PHOSPHORUS CYCLING IN A SANDY PODSOL UNDER *PINUS RADIATA*

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ABSTRACT

Phosphorus cycling through various soil pools of a podsol was measured at two *Pinus radiata* D.Don fertiliser trial sites. Tree growth rates differed markedly between sites, but the growth response to phosphorus treatment was absent at one site and small at the other.

The surface mineral soil horizons were mainly quartz sand, and the 0–15 cm layer of the soils contained very little inorganic phosphorus compared with organic phosphorus. The phosphorus in most pools increased with higher rates of phosphorus fertiliser. There was no significant increase in tree growth, litterfall, soil carbon, or microbial carbon pools, and thus the P/C ratios of soil pools generally increased. The phosphorus mineralisation rate also increased with phosphorus treatment. The microbial biomass phosphorus made up a large proportion of the forest floor phosphorus, and the solution phase in the forest floor contained large concentrations of inorganic phosphorus that probably arose from mineralisation of organic matter during turnover of the microbial biomass, together with direct leaching from needles. The concentration of inorganic phosphorus in the soil solution of the mineral soil was less than in the forest floor. Since there was little phosphorus sorption by the mineral soil, uptake of phosphorus by the trees directly from the forest floor would account for the observed drop in inorganic phosphorus. Uptake of phosphorus by the trees was highly correlated with microbial phosphorus. There appeared to have been losses of phosphorus from the ecosystem, and leaching of phosphorus had probably occurred to at least the base of the E horizon.

At the higher rate of phosphorus fertiliser, microfauna feeding on micro-organisms in the forest floor had a similar biomass to those at the lower rate of phosphorus but there were larger numbers of smaller microfaunal organisms. This suggested that there may have been shorter generation times, more microbial grazing, and enhanced nutrient cycling as a result of the improved phosphorus status of the substrates. The overall phosphorus cycling rate also probably increased with a higher rate of applied phosphorus.

Keywords: microbial biomass; phosphorus mineralisation; phosphatase; nematodes; rotifers; soil solution.

INTRODUCTION

Phosphorus (P) deficiency in *Pinus radiata* is widespread on the older landscapes in northern New Zealand (Will 1985). The Bray soil test, which was developed to predict soil phosphorus supply to *P. radiata* crops, is in some places over-predicting, and in others under-predicting phosphorus requirements, particularly for second-rotation crops (Hunter & Hunter 1991). It seems likely that the phosphorus supply to some second-rotation crops could be met by mineralisation of soil organic phosphorus. The Bray test is, however, not a good predictor of phosphorus mineralisation; some soils with a high Bray test result may have a low rate of mineralisation and an inadequate supply of phosphorus, whereas other soils with a low Bray score may have relatively high rates of mineralisation and be adequately supplied with phosphorus. Little is known about phosphorus mineralisation in northern forests in New Zealand.

Sparling *et al.* (1994) estimated that the annual turnover of nitrogen and phosphorus through *P. radiata* on Ultic soils in the Wellington region was about 50–75 kg N/ha and about 5 kg P/ha, assuming no losses or additional inputs of these nutrients. The annual flux of phosphorus through the soil microbial fraction (18 kg/ha) was about three times greater than that through *P. radiata*; the flux of nitrogen through trees and soil microbial biomass was similar. These calculations took no account of the microbial fraction in the FH material, for which there was no estimate of turnover.

In the South Island, available phosphorus levels can be higher under conifers than under adjacent grassland, and mineralisation of organic matter appeared to be the major mechanism responsible for the enrichment of nutrients under pines in Canterbury (Davis & Lang 1991).

Polglase *et al.* (1992a) studied nitrogen and phosphorus release from decomposing needles of southern pine (*Pinus taeda* L., *P. elliottii* Engelm. var. *elliottii*) plantations in Florida and found that inorganic phosphorus (P_i) made up 40% of total phosphorus (P_t) in O_i horizon needles in untreated plots and 75% in plots treated with fertiliser. The quality of organic-matter substrates in needles was increased by fertiliser and weed treatment, leading to more phosphorus being cycled (Polglase *et al.* 1992b). Mineralisation of phosphorus was consistently increased by fertiliser application, suggesting that the general composition of phosphorus substrates was altered by fertiliser application (Polglase *et al.* 1992c).

Net mineralisation of nitrogen and phosphorus was initially enhanced by application of nitrogen and phosphorus fertilisers but microbial activity and biomass were unchanged in United States Rocky Mountain coniferous forests (Prescott *et al.* 1992).

Microbial biomass and microbial detritus are likely to be the major source of the diester-phosphorus fraction in most soils (Brookes *et al.* 1984). Diester phosphate (DNA, phospholipids, etc.) was shown by ^{31}P-NMR to provide the main source of readily mineralisable P_o in tussock grassland and cropping soils (Tate & Newman 1982; Hawkes *et al.* 1984). Monoester phosphates are the main form of soil P_o, predominantly inositol polyphosphates, but these are usually in the form of aluminium and iron salts that are insoluble and therefore are not readily mineralised (Tate 1985).

Since fluxes of phosphorus through the microbial biomass can be substantial and since there is a close relationship between nutrient content of the microbial biomass and levels of mineralisable nutrients in soil (*see* Sparling *et al.* 1994), we have measured the microbial biomass phosphorus and other phosphorus pools in two *P. radiata* forests on a podsolised

sand, and related these to phosphorus uptake by the trees. The surface layers of this soil are largely quartz sand so the phosphorus is held mainly as organic phosphorus (P_o) and the phosphorus cycle is not complicated with large pools of P_i.

