Biogeochemistry **66:** 203–221, 2003.

Land-use change effects on soil C and N transformations in soils of high N status: comparisons under indigenous forest, pasture and pine plantation

R.L. PARFITT[1,*], N.A. SCOTT[2], D.J. ROSS[1], G.J. SALT[1] and K.R. TATE[1]
*[1]Landcare Research, Private Bag 11052, Palmerston North, New Zealand; [2]Woods Hole Research Center, Woods Hole, MA, USA; *Author for correspondence (e-mail: parfittr@landcare.cri.nz; phone: 64 6 357 7154; fax: 64 6 355 9230)*

Received 15 October 2001; accepted in revised form 10 April 2002

Key words: ^{14}C, ^{15}N, Ammonium, Extractable carbon, Lignin, Microbial biomass, New Zealand, Nitrate, Respiration

Abstract. Globally, land-use change is occurring rapidly, and impacts on biogeochemical cycling may be influenced by previous land uses. We examined differences in soil C and N cycling during long-term laboratory incubations for the following land-use sequence: indigenous forest (soil age = 1800 yr); 70-year-old pasture planted after forest clearance; 22-year-old pine (*Pinus radiata*) planted into pasture. No N fertilizer had been applied but the pasture contained N-fixing legumes. The sites were adjacent and received 3–6 kg ha^{-1} yr^{-1} "volcanic" N in rain; NO_3^--N leaching losses to streamwater were 5–21 kg ha^{-1} yr^{-1}, and followed the order forest < pasture = pine. Soil C concentration in 0–10 cm mineral soil followed the order: pasture > pine = forest, and total N: pasture > pine > forest. Nitrogen mineralization followed the order: pasture > pine > forest for mineral soil, and was weakly related to C mineralization. Based on radiocarbon data, the indigenous forest 0–10 cm soil contained more pre-bomb C than the other soils, partly as a result of microbial processing of recent C in the surface litter layer. Heterotrophic activity appeared to be somewhat N limited in the indigenous forest soil, and gross nitrification was delayed. In contrast, the pasture soil was rich in labile N arising from N fixation by clover, and net nitrification occurred readily. Gross N cycling rates in the pine mineral soil (per unit N) were similar to those under pasture, reflecting the legacy of N inputs by the previous pasture. Change in land use from indigenous forest to pasture and pine resulted in increased gross nitrification, net nitrification and thence leaching of NO_3^--N.

Introduction

Change in land use can affect the carbon (C) cycle and the amount of C stored in soil. Soil nitrogen (N) cycling can also be modified by change in land-use (e.g. Neill et al. (1999)), and interactions between C and N cycles may influence soil C storage (Conant et al. 2001) and regulate N availability. However, changes in C and N cycling related to land-use change may be complicated by differences in historical land-use patterns (Compton and Boone 2000).

Throughout New Zealand, large areas of pasture have been converted to plantation forests dominated by *Pinus radiata* D. Don (MAF 1999). These new forests represent a major C sink for New Zealand, offsetting about half the annual CO_2

emissions from energy and industrial uses (MfE 1997). If land-use change leads to increased N losses or reduced plant-available N, plant N uptake and forest productivity may decline over time. Moreover, the forms of N and their rate of formation influence the competitive outcome between plants and soil microorganisms for this often scarce resource (Kaye and Hart 1997) and can influence potential C storage (Nadelhoffer et al. 1999). Simulation modelling studies suggest that it is the fate of nutrients in plants vs soils that ultimately determines the C-storage potential for a site (Rastetter et al. 1992; McMurtrie et al. 2001). Although the impact of land-use change on soil C and N cycling is complex and occurs over variable time scales, understanding these interactions is critical to determining how land-use change will alter C budgets and N losses.

The Purukohukohu Experimental Catchments in central North Island, New Zealand, contain three adjoining catchments (22–37 ha) that are occupied by the following ecosystems: indigenous forest, 70-year-old pasture planted after forest clearance, and 22-year-old *P. radiata* planted in 50-year-old pasture. They have a high natural N status and lose NO_3^--N in spring water and stream water (Cooper 1986; Cooper et al. 1987). Although there are no similar catchments that allowed us to carry out a replicated study, they do enable us to study the mechanisms that affect C and N cycling for these three sites that were all under indigenous forest in 1920.

