting nutrient accumulation by stands with a given average tree size, which varied according to experimental treatments.

Residual slash and forest floor materials

The amount of coarse woody debris (>10 cm diameter) and forest floor and small woody debris (<10 cm diameter) was estimated in March 1991 using methods described by Smith *et al.* (1994). Forest floor materials were not separated by age class or state of decomposition. Nutrient estimates were based on materials collected at five random sampling locations on each subplot. Samples were analysed for total nitrogen, phosphorus, potassium, calcium, magnesium, and boron using methods described by Nicholson (1984). Nitrogen concentrations for forest floor materials were expressed on both ash-free and total-mass bases. Concentrations for phosphorus, potassium, calcium, magnesium, and boron in the forest floor were expressed on a total-mass basis. The nutrient content of these materials (kg/ha) was estimated from the product of average nutrient concentration (mg/kg) and average weight per unit area (tonnes/ha) (Smith *et al.* 1994) for the respective subplots.

Mineral soil, fine roots (<2 mm diameter), and coarse (>2 mm) roots

Mineral soil and fine root samples were collected in April 1991 using a 5-cm-diameter core, as described by Smith *et al.* (1994). Samples were collected at five systematically located sample points along three transects in each subplot, thus 15 sample points per subplot. Samples within each transect were bulked to yield three samples for each depth per subplot. Nutrient estimates for mineral soil depths of 0–10, 10–30, and 30–90 cm were based on three samples per subplot. For nitrogen, phosphorus, potassium, calcium, and magnesium, live fine roots were bulked across all mineral soil depths to yield three samples per subplot from forest floor and 0–90 cm mineral soil depths. For boron, the 10–30 cm depth was based on one sample per subplot and the 30–90 cm depth samples were bulked and based on two samples (one each for treatments with and without fertiliser). Samples were analysed for total nitrogen, phosphorus, potassium, calcium, and magnesium using methods described by Nicholson (1984). Boron was extracted from soil samples with hot acid (1% HNO_3 and 10% HCl at 95°C until the digest solution volume was reduced from 111 ml to 25 ml). The extractant was filtered and boron concentration determined colorimetrically using curcumin (Nicholson 1984). The nutrient content of the mineral soil for each depth and the profile down to 90 cm (kg/ha) was estimated from the product of average nutrient concentration (mg/kg), depth (cm), and bulk density (g/cm^3) (G.Nicholson & A.Sims unpubl. data). Fine root nutrient contents (kg/ha) were estimated from the product of average nutrient concentration (mg/kg) and fine root weight per unit area (tonnes/ha) (Smith *et al.* 1994) for the respective subplots.

Coarse root (>2 mm diameter) biomass was estimated using an equation developed by Jackson & Chittenden (1981, Eq. 1), which used tree dbh as the independent variable. Coarse root nutrient concentrations were not determined in this study.

Statistical Analyses

Data from this study have been analysed as a split-plot, randomised block design using GENSTAT (Lawes Agricultural Trust 1980). Data sets that included a soil depth component included this factor as a main effect in the analysis of variance. Transformations of data sets were made as appropriate to satisfy statistical assumptions. Least significant differences were estimated to separate means when ANOVA results indicated that there were significant treatment effects.

RESULTS

Above-ground Nutrient Concentrations

Nitrogen concentrations in all above-ground tree components were significantly increased by urea additions (Table 1). Urea additions increased 1-year foliar nitrogen concentrations by only about 0.2%N in the fifth year. Slash retention also increased nitrogen concentrations in stem wood (with treatments with and without fertiliser averaged within harvesting classes FF 0.082%N^a; WT 0.083%N^{ab}; DS 0.085%N^{abc}; SS 0.088%N^c; where different superscript letters indicate significant differences $p \leq 0.05$).

In trees with fertiliser, phosphorus concentrations were significantly lower for six components, but were higher in dead foliage (Table 2). Stem bark phosphorus concentrations were increased by retention of a single layer of slash (with treatments with and without fertiliser averaged within harvesting classes WT 0.050%P^a; FF 0.051%P^a; DS 0.052%P^a; SS 0.056%P^b; where different superscript letters indicate significant differences $p \leq 0.05$).

In trees with fertiliser, potassium concentrations were greater in dead foliage and dead branches, and lower in live branches, stem bark, and stem wood than in trees without fertiliser (Table 3). Reduced potassium concentrations in the living tissues of trees with fertiliser was a pattern similar to phosphorus, although this trend was not observed in foliage. Potassium concentrations were not affected by harvest treatments, but for most above-ground components, potassium concentrations tended to be lower in subplots with fertiliser that had greater residue removal (e.g., FF+N and WT+N).

In samples of expanding foliage from secondary branches collected in March, using standard protocols, foliar calcium and magnesium in subplots with fertiliser were significantly

TABLE 1–Average concentration (% oven-dry weight) of nitrogen in above-ground components of 5-year-old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	1.13	0.84	0.49	0.21	0.19	0.35	0.073
WT	1.07	0.82	0.54	0.20	0.18	0.36	0.073
SS	1.19	1.01	0.51	0.21	0.21	0.39	0.083
DS	1.34	1.02	0.51	0.20	0.17	0.36	0.077
FF+N	1.34	1.07	0.79	0.26	0.34	0.48	0.090
WT+N	1.34	1.01	0.82	0.27	0.29	0.47	0.093
SS+N	1.39	1.02	0.81	0.29	0.30	0.48	0.093
DS+N	1.34	0.97	0.79	0.27	0.34	0.46	0.093
No fertiliser	1.13**	0.85**	0.51**	0.20**	0.19**	0.37**	0.077**
Plus fertiliser	1.35**	1.02**	0.80**	0.27**	0.32**	0.47**	0.093**

† FF, whole-tree harvest plus forest floor removed; WT, whole-tree harvest; SS, stem-only harvest (single layer of slash); DS, stem-only harvest plus slash (double layer of slash); FF+N, whole-tree harvest plus forest floor removed plus 200 kg N/ha•year; WT+N whole-tree harvest plus 200 kg N/ha•year; SS+N, stem-only harvest (single layer of slash) plus 200 kg N/ha•year; DS+N, stem-only harvest plus slash (double layer of slash) plus 200 kg N/ha•year.

Significantly different means between classes of components with and without fertiliser are followed by * ($p \leq 0.05$) or ** ($p \leq 0.01$)

Means followed by different letters within a column are significantly different ($p \leq 0.05$)

TABLE 2–Average concentration (% oven-dry weight) of phosphorus in above-ground components of 5-year old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	0.14	0.12	0.06	0.07	0.06	0.052	0.023
WT	0.13	0.12	0.05	0.07	0.06	0.053	0.021
SS	0.14	0.12	0.06	0.08	0.07	0.060	0.019
DS	0.13	0.11	0.05	0.07	0.06	0.053	0.020
FF+N	0.11	0.10	0.06	0.05	0.04	0.050	0.021
WT+N	0.11	0.09	0.06	0.04	0.04	0.048	0.019
SS+N	0.11	0.09	0.06	0.05	0.04	0.052	0.020
DS+N	0.11	0.09	0.06	0.05	0.05	0.052	0.021
No fertiliser	0.13**	0.12**	0.056*	0.07**	0.06**	0.054*	0.022**
Plus fertiliser	0.11**	0.09**	0.060*	0.05**	0.05**	0.050*	0.020**

† For explanation of abbreviations, *see* Table 1 footnote.

higher in 1991 (Smith *et al.* 1994). Magnesium and calcium concentrations showed similar trends in several components, though concentration differences in these nutrients between treatments with and without fertiliser were significant in only three (for calcium) or four (for magnesium) of seven components at normally accepted significance levels (Tables 4 and 5). The direction of these trends was usually opposite to those for potassium.

TABLE 3–Average concentration (% oven-dry weight) of potassium in above-ground components of 5-year old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	0.58	0.46	0.13	0.30	0.10	0.49	0.13
WT	0.55	0.47	0.12	0.28	0.14	0.47	0.13
SS	0.58	0.52	0.12	0.30	0.16	0.54	0.14
DS	0.58	0.50	0.13	0.30	0.14	0.51	0.14
FF+N	0.53	0.47	0.16	0.26	0.18	0.41	0.12
WT+N	0.57	0.53	0.17	0.26	0.18	0.39	0.12
SS+N	0.58	0.50	0.18	0.28	0.20	0.45	0.13
DS+N	0.59	0.52	0.19	0.27	0.19	0.45	0.12
No fertiliser	0.57	0.49	0.13**	0.29*	0.13**	0.50**	0.14**
Plus fertiliser	0.57	0.50	0.17**	0.27*	0.19**	0.42**	0.12**

† For explanation of abbreviations, *see* Table 1 footnote.