In this paper we attempt to quantify the phosphorus cycle during 1990–91 in *P. radiata* stands growing with and without fertiliser at two sites on this soil, where P_o is expected to make the major contribution to the phosphorus nutrition of the trees.

MATERIALS AND METHODS

Trial Sites

Site 1 in Shenstone Forest was planted in 1979 with *P. radiata*, with 25 kg P/ha being applied as superphosphate at establishment; the site previously had been under manuka (*Leptospermum scoparium* J.R.et G.Forst.). A fertiliser trial was established in 1983, after a weed control operation. In our sampling two replicates of growth plots were selected; each was 0.0255 ha, treated with either 0 or 75 kg P/ha as monocalcium phosphate (MCP), and had no added nitrogen fertiliser. The tree canopy was closed at time of sampling and the site relatively free of weeds. Litter was largely from *P. radiata* although partially decomposed manuka was probably still present in the FH material.

Site 2 in Te Kao Forest was planted in 1983 and was previously under 2- to 3-m-tall manuka. The site was prepared by crushing the manuka and mounding the soil, with no additional weed control. A rock phosphate trial was established at planting; three replicates of plots (each 0.015 ha), treated with either 4 kg P or 125 kg P/ha as a 50/50 mixture of Nauru/Christmas Island rock phosphate, were selected for our study. The site contained an understorey of manuka and *Oxylobium* shrubs, and these species contributed to the LFH material.

The two sites were both on Te Kopuru sand (podsol). At each site an LFH horizon overlay an A_p horizon of about 10 cm thickness. An E horizon of about 40 cm thickness rested on indurated B_h and B_s horizons with bulk densities of close to 2.0 g/cm^3. The A_p and E horizons were composed largely of quartz sand and had phosphate retention values of zero (Blakemore *et al.* 1987); the pH in water of the A_p horizons was 4.2–4.7. The sites had been ripped to a depth of 60 cm at planting to shatter the indurated layer. The landscape has been described by Hicks (1983), and the mean annual rainfall is 1400 mm.

Phosphorus Content of *Pinus radiata* Stands

The diameter and height of trees in growth plots established in each replicate of the trials had been measured annually prior to this study. The plots were remeasured in November 1991 to provide information on the current stocking, basal area, and height.

The above-ground biomass and phosphorus content of 12 trees (2 sites × 2 treatments × 3 trees) were measured in November 1991. Each replicate at Te Kao provided one sample tree, and either one or two sample trees at Shenstone. The trees were felled at 10 cm above ground-level, and total height and stem diameter at 1.40 m were measured. Branch diameters were measured at 2.5 cm from point of attachment to stem. One typical branch was selected from each branch cluster and these were bulked by tree and divided into needles by age class, live branch, and dead branch matter. Stem disc samples were cut at 1-m intervals along the

stem, and disc length and diameter over bark were measured. Samples were dried to constant weight and weighed. The phosphorus in subsamples was determined colorimetrically after digestion with sulphuric acid and hydrogen peroxide in the presence of lithium sulphate and selenium (Nicholson 1984).

Stand phosphorus content was determined from the three trees collected by site and phosphorus treatment, using ratio methods described by Beets & Madgwick (1988).

Samples were dried to constant weight at 105°C for mineral soil, and in forced-ventilation ovens at 70°C for plant and LFH material.

Phosphorus Uptake by *Pinus radiata* Stands

Stand estimates of phosphorus uptake by the pines were obtained by site and phosphorus treatment using the NZ FRI DRYMAT model, which requires site-specific data on tree growth rate and component nutrient concentrations (Beets 1982; Beets & Brownlie 1987). Model inputs influencing stand growth rate included site productivity level (which is defined in DRYMAT as stem periodic annual volume increment at age 20), stocking rate, stand tending history, needle retention, and wood density region. Model inputs influencing phosphorus uptake include the concentration (percentage oven dry weight basis) of phosphorus in foliage by needle age-class, needle fall, branches, stems, and roots. The model was run over a range of productivities to determine the level at which the simulated volume increment matched the measured increment during 1990–91, the period of interest. Growth of non-stem components was simulated in DRYMAT using partitioning functions, which are based on biomass data described by Beets & Pollock (1987). The model estimates of tree component weights and losses owing to mortality were multiplied by the component mean phosphorus concentrations of sample trees and litterfall collected from each stand. No root samples were collected in this study, and so unpublished biomass and nutrient data from Woodhill Forest were used as a guide. Fine root (<2 mm diameter) phosphorus concentrations were assumed to equal 2-year-old needle phosphorus concentrations, and coarse root (>2 mm diameter) phosphorus concentrations were assumed to equal branch phosphorus concentrations. The phosphorus concentrations of all components were assumed to be constant at the beginning and end of the simulation period. Normally phosphorus concentrations change with increasing stand age (Beets & Madgwick 1988), and so the modelled phosphorus uptake estimates will be biassed; however, the bias is likely to be small over an increment period of only 1 year.

Organic Matter and Phosphorus Pools and Fluxes

Three litter traps were sampled in each replicate, after 8 months in July 1991 and again after 4 months in November 1991. The phosphorus content of each sample was measured after acid digestion.