We investigated the hypothesis that N fixation in leguminous pastures has long-term effects on C and N cycling processes in soil after the pasture has been converted to production forest. Here, we used laboratory incubations (Hart et al. 1994a) to investigate the interaction between the C and N cycles in soils from the pasture, *P. radiata* plantation and indigenous forest. These data, together with published data on pools (Ross et al. 1999) and NO_3^--N leaching (Parfitt et al. 2003) are used to briefly assess the effect of change in land use on N cycling in the catchments.

Materials and methods

Site descriptions

We examined soil C and N transformations in LFH material and mineral soil (0–10 cm) layers from three sites in the Purukohukohu Experimental Catchments located in the central North Island, New Zealand at 38° 36′ S, 176° 16′ E. Annual precipitation is approximately 1500 mm and the mean annual temperature is about 10 °C (Beets and Brownlie 1987). The soils are Typic Udivitrands (Oruanui sandy loams) formed from 1800-year-old pumice that is about 1 m thick (Ross et al. 1999). The soil horizons and depths are given in Table 1. The catchments contain incised streams that are fed by springs.

Briefly, the indigenous forest (broadleaf/podocarp) catchment (37 ha) had a three-tiered structure and was rich in plant species. Rimu (*Dacrydium cupressinum* Lamb.) emerged over a canopy dominated by kamahi (*Weinmania racemosa* L.F.),

Table 1. Soil horizons for the three soils and $\Delta^{14}C$ data for these horizons.

	Indigenous Forest		Pasture		Pine	
Horizon	Depth (cm)	$\Delta^{14}C$ (‰)	Depth (cm)	$\Delta^{14}C$ (‰)	Depth (cm)	$\Delta^{14}C$ (‰)
FH	8–0	182	np	np	3–0	211
Ah/Ap	0–11	8	0–9	144	0–10	124
AB	np	np	np	np	10–23	70
Bs	11–19	−80	9–20	28	23–36	nd
Bw	19–45	−109	20–44	−14	36–60	nd

np = not present; nd = not determined

hinau (*Elaeocarpus dentatus* (J.R. et G Forst.) Vahl.), rewarewa (*Knightia excelsa* R. Br.), and tawa (*Beilschmiedia tawa* (A Cunn.) Kirk). The sparse understory comprised hardwood trees, shrubs and ferns. The pine (34 ha) and pasture (22 ha) catchments had been under indigenous forest until the 1920s, when they were cleared and burned. Grass and scrub grew until 1957, when ryegrass-clover (*Lolium perenne-Trifolium repens)* pasture was sown in both catchments. The pasture was grazed regularly and fertilized (34 kg P ha^{-1} yr^{-1}) until 1969 (Beets and Brownlie 1987). In 1973, herbicide was applied to the 34 ha catchment, and *P. radiata* seedlings were planted at 2000 stems ha^{-1}. For the remaining pasture catchment, the P status of the soil remained high, white clover was present in 1995, and it was grazed regularly.

Sample collection and preparation

Sites with the same soil type and slope (4–8°) were selected in each catchment. The sites under pasture and pine were 200 m apart. Litterfall was collected every three months for one year using 15 traps (340 × 280 mm) along a 50 m transect. We sampled LFH material from the indigenous forest and pine plantation, and mineral soil (0–10 cm depth) from all sites in April 1995. Three replicate composite samples (each with 25 individual cores) were collected using an 80 -mm diameter core for LFH material, and a 25 -mm core for mineral soil. The forest floor was predominantly F and H horizons with a thin L horizon. Moss and fresh green foliage were removed where necessary from the LFH samples, but it was difficult to obtain complete separation of FH material from mineral soil. The field-moist samples were sieved through a 5 mm sieve to remove woody material, but not brown leaves, and stored for about one week at 4 °C.

Incubation procedures

Field-moist soil was weighed into 125 mL polypropylene containers, and water was added to adjust all samples to −10 kPa (about 60% of water-holding capacity). The adjusted moist weights were 7.5 g for LFH material from both sites, and 15.0 g for the mineral soil. Sufficient containers were prepared to allow for destructive sam-

pling of each replicate at several times over the incubation. The containers were covered with polyethylene (30 micron), held in place with a rubber band and placed in plastic trays containing water, enclosed in large polyethylene bags (to maintain high humidity), and placed in an incubator at 25 °C. The system had been shown to allow gas exchange (M.W. Gradwell pers. comm.). In addition, two containers of each replicate composite sample were placed in a 1 -L sealed glass jar fitted with a septum for CO_2 production measurements. Periodically, individual containers were destructively sampled for measurements of 0.5 *M* K_2SO_4-extractable C, NH_4^+-N and NO_3^--N. At the same time, additional soil samples were used for measurements of gross N mineralization and nitrification by ^{15}N isotopic dilution.