TABLE 4–Average concentration (% oven-dry weight) of calcium in above-ground components of 5-year old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	0.28	0.55	0.75	0.20	0.24a	0.26	0.05
WT	0.22	0.40	0.58	0.20	0.22ab	0.28	0.05
SS	0.25	0.45	0.60	0.19	0.24a	0.30	0.05
DS	0.26	0.41	0.60	0.18	0.20ab	0.24	0.04
FF+N	0.29	0.43	0.58	0.20	0.22ab	0.34	0.05
WT+N	0.25	0.40	0.52	0.21	0.21ab	0.28	0.05
SS+N	0.25	0.40	0.52	0.18	0.17b	0.25	0.05
DS+N	0.25	0.40	0.55	0.21	0.22ab	0.27	0.05
No fertiliser	0.26	0.45*	0.63*	0.20	0.23*	0.28	0.05
Plus fertiliser	0.26	0.41*	0.54*	0.20	0.20*	0.28	0.05

† For explanation of abbreviations, *see* Table 1 footnote.

Boron concentrations increased in the 1-year foliage of stands with increasing amount of slash retained (with treatments with and without fertiliser averaged within harvesting classes FF 12.8 mg B/kg^{a}; WT 14.6 mg B/kg^{b}; SS 15.1 mg B/kg^{bc}; DS 15.8 mg B/kg^{c}; where different superscript letters indicate significant differences $P \leq 0.05$) and in dead foliage in the same stands (with treatments with and without fertiliser averaged within harvesting classes FF 16.4 mg B/kg^{a}; WT 16.9 mg B/kg^{a}; SS 16.9 mg B/kg^{a}; DS 19.2 mg B/kg^{b}; where different superscript letters indicate significant differences $p \leq 0.05$) (Table 6).

Below-ground Nutrient Concentrations

Residual slash nutrient concentrations

Nitrogen concentrations in coarse residual slash (>10 cm diameter) were significantly ($p \leq 0.05$) higher in stands with fertiliser than in those without (Table 7). The nitrogen concentration of this material was comparable to live branches of the 5-year-old stand. Coarse woody residues were functioning as an important sink for urea-nitrogen during early plantation development.

Phosphorus and potassium concentrations in coarse residues were not affected by urea additions (Tables 8 and 9). However, concentrations of calcium, magnesium, and boron were greater in coarse residues of stands without fertiliser ($p \leq 0.05$) (Tables 10–12). Reasons for these trends were not apparent.

Forest floor nutrient concentrations

Nitrogen concentrations (ash-free basis) in the forest floor and fine woody residues (<10 cm diameter) were higher in fertiliser-treated stands (Table 7), and were related to harvesting

TABLE 5–Average concentration (% oven-dry weight) of magnesium in above-ground components of 5-year old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	0.19	0.22	0.25	0.12	0.13	0.16	0.03
WT	0.19	0.21	0.23	0.12	0.12	0.18	0.03
SS	0.20	0.22	0.22	0.11	0.12	0.18	0.03
DS	0.19	0.19	0.20	0.11	0.11	0.16	0.03
FF+N	0.21	0.22	0.28	0.11	0.12	0.16	0.04
WT+N	0.20	0.23	0.26	0.11	0.10	0.16	0.04
SS+N	0.20	0.21	0.26	0.11	0.10	0.15	0.04
DS+N	0.20	0.21	0.26	0.10	0.11	0.15	0.03
No fertiliser	0.20	0.21	0.22**	0.11	0.12*	0.17*	0.03**
Plus fertiliser	0.20	0.22	0.26**	0.11	0.11*	0.16*	0.04**

† For explanation of abbreviations, *see* Table 1 footnote.

TABLE 6–Average concentration (mg/kg oven-dry weight) of boron in above-ground components of 5-year old *Pinus radiata*.

Treatment†	Component						
	1-year foliage	≥2-year foliage	Dead foliage	Live branches	Dead branches	Stem bark	Stem wood
FF	13.1	15.0	17.2	7.7	9.8	18.3	2.5
WT	14.5	14.0	16.4	7.5	9.5	19.1	2.5
SS	15.0	15.2	17.0	8.3	9.1	18.1	2.7
DS	15.6	15.1	18.2	7.6	8.5	18.8	2.6
FF+N	12.5	12.4	15.6	7.7	8.6	16.2	2.7
WT+N	14.6	13.7	17.4	8.1	7.2	16.2	2.7
SS+N	15.2	13.0	16.9	8.4	7.5	17.6	2.8
DS+N	16.0	15.3	20.1	8.2	8.7	19.4	3.1
No fertiliser	14.6	14.2	17.2	7.8	9.2	18.6*	2.6*
Plus fertiliser	14.6	14.2	17.5	8.1	8.0	17.4*	2.8*

† For explanation of abbreviations, *see* Table 1 footnote.

TABLE 7–Concentration of total nitrogen (g/100 g oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year-old second-rotation stand of *Pinus radiata*.

Treatment	Coarse litter	Forest floor		Mineral soil			Fine roots (<2 mm)			
				0–10 cm	10–30 cm	30–90 cm	Litter layer		Mineral soil	
	afb†	tmb‡	afb	tmb	tmb	tmb	tmb	afb	tmb	afb
FF	–	0.407	0.800	0.0083	0.0035	0.0026	–	–	0.240	0.660
WT	–	0.370	1.402	0.0110	0.0048	0.0030	0.745	0.915	0.237	0.553
SS	0.251ab	0.443	1.073	0.0102	0.0038	0.0033	0.830	1.020	0.280	0.698
DS	0.173a	0.497	0.902	0.0087	0.0037	0.0030	0.897	1.149	0.230	0.681
FF+N	–	0.543	1.223	0.0135	0.0108	0.0030	–	–	0.480	1.044
WT+N	–	0.527	1.785	0.0110	0.0056	0.0043	0.850	1.281	0.423	0.901
SS+N	0.249ab	0.617	1.516	0.0150	0.0049	0.0038	1.003	1.197	0.430	0.967
DS+N	0.270b	0.717	1.325	0.0151	0.0057	0.0042	1.315	1.581	0.457	0.907
No fertiliser	0.212*		1.044**	0.010	0.004	0.003		1.032**		0.648**
Plus fertiliser	0.260*		1.462**	0.014	0.007	0.004		1.383**		0.955**

† afb = nitrogen concentration expressed on ash-free basis

‡ tmb = nitrogen concentration expressed on total mass basis (statistical analysis performed on afb only)

For explanation of additional abbreviations, *see* Table 1 footnote.

TABLE 8–Concentration of total phosphorus (g/100 g oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year old second-rotation stand of *Pinus radiata*, expressed on total mass basis.

Treatment	Coarse litter (>10 cm)	Forest floor (<10cm)	Mineral soil			Fine roots (<2 mm)	
			0–10 cm	10–30 cm	30–90 cm	Litter layer	Mineral soil
FF	–	0.043	0.031	0.031	0.030	–	0.063
WT	–	0.036	0.032	0.033	0.031	0.074	0.047
SS	0.020	0.034	0.033	0.032	0.032	0.093	0.054
DS	0.014	0.037	0.033	0.030	0.031	0.086	0.052
FF+N	–	0.049	0.030	0.031	0.030	–	0.054
WT+N	–	0.035	0.033	0.032	0.031	0.057	0.050
SS+N	0.017	0.036	0.034	0.032	0.031	0.064	0.051
DS+N	0.021	0.038	0.032	0.031	0.030	0.074	0.052
No fertiliser	0.017		0.031	0.031	0.030		
Plus fertiliser	0.019		0.033	0.033	0.031		

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 9–Concentration of total potassium (g/100 g oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year old second-rotation stand of *Pinus radiata* expressed on total mass basis.