Four samples of LFH horizon (300 cm^2) were taken from each replicate in November 1990. Twenty cores of soil (0–5 cm and 5–15 cm depth) were taken along two diagonal transects in each replicate. In November 1990 the samples from each diagonal from all replicates were bulked; in later samples for microbial biomass phosphorus measurements and phosphorus mineralisation, the samples from diagonals were kept separate. All samples were stored field moist in plastic bags at 4°C. Bulk densities were estimated from the mass, diameter, and depth of the samples.

Soil solutions were extracted immediately on return to the laboratory by centrifuging at 3500 RCF (7000 rpm) for 20 minutes. After filtering through 0.2-μm filters the solutions were analysed for anions by ion chromatography and for phosphorus by an ammonium molybdate method.

Total carbon was measured on LFH samples which were cut up and mixed, and soil samples which were sieved through a 2-mm sieve. A Leco furnace was used.

Microbial biomass carbon and biomass phosphorus were measured by chloroform fumigation-extraction methods (Brookes *et al.* 1982; Vance *et al.* 1987). Litter (LFH) P_i was estimated by extraction with 0.5M bicarbonate for 2 h. Bicarbonate was also used to extract soil phosphorus; P_i was measured using ammonium molybdate and organic phosphorus (P_o) was measured by difference after acid digestion of the bicarbonate extract. Total phosphorus was estimated by digestion with sulphuric acid. Resin phosphorus was measured by shaking 2.5 g soil with 25 ml water in the presence of an anion exchange membrane; membranes were also used to extract the phosphorus mineralised after incubation of the soil at 39°C (Parfitt *et al.* 1994). Extractable phosphorus was also measured using 2.5 g soil samples and 25 ml 0.1 M NaOH for 24 h; charcoal was added, the samples acidified rapidly to pH 1.5, centrifuged, and filtered to remove colour and solids before analysing for phosphorus. Phospho-diesterase activity was measured by the method of Sparling *et al.* (1986).

The ^{31}P NMR methods using sodium hydroxide extracts to estimate phosphorus compounds in soils have been described by Tate & Newman (1982). In this study, 0.1M NaOH rather than 0.5M NaOH was used as the extractant. Although broader peaks were obtained with the lower concentration of alkali (data not shown), the spectra are considered more representative of the phosphorus-containing biopolymers in soil organic matter. Cross polarisation/magic angle spinning ^{13}C NMR methods have been given by Newman & Tate (1991). Subspectra were separated by an inversion-recovery pulse sequence for both ^{13}C NMR and ^{31}P NMR; recovery intervals were 17 and 49 ms. This method was applied to soil organic matter which was physically separated from the quartz sand upon air drying.

Nematodes

Duplicate samples of LFH horizons with field moist weights of 30–40 g, and 0–5 cm mineral soil with field moist weights of 50 g, were extracted for nematodes using Whitehead and Hemming trays as described by Yeates (1978); when live samples were counted at 50× magnification, rotifers were also observed and counted. After fixation, an average of 116 nematodes per LFH sample, and 42 nematodes per 0–5 cm sample, were identified to genus, their live biomass was determined by the Andrássy method (Yeates 1988), and they were allocated to a feeding group. Using relative dimensions, rotifers were assumed to have an individual biomass of 0.43 μg.

RESULTS AND DISCUSSION

Pinus radiata Productivity Levels and Phosphorus Status

The stands were stocked at approximately 1000 trees/ha. Stem volume at Te Kao was 29.4 and 30.8 m^3/ha in the control and treated plots at age 8, suggesting a productivity level of 11 m^3/ha/year in both control and treated stands, with no apparent growth response to added phosphorus. This may have arisen from poor physical conditions at the site. Stem volume at

Shenstone was 112 and 126 m^3/ha at age 11, suggesting productivity levels of 22 and 24 m^3/ha/year in the control and treated stands, respectively. A small growth response to the fertiliser phosphorus treatment seems to have occurred at Shenstone. The differences in tree growth rate with site but not phosphorus fertiliser treatment were reflected in the litterfall measurements (Table 1).

TABLE 1–Additions to forest floor (LFH) between November 1990 and November 1991, mass of LFH, LFH and microbial biomass carbon, soil and microbial biomass carbon. All data in kilograms per hectare; means ± SE.

	Shenstone		Te Kao	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
Litterfall to Nov.1991	3 850±720	3 250±960	2 230±790	2 220±900
LFH mass Nov.1990	26 700±5800	21 000±7100	9 060±3000	10 200±4700
LFH C	9 150	7 350	3 110	3 870
LFH biomass C	153±32	111±34	43±15	61±24
Soil C 0–5 cm	30 000	27 600	17 300	16 700
Soil C 5–15 cm	70 000	63 600	40 800	36 500
Soil biomass C 0–5 cm	274±1	265±18	158±2	137±6

Crop nutritional monitoring (Will 1985) undertaken at these trials indicated that the foliar phosphorus status at Te Kao remained constant with stand age in control stands and improved with stand age in phosphorus-treated stands. In contrast, foliar phosphorus status declined with stand age in Shenstone, both in phosphorus-treated and control stands. The phosphorus status of trees at Shenstone was superior to trees at Te Kao when the stands were 5 years old, but by 1991 the foliar phosphorus concentrations were similar. However, the foliar phosphorus concentrations of treated stands were significantly higher than control stands at both sites, suggesting luxury consumption of phosphorus, with implications for phosphorus concentrations of all ecosystem components.

