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G.W. Yeates · M.F. Hawke · W.C. Rijkse

Changes in soil fauna and soil conditions under *Pinus radiata* agroforestry regimes during a 25-year tree rotation

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Abstract *Pinus radiata* was planted in a grazed pasture at Tikitere, New Zealand in 1973; final tree stocking rates were 0, 50, 100, 200 and 400 stems ha⁻¹; trees were harvested in 1999. We sampled the loamy sand for chemistry, earthworms, enchytraeids and nematodes during crop growth. There were no visible changes in the soil profile between years 2 and 25 of the *P. radiata* rotation, but marked changes in soil chemistry with pH declining at all depths. Topsoil pH declined but plant-available P and the soil C:N ratio increased. That similar trends occurred in pasture may have reflected reduced inputs. Lumbricid earthworms declined with increasing time and tree stocking rate; significant populations were found only in pasture at 25 years; no related changes in soil bulk density were detected. Enchytraeids were abundant but declined in the plots with 200 and 400 stems ha⁻¹. The composition of the nematode fauna at a soil depth of 0–10 cm varied, and there were changes in the “control” pasture. *Pratylenchus* sp. and *Pungentus* sp. were characteristic of pasture; *Diphtherophora* sp. appeared at higher tree stocking rates. In addition to changes related to the change in landuse there were temporal changes that affected faunal composition across tree stocking rates: *Heterodera* sp. and *Paratylenchus* sp. were rare after year 6; *Prismatolaimus* sp. was most abundant in years 2, 13 and 25; *Axonchium* sp. occurred in year 6 and *Alaimus* sp. mainly in year 25. Overall, the changes in soil chemistry reflected the change from pasture to forest. Parallel changes in soil microfauna and macrofauna also reflected the

change in landuse, from fertilised pasture to coniferous forest, and are considered reversible.

Key words Nematodes · Earthworms · Acidification · Enchytraeids · Agroforestry

Introduction

Although agroforestry emerged as a defined landuse in the 1970s, the practice of intercropping of woody and non-woody plant species is as old as agriculture itself. Particularly in the tropics, alley cropping between rows of leguminous trees is widespread and it was with knowledge of this type of landuse that Kidd and Pimentel (1992) wrote: “Agroforestry systems will be able to mimic or replicate many of the nutrient-cycling and favourable environmental influences found with forest ecosystems, while generating the exportable outputs achieved with agricultural systems”. In the 1970s, establishment of widely spaced coniferous [*Pinus radiata* (D. Don.)] plantations in improved New Zealand pastures dominated by ryegrass (*Lolium perenne* L.)/white clover (*Trifolium repens* L.) was advocated, principally with the idea that income from stock grazing the pasture would provide some financial return during part of the, typically 25-year, production of high value sawlogs (Hawke and Knowles 1997). Agroforestry was also seen as contributing to the stabilisation of hill country (Hawke 1991).

Not only do the trees in a pasture modify the microclimate (Hawke and Wedderburn 1994; Brenner 1996), with all that implies for pasture growth and stock health, but they also affect physical, chemical and biological properties of the soil – the very reason why alley cropping between leguminous trees is practised in the tropics. Forestry worldwide, particularly coniferous forestry, has been associated with soil acidification (Page 1974; Gilmore and Matis 1981; Miles 1985; Turner and Lambert 1988; Hawke and O'Connor 1993; Giddens et al. 1997). Such acidification must be contrasted with the

G.W. Yeates (✉)
Landcare Research, Private Bag 11052, Palmerston North,
New Zealand
e-mail: yeatesg@landcare.cri.nz
Tel.: +64-6-3567154
Fax: +64-6-3559230

M.F. Hawke
AgResearch, Private Bag 3020, Rotorua, New Zealand

W.C. Rijkse
Landcare Research, Private Bag 3127, Hamilton, New Zealand

pastoral agricultural practice of applying lime to increase soil pH to enhance populations of agronomically important topsoil-mixing lumbricid earthworms (Springett 1983; Edwards and Bohlen 1996) and to give a soil pH of 5.5–6.5 for optimum growth of temperate pasture plants and nodulation of legumes (Langer 1977). As soil macrofauna has a profound effect on soil structure (Lavelle et al. 1997), and as soil microfaunal activity stimulates nutrient cycling (Ingham et al. 1985; Bouwman et al. 1994), an understanding of how soil faunal populations change during an agroforestry rotation is important in interpreting the impact of this land-use on soil processes and assessing its sustainability. Further, the use of lower tree stocking rates in agroforestry may ameliorate some of the effects of planted forests discussed by Maclaren (1996).

This paper reports changes primarily in nematode and earthworm populations, and related soil properties, at intervals from 1975 to 1998 in the Tikitere Agroforestry Trial on volcanic soil near Rotorua, New Zealand. The duration of the sampling not only describes treatment effects but also provides a time-series of faunal estimates. Soil chemical properties at the beginning and end of a *P. radiata* rotation are also given.

Materials and methods

The site

The Tikitere Agroforestry Trial of 93 ha is located on volcanic soils 15 km north east of Rotorua, New Zealand, at 38°04'S, 176°20'E. Overviews of the trial, which has been described as "silvopastoral", include those of Percival et al. (1984a) and Hawke and Knowles (1997). In July 1973 (year 0), *P. radiata* seedlings were planted in relatively high fertility, improved [ryegrass (*Lolium perenne* L.)/white clover (*Trifolium repens* L.) dominant], grazed pasture at tree stocking rates of 0, 250, 500, 1000 and 2000 stems ha⁻¹ (Hawke and O'Connor 1993). The site had a 50 to 60-year history of pastoral landuse. There were four replicate plots of each treatment, with each plot having a treated, but unsampled, buffer zone 27 m wide, and effective experimental areas of 2 ha. During the crop cycle they were subject to normal forest management. Cull trees were thinned to waste at each pruning lift with final stocking rates of 0, 50, 100, 200 and 400 stems ha⁻¹ by year 8 (1981) when the trees were ~10 m; these final stocking rates are used to identify the treatments throughout this paper. Final crop trees were pruned in four lifts to give clear logs of 5.8 m. The trees were scheduled for felling in the winter of year 26 (1999). The trial was rotationally grazed, on a within-treatment basis, up to year 16 (1989) on a year-round basis, mainly with sheep although cattle were used to control surplus feed. Annual fertiliser applications were made from the air from year 2 to year 16; applications to plots of 400 stem ha⁻¹ ceased in year 10 and those to plots of 200 stem ha⁻¹ in year 13. From 1975–1983 nutrients applied annually were: 13–41 kg P ha⁻¹, 16–56 kg K ha⁻¹, 15–48 kg S ha⁻¹ and 8–16 kg Mg ha⁻¹. In 1991 and 1992 the plots of 0 stem ha⁻¹ and 50 stem ha⁻¹ were fertilised by ground spreading (Hawke and O'Connor 1993). From year 16 the area was grazed as one paddock with breeding ewes and beef cattle (Hawke and O'Connor 1993; Hawke and Knowles 1997).

The following sampling was restricted to the contiguous plots of one replicate in which the flat to easy rolling land was most uniform and the soil least variable. The centre of the area is at grid reference NZMS 260 sheet U15 032 441; altitude 350 m above sea level. The soils are mapped by Rijkse (1979) as Rotoiti

loamy sand, a Typic Orthic Pumice soil (Hewitt 1992) derived from patchy Rotomahana Mud on Kaharoa Tephra on older Rhyolitic Tephra; in Soil Taxonomy the soil is a Typic Udivitrand (Soil Survey Staff 1996). Thirty-year (1950–1980) climate normals include an average annual rainfall of 1490 mm (the monthly range being 90 mm in January to 146 mm in August) and a mean daily air temperature of 12.7 °C (7.3° in July to 17.8° in February) (New Zealand Meteorological Service 1983a,b). Data for 1963–1980 showed soil moisture deficits of 6–55 mm under pasture from November to February (New Zealand Meteorological Service 1983c). Previous soil biological work on this replicate has been reported by McMillan (1981), Percival et al. (1984a), Sparling et al. (1989), Yeates (1978a, 1980, 1981, 1988) and Yeates and Boag (1995), and where appropriate those results are included in this paper.

Soil profile

In May 1975 (year 2) the soil profile between *P. radiata* trees planted two years earlier was described (Appendix I) and sampled to 70 cm depth. The soil profile was again described and sampled in May 1998 (year 25) under a final stocking rate of 400 *P. radiata* stems ha⁻¹; the description was by the same pedologist and this profile was within 3 m of that of 1975. Soil chemical analyses on both sets of samples followed the methods of Blakemore et al. (1987); care was taken to ensure strictly comparable analytical laboratory operating procedures were used for both sets of samples.