Treatment	Coarse litter (>10 cm)	Forest floor (<10cm)	Mineral soil			Fine roots (<2 mm)	
			0–10 cm	10–30 cm	30–90 cm	Litter layer	Mineral soil
FF	–	0.179	0.237	0.244	0.217	–	0.312
WT	–	0.238	0.236	0.256	0.212	0.272	0.327
SS	0.132a	0.201	0.230	0.237	0.202	0.274	0.351
DS	0.058b	0.146	0.227	0.201	0.200	0.265	0.339
FF+N	–	0.186	0.213	0.231	0.209	–	0.346
WT+N	–	0.194	0.234	0.248	0.212	0.315	0.357
SS+N	0.015b	0.183	0.238	0.220	0.212	0.302	0.354
DS+N	0.083ab	0.150	0.225	0.211	0.198	0.286	0.361
No fertiliser	0.095		0.233	0.234	0.208		
Plus fertiliser	0.049		0.227	0.228	0.208		

For explanation of abbreviations, *see* Table 1 footnote.

treatments (with treatments with and without fertiliser averaged within harvesting classes FF 1.01%N[a]; DS 1.11%N[a]; SS 1.30%N[b]; WT 1.59%N[c]; where different superscript letters indicate significant differences $p \leq 0.01$).

Differences in forest floor phosphorus concentrations did not reflect trends in above-ground tree components, although the range in concentrations was very similar (Table 8). For phosphorus, potassium, calcium, magnesium, and boron, the general trend was for the WT and FF treated stands to have the highest concentrations, while DS stands had the lowest (Tables 8–12). These trends reflected the greater fraction of dilute woody residues in SS and DS treatments, relative to nutrient-rich foliage retained in FF and WT treatments, and may be due to comminution-related inputs to the fine woody fraction over time.

TABLE 10–Concentration of total calcium (g/100 g oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year old second-rotation stand of *Pinus radiata*, expressed on total mass basis.

Treatment	Coarse litter (>10 cm)	Forest floor (<10cm)	Mineral soil			Fine roots (<2 mm)	
			0–10 cm	10–30 cm	30–90 cm	Litter layer	Mineral soil
FF	–	0.489	0.293	0.296	0.261	–	0.418
WT	–	0.390	0.295	0.309	0.261	0.392	0.433
SS	0.210a	0.393	0.287	0.290	0.260	0.374	0.492
DS	0.093ab	0.380	0.287	0.243	0.249	0.443	0.421
FF+N	–	0.445	0.277	0.291	0.255	–	0.441
WT+N	–	0.359	0.291	0.303	0.261	0.338	0.442
SS+N	0.038b	0.397	0.293	0.281	0.262	0.307	0.443
DS+N	0.108ab	0.398	0.285	0.256	0.244	0.355	0.455
No fertiliser	0.151*		0.290	0.284	0.258	0.484	
Plus fertiliser	0.073*		0.286	0.283	0.256		

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 11–Concentration of total magnesium (g/100 g oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year old second-rotation stand of *Pinus radiata*, expressed on total mass basis.

Treatment	Coarse litter (>10 cm)	Forest floor (<10cm)	Mineral soil			Fine roots (<2 mm)	
			0–10 cm	10–30 cm	30–90 cm	Litter layer	Mineral soil
FF	–	0.238	0.255	0.260	0.242	–	0.223
WT	–	0.214	0.252	0.277	0.246	0.231	0.222
SS	0.108b	0.194	0.244	0.264	0.244	0.207	0.231
DS	0.042ab	0.183	0.244	0.227	0.240	0.216	0.229
FF+N	–	0.274	0.232	0.252	0.254	–	0.229
WT+N	–	0.215	0.249	0.266	0.248	0.163	0.242
SS+N	0.016a	0.202	0.266	0.249	0.256	0.135	0.230
DS+N	0.050ab	0.190	0.239	0.235	0.240	0.147	0.219
No fertiliser	0.075*		0.249	0.250	0.245		
Plus fertiliser	0.033*		0.246	0.250	0.245		

For explanation of abbreviations, *see* Table 1 footnote.

Mineral soil nutrient concentrations

Mineral soil total nitrogen concentration (0–90 cm average) was increased 0.003% ($p \leq 0.01$) by urea additions. The top 10 cm had a higher nitrogen concentration than the lower depths ($p \leq 0.01$), which reflects the A over C-horizon soil profile at this site (Table 7). Mineral soil nitrogen concentrations were not significantly different among harvesting treatments. Total nitrogen concentrations were very low, reflecting the young age and lack of humus accumulation in these sand dune soils.

Although there were significant differences, there was no consistent relationship between harvesting treatments and mineral soil concentrations of phosphorus, potassium, calcium, magnesium, and boron (Tables 8–12).

TABLE 12–Concentration of total boron (mg/kg oven-dry weight) in coarse litter (>10 cm diameter), forest floor (<10 cm diameter), mineral soil, and fine roots (<2 mm diameter) in a 5-year old second-rotation stand of *Pinus radiata*, expressed on total mass basis.

Treatment	Coarse litter (>10 cm)	Forest floor (<10cm)	Mineral soil			Fine roots (<2 mm)	
			0–10 cm	10–30 cm	30–90 cm	Litter layer	Mineral soil
FF	–	8.3	16.0	9.8	19.7	–	3.7
WT	–	4.4	13.9	14.0	19.7	6.0	4.5
SS	4.1b	4.7	10.1	15.0	19.7	6.7	7.3
DS	2.9ab	5.6	12.3	19.0	19.7	8.2	3.6
FF+N	–	8.2	13.5	11.0	19.7	–	6.1
WT+N	–	3.6	14.0	11.0	19.7	4.7	9.8
SS+N	1.5a	4.8	10.8	11.0	19.7	7.0	14.0
DS+N	3.1ab	6.3	16.3	17.0	19.7	6.2	15.3
No fertiliser	3.5*		13.1	14.5	19.7		
Plus fertiliser	2.3*		13.6	12.5	19.7		

For explanation of abbreviations, *see* Table 1 footnote.

Concentrations of phosphorus, potassium, calcium, and magnesium generally decreased with depth (Tables 8–11), reflecting the importance of soil profile development and increases in soil organic matter since sand dune stabilisation.

Fine root nutrient concentrations

Fine root nitrogen concentrations (ash-free basis) were increased by urea additions ($p \leq 0.01$), and were greater in the forest floor horizon than the underlying mineral soil ($p \leq 0.01$) (Table 7). Nitrogen concentrations were not affected by harvesting treatments. Fine root nitrogen concentrations in fertiliser-treated stands and in forest floor horizons were comparable to 1-year foliage, indicating the importance of fine roots as nitrogen sinks.

Stands without fertiliser had higher concentrations of phosphorus, calcium, and magnesium in fine roots than fertiliser-treated stands, which was similar to the foliar concentration trend for phosphorus (Tables 8, 10, 11).

Fine roots growing in mineral soil generally had higher concentrations of potassium, calcium, magnesium, and boron than fine roots in the forest floor (Tables 8–12). This is in contrast to fine root nitrogen and phosphorus concentrations, which were higher in the forest floor. These trends may be partially explained by differences in forest floor and mineral soil concentrations of total amounts of these elements, since the mineral soil had somewhat higher concentrations of total potassium, magnesium, and boron. Total calcium concentrations were somewhat higher in the forest floor than mineral soil.

Above-ground Nutrient Content

The trends in total nutrient content (kg/ha) of the above-ground biomass (Tables 13–18) reflected the combined effects of harvesting and fertiliser application on biomass accumulation and nutrient concentration. Above-ground biomass estimates have been published previously (Smith *et al.* 1994, Table 4). In summary, stand biomass (tonnes/ha) was ranked according to three productivity levels, FF < WT = SS = DS < FF+N = WT+N = SS+N = DS+N, which

TABLE 13–Total nitrogen (kg/ha) in components of 5-year-old *Pinus radiata* ecosystem.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-yr foliage	57.63	71.69	71.22	68.14	108.54	110.13	112.59	109.63
2+yr foliage	31.81	40.33	37.09	40.05	57.62	54.54	54.92	52.38
Dead foliage	3.45	4.83	4.06	4.08	17.45	17.97	17.89	17.38
Live branches	19.25	24.03	23.00	21.67	54.97	56.97	60.61	56.34
Dead branches	0.57	0.71	0.64	0.67	4.38	3.73	3.90	4.38
Stem bark	7.35	10.16	9.83	9.08	15.74	15.88	15.84	15.74
Stem wood	10.73	14.02	14.11	13.40	19.62	20.46	20.27	20.46
Sum above-ground	130.79	165.77	159.95	157.08	278.31	279.68	286.02	276.31
Coarse litter (>10 cm)	0.00	0.00	2.51	35.98	0.00	0.00	9.46	55.89
Forest floor (<10 cm)	19.20	260.77	459.24	736.93	39.14	374.85	532.12	878.48
Mineral soil								
0–10 cm	114.96	152.35	141.27	120.50	186.98	152.35	207.75	209.14
10–30 cm	109.90	150.72	119.32	116.18	339.12	175.84	153.86	178.98
30–90 cm	244.92	282.60	310.86	282.60	282.60	405.06	357.96	395.64
Sum soil	469.78	585.67	571.45	519.28	808.70	733.25	719.57	783.76
Fine roots (<2 mm)								
Litter layer	0.00	6.41	8.26	13.10	0.00	11.27	16.40	13.28
Mineral soil	14.98	12.66	14.10	14.44	40.92	35.23	42.55	70.84
Sum fine roots	14.98	19.07	22.36	27.54	40.92	46.50	58.95	84.12
Sum below-ground	516.36	883.71	1070.77	1335.53	921.16	1187.54	1352.49	1835.18
Total ecosystem	635	1031	1216	1477	1167	1434	1607	2078