Litter Inputs and Forest Floor Carbon

The litterfall dry matter content differed by site but not with phosphorus treatment in the 12 months to November 1991 (Table 1). The mass of LFH horizon was greater at Shenstone where the trees were aged 11 years compared with age 7 years at Te Kao, and productivity and litterfall were greater (Table 1). At Shenstone the bulk density of the LFH horizon was 0.10 g/cm^3 for 25 kg P/ha and 0.06 g/cm^3 for 100 kg P/ha, where the horizon had a greater thickness (data not presented); soil faunal activity may be greater after phosphorus treatment. The LFH horizons at Te Kao had a large variation in bulk density, thickness, and composition.

The ratio of mass of LFH to litterfall (Table 1) and the ratio of LFH phosphorus to litterfall phosphorus (Table 2) were similar within each site, indicating similar rates of turnover for both the litter (LFH) and the phosphorus fraction in the litter. The ratios were lower at Te Kao than at Shenstone. The amount of LFH material was greater than expected had pine litter been the only input, suggesting that LFH from understorey vegetation and the previous land-use were influencing the LFH weight.

TABLE 2–Phosphorus (kg P/ha) in litterfall, various LFH pools, and soil pools including microbial biomass; means ± SE.

	Shenstone		Te Kao	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
Litterfall P 1991	1.5±0.5	1.8±0.5	0.9	1.3
LFH P	12.6±2.7	11.7±3.8	3.0±1.3	6.6±3.7
LFH P HCO_3	0.2	0.3	0.2	0.5
LFH biomass P	5.4±0.8	5.3±0.9	3.2±1.2	3.8±0.6
Soil P_t H_2SO_4 0–5 cm	31.0±2.0	43.0±4.0	17.0±1.0	30.0±1.0
Soil P_t H_2SO_4 5–15 cm	91.0±2.0	92.0±6.0	45.0±1.0	82.0±3.0
Soil biomass P 0–5 cm	15.7±1.0	21.0±3.0	7.1±0.6	10.8±1.0
Soil biomass P 5–15 cm	15.5±0.1	19.8±2.0	nd	nd

nd = not determined.

Microbial biomass carbon was a smaller proportion of the 0–5 cm soil carbon than of the LFH carbon (Table 1). At both sites the ratio of soil microbial carbon to total carbon was similar (0.9%); these values are typically low compared to those of heavier textured soils (Wardle 1992).

The carbon pools reported in Table 1 showed no increase with phosphorus treatment, which was as expected given that tree growth rate was hardly influenced by phosphorus treatment.

Phosphorus in Litter and Mineral Soil

The P_i in 0–5 cm samples from Te Kao measured using bicarbonate and resin extraction was very low (<2 kg/ha) (Table 3). The resin-extractable phosphorus changed very little with longer extraction time between 24 and 70 hours (data not shown) suggesting very little desorption occurred (Parfitt *et al.* 1994). The phosphorus extracted with sodium hydroxide was similar to or twice the phosphorus extracted with resin in 24 hours (Table 3). The P_o can hydrolyse at high pH so this fraction may represent a readily hydrolysable pool together with a soluble inorganic pool. During estimation of microbial biomass phosphorus in the Te Kao

TABLE 3–Phosphorus (kg P/ha) extracted from 0–5 cm soil by various procedures.

	Shenstone		Te Kao	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
P_t H_2SO_4	31.0	43.0	17.0	30.0
P biomass	15.7	21.0	7.1	10.8
P_o HCO_3^{-1}	5.7	6.4	nd	nd
P_i HCO_3^{-1}	0.5	2.4	0.5	1.0
P_i resin 4 h	0.5	1.6	0.4	0.7
P_i resin 24 h	0.9	3.5	0.8	1.7
P 0.1M NaOH	0.6	5.1	2.0	3.3
P_i min 39°C	0.6	3.1	1.0	2.6

P_o = organic phosphorus
P_i = inorganic phosphorus
nd = not determined.

samples none of the phosphorus spike (27 mg P/kg soil) was adsorbed, indicating that no adsorption sites were available; this suggests only very small amounts of iron or aluminium compounds were present in these samples and explains the low desorption. The P_o can be measured by subtraction ($P_t - P_i$); since P_i was very low, P_o comprised most of the phosphorus in the 0–5 cm soil layer.

The samples from Shenstone adsorbed about half of the spike (data not shown), indicating that some iron or aluminium compounds were present. The resin-extractable phosphorus values were higher than for the Te Kao samples and based on sodium hydroxide extraction there may be as much as 5 kg P_i/ha (11 mg P_i/kg) in the samples with 100 kg P fertiliser. This is a small proportion of the P_t (43 kg/ha).

The microbial biomass phosphorus comprised a large proportion (about half) of both the LFH and 0–5 cm mineral soil P_t (Table 3), P_t being low compared with heavier textured soils (Sparling *et al.* 1994). The phosphorus content of the microbial biomass in the mineral soil increased slightly with increasing amount of fertiliser but the microbial biomass carbon remained almost the same (Tables 1 and 2). This general increase in the P/C ratio of the microbial biomass suggests that the phosphorus in the biomass may be a readily mineralisable phosphorus source.

All extraction methods showed an increase in phosphorus in the 0–5 cm soil samples from the plots treated with the higher rates of phosphorus (Table 3). At Shenstone the sodium-hydroxide-extractable phosphorus increased by 4.5 kg/ha and this may represent a labile pool in this soil.