Annelida and soil physics

Lumbricid earthworms were first sampled in 1975–1976 by McMillan (1981), who reported results from quarterly samples from three hand-sorted, replicate 0.1-m² pits from each of the five tree stocking rates. Yeates' (1988) sampling grid was only partly sampled in the 1986–1987 programme, which included four replicate earthworm samples each quarter. Ten replicate 91-mm-diameter × 77-mm-deep rings plot⁻¹ were taken for soil bulk density in July 1987 and August 1991 (Yeates 1988; Yeates and Boag 1995). In May 1998, sampling for lumbricid earthworms and soil bulk density was made at four grid points in each plot, using the methods described by Yeates (1988). Intact cores were collected from depths of 0–2.5 and 2.5–5.0 cm for extraction of Enchytraeidae by wet funnels in 1986–1987 and 1998, there being ten replicate cores from each tree stocking rate; the methods were described by Yeates (1988). The various sampling events are referred to as years 2 (1975), 13 (1986–1987), 18 (1991) and 25 (1998).

Soil nematodes and topsoil chemistry

In October 1975, an area about 2 × 10 m in each of five plots with final tree stocking rates of 0 (pasture control), 50, 100, 200 and 400 trees ha⁻¹ (experimental plots E, L, G, I, H) was selected to give greatest similarity of soil and topography between treatments. In each case the "sampling line" ran midway between parallel rows of trees to standardise any "distance-from-tree" effect; at 400 trees ha⁻¹ there were two 5-m sampling lines in two adjacent alleys. Each plot was sampled in October 1975, October 1977, October 1979, October 1986 and May 1998. On each sampling occasion ten cores, each approximately 25 mm in diameter, were collected from a soil depth of 0–10 cm, divided into depths of 0–5 and 5–10 cm, and the soil nematodes extracted separately from each using a variant of the Whitehead and Hemming tray method (Yeates 1978b); after counting the microfauna the suspensions for each plot and depth were bulked and fixed. All nematode identifications were made in 1998, with an average of 136 and 114 nematodes from 0–5 and 5–10 cm depths, respectively, being identified to nominal genus for each sampling date. These genera were allocated to feeding groups following Yeates et al.

(1993a,b), and all populations are expressed on a per square metre basis. Indices of diversity, evenness, richness, dominance and maturity of the nematode fauna were calculated according to Yeates and Bongers (1999). Soil moisture determinations (expressed as % 105 °C dry mass) and soil pH measurements on field-moist soil (soil:water=1:2.5) were made within 2 weeks of each sample collection.

In April 1987 a pit was dug in the plot of 400 stems ha⁻¹, near the profile described in Appendix 1, and samples for soil nematode extraction collected, over 10-cm increments, to a depth of 80 cm. Nematodes were extracted from duplicate 200-g field-moist samples from each depth increment.

On each date nematodes were sampled from the five tree stocking rates an additional five cores were collected from each plot, bulked and dried for later determination of soil chemical conditions. These analyses were all made in 1998, using the methods of Blakemore et al. (1987).

With time incremental changes in surface organic horizons varied with tree stocking rate, and no attempt was made to distinguish between soil fauna in the organic horizons and the upper soil. The surface level was taken as 0 cm, and samples taken from that reference point.

Data analysis

The collections of nematodes and soils made in 1975, 1977, 1979, 1986 and 1998 (years 2, 4, 6, 13, 25) were all analysed, using identical methods, at the end of the programme, and arithmetic data have been statistically analysed using Systat; statistical probabilities are derived from ANOVA. As other data are rather more variable, in both sampling and analysis, emphasis is placed on the long-term trends they show rather than statistical analysis.

Results

Soil chemistry

Apart from the presence of a surface LFH horizon, there were no visible changes in the soil profile (Appendix 1) over 23 years of *P. radiata* growth. The pH of all mineral soil layers was lower, by 0.2–0.5 units, at harvest in year 25 than under young trees in year 2 and under pasture at year 25, but all values (Table 1) are rated as acid, according to the ratings of Blakemore et

al. (1987). At pH 4.7–4.9, the topsoil (0–18 cm soil) was strongly acid. The value changed from moderately acid (pH 5.4) to strongly acid (pH 4.9) in the Bw1 horizon. At a depth of 30–40 cm it was uniformly moderately to strongly acid, while at 40–60 cm depth the pH changed from slightly acid to strongly acid. The litter layer was extremely acid (pH 4.3).

Although mineral soil C contents were generally lower in year 25 (e.g. 47.0%, 44.5% at a soil depth of 0–18 cm) the ratings were similar to those for year 2, with the contents at depths of 0–18, 30–40 and 40–60 cm being very high and that at a depth of 18–30 cm (B horizon) being high (Table 1). While the N contents of all mineral soil horizons were lower in year 25 (Table 1), at the end of the crop, all values were rated as high or very high. Soil C:N ratios were all initially medium (13–16) and ended as medium to high (14–20), indicating additions of slowly decomposing organic matter.

While acid-extracted-P values in year 25 were 39–81% of those in year 2, they still remained “very high” (>40) according to Blakemore et al. (1987). In contrast, the inorganic P contents of year 25 had increased to 473–584% of those of year 2; all soil values were “very high” but that for LFH was 0. Soil organic P values were all slightly lower but remained “very high” (>70). There were no significant changes in PO₄³⁻ retention (Table 1) which was expected to be unlikely even over a 23-year period.

Apart from the Bw1 horizon, which had a very low cation exchange capacity (CEC) in both years 2 and 25, the CEC of three horizons dropped slightly while retaining medium-to-low ratings (Table 2). Although they began with low-to-very-low ratings, by year 25 the levels of total cations had dropped in all mineral soil horizons, and this reflected marked drops in both exchangeable Ca and K to 25–38% and 27–53% of year-2 values, respectively. Below a depth of 18 cm there was a general increase in Na concentration (Table 2).

In the presence of lower cation concentrations, base saturation decreased from low-medium to very low-low

Table 1 Chemical properties of a profile sampled in year 2 (1975; under pasture) and again in year 25 (1998; under 400 stems ha⁻¹ *Pinus radiata*). See also Table 2. *n.d.* Not determined

Horizon	Depth (cm)	pH (1:2.5 H ₂ O)		Organic matter						P									
				C		N		C:N		0.5 M H ₂ SO ₄ (mg kg ⁻¹)		Inorganic (mg kg ⁻¹)		Organic (mg kg ⁻¹)		Total (mg kg ⁻¹)		P-retention (%)	
				(g kg ⁻¹)		(g kg ⁻¹)													
		1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998
LFH	4–0	– ^a	4.3	–	208	–	10.25	–	20	–	214	–	0	–	787	–	540	–	29
Ap	0–18	4.9	4.7	47.0	44.5	3.6	3.08	13	14	970	376	103	488	510	421	1540	909	36	40
Bw1	18–30	5.4	4.9	16.0	14.5	1.0	0.80	16	18	150	95	25	146	170	155	420	301	27	27
2bA ₂	30–40	5.3	5.2	43.0	24.6	2.9	1.63	14	15	260	175	28	142	460	312	740	454	90	81
2bA ₃	40–60	6.1	5.6	23.0	22.0	1.7	1.55	13	14	200	161	26	136	290	278	550	414	96	90
3bBC	60–70	6.2	n.d.	8.0	n.d.	0.6	n.d.	13	n.d.	150	n.d.	30	n.d.	100	n.d.	400	n.d.	81	n.d.
Ap	0–7.5	–	4.6	–	50.0	–	3.44	–	15	–	437	–	586	–	425	–	1011	–	38
	7.5–18	–	4.8	–	40.6	–	2.83	–	14	–	332	–	418	–	418	–	836	–	42

^a LFH horizon not present under pasture

Table 2 Chemical properties of a profile sampled in year 2 (1975; under pasture) and again in year 25 (1998; under 400 stems ha⁻¹ *P. radiata*). See also Table 1. CEC Cation exchange capacity, BS base saturation

Hori- zon	Depth (cm)	CEC														Oxalate extractable					
		CEC		Total cations		BS		Ca		Mg		K		Na		Al		Fe		Si	
		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		[cmol(+) kg ⁻¹]		(g kg ⁻¹)		(g kg ⁻¹)		(g kg ⁻¹)	
		1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998	1975	1998
LFH	4–0	– ^a	47.9	–	13.79	–	29	–	9.19	–	2.91	–	1.40	–	0.29	–	3.7	–	3.0	–	0.4
Ap	0–18	16.0	13.5	6.8	2.24	43	16	5.4	1.36	0.56	0.36	0.58	0.31	0.27	0.21	4.5	5.8	4.8	3.6	1.0	1.2
Bw1	18–30	3.8	4.2	0.8	0.39	21	9	0.6	0.23	0.05	0.06	0.15	0.04	0.03	0.06	3.1	3.8	1.1	1.4	0.8	1.3
2bA ₂	30–40	13.4	9.0	2.4	0.93	18	10	1.6	0.46	0.15	0.13	0.54	0.17	0.09	0.17	22.0	20.6	11.0	7.0	7.7	7.7
2bA ₃	40–60	10.1	8.9	2.6	1.26	26	14	1.7	0.64	0.13	0.23	0.66	0.21	0.07	0.18	34.0	28.1	20.0	9.9	15.0	11.3
3bBC	60–70	5.0	n.d.	1.4	n.d.	28	n.d.	1.1	n.d.	0.09	n.d.	0.09	n.d.	0.07	n.d.	13.0	n.d.	15.0	n.d.	13.0	n.d.
Ap	0–7.5	–	15.2	–	2.74	–	18	–	1.73	–	0.44	–	0.40	–	0.17	–	5.7	–	3.8	–	1.3
	7.5–18	–	12.2	–	1.88	–	15	–	1.09	–	0.30	–	0.25	–	0.24	–	5.9	–	3.5	–	1.1

^a LFH horizon not present under pasture

over 23 years (Table 2). Oxalate-extractable Al and Si increased in the upper horizons and decreased in the lower horizons (Table 2), but the changes were very small. Oxalate-extractable Fe generally decreased, except for the Bw1 horizon.