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 14–Total phosphorus content (kg/ha) in components of 5-year-old *Pinus radiata*.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-year foliage	7.19	8.58	8.28	7.87	9.23	8.69	8.91	9.10
2+year foliage	4.75	5.78	5.32	5.13	5.45	4.75	4.81	4.97
Dead foliage	0.41	0.49	0.44	0.42	1.30	1.30	1.30	1.34
Live branches	6.88	8.54	8.21	7.81	10.03	9.50	10.24	10.76
Dead branches	0.19	0.22	0.20	0.22	0.59	0.52	0.57	0.70
Stem bark	1.09	1.48	1.50	1.33	1.65	1.63	1.72	1.77
Stem wood	3.38	4.03	3.74	3.83	4.58	4.18	4.36	4.62
Sum above-ground	23.90	29.12	27.69	26.61	32.83	30.57	31.90	33.26
Coarse litter (>10 cm)	0	0	0	3	0	0	1	4
Forest floor (<10 cm)	2	25	35	55	4	25	31	46
Mineral soil								
0–10 cm	429	443	457	457	416	457	471	443
10–30 cm	973	1036	1005	942	973	1005	1005	973
30–90 cm	2826	2920	3014	2920	2826	2920	2920	2826
Sum soil	4229	4400	4476	4319	4215	4382	4396	4243
Fine roots (<2 mm)								
Litter layer	0	1	1	1	0	1	1	1
Mineral soil	4	3	3	3	5	4	5	8
Sum fine roots	4	3	4	5	5	5	7	9
Sum below-ground	4235	4428	4515	4382	4223	4412	4434	4302
Total ecosystem	4259	4457	4543	4408	4256	4443	4466	4335

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 15–Total potassium content (kg/ha) in components of 5-year-old *Pinus radiata*.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-year foliage	29.53	36.78	34.92	35.38	42.85	47.07	47.06	48.05
2+year foliage	17.44	22.83	23.01	22.59	25.60	28.40	26.78	28.19
Dead foliage	0.90	1.11	1.00	1.04	3.48	3.70	3.87	4.16
Live branches	27.99	33.92	31.97	33.00	53.92	55.92	59.15	56.13
Dead branches	0.31	0.54	0.48	0.56	2.31	2.34	2.60	2.46
Stem bark	10.21	13.08	13.40	12.73	13.66	13.29	14.82	15.16
Stem wood	19.40	24.96	23.80	24.01	27.03	27.28	27.90	27.50
Sum above-ground	105.78	133.22	128.58	129.31	168.85	178.00	182.19	181.65
Coarse litter (>10 cm)	0	0	1	12	0	0	1	17
Forest floor (<10 cm)	9	169	212	220	14	139	160	184
Mineral soil								
0–10 cm	3282	3269	3186	3144	2950	3241	3296	3116
10–30 cm	7662	8038	7442	6311	7253	7787	6908	6625
30–90 cm	20441	19970	19028	18840	19688	19970	19970	18652
Sum soil	31385	31277	29656	28295	29891	30999	30175	28393
Fine roots (<2 mm)								
Litter layer	0	2	3	4	0	4	5	2
Mineral soil	21	18	19	22	30	30	39	57
Sum fine roots	21	20	21	26	30	34	44	59
Sum below-ground	31415	31466	29891	28553	29935	31171	30380	28653
Total ecosystem	31520	31599	30019	28682	30104	31349	30562	28835

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 16–Total calcium content (kg/ha) in components of 5-year-old *Pinus radiata*.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-year foliage	14.18	14.47	15.24	16.10	23.81	20.58	20.49	20.42
2+year foliage	20.98	19.40	19.80	18.32	23.27	21.65	21.65	21.76
Dead foliage	5.28	5.20	4.80	4.82	12.87	11.33	11.51	12.03
Live branches	18.97	25.01	20.30	19.58	42.43	43.89	38.25	45.15
Dead branches	0.73	0.87	0.72	0.82	2.87	2.68	2.22	2.85
Stem bark	5.42	7.76	7.43	6.10	11.12	9.52	8.38	9.21
Stem wood	7.35	9.41	8.16	7.31	10.25	11.00	10.03	10.34
Sum above-ground	72.90	82.12	76.45	73.04	126.63	120.65	112.53	121.77
Coarse litter (>10 cm)	0	0	2	19	0	0	1	22
Forest floor (<10 cm)	23	275	410	569	32	256	348	489
Mineral soil								
0–10 cm	4058	4086	3975	3975	3740	4030	4058	3947
10–30 cm	9294	9703	9106	7630	9137	9514	8823	8038
30–90 cm	24586	24586	24492	23456	24021	24586	24680	22985
Sum soil	37939	38375	37573	35061	36898	38131	37562	34970
Fine roots (<2 mm)								
Litter layer	0	3	4	7	0	4	5	3
Mineral soil	27	23	26	27	38	37	49	71
Sum fine roots	27	26	30	34	38	41	54	74
Sum below-ground	37989	38676	38014	35682	36968	38428	37965	35556
Total ecosystem	38062	38758	38091	35755	37095	38549	38078	35678

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 17–Total magnesium content (kg/ha) in components of 5-year-old *Pinus radiata*.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-year foliage	9.64	12.80	11.88	11.59	17.17	16.65	16.52	16.81
2+year foliage	8.47	10.09	9.50	8.64	12.15	12.42	11.18	11.34
Dead foliage	1.74	2.05	1.80	1.58	6.09	5.79	5.65	5.68
Live branches	11.25	14.15	12.10	11.99	22.36	23.84	22.57	21.94
Dead branches	0.39	0.50	0.35	0.43	1.52	1.37	1.34	1.39
Stem bark	3.34	4.96	4.50	4.05	5.35	5.27	5.08	5.20
Stem wood	4.70	6.53	5.78	5.74	7.63	8.14	8.28	7.48
Sum above-ground	39.54	51.08	45.91	44.02	72.28	73.47	70.63	69.84
Coarse litter (>10 cm)	0	0	1	9	0	0	1	10
Forest floor (<10 cm)	11	151	205	275	20	154	177	234
Mineral soil								
0–10 cm	3532	3490	3379	3379	3213	3449	3656	3310
10–30 cm	8164	8698	8290	7128	7913	8352	7819	7379
30–90 cm	22796	23173	22985	22608	23927	23362	24115	20912
Sum soil	34492	35361	34654	33115	35053	35163	35590	31602
Fine roots (<2 mm)								
Litter layer	0	1	2	3	0	2	2	1
Mineral soil	15	12	13	15	20	20	26	35
Sum fine roots	15	14	15	18	20	22	29	36
Sum below-ground	34518	35526	34874	33417	35093	35339	35796	31882
Total ecosystem	34558	35577	34920	33461	35165	35413	35867	31951

For explanation of abbreviations, *see* Table 1 footnote.

TABLE 18–Total boron content (kg/ha) in components of 5-year-old *Pinus radiata*.