There was 13 kg more P_t / ha in the 0–15 cm layer of the 100-kg plots than in the 25-kg plots at Shenstone (Table 2). At Te Kao there was 50 kg P/ha more in the 125-kg plots than the 4-kg plots. The higher value at Te Kao may arise from the use of rock phosphate which is less soluble than the MCP used at Shenstone. Because of the low pH values (4.5), together with 1400-mm rainfall and with the low resin-phosphorus values (Table 3), we conclude most of the rock phosphate has probably dissolved and been transferred slowly to the organic pool. The MCP by contrast may have been transferred more rapidly and more lost through leaching during 1983–91. The build-up of phosphorus in organic pools probably results in an increase in the monoester and diester phosphates, which are usually the most abundant forms of soil P_o (Tate & Newman 1982).

The rate of phosphorus mineralisation was greater in plots which had received more phosphorus (Table 3) (Polglase *et al.* 1992c). Rates were similar at both Shenstone and Te Kao for the low phosphorus plots, and also were similar for the high phosphorus plots. The mineralisation of P_o in the LFH and 0–10 cm A_p horizons was probably an important source of phosphorus to the trees since most phosphorus was in organic forms, and most feeding roots were found within this soil depth. A large part of the P_o, however, was probably present in the soil at Shenstone as inositol polyphosphate or as salts of inositol polyphosphate which are relatively insoluble, and consequently may be slow to mineralise.

Enzyme Activity, Monoesters, and Diesters

Phosphodiesterase activity was greater in the soils with the lower additions of phosphorus fertiliser (Table 4). This may arise from either more enzyme being produced in soils of low phosphorus status or the enzyme activity being suppressed by the high concentration of

TABLE 4–Soil phospho-diesterase activities in nmol *p*-nitrophenol/g soil; means ± SE.

	Shenstone		Te Kao	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
LFH	9.6±1.8	5.1±0.3	14.2±5.0	4.8±0.2
0–5 cm	5.3	1.6	4.5	0.8

phosphorus in soil solution in the high phosphorus status soils (Table 5). The differences were particularly marked for the 0–5 cm samples from Te Kao where activity was five times greater with 4 kg P than with 125 kg P, while the soil solution phosphorus was one-tenth. The phosphomonoesterase activities are usually similar to the diesterase activities (T. W. Speir pers. comm.). It should be noted that the presence of these enzymes facilitates mineralisation of the P_o which is in soil solution.

TABLE 5–Phosphate concentrations (μmol/ℓ) in soil water and LFH water; means ± SE.

	Shenstone		Te Kao	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
LFH	85±50	166±58	157±150	355±170
0–5 cm soil	8±2	13±2	18±2	180±10
5–15 cm soil	6±1	9±4	46±20	159±70

The ^{31}P-NMR spectra of 0.1M NaOH extracts for the 0–5 cm Shenstone samples were similar for both levels of phosphorus fertiliser. The proportions of the phosphate groups were: diesters 15%, monoesters 43%, pyrophosphate 16%, and orthophosphate (P_i) 25%. Use of sodium hydroxide can cause hydrolysis of P_o to P_i, although 0.1M NaOH causes less hydrolysis than 0.5M NaOH (K.R.Tate unpubl. data); monoesters, however, usually predominate in soil organic matter but diesters are the main source of mineralised phosphorus (Tate & Newman 1982).

The ^{13}C NMR and ^{31}P NMR subspectra of solid soil organic matter from the Te Kao samples revealed two types of organic matter, one containing more CH_2 and fewer carbohydrate groups, which was probably a more recalcitrant fraction of organic matter (Theng *et al.* 1992). This type also contained polyphosphate phosphorus together with orthophosphate, monoesters, and diesters. The other type had carbohydrate groups and lacked CH_2 groups, probably indicating more decomposable organic matter (Newman & Tate 1991). This type did not contain polyphosphate but the spectrum had a shoulder possibly arising from pyrophosphate. The presence of pyrophosphate indicates hydrolysis of more complex phosphates (Tate & Newman 1982).

Microfauna

The numbers of fungal- and bacterial-feeding nematodes and bacterial-feeding rotifers (Donner 1966) in the LFH horizons at Shenstone with 100 kg P were 2–7 times those in the horizons from the 25-kg P plots (Table 6). The numbers of total nematodes in the 0-5 cm mineral soil were much lower: 122 nematodes/50 g for the 100-kg P/ha plots, and 60 for the

TABLE 6–Microfauna in 50-g field moist LFH samples.

	Shenstone	
	25 kg P/ha	100 kg P/ha
Number (individuals/50 g)		
Nematodes		
Root-feeding nematodes	0	0
Fungal-feeding nematodes	162	776
Bacterial-feeding nematodes	470	926
Predatory nematodes	15	22
Omnivorous nematodes	460	359
Total nematodes	1107	2083
Rotifers	25	173
Biomass (μg/50 g)		
Nematodes		
Root-feeding nematodes	0	0
Fungal-feeding nematodes	21	59
Bacterial-feeding nematodes	213	201
Predatory nematodes	34	88
Omnivorous nematodes	1064	1092
Total nematode biomass	1332	1440
Rotifer biomass	11	75

25-kg P/ha plots. However, the biomass of these two nematode groups, and total nematodes, differed little between treatments (Table 6). This suggests that the smaller nematodes in the 100 kg P/ha plots had shorter generation times and that their higher rate of grazing on the microbial biomass was likely to maintain the microbial populations in their logarithmic growth phase and thus enhance the cycling of plant nutrients (Ingham *et al.* 1985). The higher grazing rate was probably a function of the higher P/C ratio of substrates, i.e., better quality nutrition (Polglase *et al.* 1992b) for micro-organisms and their grazers, thus reducing limitations on them.