The mass of the surface organic horizons increased with time and tree stocking rates (Table 3). At 200 and 400 stems ha⁻¹ it was about 5 t ha⁻¹ before harvest. The mass of 12 t ha⁻¹ at 400 stems ha⁻¹ in year 13 reflected the large amount of slash present following the final pruning lift and thinning carried out in 1981 (year 8); on an area basis such inputs would have been greatest in the treatment where the greatest number of stems were thinned.

Results for sets of samples from soil depths of 0–5 cm and 5–10 cm collected in parallel with nematodes in 1975, 1977, 1979, 1986 and 1998 and analysed in a single block are given in Tables 4 and 5. Soil pH, on air-dried material, was, with the exception of soil from a depth of 0–5 cm in pasture, greatest at both depths in year 4 (Table 4). Lowest values in soil at a depth of 0–5 cm were found in year 13 for pasture and under a tree stocking rate of 50 stems ha⁻¹, and in year 25 for tree stocking rates of 100, 200 and 400 stems ha⁻¹. For soil at a depth of 5–10 cm lowest values were

distributed across the other five sampling dates. ANOVA showed a significant ($P < 0.001$) time effect (Fig. 1a).

Soil pH measurements were also made on fresh, moist soil samples. Again, there was a decline in pH with falls exceeding 0.5 units at a soil depth of 0–5 cm under stocking rates of 100, 200 and 400 stems ha⁻¹ and at a soil depth of 5–10 cm at 400 stems ha⁻¹ over the 23 years. A significant ($P < 0.001$) time effect was found by ANOVA (data not shown).

Olsen P values in soil at a depth of 0–10 cm were all greater at the end of the rotation than at planting, and for the four stocking rates of *P. radiata* there were marked increases to years 13 and 25 from lows in year 6 (Table 4). Under pasture there was a 51% increase in Olsen P at a soil depth of 0–10 cm from year 13 to year 25, and a 135% increase at a soil depth of 5–10 cm. Overall trends with time and tree stocking rates were marginally significant ($P = 0.057$, $P = 0.053$, respectively) (Fig. 1b).

Soil C contents were greatest in seven of ten sampling units at the beginning of the programme, in 1975. For the remaining three (0–5 cm depth under pasture, 100 and 400 stems ha⁻¹) soil C was highest in the final, 1998 samples. The trends in C contents were not consis-

Table 3 Mass of surface litter and soil bulk density on an oven-dry (105°C) basis sampled under five stocking rates of *P. radiata* in years 13, 18 and 25 (means ± SEs)

Depth	Stems ha ⁻¹														
	0			50			100			200			400		
	13	18	25	13	18	25	13	18	25	13	18	25	13	18	25
Year	13	18	25	13	18	25	13	18	25	13	18	25	13	18	25
LF ^a (kg ha ⁻¹)	0	n.d.	0	168 ± 68	n.d.	265 ± 94	736 ± 76	n.d.	1468 ± 678	3204 ± 977	n.d.	5040 ± 429	11992 ± 2109	n.d.	4780 ± 303
(n = 4)															
0–10 cm (t m ⁻³)	0.96 ± 0.05	1.01	0.93 ± 0.02	1.00 ± 0.02	1.05	1.00 ± 0.01	0.94 ± 0.02	0.96	0.92 ± 0.01	0.99 ± 0.01	0.95	0.97 ± 0.02	1.03 ± 0.04	1.01	0.92 ± 0.02
(n = 10)															
10–20 cm (t m ⁻³)	1.02 ± 0.057	1.01	0.97 ± 0.01	1.04 ± 0.02	1.05	0.98 ± 0.01	0.95 ± 0.03	0.98	0.97 ± 0.01	1.06 ± 0.02	0.99	0.99 ± 0.02	1.05 ± 0.06	1.02	0.90 ± 0.02
(n = 10)															

^a *Pinus radiata* needle and twig material; excludes any pasture sward material

Table 4 Chemical analyses of soil samples collected from soil depths of 0–5 and 5–10 cm in years 2, 4, 6, 13 and 25, dried and ground; all analyses were carried out in 1998–1999 using constant methodology. See also Table 5

Stems ha ⁻¹	Depth (cm)	pH (1:2.5 soil:H ₂ O)						Olsen P (mg kg ⁻¹)					
		2	4	6	13	25	Shift	2	4	6	13	25	Shift
0	0–5	4.99	4.95	4.80	4.77	4.83	–0.16	48.9	81.3	83.9	63.9	96.6	+47.7
	5–10	4.82	5.17	4.84	4.93	5.06	+0.24	59.8	46.2	45.9	38.9	91.6	+31.8
50	0–5	4.82	5.10	4.76	4.72	4.78	–0.04	65.1	67.9	39.4	58.4	65.2	+0.1
	5–10	4.82	5.15	4.81	4.77	5.09	+0.27	48.5	35.9	18.6	36.8	29.5	–19.0
100	0–5	4.99	5.15	5.07	5.02	4.77	–0.22	65.6	88.4	52.2	57.4	84.0	+18.4
	5–10	4.83	5.30	4.87	4.91	5.01	+0.18	77.9	59.9	28.8	47.5	77.8	–0.1
200	0–5	5.05	5.18	4.67	4.57	4.32	–0.73	43.1	46.3	44.4	80.9	76.6	+33.5
	5–10	4.97	5.36	4.62	4.87	5.03	+0.06	27.0	17.5	25.7	36.1	25.9	–1.1
400	0–5	4.88	5.05	4.95	4.64	4.13	–0.75	79.1	62.8	53.4	67.2	101	+21.9
	5–10	4.95	5.19	4.95	4.89	4.72	–0.23	63.8	29.0	22.5	42.8	51.7	–12.1

Table 5 Chemical analyses of soil samples collected from soil at a depth of 0–5 and 5–10 cm in years 2, 4, 6, 13, and 25, dried and ground; all analyses were carried out in 1998–1999 using constant methodology. See also Table 4

Stems ha ⁻¹	Depth (cm)	C (%)						N (%)						C:N					
		2	4	6	13	25	Shift	2	4	6	13	25	Shift	2	4	6	13	25	Shift
0	0–5	6.37	7.66	6.94	7.00	7.69	+1.32	0.491	0.575	0.550	0.522	0.652	+0.161	13	13	13	13	12	–1
	5–10	6.60	3.65	4.44	4.93	3.24	–3.36	0.526	0.299	0.338	0.334	0.243	–0.283	13	12	13	13	13	–
50	0–5	8.92	7.81	7.45	7.48	7.96	–0.96	0.712	0.625	0.592	0.651	0.570	–0.142	13	12	13	11	14	+1
	5–10	6.76	4.66	4.65	4.03	4.03	–2.73	0.551	0.370	0.344	0.298	0.294	–0.257	12	13	13	14	14	+2
100	0–5	8.33	6.32	5.81	6.72	8.78	+0.45	0.630	0.473	0.415	0.543	0.538	–0.092	13	13	14	12	16	+3
	5–10	8.94	3.49	3.61	3.88	3.93	–5.01	0.693	0.284	0.251	0.271	0.284	–0.409	13	12	14	14	14	+1
200	0–5	10.67	7.50	7.42	6.59	9.38	–1.29	0.848	0.593	0.606	0.485	0.574	–0.274	13	13	12	14	16	+3
	5–10	7.48	4.11	4.53	3.69	3.67	–3.81	0.594	0.336	0.357	0.261	0.248	–0.346	13	12	13	14	15	+2
400	0–5	6.98	6.68	6.44	7.58	8.81	+1.83	0.501	0.470	0.458	0.488	0.476	–0.025	14	14	14	16	18	+4
	5–10	5.24	3.87	3.80	4.32	3.59	–1.65	0.382	0.292	0.251	0.302	0.234	–0.148	14	13	15	14	15	+1

tent, with five of eight layers under *P. radiata* having their lowest values in year 6 or year 13. In all *P. radiata* plots soil N levels were greatest in year 2, at both depths (Table 5). For four *P. radiata* samples lowest values were in year 25, with other lows being recorded in years 6 and 13. Soil at a depth of 0–5 cm from pasture was unusual in having its greatest C content in year 25. While both soil C and N varied significantly ($P < 0.001$) with depth (0–5 vs 5–10 cm depth) no time or stocking rate effect was found by ANOVA ($P > 0.05$). Soil C:N ratios were at their greatest for all treatments and depths in year 25, except for soil at a depth of 0–5 cm under pasture which was then at its lowest. ANOVA showed both time and stems ha⁻¹ to have significant ($P < 0.001$) effects on the soil C:N ratio (Fig. 1c).