Component	Treatment							
	FF	WT	SS	DS	FF+N	WT+N	SS+N	DS+N
1-year foliage	0.07	0.10	0.09	0.10	0.10	0.12	0.12	0.13
2+year foliage	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.08
Dead foliage	0.01	0.01	0.01	0.01	0.03	0.04	0.04	0.04
Live branches	0.07	0.09	0.09	0.08	0.16	0.17	0.18	0.17
Dead branches	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01
Stem bark	0.04	0.05	0.05	0.05	0.05	0.06	0.06	0.07
Stem wood	0.04	0.05	0.05	0.05	0.06	0.06	0.06	0.07
Sum above-ground	0.29	0.38	0.35	0.36	0.49	0.53	0.53	0.58
Coarse litter (>10 cm)	0.00	0.00	0.00	0.06	0.00	0.00	0.01	0.06
Forest floor (<10 cm)	0.04	0.28	0.43	0.82	0.06	0.23	0.39	0.73
Mineral soil								
0–10 cm	22	19	14	17	19	19	15	23
10–30 cm	31	44	47	60	35	35	35	53
30–90 cm	186	186	186	186	186	186	186	186
Sum soil	239	249	247	262	239	240	235	262
Fine roots (<2 mm)								
Litter layer	0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.01
Mineral soil	0.02	0.02	0.04	0.02	0.05	0.07	0.15	0.22
Sum fine roots	0.02	0.03	0.05	0.03	0.05	0.08	0.16	0.23
Sum below-ground	239.06	249.31	247.48	262.91	239.11	240.31	235.56	263.02
Total ecosystem	239.35	249.69	247.83	263.27	239.47	240.84	236.09	263.60

For explanation of abbreviations, *see* Table 1 footnote.

indicated the influence of forest floor removal and fertiliser on growth over the first 5 years. These three levels were also observed for nutrient contents of all six nutrients because of dominant effects of biomass accumulation. Stand nutrient contents were generally in the order N=K>Ca>Mg=P>B for stands without fertiliser, the fertiliser treatment affecting not the rank but the magnitude of differences between element contents in the order N>K>Ca>Mg>P>B.

The total above-ground nitrogen content of the fertiliser-treated stands at 5 years (Table 13) ranged from 278 (FF+N) to 286 kg N/ha (SS+N). Stands without fertiliser contained 47% (FF) to 59% (WT) of the amount in fertiliser-treated stands. Foliar nitrogen contents ranged from 93 (FF) to 117 (WT) kg N/ha in stands without fertiliser, and 179 (DS+N) to 185 (SS+N) kg N/ha in fertiliser-treated stands. Foliage contained 65 to 71% of total above-ground nitrogen, while branches contained 14 to 23% and stems 13 to 15%. In contrast, the 42-year-old first-rotation stand (Dyck *et al.* 1991) had 24% of total above-ground nitrogen in foliage, 27% in branches, and 46% in stems, largely due to age-related differences in biomass proportions among tree components.

Phosphorus contents of stands without fertiliser were from 78 to 95% (4–10 kg P/ha lower) of those estimated for fertiliser-treated stands (Table 14). Foliage contained 46 to 52% of above-ground phosphorus, while branches contained 30 to 34% and stems 19%.

Potassium contents of stands without fertiliser were 59 to 75% of those of fertiliser-treated stands (Table 15). Foliage contained 43 to 46% of above-ground potassium, while branches contained 25 to 34% and stems 23 to 29%. Stands with forest floor removed (FF) had lower potassium contents than other stands without fertiliser with intact forest floor (WT, SS, DS).

Calcium contents of stands without fertiliser were 60 to 68% of those of fertiliser-treated stands (Table 16). Foliage contained 44 to 55% of above-ground calcium, while branches contained 27 to 39% and stems contained 17 to 21%. The ranking of treatments by calcium content (FF = DS = SS < WT < SS+N = WT+N = DS+N = FF+N) reflected the influence of woody biomass accumulation in branches and stems of the respective treatments (Smith *et al.* 1994).

Magnesium contents of stands without fertiliser were 54 to 70% of those of fertiliser-treated stands (Table 17). Foliage contained 47 to 51% of above-ground magnesium, while branches contained 27 to 34% and stems contained 18 to 22%. Mg:K ratios ranged from 0.37 to 0.49 in foliage, and from 0.34 to 0.43 for total above-ground contents.

Boron contents of stands without fertiliser were 55 to 72% of those of fertiliser-treated stands (Table 18), largely reflecting differences in above-ground biomass among the treatments. Foliage contained 42 to 48% of above-ground boron, while branches contained 24 to 35% and stems contained 22 to 27%.

Below-ground Nutrient Contents

Below-ground nitrogen contents ranged from 79 to 90% of the ecosystem total. For stands with and without fertiliser, the below-ground fraction was proportional to residue retention (i.e., FF<WT<SS<DS) (Table 13). For phosphorus, potassium, calcium, magnesium, and boron, the below-ground contents were greater than 99% of the ecosystem total, and were similar for all harvesting treatments (Tables 14–18).

The forest floor contained 4% (FF) to 55% (DS) of total below-ground nitrogen in stands without fertiliser, and 4.2% (FF+N) to 48% (DS+N) in fertiliser-treated stands. The forest floor fraction of total nitrogen was positively related to residue retention, and was not substantially changed by fertiliser application. The forest floor fraction of below-ground nutrient content was small for phosphorus (0.05 to 1.3%), potassium (0.03 to 0.7%), calcium (0.06 to 1.6%), magnesium (0.03 to 0.8%), and boron (0.02 to 0.3%).

Fine roots contained 2% (SS and DS) to 3% (FF) of total below-ground nitrogen in stands without fertiliser, and 4% (WT+N) to 5% (DS+N) in fertiliser-treated stands. Fine root nitrogen content generally reflected trends in fine root biomass (Smith *et al.* 1994), and increased with residue retention and fertiliser application. The fine root fraction of below-ground nutrient content was very small for phosphorus (0.07 to 0.2%), potassium (0.06 to 0.2%), calcium (0.07 to 0.2%), magnesium (0.04 to 0.1%), and boron (0.008 to 0.09%).

Ecosystem Nutrient Contents

The total ecosystem nitrogen contents ranged from 635 (FF) to 2078 kg N/ha (DS+N) (Table 13). Above-ground nitrogen contents ranged from 10% (DS) to 21% (FF+N) of total ecosystem nitrogen.

Total ecosystem nutrient contents for phosphorus were similar across all treatments, ranging from 4223 to 4515 kg P/ha (Table 14). Above-ground phosphorus contents were a relatively small percentage of total ecosystem phosphorus, ranging from 0.6 to 0.8%. Total ecosystem contents of potassium, calcium, and magnesium were an order of magnitude greater than nitrogen and phosphorus (Tables 15–17). However, the above-ground components contained proportions of total ecosystem potassium (0.3 to 0.6%), calcium (0.2 to 0.3%), and magnesium (0.1 to 0.2%) similar to that observed for phosphorus.

Total ecosystem boron content ranged from 236 to 264 kg B/ha (Table 18). Above-ground portions of the ecosystem contained small amounts (0.1 to 0.2%) of total ecosystem boron.

Above-ground phosphorus, potassium, calcium, magnesium, and boron contents appeared to be proportional to the ecosystem total (0.1 to 0.8%) even though total amounts differed by one or two orders of magnitude. In contrast, above-ground nitrogen contents were a relatively high proportion of the total in this nitrogen-poor ecosystem.

DISCUSSION

Above-ground Nutrient Concentrations

Nitrogen concentrations in 1-year needles were considered deficient in trees without fertiliser, and even marginal in trees that had received 200 kg N/ha•year, using criteria of Will (1985). However, nitrogen uptake and biomass production were substantially increased by urea additions. Hunter & Hoy (1983) also observed marginal foliar nitrogen concentrations in *P. radiata* growing on recent sands of the Santoft Forest after treatment with calcium ammonium nitrate, although nitrogen additions substantially increased basal area growth. These results suggest that the threshold for "marginal" foliar nitrogen concentrations should be reduced on nitrogen-deficient sand dune soils.

The potassium concentrations observed in 1-year foliage, live branches, bark, and wood were substantially lower than those reported by Madgwick *et al.* (1977, Fig. 6). Potassium concentrations of these four *P. radiata* components growing on the potassium-rich Matahina gravels or Matahina hill soils of the north-eastern Kaingaroa Forest were a factor of 1.3 to 1.8 greater than observed in this study on coastal Pinaki sands.

Relative to the first-rotation stand at this site, foliar calcium and magnesium increased by 15% and foliar potassium concentrations decreased by 37% in subplots without fertiliser (P.N.Beets unpubl. data). Considerable potassium was removed from the site during harvesting; however, magnesium would have been largely replaced by atmospheric inputs of around 10 kg/ha•year (Metson 1974).