Thus the microbial population in general probably was turning over more rapidly in the 100 kg P/ha plots with more release of P_o to soil solution. This is consistent with phosphorus mineralisation occurring 500% faster with the higher amounts of fertiliser while microbial biomass phosphorus increased by only a third (Table 3).

As the microfauna generally makes a relatively small contribution to soil microbial biomass (Yeates 1988) any differences in microfaunal biomass between treatments is unlikely to have a significant effect on total microbial biomass.

Soil Solution

The concentration of P_i in the LFH solution was higher with the higher rate of fertiliser at both sites (Table 5). The P_i in the LFH solution was greater than in the soil and this is consistent with release of P_i by mineralisation of fresh litter and direct leaching from needles (Polglase *et al.* 1992a). Uptake of P_i from the LFH by the mycorrhizal roots of the trees found in this layer would reduce the leaching of phosphorus from the LFH to the A_p horizon, and would explain the lower concentrations of phosphorus in the mineral soil solution. Yanai

(1991) found for a northern hardwood forest that there was a flux of phosphorus in solution from the forest floor pool (85 kg P/ha) to the B horizon; the rate of transfer was estimated at 0.3 kg/ha/year.

The P_i in the 0–5 cm soil solution was lower at Shenstone than at Te Kao, possibly as a result of sorption by traces of iron or aluminium compounds in the A_p horizon at Shenstone. With 125 kg P applied fertiliser at Te Kao. the P_i in soil solution was very high (159-180 μmol/ℓ) compared with 4 kg applied P (18–46 μmol/ℓ) in both the 0–5 cm and the 5–15 cm layers. There was probably an excess of phosphorus in solution in the plots which had received 125 kg P/ha and leaching losses of phosphorus are likely in quartz sand.

Phosphorus Pools and Cycle

Phosphorus content of the ecosystem pools is given in Table 7. The phosphorus content of the LFH horizon and the 0–15 cm layer were taken from Table 2. The phosphorus content in the understorey is based on data by Hunter & Hunter (1991). The phosphorus in the above-ground tree components was estimated from the biomass study, while phosphorus in below-ground tree components and phosphorus uptake in 1990–91 were estimated using the DRYMAT model, as described previously.

TABLE 7–Phosphorus content (kg/ha) of ecosystem pools

	Shenstone 11 years		Te Kao 7 years	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
LFH	12	11	3	6
Understorey	1	1	4	4
Pine - measured	27	33	8	13
- (modelled)	(25)	(32)	(7)	(12)
Soil 0–15 cm	122	135	62	112
Total	162	180	77	135
Treatment effect		+18		+58

At Shenstone only 18 kg P/ha could be accounted for out of the extra 75 kg applied at the higher rate of MCP. An amount of 57 kg P/ha (75 – 18) has apparently been lost from the ecosystem, presumably by leaching to the soil layers below 15 cm. Since the E horizon was quartz sand to a depth of about 50 cm, the phosphorus was probably leached to at least that depth. Where the indurated B horizon had been ripped the phosphorus may have moved into the rip lines and either been leached further or been sorbed onto iron or aluminium compounds.

At Te Kao, 58 kg P/ha was accounted for out of the extra 121 kg applied at the higher rate of rock phosphate, suggesting that 63 kg P/ha (121 – 58) has been lost to the subsoil by leaching.

We estimate that phosphorus uptake by the trees at age 7 is 3-5 kg/ha/year at Te Kao and phosphorus uptake at age 11 is 6–8 kg/ha/year at Shenstone (Table 8). Foliar analysis indicated that the low productivity level at Te Kao was not associated with phosphorus deficiency, which is consistent with most of the soil indices of plant available phosphorus examined in this study. Phosphorus uptake by the trees was highly correlated with the soil

TABLE 8–Phosphorus uptake rate (kg/ha/year) by *Pinus radiata*

	Shenstone 11–12 years		Te Kao 7–8 years	
	25 kg P/ha	100 kg P/ha	4 kg P/ha	125 kg P/ha
Above-ground	3.1	4.5	1.8	2.8
Below-ground	2.9	3.6	1.7	2.3
Total tree	6.0	8.1	3.5	5.1

microbial biomass phosphorus (Table 3) which is consistent with the turnover of the microbial biomass being an important source of phosphorus to the trees. The phosphorus fertiliser probably has been transferred into the organic phosphorus cycle within the 7–11 years after application.

The phosphorus extracted by resin indicates about 1–3 kg was in the available pool in the 0–5 cm layer at time of sampling. Assuming this pool supplies the phosphorus to the tree, the resin-phosphorus pool would need to turn over about three times a year to supply the phosphorus taken up by the trees.

If 30% of the microbial biomass phosphorus does turn over in 1 year (Sparling *et al.* 1994), then, using the data in Table 2, the turnover in the 0–15 cm layer is 5–12 kg/ha/year. The rate of turnover, however, may be more rapid at these Northland sites because there are no clays to slow the process, and because temperatures are higher than elsewhere in New Zealand. The rate is probably also higher with the higher level of phosphorus. No turnover rates are available for the LFH horizon. Both Polglase *et al.* (1992c) and Sparling *et al.* (1994) suggested that phosphorus mineralisation and phosphorus turnover through the microbial biomass were more rapid than phosphorus uptake by pine, which is consistent with our findings.

Representations of the phosphorus cycle at Shenstone and Te Kao are shown in Fig. 1 and 2.