Soil bulk density

Mean soil bulk density values were in the range 0.90–1.06 t m⁻³ (Table 3); all values lay within the moderate-low rating of McQueen (1988). While statistically significant differences between years and treatments could be demonstrated, such differences were minor in

terms of the range of soil bulk densities. Under all treatments, mean bulk densities of soil at a depth of 0–20 cm were higher for year 13 than for year 25 (viz 0.99 > 0.95, 1.02 > 0.99, 0.95 > 0.94, 1.03 > 0.98, 1.04 > 0.91 t m⁻³); the grand mean was 0.99 t m⁻³. In the absence of data for other depths, and as treatment had no systematic effect on bulk density in this grazed trial, a uniform bulk density of 1.00 t m⁻³ could be used to convert chemical data to an area basis, if required.

Annelids

Populations of introduced, topsoil-mixing lumbricid earthworms estimated at three stages of the crop cycle are given in Table 6. While the results for years 2 and 13 are each means of four seasonal sampling occasions, those for year 25 represent a single, winter (May) sampling. Under pasture, total earthworm abundance and biomass were similar over the 23-year period, with some variation but no apparent trend. In contrast, under all *P. radiata* treatments there was a significant downward trend in abundance and biomass with time. In 1975, all treatments had similar populations to those in pasture (287–435 cf 547 individuals m⁻², 64–99 cf

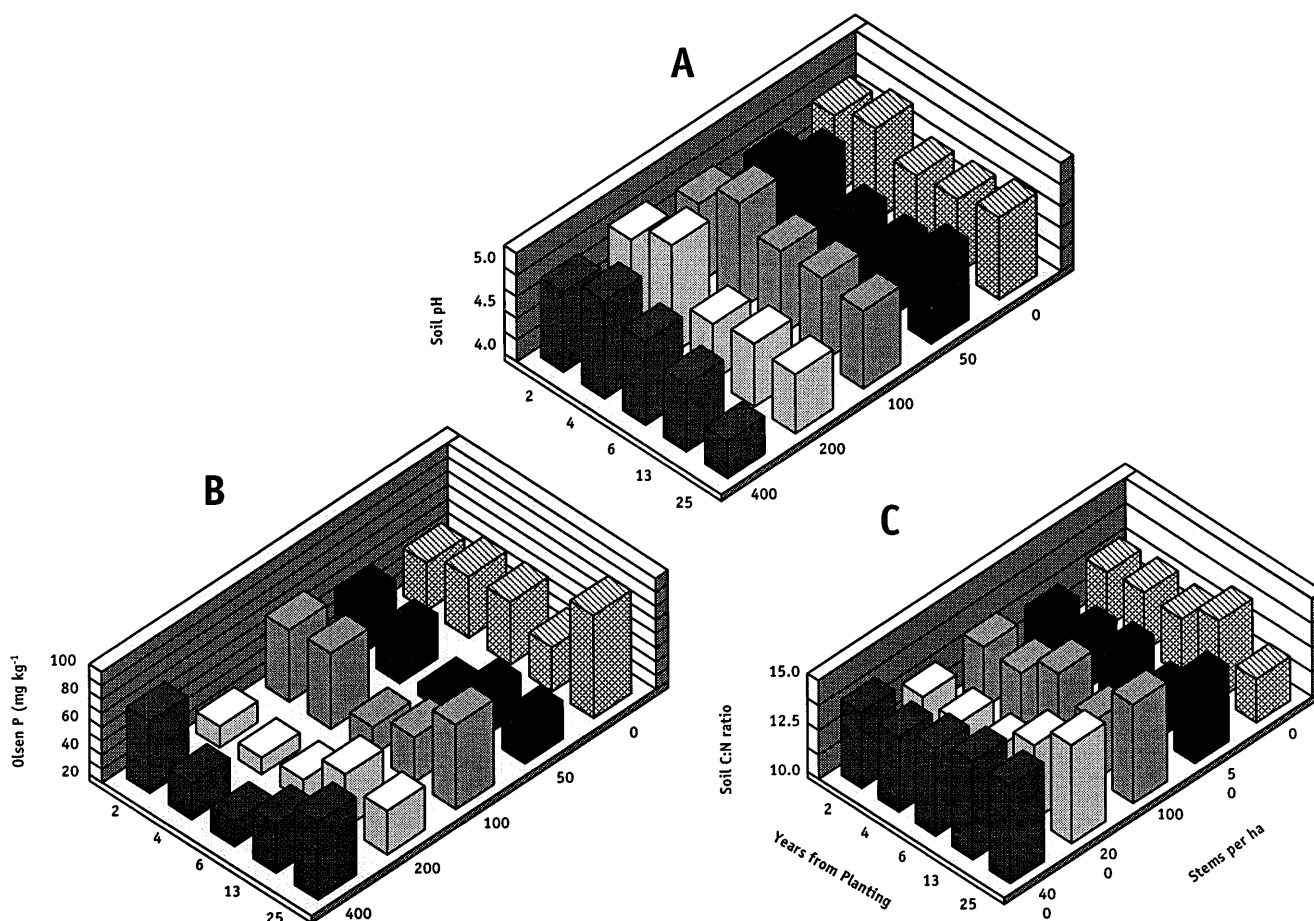


Fig. 1A–C Changes in chemical properties of soil at a depth of 0–10 cm under five *P. radiata* stocking rates during the course of the rotation. **A** pH of air-dried soil, **B** Olsen P, **C** soil C:N ratio

106 g m⁻²), but by 1998 the populations in all *P. radiata* treatments were negligible, and at the threshold of the level of detection.

The widespread *Aporrectodea caliginosa* was the dominant lumbricid. *Lumbricus rubellus*, commonly associated with dung of grazing animals, was not detected after 1986. No native, megascolecid earthworms were detected.

Samples were collected and extracted for enchytraeids in years 13 and 25. The population estimates given in Table 7 show the typical high variability associated with enchytraeid populations. For year 13 significant ($P < 0.001$) tree-stocking-rate and seasonal effects were reported by Yeates (1988), with the lowest average population (1380 m⁻²) being found in January. Comparison of results for April 1987 (year 14) and May 1998 (year 25) showed a significant decline in the enchytraeid population at a soil depth of 0–2.5 cm at both 200 and 400 stems ha⁻¹. The plot with a stocking rate of 50 stem ha⁻¹ had the greatest populations in both years (Table 7).

Soil nematodes

A total of 50 nematode taxa were discriminated (Appendix 2) in the 50 samples comprising the time series, and an average of 136 and 114 specimens were identified from samples of soil at depths of 0–5 and 5–10 cm, respectively. ANOVA showed significant ($P < 0.05$) differences in the abundance of the following 17 taxa between 0–5 and 5–10 cm depths: *Paratylenchus*, *Rhabditis*, *Panagrolaimus*, *Cephalobus*, *Heterocephalobus*, *Acrobeles*, *Teratocephalus*, *Plectus*, *Anaplectus*, *Chromadorida*, *Dorylaimus*, *Aporcelaimus*, *Nygolaimus*, *Doryllium*, *Tylencholaimus*, *Clarkus*, *Alaimus*. Total nematode populations also varied significantly ($P < 0.001$) with depth. When the effects of year and tree stocking rate were examined nine taxa showed significant ($P < 0.05$) effects, and these are shown in Fig. 2. *Heterodera* juveniles (representing the clover cyst nematode, *H. trifolii* Goffart, 1932), were most abundant in years 4 and 6 ($P < 0.001$) (Fig. 2b); while there were also greater populations in those years at 0 and 50 stems ha⁻¹, the stem effect was not significant. The root lesion nematode, *Pratylenchus*, showed a marked ($P < 0.001$) stem effect, the greatest populations in each year being found under pasture (Fig. 2c). In the case of *Paratylenchus*, year was significant ($P = 0.012$), with highest populations in years 2 and 4, and lowest in years 13 and 25

Table 6 Earthworm populations [means \pm SEs based on three (1975) or four replicate, hand-sorted 0.1-m² samples per tree stocking rate]. The populations given for 1975 and 1986 are based on four quarterly samples whereas those for 1998 are based on a

single, May, sampling. Biomass estimates in 1975 are based on specimens with evacuated intestines, those for 1986 and 1998 on specimens placed directly into 10% ethanol