Vector analysis (after Timmer 1991), conducted with foliage samples collected in March 1991 using standard protocols, indicated urea fertiliser had substantial effects on the concentration of various nutrients (Smith *et al.* 1994). Based on those results, reduced phosphorus concentrations in fertiliser-treated stand components reported here (Table 2) appear to be due to nutrient antagonism and reduced phosphorus uptake caused by high urea additions. However, greater productivity was achieved in fertiliser-treated stands despite lower phosphorus concentrations than in untreated ones, suggesting that phosphorus was not limiting growth on this site. In the first 4 years, potassium concentrations in foliage sampled with standard protocols were significantly lower on subplots with fertiliser, and vector analysis suggested that this was due to biomass dilution, rather than reduced uptake (Smith *et al.* 1994). Those results suggested that the availability of potassium was reduced with greater removal of organic matter. Vector analysis of foliar calcium and magnesium indicated that increased uptake of these elements occurred after urea application on all harvesting treatments (Smith *et al.* 1994).

Above-ground Nutrient Content

The order of stand nutrient contents (N=K>Ca>Mg=P>B) is consistent with the findings of Madgwick *et al.* (1977) for *P. radiata* stands ranging from 2 to 22 years old. Heavy urea application has increased the difference between nitrogen and potassium because of high uptake of nitrogen; and has increased the difference between magnesium and phosphorus because of reduced phosphorus uptake caused by urea-related antagonism.

Above-ground nitrogen accumulation in the present study was greater than the 88 kg N/ha observed in tree "tops" of a 5-year-old first-rotation *P. radiata* stand by Gadgil (1979). However, nitrogen accumulated above ground in the FF treatment was comparable to the 140 kg N/ha report by Gadgil (1979) as being accumulated in tree plus herbaceous "tops". The range in total above-ground nitrogen was comparable to that observed in a 7-year-old first-rotation *P. radiata* stand at Woodhill Forest described by Beets & Madgwick (1988, Table 15) (Fig. 1).

In the present study, the total above-ground nitrogen content of the stands with fertiliser at 5 years (Table 13) was equivalent to the 284 kg N/ha contained above-ground in the 42-year-old first-rotation stand on this site (Dyck *et al.* 1991). Stands in all treatments had greater foliar nitrogen contents than the 68 kg N/ha contained in foliage of the 42-year-old first-rotation stand. The nitrogen accumulated by the second-rotation stand suggests the first rotation has enriched the nitrogen fertility of the site. However, stands grown on recent sand dunes accumulate substantially less nitrogen than on nitrogen-rich sites. For example, the highest nitrogen accumulation observed in this study was about 190 kg N/ha less than estimated to be in a 4-year-old stand at the nitrogen-rich Purukohukohu (Puruki-Tahi) study area (Beets & Pollock 1987) (Fig. 1).

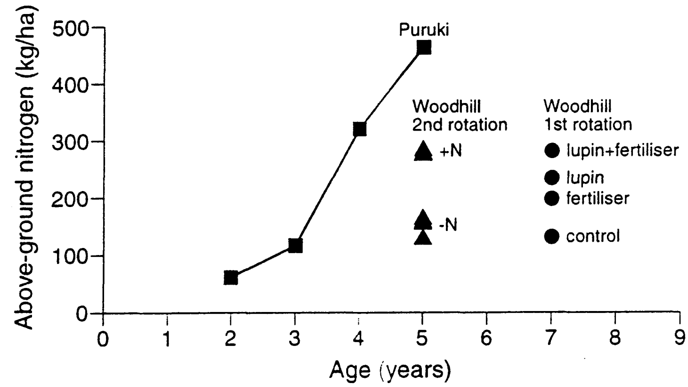

FIG. 1–Above-ground nitrogen (kg N/ha) in the present second-rotation study at stand age 5 years (■), at the Tahi sub-catchment at Puruki at ages 2, 3, 4, and 5 years (Beets & Pollock 1987) (▲), and for a first-rotation stand in Woodhill Forest (●) receiving fertiliser, lupins, and no amendments (control) at age 7 years (Beets & Madgwick 1988). All values estimated for stocking of 2500 stems/ha in the present study.

Boron contents of stands with fertiliser and stands without fertiliser and with intact forest floor (i.e., WT, SS, DS) were similar to those observed by Beets & Madgwick (1988). Although vector analysis of foliar boron and phosphorus indicated urea fertiliser antagonism (Smith *et al.* 1994) and reduced uptake, above-ground contents of these elements were somewhat increased by fertiliser application. Increased biomass production apparently offset reduced concentrations. These results indicate the need to interpret vector analysis results with caution.

Above-ground nutrient accumulation by fertiliser-treated stands in this study was of similar magnitude to 5-year-old stands described by Madgwick *et al.* (1977), who reported above-ground accumulation of approximately 220 kg N/ha, 160 kg K/ha, 90 kg Ca/ha, 30 kg Mg/ha, and 30 kg P/ha (values taken from Fig. 7). However, the fertiliser-treated stands in the present study at Woodhill Forest had greater accumulation of calcium (120 kg/ha) and magnesium (72 kg/ha), perhaps reflecting the influence of parent materials, Tasman Sea salt inputs, or urea on mineral solubility. Nutrient contents of this 5-year-old second-rotation stand were also comparable to a 7-year-old first-rotation stand at Woodhill Forest (Beets & Madgwick 1988). Urea fertiliser generally increased the accumulation rates of phosphorus, potassium, calcium, magnesium, and boron. Urea fertiliser increased the productivity of these sand dunes, and increased stand nutrient demand for elements not added in fertiliser. Thus, intensive management involving fertiliser and shorter rotations may increase the rate of nutrient depletion, and increase the need for future additional fertiliser amendments.

Above-ground Nutrient Partitioning

For all nutrients, the foliage and stems in fertiliser-treated stands contained a lower proportion of above-ground content than untreated stands. Branches in stands with fertiliser contained a greater proportion of above-ground nutrients than those in untreated stands. This reflected the tendency for *P. radiata* treated with nitrogen (Will & Hodgkiss 1977; Smith *et al.* 1994), or growing on ex-pasture sites (Birk 1992), to have biomass partitioning shifts from stems to branches.

In these 5-year-old trees, nutrients were generally accumulated by the above-ground components in the order stem < branches < foliage. However, *P. radiata* accumulates a greater proportion of potassium (23 to 29% of above-ground total) and boron (22 to 27%) in stem wood and bark than observed for nitrogen, phosphorus, calcium, and magnesium, which generally had from 13 to 22% of the above-ground content in stems. Similar observations have been made by Cromer *et al.* (1985), Madgwick *et al.* (1977), Orman & Will (1980), and Will (1964). These proportions are expected to change as trees age and develop greater stem size; however, these results indicate that commercial thinning in young stands of *P. radiata* will have a greater effect on potassium and boron depletion rates than on the other elements studied.

Forest Floor Nutrient Concentrations

Total nitrogen concentrations (ash-free basis) of the forest floor were positively correlated ($r=0.695$, $p\leq0.01$) with tree dbh at age 5 years (Fig. 2) (Smith *et al.* 1994). Smethurst & Nambiar (1990) emphasised that the concentration of nitrogen in the root zone may have a greater effect on growth than overall nitrogen mineralisation rates in young plantations. It is not clear how different organic fractions (e.g., humus, fresh litter, woody litter) contribute to the average nitrogen concentration of the forest floor materials at the site; however, the relationship appears to be dominated by the combined influences of the higher C:N ratio of the woody residues in slash, urea additions, and, in the FF treatment, the low nitrogen concentration of litter inputs during the 5-year period after trial establishment. This relationship may be related to differences in nitrogen availability among harvest treatments, since litter nitrogen concentration has been shown to be positively related to nitrogen mineralisation (Raison *et al.* 1987) and to growth (Hunter *et al.* 1985). If this relationship is indicative of differences in nitrogen mineralisation, it may also explain why growth has been

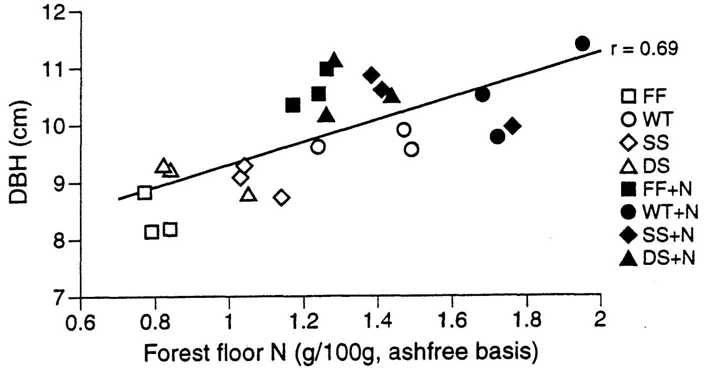

FIG. 2–Relationship between forest floor nitrogen concentration (%N, ash-free basis) and average dbh for each sub-plot in the present study. The relationship can be described by the equation [dbh, cm = 7.361 + 1.947(%N, afb)] ($r=0.695$, $p<0.01$).

somewhat greater in stands that were whole-tree harvested (WT) than those retaining slash (e.g., SS and DS) as reported by Smith *et al.* (1994). These results support other research indicating that retention of woody residues with high C:N ratio may increase nitrogen immobilisation for some period of time after harvesting (Vitousek & Matson 1985).