Microbial C and N were measured in an associated study (D.J. Ross unpublished data) in which equal portions of the field replicate samples were pooled and subdivided into triplicate portions of about 60 g for the LFH material and 200 g for each mineral soil. These samples were placed in 600 mL jars, adjusted to −10 kPa water content, covered with polyethylene film, and incubated at 25 °C for up to one year. Water content was checked fortnightly and replenished as necessary.

Analytical procedures

The pH of mineral soil and LFH material was measured on a 1:2.5 w/v mixture of sample and water. Total C and N were measured on a LECO FP-2000 CNS analyser. Lignin and cellulose were determined using the acid-detergent fibre method of Rowland and Roberts (1994). The $\Delta^{14}C$ values of soil organic matter were determined by Accelerator Mass Spectrometry, as described by Tate et al. (1993), using air-dry samples (< 5 mm; finely ground to < 0.25 mm) that had been taken from each horizon from a representative profile at each site in September 1992 (Table 1); determinations were unreplicated, except for the pasture 20–44 cm sample (duplicate) and pine 0–10 cm sample (triplicate).

Microbial C was determined on days 0, 96, 250 and 340, and microbial N on days 0 and 340, by chloroform fumigation-extraction methods (Ross and Tate 1993), using triplicate samples and a k_{EC} factor of 0.34 and a k_{EN} factor of 0.45 (Ross et al. 1999). At the end of the incubation, large amounts of NO_3^--N and NH_4^+-N in many of the samples would have made it difficult to measure the small microbial N pools. The samples were, therefore, pre-extracted with 0.5 *M* K_2SO_4 before chloroform fumigation, using a modification of the procedure of Widmer et al. (1989) as described by Scott et al. (1998).

Other analytical procedures closely followed those of Scott et al. (1998). Briefly, CO_2 production was measured periodically by measuring the accumulation of headspace CO_2 between sample intervals using gas chromatography. When necessary, deionized water was added to maintain constant soil moisture. After each set of measurements, jars were flushed with ambient air, re-sealed and returned to the incubator at 25 °C.

We estimated gross rates of N transformations using isotopic dilution with both $^{15}NO_3^-$-N and $^{15}NH_4^+$-N (Brooks et al. 1989; Hart et al. 1994b) on days 0, 21, 42, and 84; after this, mineral-N pools became so large in some samples that it was

difficult to get reliable pre- and post-incubation results without adding a very large ^{15}N spike. At each sampling time, two containers of each soil were removed. One received 1 mL of 3.21 m*M* $K^{15}NO_3$ (99.5 atom percent enrichment), and the other 1 mL of 1.605 m*M* $(^{15}NH_4)_2SO_4$ (99.5 atom percent) added dropwise across the soil surface; the treated samples were then incubated for 24 hours. The diffusion protocols and extraction procedure are described in Scott et al. (1998). All ^{15}N analyses were conducted at Michigan State University's Isotope Mass Spectrometry Laboratory. Previous work has shown that a significant portion of the added $^{15}NH_4$-N can be rapidly removed from the extractable pool (Hart and Firestone 1991; Hart et al. 1994a). We therefore measured the quantity of labelled NH_4^+ lost from the extractable NH_4^+-N pool 15 minutes after addition of the isotope at day 0. About 35% of the added $^{15}NH_4^+$-N could not then be recovered in a 0.5 *M* K_2SO_4 extract. However, by the next sampling date (21 days), a significant pool of NH_4^+-N had accumulated in both the LFH material and mineral soil, and we assumed that no further loss of the ^{15}N label occurred except via biological transformations. Nitrogen transformation rates were, therefore, based on the reduced size of the initial labelled extractable pool at day 0 and were calculated using isotope dilution equations presented in Kirkham and Bartholomew (1954).

Statistical analyses

We examined between-site differences in soil C and N transformations in a) LFH material and b) mineral soil over the whole incubation period using repeated measures within the general linear models procedure in MGLH (SYSTAT 1992). At the beginning and end of the incubation, the significance of differences in properties of all samples considered together was assessed by ANOVA using log-transformed data and Fisher's LSD test. Repeated measures and ANOVA were also used to compare gross NH_4^+-N and NO_3^--N rates of production and consumption in our different systems. We compared C mineralization to radiocarbon concentrations and N mineralization using regression analysis under procedure MGLH in SYSTAT. For all data, all differences that are reported in the text were tested and considered significant at $P \leqslant 0.05$, unless stated otherwise.