Population	Stems ha ⁻¹														
	0			50			100			200			400		
	1975 ^a	1986	1998	1975	1986	1998	1975	1986	1998	1975	1986	1998	1975	1986	1998
<i>Aporrectodea caliginosa</i> (Savigny) (individuals m ⁻²)	452 \pm 76	321 \pm 109	328 \pm 98	358 \pm 98	238 \pm 18	0	220 \pm 53	119 \pm 63	0	336 \pm 55	0	0	241 \pm 58	1.25 \pm 1.25	8 \pm 7
<i>Lumbricus rubellus</i> (Hoffmeister) (individuals m ⁻²)	90 \pm 21	44 \pm 24	38 \pm 10	73 \pm 19	43 \pm 25	0	84 \pm 23	28 \pm 17	5 \pm 4	52 \pm 23	0	0	44 \pm 13	0	0
<i>Octolasion cyaneum</i> (Savigny) (individuals m ⁻²)	5	3 \pm 6	0	4	0	0	0	0	0	2	0	0	2	0	0
Total Lumbricidae (individuals m ⁻²)	547 \pm 65	368 \pm 65	365 \pm 98	435 \pm 103	281 \pm 46	0 ^b	304 \pm 68	147 \pm 10	5 \pm 4	389 \pm 54	0	0	287 \pm 66	1.25 \pm 1.25	8 \pm 7
Biomass of Lumbricidae (g fresh weight m ⁻²)	106	128 \pm 24	140 \pm 38	90	113 \pm 20	0	64	63 \pm 16	6 \pm 5	86	0	0	99	0.1 \pm 0.1	1 \pm 1

^a Results for 1975 are taken from McMillan (1981) and are given as means of his four quarterly means and SEs

^b Low numbers were seen but none were found in sampling units

(Fig. 2d). Overall, populations of the bacterial-feeding *Prismatolaimus* showed a significant ($P=0.023$) stem effect; the effect reflected smaller populations at intermediate stocking rates (Fig. 2e). *Pungentus* showed a significant ($P<0.001$) stem effect, always having its greatest population at 0 stems ha⁻¹ (Fig. 2f). *Axonchium* was found only in year 6 and showed a significant ($P=0.002$) time effect (Fig. 2g). The fungal-feeding *Diphtherophora* and plant-feeding *Trichodorus* both showed significant time and stem effects in soil at a depth of 0–10 cm, and significant ($P<0.001$) interactions between these. *Diphtherophora* was associated with higher stocking rates ($P<0.001$) in later years ($P<0.001$) (Fig. 2h). The greatest abundance of *Trichodorus* was in year 6 at 200 and 100 stems ha⁻¹, in year 13 at 50 stems ha⁻¹, and in year 25 at 0 stems ha⁻¹ (Fig. 2i); the year and stem effects were significant at $P=0.010$ and $P=0.029$ respectively. The bacterial-feed-

ing *Alaimus* occurred principally in years 13 and 25 ($P=0.030$) (Fig. 2j). A full list of nematode taxa discriminated and their populations in year 25 are given in Appendix 2.

When nematode taxa were aggregated into feeding or functional groups their total abundance at a depth of 0–10 cm over the 23 years showed neither year nor stocking-rate effects (data not shown). However, the proportional contribution of bacterial, fungal and plant-feeding groups all showed significant stocking-rate effects ($P=0.011$, $P=0.044$, $P=0.001$ respectively) and the effect of year was significant in bacterial ($P=0.004$) and plant-feeding ($P=0.005$) groups (Fig. 3). The indices of the nematode fauna at a soil depth of 0–10 cm showed no significant effects of time or tree stocking rates; values are given in Appendix 3.

Under 400 stems ha⁻¹ the abundance and composition of the nematode fauna at 13 years after planting

Table 7 Estimates of abundance of Enchytraeidae (mean m⁻² \pm SE) based on undisturbed cores from 0–2.5 and 2.5–5 cm depth collected quarterly in 1986–1987 and in May 1998. n.s. Non-significant

Stems ha ⁻¹	Depth (cm)	Average 1986–1987 (n=40)	April 1987 (n=10)	May 1998 (n=10)	Time effect 1987 vs 1998
0	0–2.5	942 \pm 418	294 \pm 132	3182 \pm 1121	n.s.
	2.5–5	9704 \pm 2300	3524 \pm 1444	5385 \pm 2414	n.s.
	0–5	10647 \pm 2530	3818 \pm 1547	8567 \pm 2742	n.s.
50	0–2.5	27669 \pm 4814	9252 \pm 4322	61337 \pm 46333	n.s.
	2.5–5	36309 \pm 5919	44066 \pm 13985	6658 \pm 3519	n.s.
	0–5	63978 \pm 8633	53258 \pm 13456	67994 \pm 49450	n.s.
100	0–2.5	13119 \pm 5195	2937 \pm 1787	2203 \pm 690	n.s.
	2.5–5	8273 \pm 2284	3035 \pm 871	1126 \pm 465	n.s.
	0–5	21391 \pm 2284	5972 \pm 2364	3329 \pm 1026	n.s.
200	0–2.5	35477 \pm 8376	29615 \pm 7714	4455 \pm 1268	<0.05
	2.5–5	3794 \pm 595	3720 \pm 1013	1322 \pm 527	n.s.
	0–5	39270 \pm 8709	33335 \pm 7827	5776 \pm 1449	<0.05
400	0–2.5	27534 \pm 5435	36810 \pm 9521	3476 \pm 1228	<0.05
	2.5–5	3671 \pm 1231	4601 \pm 1841	1567 \pm 685	n.s.
	0–5	31206 \pm 6336	41412 \pm 9932	5042 \pm 1862	<0.05

Nematode abundance (thousand per sq m)

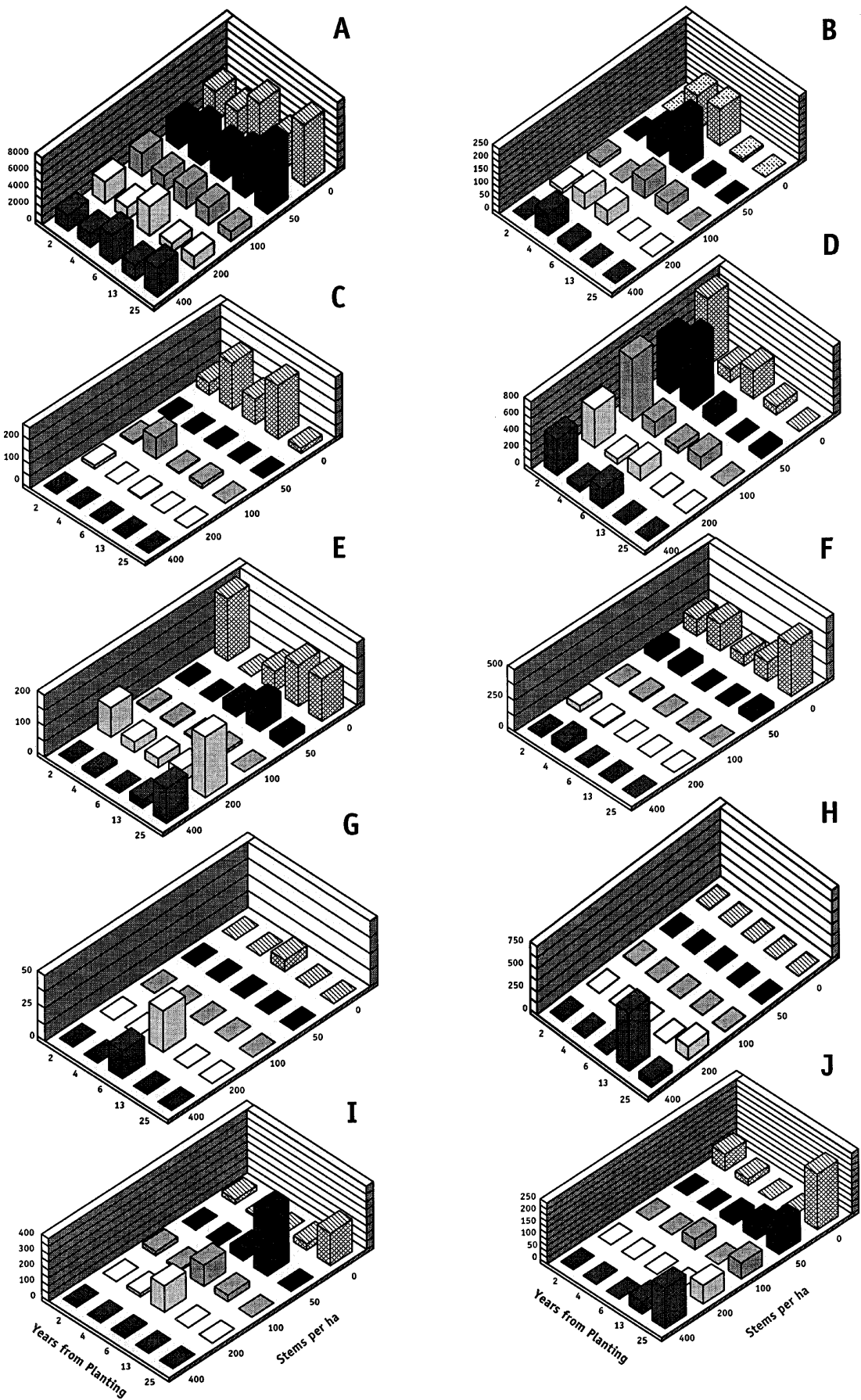


Fig. 2A–J Changes in soil nematode populations in soil at a depth of 0–10 cm under five *P. radiata* stocking rates during the course of the rotation; using ANOVA all these genera showed significant ($P < 0.05$) effects of year and stocking rate. **A** Total nematodes, **B** *Heterodera* juveniles, **C** *Pratylenchus*, **D** *Paratylenchus*, **E** *Prismatolaimus*, **F** *Pungentus*, **G** *Axonchium*, **H** *Diphtherophora*, **I** *Trichodorus*, **J** *Alaimus*