CONCLUSIONS

Soils developed in quartz sand are useful for studying the cycling of phosphorus through various soil biological pools since there are only traces of iron and aluminium compounds in the topsoils which would otherwise tie up phosphorus. The surface 0–15 cm of the soil contained very little P_i compared with P_o.

The phosphorus in most pools increased with larger additions of phosphorus fertiliser but there was no significant increase in the carbon pools. This was expected because the trees showed no or only a small growth response to phosphorus treatments. The phosphorus mineralisation in mineral soil also increased with phosphorus fertiliser, and this probably results from increases in the P/C ratio of the microbial biomass.

The microbial biomass phosphorus made up a large proportion of the forest floor (LFH) phosphorus and the solution phase in the LFH horizon contained large concentrations of P_i that probably arose from mineralisation during turnover of the microbial biomass together with leaching directly from needles. The concentration of P_i in the mineral soil was less than in the forest floor. If no sorption occurred on the quartz sand then there must have been uptake of phosphorus by the trees directly from the forest floor. There appeared to have been losses

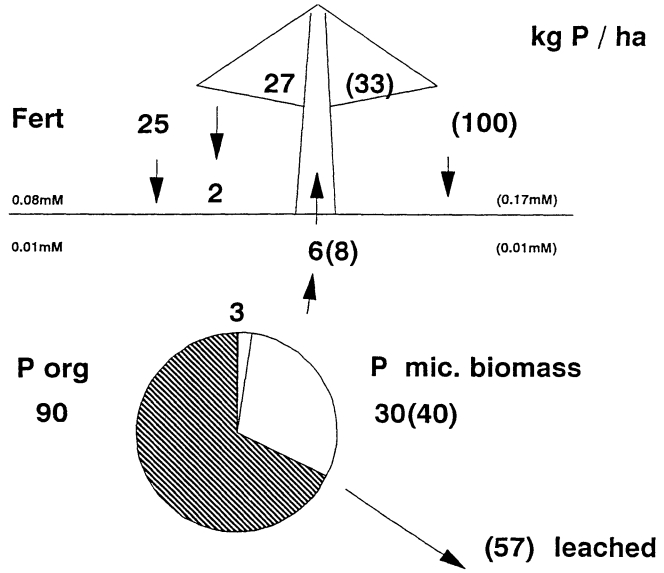

FIG. 1–Phosphorus cycle for the plots at Shenstone forest; pools are expressed in kilograms of phosphorus per hectare, 100 kg P/ha data are in parentheses; annual fluxes are 2 kg/ha in litterfall and 6(8) for uptake; the leaching loss in 11 years from the extra 75 kg P is 57 kg/ha.

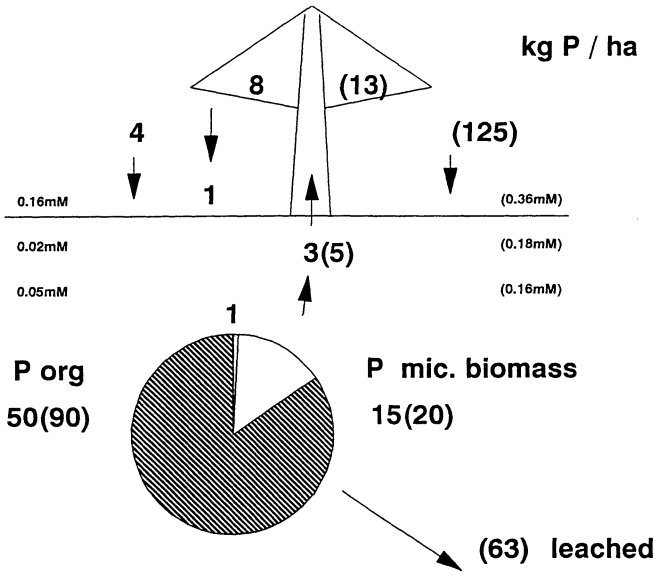

FIG. 2–Phosphorus cycle for the plots at Te Kao forest; pools are expressed in kilograms of phosphorus per hectare, 125 kg P/ha data are in parentheses; annual fluxes are 1 kg/ha in litterfall and 3(5) for uptake; the leaching loss in 7 years from the extra 121 kg P is 63 kg/ha.

of phosphorus from the ecosystem in the past, and leaching of phosphorus had probably occurred to at least the base of the E horizon.

There were larger numbers of nematodes and rotifers, which feed on the microbial biomass, at the higher rate of phosphorus fertiliser; the total mass of these fauna was not greatly different. This suggests that there may have been shorter generation times, more microbial grazing and enhanced nutrient cycling as a result of the improved nutritional quality of both substrates and micro-organisms. The general phosphorus cycling rate may also have increased with higher rate of applied phosphorus.

This study underlines the importance of retaining forest litter and topsoil during forestry operations. In less versatile soils such as sands most of the available phosphorus is stored in the litter and topsoil as P_o which is a major source of the phosphorus required for tree growth.

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REFERENCES

BEETS, P. N. 1982: Modelling dry matter content of a managed stand of Pinus radiata in New Zealand. Ph.D. Thesis, University of Georgia, Athens, United States. 217.p.

BEETS, P.N.; BROWNLIE, R.K. 1987: Puruki experimental catchment: site, climate, forest management, and research. *New Zealand Journal of Forestry Science 17*: 137–60.

BEETS, P.N.; MADGWICK, H.A.I. 1988: Above-ground dry matter and nutrient content of *Pinus radiata* as affected by lupin, fertiliser, thinning, and stand age. *New Zealand Journal of Forestry Science 18*: 43–64.