Below-ground Nitrogen Contents

Below-ground nitrogen contents (Table 13) were 38 to 136% of pre-harvest contents (1346 kg N/ha) observed by Dyck *et al.* (1991), including forest floor, mineral soil (0–90 cm), and roots. Only stands with DS, SS+N, and DS+N treatments had below-ground nitrogen contents equal to or greater than the pre-harvest stand. Harvesting removals and redistributions, and leaching losses of nitrogen in stands that received other treatments will have to be replaced by some combination of atmospheric deposition, nitrogen fixation, and fertiliser inputs for nitrogen contents to fully recover to pre-harvest levels.

Productivity to Nutrient Accumulation (P/NA) Ratios

Productivity to nutrient accumulation (P/NA) ratio, defined as above-ground production (tonne/ha) per unit of nutrient accumulation (e.g., kg N/ha), was 0.27 tonne/kg N for treatments without fertiliser, 0.23 tonne/kg N for treatments with fertiliser, and estimated to be 0.16 tonne/kg N at Puruki-Tahi (Purukohukohu). These results were consistent with those of Beets & Madgwick (1988), where P/NA, on an above-ground basis, was greatest in control stands (0.38 tonnes/kg N), and was lower in stands where the fertility of the sand dunes was supplemented by lupins (0.27 tonnes/kg N), fertiliser (0.29 tonnes/kg N), and lupin plus fertiliser (0.23 tonnes/kg N).

Nitrogen P/NA values appear to differ substantially between stands on sand dunes and nitrogen-rich Oruanui loamy sands of the Purukohukohu Experimental Basin (Puruki-Tahi). While this study did not measure all components of nitrogen flux, P/NA trends for nitrogen are expected to be indicative of differences in nitrogen-use efficiency among sites. These differences suggest *P. radiata* grows more efficiently (albeit more slowly), from a nutrient-use perspective, on nitrogen-deficient sands than on nitrogen-rich sites. Decreased nitrogen-use efficiency (NUE) with increasing nitrogen availability was also observed by Birk & Vitousek (1986) in *Pinus taeda* L. stands on the upper coastal plain of South Carolina. They hypothesised that more carbon was fixed into organic matter per unit of tissue nitrogen at low levels of nitrogen availability. However, analyses on a foliar basis may support hypotheses different from analyses based on above-ground total nitrogen contents. For example, preliminary work in 1991 at this Woodhill Forest study area by Beets & Whitehead (1992) indicated that net photosynthesis per unit of leaf area increased with foliar nitrogen status. Decreasing P/NA with increasing nitrogen availability, as seen in differences between Woodhill Forest and Puruki, may merely be due to "luxury" accumulation of nitrogen in tissues that are not directly involved in carbon fixation.

Foliar nitrogen concentrations on sandy sites are generally lower than on other sites in New Zealand (Madgwick 1985). In this trial, fertiliser-treated trees had lower than expected foliar nitrogen concentrations (Smith *et al.* 1994). Beets & Madgwick (1988) also observed that fertiliser-treated trees in Woodhill Forest had foliar nitrogen concentrations below the critical levels established by Will (1985). It is likely that critical foliar nitrogen levels established for *P. radiata* may require modification to account for different NUE among sites and climatic regimes.

Higher NUE on low-nitrogen sandy sites would refute the suggestion of Beets & Pollock (1987) that Puruki nitrogen uptake estimates could be used to predict nitrogen demand for maximum growth. Puruki-derived estimates would probably over-estimate nitrogen demand for low-nitrogen sites (Fig. 1). These results have important implications for attempts to model and manage long-term site fertility and productivity using the approach suggested by Beets & Pollock (1987).

Because nitrogen additions altered the productivity of these stands, it is probably inappropriate to apply the term "nutrient use efficiency" to the elements phosphorus, potassium, calcium, magnesium, and boron. However, analysis of P/NA ratios for these elements is instructive for determining whether the soil supply of these nutrients is sufficient to maintain constant proportionality in P/NA for all nutrients when heavy additions of single element fertiliser cause rapid increased growth. Analysis of P/NA ratios between stands with and without fertiliser showed that urea additions resulted in "dilution" of above-ground phosphorus (1.97 for treated *v.* 1.56 tonnes/kg P for untreated stands) and potassium (0.36 *v.* 0.34, respectively) in this study; whereas nitrogen, calcium (0.53 *v.* 0.55), magnesium (0.89 *v.* 0.93), and boron (119.4 *v.* 121.6, respectively) were more concentrated in treated trees. "Nutrient dilution" (as used by Jarrell & Beverly 1981) would occur when increased biomass accumulation rates were not matched by nutrient uptake. These differences may be useful for identifying nutrients that may begin to limit growth after fertiliser application because of slow rates of various processes contributing to nutrient availability. Of course, one must be careful to distinguish between "nutrient dilution" due to altered P/NA and apparent dilution due to age-related differences in biomass partitioning between nutrient-poor stems and nutrient-rich crown components.

The observed dilution of phosphorus may have been due to an antagonism between phosphorus and nitrogen caused by high rates of urea additions, as discussed by Smith *et al.* (1994) and supported by vector analysis of foliar nutrient differences among treatments using techniques of Timmer (1991).

Boron was generally more concentrated in treatments with than without fertiliser, as indicated by lower P/NA ratios for WT+N, SS+N, and DS+N than corresponding treatments without fertiliser. However, the boron P/NA ratio for FF (124 tonne/kg B) was lower than for FF+N (129 tonne/kg B), indicating a dilution in above-ground components of fertilised stands. This supports the results of vector analysis indicating antagonism between boron and urea-derived nitrogen in stands where the forest floor was removed (Smith *et al.* 1994), and suggests that removal of forest floor materials reduces the availability of boron to fast-growing fertiliser-treated trees.

Nutrient Requirements with Intensified Management

Webber (1978) predicted that intensified management could increase nutrient depletion rates, and increase the need for fertilisers to maintain productivity. The results of this study support that prediction, since treatment with urea substantially increased the productivity of the sand dunes, and increased stand accumulation of elements not applied with fertiliser as well. Mean annual above-ground biomass productivity for this trial ranged from 7.2 to 12.7

tonnes/ha. Mean annual nitrogen accumulation rates ranged from 26 to 57 kg N/ha, and for other nutrients were: 4.8 to 6.6 kg P/ha, 21 to 36 kg K/ha, 14.6 to 25.3 kg Ca/ha, 7.9 to 14.7 kg Mg/ha, and 0.06 to 0.12 kg B/ha.

Increased biomass production was not in constant proportion with increased nutrient accumulation. In this trial, the ratio of above-ground biomass production in stands with fertiliser to those without was 1.75 (FF), 1.35 (WT), 1.51 (SS), and 1.49 (DS). The ratio between treated and untreated stands for nutrient accumulation should indicate whether soil supplies of nutrients are greater than, equal to, or less than adequate to meet increased tree demand due to increased biomass productivity. The ratio of treated and untreated stand nutrient contents was 1.7-2.1 for N, 1.2-1.4 for P, 1.3-1.6 for K, 1.5-1.7 for Ca, 1.4-1.8 for Mg, and 1.4-1.7 for B. These results indicate nitrogen and magnesium supplies were increased; reduced for phosphorus and potassium; varied between unchanged and increased for calcium; and for boron, reduced in FF treatments, unchanged in WT and SS, and increased in DS treatments. These results generally support conclusions based on analysis of P/NA ratios and vector analysis of foliar nutrients.