varied markedly with depth (Table 8). In soil at a depth of 0–10 cm there were over 1600 nematodes from 18 taxa per 100 g soil. The next increment, 10–20 cm, had only 210 nematodes from 11 taxa per 100 g soil, and at a depth of 70–80 cm there were only eight nematodes from five taxa in 100 g soil. Only at a soil depth of 0–10 cm were all six trophic groups represented. There was a change from a predominance of bacterial-feeding nematodes at soil increments of 0–10 and 10–20 cm (87% and 77% of all microbial-feeding nematodes, respectively) to 18–29% over the depth range of 20–60 cm. Correspondingly, the contribution of fungal-feeding nematodes increased with depth; they com-

prised >70% of the fauna between a depth of 20 cm and 50 cm.

Discussion

After 25 years under a final crop of 400 stems *Pinus radiata* ha⁻¹ there were no visible changes in the profile of the previously fertilised soil, although the pasture sward had been replaced by an acidic litter layer. The changes in chemistry of the upper horizons were broadly similar to those reported by McIntosh (1980) who compared unfertilised soil beneath 45-year-old *P. radiata* and manuka (*Leptospermum scoparium* J.R. and G. Forst.) at a site on Rhyolitic Pumice soil some 40 km

Fig. 3A–D Changes in the proportions of nematode feeding groups in soil at a depth of 0–10 cm under five *P. radiata* stocking rates during the course of the rotation. **A** Bacterial-feeding, **B** fungal-feeding, **C** predacious, **D** plant-feeding

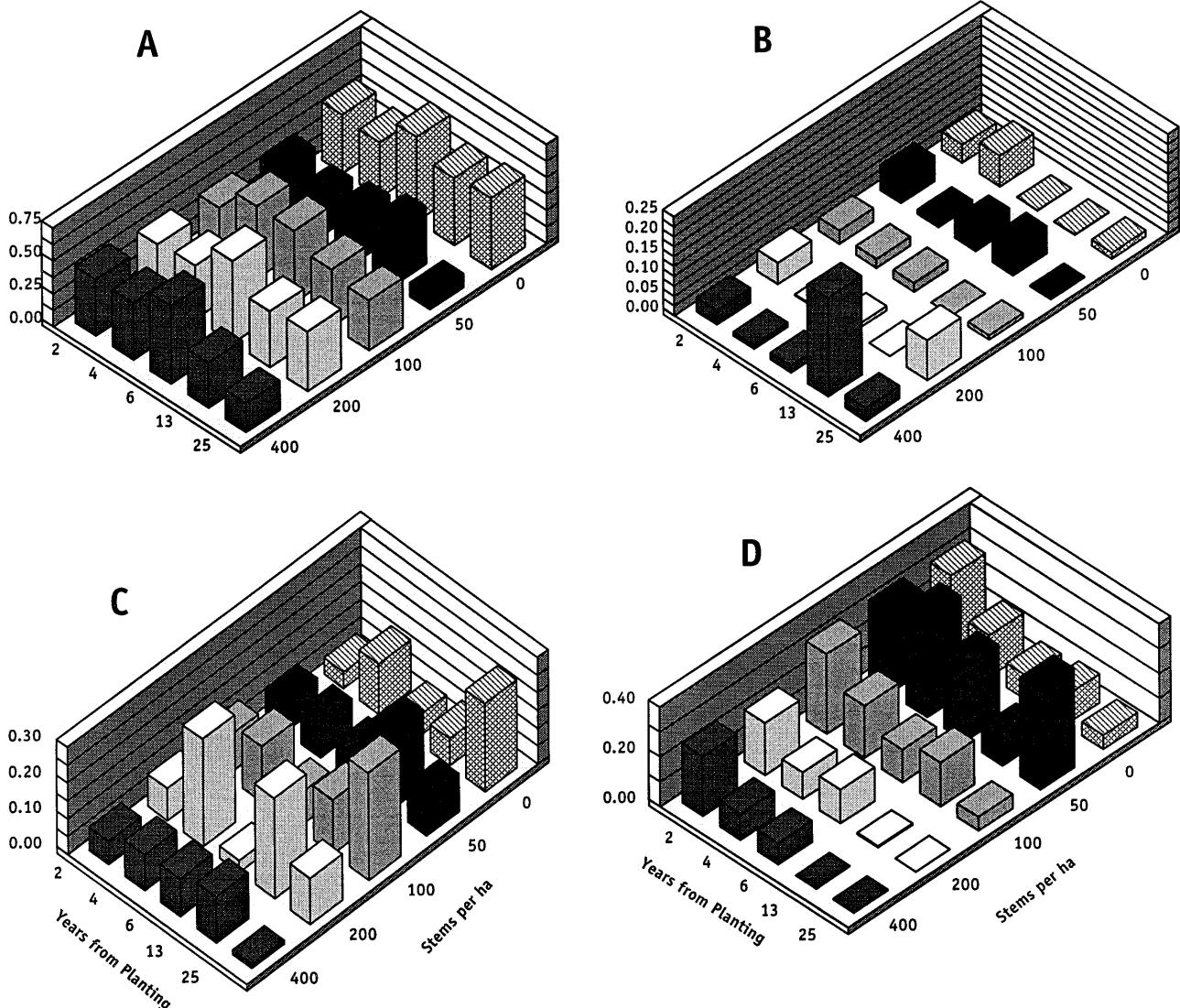


Table 8 Vertical distribution of nematode taxa (no. 100 g⁻¹ field-moist soil) and feeding groups beneath a stand of 400 stems ha⁻¹ *P. radiata* in April 1987

Taxon/group	Depth increment (cm)							
	LFH + 0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80
<i>Paratylenchus</i>	34	—	—	—	—	1	—	—
<i>Aphelenchoides</i>	—	222	—	—	—	—	—	—
<i>Rhabditis</i>	128	2	—	—	—	—	+	1
<i>Cephalobus</i>	170	38	20	9	—	1	2	2
<i>Heterocephalobus</i>	51	—	—	—	—	—	—	—
<i>Cervidellus</i>	34	40	7	6	8	7	2	—
<i>Acrobeles</i>	394	—	—	—	—	—	+	—
<i>Teratocephalus</i>	69	—	—	—	—	—	—	—
<i>Plectus</i>	92	2	—	—	—	—	—	—
<i>Anaplectus</i>	9	—	—	—	—	—	—	—
<i>Chronogaster</i>	137	45	4	1	—	—	—	—
<i>Rhabdolaimus</i>	—	19	2	2	1	2	—	—
<i>Chromadorida</i>	137	7	—	—	—	—	+	—
<i>Eudorylaimus</i>	9	—	—	—	—	—	—	—
<i>Pungentus</i>	17	—	—	—	—	—	—	—
<i>Aporcelaimus</i>	9	11	1	4	6	8	3	2
<i>Nygolaimus</i>	51	—	—	—	—	—	—	—
<i>Sectonema</i>	—	—	+	—	—	—	—	—
<i>Tylencholaimus</i>	17	40	2	10	8	12	3	2
<i>Diphtherophora</i>	171	4	76	55	32	12	3	1
<i>Clarkus</i>	77	—	—	—	—	—	—	—
Total nematodes	1606	210	112	87	55	43	13	8
Proportions in each feeding group								
Bacterial-feeding	0.760	0.73	0.29	0.21	0.16	0.23	0.31	0.38
Fungal-feeding	0.12	0.22	0.70	0.75	0.73	0.56	0.46	0.38
Predacious	0.080	—	—	—	—	—	—	—
Plant-feeding	0.021	—	—	—	—	0.02	—	—
Plant-associated	0.011	—	—	—	—	—	—	—
Omnivorous	0.011	0.05	0.01	0.04	0.11	0.19	0.23	0.24
Ratio bacterial-feeding:(bacterial-feeding + fungal-feeding)	0.87	0.77	0.29	0.22	0.18	0.29	0.40	0.50

south of Tikitere. In contrast, in the South Island high country Davis and Lang (1991) demonstrated increased nutrient availability in the topsoil of native soils under *P. radiata*; this was attributed to mineralisation of organic matter or transfer of nutrient from deeper horizons. Gilmore and Matis (1981) have discussed the relationship between past agricultural practices and the growth of *Pinus* spp. in Illinois.