BEETS, P.N.; POLLOCK, D.S. 1987: Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. *New Zealand Journal of Forestry Science 17*: 246–71.

BLAKEMORE, L.C.; SEARLE, P.L.; DALY, B.K. 1987: Methods for chemical analysis of soils. *DSIR, NZ Soil Bureau Scientific Report 80.*

BROOKES, P.C.; POWLSON, D.S.; JENKINSON, D.S. 1982: Measurement of microbial biomass phosphorus in soil. *Soil Biology and Biochemistry 14*: 319–29.

——1984: Phosphorus in the soil microbial biomass. *Soil Biology and Biochemistry 16*: 169–75.

DAVIS, M.R.; LANG, M.H. 1991: Increased nutrient availability in topsoils under conifers in the South Island high country. *New Zealand Journal of Forestry Science 21*: 165–79.

DONNER, J. 1966: "Rotifers". Warne, London. 80p.

HAWKES, G.E.; POWLSON, D.S.; RANDALL, E.W.; TATE, K.R. 1984: ^{31}P-nuclear magnetic resonance study of the phosphorus species in alkali extracts of soils from long-term field experiments. *Journal of Soil Science 35*: 35–45.

HICKS, D. 1983: Landscape evolution in consolidated coastal dunesands. *Zeitscrift für Geomorphology 45*: 245–50.

HUNTER, I. R.; HUNTER, J. A. C. 1991: Apparent phosphorus uptake and change in nitrogen content of *Pinus radiata* growing on soils of different phosphorus retention, treated with superphosphate and A-grade rock phosphate. *New Zealand Journal of Forestry Science 21*: 50–61.

INGHAM, R.E.; TROFYMOW, J.A.; INGHAM, E.R.; COLEMAN, D.C. 1985: Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecological Monographs 55*: 119–40.

NEWMAN, R.H.; TATE, K.R. 1991: ^{31}C NMR characterization of humic acids from soils of a development sequence. *Journal of Soil Science 42*: 39–46.

NICHOLSON, G. 1984: Methods of soil, plant, and water analysis. *New Zealand Forest Service, FRI Bulletin No.70.*

PARFITT, R.L.; TATE, K.R.; McKERCHER, R.B. 1994: Measurement of phosphorus mineralisation using an anion exchange membrane. *Communications in Soil Science and Plant Analysis 25*: 3209–19.

POLGLASE, P.J.; JOKELA, E.J.; COMERFORD, N.B. 1992a: Phosphorus, nitrogen and carbon fractions in litter and soil of Southern pine plantations. *Soil Science Society of America Journal 56*: 566-72.

——1992b: Nitrogen and phosphorus release from decomposing needles of Southern pine plantations. *Soil Science Society of America Journal 56*: 914–20.

——1992c: Mineralization of nitrogen and phosphorus from soil organic matter in Southern pine plantations. *Soil Science Society of America Journal 56*: 921–7.

PRESCOTT, C.E.; CORBIN, J.P.; PARKINSON, D. 1992: Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. *Plant and Soil 143*: 1–10.

SPARLING, G.P.; SPEIR, T.W.; WHALE, K.N. 1986: Changes in microbial biomass C, ATP content, soil phospho-monoesterase and phospho-diesterase activity following air-drying of soils. *Soil Biology and Biochemistry 18*: 363–70.

SPARLING, G.P.; HART, P.B.S.; AUGUST, J.A.; LESLIE, D.M. 1994: A comparison of soil and microbial carbon, nitrogen and phosphorus content and macro-aggregate stability of a soil under native forest and after clearance for pasture and plantation forest. *Biology and Fertility of Soils 17*: 91–100.

TATE, K.R. 1985: Soil phosphorus. Pp.329–77 *in* Vaughan, D.; Malcolm, R.E. (Ed.) "Soil Organic Matter and Biological Activity". Martinus Nijhoff / Dr W.Junk Publishers, Dordrecht, The Netherlands.

TATE, K.R.; NEWMAN, R.H. 1982: Phosphorus fractions of a climosequence of soils in New Zealand tussock grassland. *Soil Biology and Biochemistry 14*: 191–6.

THENG, B.K.G.; TATE, K.R.; BECKER-HEIDMANN, P. 1992: Towards establishing the age, location and identity of the inert soil organic matter of a Spodosol. *Zeitschrift für Planzenernährung und Bodenkunde 155*: 181–4.

VANCE, E.D.; BROOKES, P.C.; JENKINSON, D.S. 1987: An extraction method for measuring soil microbial C. *Soil Biology and Biochemistry 19*: 703–7.

WARDLE, D.A. 1992: A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Reviews 67*: 321–58.

WILL, G. 1985: Nutrient deficiencies and fertiliser use in New Zealand exotic forests. *New Zealand Forest Service, Forest Research Institute, FRI Bulletin No.97.*

YANAI, R.D. 1991: Soil solution phosphorus dynamics in a whole tree harvested Northern hardwood forest. *Soil Science Society of America Journal 55*: 1746–52.

YEATES, G.W. 1978: Populations of nematode genera in soils under pasture. I. Seasonal dynamics in dryland and irrigated pasture on a southern yellow-grey earth. *New Zealand Journal of Agricultural Research 21*: 321–30.

——1988: Contribution of size classes to biovolume with special reference to nematodes. *Soil Biology and Biochemistry 20*: 771–3.