Nutrient Accumulation and Retention

Total ecosystem nitrogen contents were from 39 to 126% of pre-harvest total of 1645 kg N/ha (Dyck *et al.* 1991; Smith *et al.* 1994). Based on these estimates, only DS+N treated sites had recovered from harvesting-related nitrogen removals (Fig. 3). Above-ground nitrogen contents ranged from 23% (FF+N) to 11% (DS) of total ecosystem nitrogen, which would be higher than typical of ecosystems with higher soil nitrogen content. This indicates the susceptibility of sand dune forests to nutrient depletion or reduced productivity due to harvest removals of organic matter. As expected, those stands with greatest below-ground nitrogen are least susceptible to nutrient depletion by whole-tree harvest of young stands (e.g., pre-commercial thinning removals).

It is noteworthy that there had been declines in total ecosystem nitrogen since trial establishment in 1986 for all stands without fertiliser (Fig. 3). Declines ranged from 200 to 338 kg N/ha, and indicated the poor ability of the combined accumulation potential of the

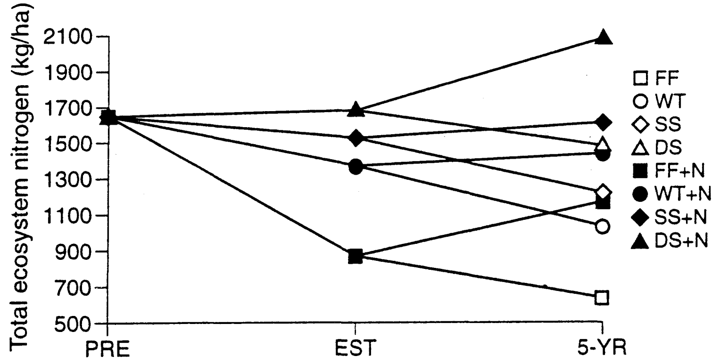

FIG. 3–Total nitrogen contained in above- and below-ground components of stands at times corresponding to pre-harvest (Dyck *et al.* 1991), immediately after trial establishment (Smith *et al.* 1994), and at stand age 5 years. Treatment abbreviations are described in Table 1 footnote.

trees and soils (via microbial immobilisation) to prevent nitrogen leaching losses in the first 2 to 3 years after harvesting. Smethurst & Nambiar (1990) reported losses of the same magnitude (242 kg N/ha) from the top 30 cm of a sandy podzol in south-eastern Australia. Slash retention appeared to increase the ecosystem nitrogen retention capacity substantially, as retention (age 5-year ecosystem total expressed as a percentage of the amount present immediately after trial establishment) increased in the order FF<WT<SS<DS. The DS treatment retained 88% of the amount present at establishment, compared with FF (73%), WT (75%), and SS (80%) treatments.

Stands treated with fertiliser accumulated from 391 to 601 kg N/ha more than untreated stands over the 5 years from trial establishment. However, only 43 to 67 % of the 900 kg N/ha added was retained in the top 90 cm of the ecosystem. Fertiliser-treated stands had somewhat lower retention than untreated stands of the total amount of nitrogen added over the first 5 years plus that present at trial establishment. Retention of nitrogen was in the order: WT+N (63%), SS+N (66%), FF+N (76%), DS+N (81%). Only the DS+N treatment had accumulated enough nitrogen to surpass the 1700 kg N/ha present in the 42-year-old first-rotation stand.

These results indicate the importance of residue retention for conservation of nitrogen, probably as a result of microbial immobilisation in residues that have high C/N ratios. In addition to woody residues with high C/N ratios, significant nitrogen immobilisation capacity has been observed in litter derived from *P. radiata* foliage (Will *et al.* 1983). Nitrogen-deficient sand dune ecosystems have been found to have high nitrogen-immobilisation capacity in studies by Miller *et al.* (1979); however, sand dune mineral soils without organic residues would have negligible nitrogen-retention capacity because of low capacity to adsorb inorganic nitrogen.

Nutrient Depletion with Harvesting

Sand dune forests are expected to be more susceptible to nitrogen depletion due to harvest removals than more fertile sites. For example, Crompton & Cole (1991) found that infertile sands were more susceptible to nutrient depletion due to harvesting Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) than fine-textured, more fertile soils in British Columbia. Birk (1993) reached similar conclusions for Australian sites, where intensive management resulted in more rapid accumulation of biomass and nutrients than on unimproved sites, and where the proportion of nutrients contained in the above-ground biomass was large relative to that contained in the soil.

For the present study site, whole-tree harvesting removed 18.6% of the ecosystem nitrogen. The results of this study indicated that above-ground the stand already contained a substantial proportion of total ecosystem nitrogen (9.6 to 18.7%) at age 5 years, as compared with the distribution of the other nutrients studied. For phosphorus, potassium, calcium, magnesium, and boron, above-ground contents were less than 1% of the ecosystem total. In a 5-year-old first-rotation *P. radiata* stand in Woodhill Forest, Gadgil (1979) found that above-ground tree components contained 5% of the ecosystem nitrogen content.

Reductions in growth were observed in this trial in stands receiving the FF treatment (Smith *et al.* 1994), where the total ecosystem nitrogen content at trial establishment was 869 kg N/ha. We hypothesise that the growth reductions observed here represent the combined effects of the low total nitrogen content of the site and the removal of readily mineralisable forest floor materials. These results indicate that 869 kg N/ha contained in relatively recalcitrant mineral soil organic matter was not sufficient to maintain productivity in the second rotation, and that it was essential to retain the more labile forest floor materials containing 462 kg N/ha, because of greater mineralisation potential.

At this time, it is not easy to objectively resolve differences in management approaches suggested by analysis of growth data and nutrient depletion estimates. Somewhat greater growth in stands receiving whole-tree harvesting (WT) than residue retention (SS and DS) might suggest that forest managers select harvesting systems that increase nutrient depletion rates (e.g., WT), since this would help avoid fertility limitations in the first 5 years associated with nitrogen immobilisation by coarse woody slash. A more conservative approach would be to achieve long-term balance between nutrient removals and additions. Ultimately, we may be able to develop management systems that would be based on a combination of ecological and economic principles, and where residue retention decisions are based on relative costs associated with different harvesting systems, potential growth decline or increase, and fertiliser amendment efficiency and cost.

Reductions in nutrient availability caused by harvest removals of organic matter can be easily, albeit expensively, corrected by fertiliser additions. However, we require greater understanding of the role of organic sources of nutrients in regulating nutrient availability in managed forests. It is likely that reductions in growth due to reduced boron availability will be a minor consideration in comparison to reduced nitrogen availability, because of the importance of nitrogen for tree growth. Based on studies by Miller (1981), we expect the nitrogen immobilisation capacity of the Pinaki sands to be of significance to later stand development. It remains to be seen whether the urea added in this trial has the potential to increase long-term nitrogen availability and stand productivity, or has been just of short-term benefit to the trees, since the nitrogen additions have been substantial relative to the nitrogen capital of the site. Miller (1981) indicated that there is little potential for fertiliser to have long-term benefits to site productivity. Research in first-rotation *P. radiata* plantations established on recent sands in Santoft Forest (Hunter & Hoy 1983) and Woodhill Forest (P.N.Beets unpubl. data) also indicate that trees will again become nitrogen deficient several years after fertiliser application ceases.

It is not certain how increases in soil organic matter will benefit sand dune productivity in the long term. However, these results indicate the importance of organic matter as a store of nitrogen on the Pinaki sands, and the importance of forest floor materials in supplying second-rotation *P. radiata* with nitrogen and boron. Nitrogen loss from the system was positively related to organic matter removal. Productivity was reduced only by removal of the forest floor and was increased in all harvest treatments by the addition of urea. It is necessary to retain all harvest residues and add fertiliser nitrogen to maintain the nitrogen content of this ecosystem at pre-harvest levels.

The results of this study may not be applicable to older stands because biomass and nutrient partitioning will change as stands age, and as stem wood increases relative to crown branch and foliage. We hypothesise that nutrient shortages (e.g., nitrogen) occurring in the early stage of stand development examined in this trial, when tree crowns were rapidly expanding, will become less critical as the stands age because a large proportion of stand nutrient demand can be met by internal retranslocation and a reduction in stand nutrient demand (Miller 1981). Nevertheless, removal of the forest floor reduced site productivity of the Pinaki sands, and we hypothesise that total volume production at the end of the second rotation will be less than in stands retaining the forest floor. These hypotheses will be tested by observing whether growth trends among the experimental stands are divergent, convergent, or parallel (after Snowdon & Khanna 1989).

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