There was a decline in soil pH over the 25-year tree rotation. Measurements on both fresh and dried samples showed that the decline was greater at 200 and 400 *P. radiata* ha⁻¹ than at other tree stocking rates (Table 4). While this acidification can in part be attributed to the effect of conifer growth, it may also reflect cessation of the previous regular fertilising and liming of the trial area for pastoral production. McIntosh (1980) also reported a decline in pH in most horizons of a similar soil under *P. radiata*. The marked increase in plant-available Olsen P in most plots (Table 4, Fig. 1c) was apparently a result of solubilisation of PO₄³⁻ from soil minerals or solubilisation of residual inorganic P under the prevailing pH regime. While the Olsen P results reported here are somewhat greater than those reported by Hawke and O'Connor (1993) for the four replicates

of the trial, for most stocking rates their data also show an increase in values in latter years. Similar trends have been reported from other sites following afforestation (e.g. Fisher and Stone 1969; Davis and Lang 1991; Sparling et al. 1994; Giddens et al. 1997).

That the C:N ratio of soil at a depth of 0–10 cm increased between years 2 and 25 in all plots with *P. radiata* (Table 5) suggested a decline in the availability of plant nutrients in the topsoil (DeAngelis 1992). However, while actual changes in soil C contents were variable (Table 5), any accumulation of C in the system should be regarded as ephemeral as it is likely to be metabolised if other nutrients or moisture become non-limiting. Further, land management practices such as forestry operations and effluent disposal may result in the loss of surface organic matter (Yeates 1995; Robertson 1998).

As noted above, the bulk density of soil at a depth of 0–20 cm varied between 0.90 and 1.06 t m⁻³ (Table 3). Yeates and Boag (1995) reported that although biopores, saturated hydraulic conductivity and air permeability were higher in pasture than any of the *P. radiata* treatments, the tree sites would still sustain infiltration of rainfall of up to 72 mm h⁻¹. They found no

reliable relationships between soil physical properties and earthworm populations, and this could be attributed to the high inherent total porosity and macroporosity of such pumice soils (McDonald and Birrell 1968). The variations we found in bulk densities were smaller than those which occur under various forest managements and animal stocking practices (Wingate-Hill and Jakobsen 1982; Firth and Murphy 1989; Singleton and Addison 1999).

Microclimatic effects occurred. Hawke and Wedderburn (1994) reported that agroforestry regimes raised grass minimum temperatures at all tree stocking rates, but reduced soil temperature at 200 and 400 stems ha^{-1} . That patterns of seasonal pasture growth differed between treatments (Hawke and Knowles 1997) would reflect this, the interception of rainfall by *P. radiata*, and increased evapotranspiration under forest.

Introduced, topsoil-mixing earthworms are a feature of modified landuses in New Zealand, and pastures are limed to enhance their populations and associated beneficial activities (Stockdill 1981; Springett 1984). That these lumbricids were essentially lost from *P. radiata* plots (Table 6) was a natural consequence of the change in landuse, and the sequence of loss was related to *P. radiata* stocking rates. While some of the changes in soil chemistry were correlated with the reduction in earthworm abundance, the changes were relatively minor and within the accepted ranges for the various earthworm species (Bouché 1972; Lee 1985). In the light of work on the effect of food quality, in particular litter type, on earthworms summarised by Edwards and Bohlen (1996), the general increase in the amount of *P. radiata* litter during the rotation (Table 3) probably indicated an effective decline in food quality for lumbricids, and may have been the chief factor responsible for their decline under *P. radiata*. The changes in soil physical conditions (Table 3) (Yeates and Boag 1995) did not appear to have adverse effects on sustainable landuse. There is evidence from New Zealand (Lee 1959; Yeates et al. 1998) and overseas (Edwards and Bohlen 1996) that, once established in a region, earthworms will colonise suitable areas, and we consider that the loss of such peregrine lumbricids from *P. radiata* plots is reversible. The Volcanic Plateau has a distinctive native, megascolecid, earthworm fauna (Lee 1959). When the natural vegetation was replaced by pasture the native megascolecids in the topsoil would have been lost (Lee 1961), and we failed to detect them or any subsoil species in our sampling. Sampling of sites at which there has been a direct conversion from native forest to exotic forest, without a transitional pasture phase, would be necessary to determine whether populations of native megascolecid earthworms can live in *P. radiata* forests. Dispersal and establishment of megascolecids in exotic forests established after a period of exotic grassland is another question.

That populations of root-feeding larvae of *Costelytra zealandica* (White) (Coleoptera, Scarabaeidae) were significantly lower in plots of 200 or 400 *P. radiata* ha^{-1}

in 1977, 1979 and 1980 was thought to reflect lower white clover content of the grass sward (Percival et al. 1984b). Soil populations of *Inopus rubriceps* (Macquart) (Diptera, Stratiomyidae) larvae at 200 *P. radiata* ha^{-1} were about half those in pasture (Percival et al. 1984b), and this again appeared to be a straightforward "dilution" effect.

Populations of Enchytraeidae are generally clustered horizontally (Didden 1993) and the present plots were no exception. The summer low reported by Yeates (1988) was moisture related. It is uncertain why the plot of 50 stems ha^{-1} had the greatest average populations (Table 7), but in nine out of ten comparisons the soil C content was greater in that plot than in those of 0 or 100 stems ha^{-1} (Table 5). While the significant declines in enchytraeid abundance at 200 and 400 stems ha^{-1} from year 13 to year 25 were associated with increases in soil C, the parallel increases in the C:N ratio probably counteracted them; lower soil temperatures may also have been a factor. Given the important contribution of soil fauna such as Enchytraeidae to the decomposition of forest litter (Setälä et al. 1988), this decline in populations and their activity may be significant factors in the regulation of nutrient cycling in coniferous forests. As enchytraeid species vary in their responses to shifts in soil pH (Abrahamsen 1983; Chalupský 1995) and soil organic matter (Lundkvist 1983), the response of the enchytraeid fauna probably reflected changes in a range of species.

The composition of the nematode fauna in soil at a depth of 0–10 cm changed with both site and year. The root-lesion nematode, *Pratylenchus*, was clearly associated with pasture (Fig. 2c), and the strong association of *Pungentus maorium* Clark, 1963 with pasture (Fig. 2f) suggests that this species, which is abundant in many improved New Zealand pastures (Yeates 1984a), is another example of an endemic species which has exploited modified habitats (Yeates 1991). In contrast, both *Axonchium* and *Diphtherophora* (Fig. 2g,h) were found under higher *P. radiata* stocking rates. The composite trends in feeding groups suggested an increase in fungal-feeding nematodes at 200 and 400 stems ha^{-1} . Under 400 stems ha^{-1} the nematode fauna below 20 cm was dominated by fungal-feeding nematodes in year 13; this represented not only a change from the situation in soil at a depth of 0–20 cm, but also a contrast with the situation under pasture where significant populations of bacterial-feeding, plant-feeding and omnivorous nematodes occurred below 20 cm (Yeates 1980). Mycorrhizal fungi form a significant part of *P. radiata* forest systems (Chu-Chou and Grace 1990), but in the present situation bacterial-mediated foodwebs dominate in the upper 10 cm of soil where our sampling was concentrated.

Overall, during the course of the rotation total nematodes at a soil depth of 0–10 cm became more abundant at 0 and 50 stems ha^{-1} (Fig. 2a). Despite this general trend there were some remarkable temporal trends that occurred across treatments. Juveniles of the clover

cyst nematode, *Heterodera trifolii* Goffart 1932, were most abundant in years 4 and 6 (Fig. 2b), while *Paratylenchus* had lower numbers after year 4 or year 6 (Fig. 2d). *Prismatolaimus* was most abundant in years 2 and 25, while *Axonchium* was only detected in year 6 (Fig. 2e,g). The bacterial-feeding *Alaimus* was most abundant in all treatments in year 25 (Fig. 2j). While the plant-feeding *Trichodorus* was present in the pasture in year 2 and much more abundant in year 25; substantial numbers were present in the plots of 50, 100 and 200 stems ha^{-1} in years 6 or 13 (Fig. 2i). As all these plots received aerial applications of fertiliser to year 13, and the 0 and 50 stems ha^{-1} plots were ground treated in years 18 and 19 (Hawke and O'Connor 1993), the trend was not a fertiliser effect.

Regular sampling of New Zealand pastures has demonstrated that, although the seasonal nematode populations under grazed pastures do vary from year to year (Yeates 1982, 1984b), there can still be distinct, climate-driven seasonal cycles in species such as *H. trifolii* (Yeates and Risk 1976). In British arable lands there are also both distinct year-to-year differences in the composition of the nematode faunas (Boag et al. 1998) and seasonal effects that may be not only climate-driven but also related to crop-loss situations (Jones et al. 1969; McSorley and Phillips 1993). In a given soil there may be both short-term, successional changes, such as have been demonstrated in the nematode fauna of forest litter (Sohlenius 1983; Arpin and Ponge 1986; Ruess 1995) and also long-term shifts in faunal composition reflecting effects of pasture sward composition, agrochemical application, grazing management and landuse changes (Sohlenius 1996, 1997; Yeates and Bongers 1999). The year-to-year variation in populations of nematodes such as *Plectus*, *Aphelenchoides* and *Acrobeloides* that Sohlenius (1997) reported from various management regimes in a 120- to 140-year-old *Pinus sylvestris* L. stand in Sweden illustrated not only that microfaunal populations in forests in both hemispheres fluctuate but also that such populations' fluctuations may be similar across various forestry regimes. At Tikitere there were similar fluctuations in measured soil chemical properties. These changes occurred independent of, but perhaps overlain by, long-term climate change such as recorded by Menzel and Fabian (1999).

In conclusion:

1. Although there were no visible changes in the soil profile under 400 *P. radiata* ha^{-1} between years 2 and 25 of the *P. radiata* rotation, there were marked changes in soil chemistry with pH declining at all depths. Topsoil pH declined but plant-available P and soil C:N increased at 0–400 *P. radiata* ha^{-1} . These are typical of changes reported following afforestation. That similar trends occurred in pasture may have reflected reduced intensity of management.
2. Topsoil-mixing, lumbricid earthworms declined with loss of grass cover and with pH; significant popula-

tions were found only in pasture at 25 years. No related changes in soil bulk density were detected.

3. That total enchytraeid abundance declined between years 13 and 25 in the plots of 200 and 400 stems ha^{-1} may have reflected a changed microclimate at those stocking rates.
4. There were significant shifts with time (1975–1998) and tree stocking rates in the composition of the nematode fauna in soil at a depth of 0–10 cm, and there were changes under the “control” pasture. In addition to changes related to the change in landuse there were temporal changes that affected the fauna irrespective of tree stocking rates.
5. The changes in soil chemistry associated with the *P. radiata* rotation reflected a change from limed pasture to forest and are regarded as reversible. The parallel changes in soil microfauna and macrofauna reflected this change in landuse and the related differences in patterns of turnover of C and soil nutrients. They, too, given recolonisation from a patchy environment, are reversible.

Appendix 1 Description of soil profile made under young *Pinus radiata* seedlings in 1975 (year 2)

Rotoiti loamy sand	New Zealand soil classification: Typic Orthic Pumice soil
Classification	New Zealand genetic classification: composite recent soil on yellow-brown pumice soil
Site details	USDA soil taxonomy: Typic Udivitrand NZMS 260 U15 032 440; altitude 335 m; annual rainfall 1400 mm; profile described and sampled 15 May 1975
Parent material	Five to 19 cm Rotomahana Mud on more than 20 cm Kaharoa Tephra, on Taupo Pumice, Rotokawa Tephra, Mamaku Tephra, Rotoma Tephra, Waiohau Tephra and Rotorua Tephra
Soil profile description	
Ap 0–18 cm	Very dark greyish brown (10YR 3/2) loamy sand; friable; moderately developed fine nut and crumb structure; lumps of greyish brown sandy loam (Rotomahana Mud); indistinct boundary
Bw1 18–30 cm	Brown (7.5YR 4/4) gritty sand; very friable to loose; weakly developed crumb to single grain structure (Kaharoa Tephra); distinct boundary
2bA ₂ 30–40 cm	Brown (7.5YR 4/4) gritty sandy loam; very friable; weakly developed nut structure; few medium Taupo Lapilli (Taupo Pumice and Rotokawau Tephra); indistinct boundary
3bA ₃ 40–60 cm	Brown (7.5YR 4/4) slightly greasy fine sandy loam; friable; weakly developed nut structure (Rotokawau Tephra); distinct boundary
3bBC 60–70 cm	As above, with many to abundant very coarse dark greyish brown (2.5Y 4/2) hard fragments of basalt (Rotokawau basal layer); distinct boundary
4bBw ₂ 70–600 cm +	Yellowish brown (10YR 5/8) greasy loamy sand; friable; weakly developed nut to single grain structure

Appendix 2 Abundance of nematode taxa (thousands m⁻² in soil at a depth of 0–10 cm) under each stocking rate of *Pinus radiata* at year 25 (May 1998) and their grand means for all five stocking rates and five sampling times (*n*=25)

Taxon	May 1998 Final crop of <i>P. radiata</i> ha ⁻¹					Mean
	0	50	100	200	400	
<i>Tylenchus</i>	62	44	45	104	1001	94
<i>Cephalenchus</i>	122	0	1	0	0	19
<i>Ditylenchus</i>	77	0	0	0	0	10
<i>Heterodera</i> juvenile	0	0	0	0	0	38
<i>Meloidogyne</i> juvenile	0	0	0	0	0	7
<i>Helicotylenchus</i>	191	5982	54	0	2	350
<i>Pratylenchus</i>	21	0	0	0	0	29
<i>Paratylenchus</i>	0	39	0	0	0	234
<i>Aphelenchus</i>	0	0	0	0	19	11
<i>Aphelenchoides</i>	38	8	9	0	2	12
<i>Rhabditis</i>	717	121	46	56	125	172
<i>Bunonema</i>	0	0	1	0	0	0
<i>Panagrolaimus</i>	505	126	0	0	2	124
<i>Diplogaster</i>	0	0	0	0	0	2
<i>Cephalobus</i>	320	92	38	101	204	265
<i>Heterocephalobus</i>	609	42	0	0	0	95
<i>Eucephalobus</i>	0	0	0	25	57	5
<i>Cervidellus</i>	52	0	1	8	12	6
<i>Acrobeles</i>	407	213	122	0	0	78
<i>Teratocephalus</i>	0	0	0	25	0	1
<i>Plectus</i>	629	8	50	37	7	175
<i>Anaplectus</i>	191	0	0	0	0	177
<i>Wilsonema</i>	0	0	0	126	38	12
<i>Prismatolaimus</i>	136	23	0	194	110	49
<i>Chromadorida</i>	129	8	56	3	0	100
<i>Monhystera</i>	38	55	0	0	0	13
Enoplid	0	3	0	0	0	5
“Marine”	0	0	1	0	0	18
<i>Tripyla</i>	0	0	0	0	2	14
<i>Dorylaimus</i>	38	0	0	0	0	8
<i>Mesodorylaimus</i>	38	0	0	0	0	16
<i>Eudorylaimus</i>	35	5	13	278	31	30
<i>Pungentus</i>	413	44	0	0	0	53
<i>Aporcelaimus</i>	340	10	210	76	1409	376
<i>Dorylaimellus</i>	0	0	0	3	7	30
<i>Axonchium</i>	0	0	0	0	0	2
<i>Nygolaimus</i>	73	3	13	14	12	46
<i>Sectonema</i>	0	0	0	0	0	8
<i>Tylencholaimellus</i>	0	0	0	0	0	1
<i>Doryllium</i>	0	0	0	0	0	25
<i>Leptonchus</i>	0	0	0	0	0	5
<i>Tylencholaimus</i>	0	3	0	9	12	9
<i>Longidorus</i>	0	0	7	0	7	1
<i>Diphtherophora</i>	0	0	3	137	72	34
<i>Trichodorus</i>	205	0	0	0	0	49
<i>Clarkus</i>	1708	636	232	173	26	277
<i>Cobbonchus</i>	0	0	0	0	0	4
<i>Iotonchus</i>	0	0	95	0	0	37
<i>Mylonchulus</i>	38	197	7	0	0	10
<i>Alaimus</i>	230	118	65	76	165	37
Total nematodes	7362	7780	1113	1446	3325	3173

Appendix 3 Abundance of nematode feeding groups (thousands m^{-2} in soil at a depth of 0–10 cm) and values of indices of the nematode fauna under each stocking rate of *P. radiata* at year 25

(May 1998) and the grand mean of these for all five stocking rates and five sampling times ($n=25$)

Taxon	May 1998 Final crop of <i>P. radiata</i> ha^{-1}					Mean
	0	50	100	200	400	
Bacterial-feeding	3961	806	422	651	721	1328
Fungal-feeding	115	10	12	146	105	110
Predacious	1819	836	348	187	38	382
Plant-feeding	417	6022	62	0	10	708
Plant-associated	597	88	47	107	1009	196
Omnivorous	452	18	223	355	1442	450
Taxa	24	11	14	15	12	17.9
H'	2.619	0.913	2.324	2.392	1.567	2.370
SR	4.494	1.912	2.788	2.813	2.160	3.461
Evenness	0.824	0.381	0.881	0.883	0.631	0.822
Dominance	0.110	0.635	0.123	0.109	0.302	0.143
H2	2.206	0.454	2.098	2.218	1.196	2.076
Sigma MI	2.790	3.005	3.396	3.248	3.479	2.906
c-p 1	0.186	0.032	0.047	0.021	0.037	0.096
c-p 2	0.335	0.053	0.283	0.290	0.411	0.410
c-p 3	0.066	0.791	0.104	0.172	0.031	0.141
c-p 4	0.329	0.123	0.358	0.455	0.080	0.175
c-p 5	0.084	0.000	0.208	0.062	0.442	0.717

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