Results and discussion

Soil C and N

All the soils have high N contents (Table 2). The addition of 3–6 kg N ha^{-1} yr^{-1} in wet deposition is likely to be a major contributor to the high natural N status of the catchments (Dyck et al. 1987; Nichol et al. 1997; Ross et al. 1999). Additions in dry deposition have not been measured but are probably similar. It is known that volcanic steam vents in the area emit ammonium-N (Ellis and Mahon 1977), and these are the likely source of the atmospheric N additions. A simulation of the C

Table 2. Litter and C and N pools. SE shown in parentheses (n = 3). Values in each row not marked with the same letter differ significantly ($P < 0.05$) from each other.

	Indigenous Forest	Pasture	Pine
Leaf/twig-fall (t C ha^{-1} yr^{-1})	4.3	np	3.7
LFH material (t ha^{-1})[x]	82(3) a	np	33 (1) b
N content of LFH (t ha^{-1})[y]	1.6 (0.1) a	np	0.5 (0.1) b
N in 0–10 cm mineral soil (t ha^{-1})[y]	1.8 (0.1) b	3.9 (0.2) a	2.1 (0.1) b
C content of LFH (t ha^{-1})[y]	34 (1) a	np	14 (1) b
C in 0–10 cm mineral soil (t ha^{-1})[y]	35 (2) b	56 (2) a	36 (1) b

np = not present [x]Calculated from 84 measurements for indigenous forest and 94 for the pine [y]Calculated using bulk density data in Ross et al. (1999)

and N cycle using the CENTURY model suggest that inputs of 5 kg N ha^{-1} yr^{-1} lead to high soil N after 1800 years, and that current N inputs are approximately equal to N losses under indigenous forest (Parfitt et al. 2001).

No N fertilizer had been applied to any of the ecosystems, but the pasture soil had received large amounts of P fertilizer between 1957 and 1969. White clover pastures on similar soils with high P status in New Zealand fix 140–170 kg N ha^{-1} yr^{-1} and so increase the N status of the soils (O'Connor et al. 1979).

Total C concentration in 0–10 cm mineral soil followed the order: pasture > pine = forest, N concentration: pasture > pine > forest, and C/N ratio: pasture < pine < forest (Table 3). However, the C/N ratio was higher in LFH material from the pine plantation than from the indigenous forest.

C and N mineralization on a mass basis

Soil temperature and moisture were controlled during the incubation, so the differences in C mineralization and N cycling in the samples from the three land uses would have arisen from other variables such as substrate quantity and quality.

Total C mineralization in the mineral soil (per g dry weight) over 250 days was highest in the pasture samples and lowest in the indigenous forest samples (Table 3). The high mineralization in the pasture sample may have been partly related to the high initial soil C concentration.

The initial extractable NH_4^+-N in the mineral soil followed the order: forest > pasture > pine, while the initial extractable NO_3^--N followed the order: pasture > pine > forest; no extractable NO_3^--N was detected in the sample under indigenous forest (Table 3). Net nitrification occurred rapidly during incubation of the mineral soil samples under pasture and pine, and more slowly for the indigenous forest soil (see Figure 1b). The extractable NH_4^+-N in the indigenous forest sample decreased during the incubation while net nitrification proceeded. (The results in Figures 1 and 2 are expressed on a mass of N basis that will be discussed later).

Carbon mineralization (after 250 days) in the LFH material was similar in the indigenous forest and the pine samples (Table 3). Net nitrification in the LFH material under pine began immediately, and NO_3^--N accumulated in the first 50 days,

Table 3. Properties of LFH material and mineral soil (0–10 cm) before and after incubation of the samples from indigenous forest, pasture and pine. SE shown in parentheses (n = 3). Values in each row not marked with the same letter differ significantly ($P < 0.05$) from each other.

	Indigenous Forest		Pasture	Pine	
	LFH	0–10 cm	0–10 cm	LFH	0–10 cm
pH initial	4.4 (0.03) c	4.2 (0.1) d	5.0 (0.04) a	4.2 (0.02) d	4.7 (0.05) b
pH final	4.8 (0.2) a	4.4 (0.02) b	4.0 (0.02) c	4.5 (0.06) b	4.0 (0.02) c
Total C (g kg^{-1})	415 (7) a	65 (1) c	100 (12) b	424 (9) a	70 (0.6) c
Total N (g kg^{-1})	19.5 (0.3) a	3.3 (0.1) e	7.0 (0.6) c	14.9 (0.1) b	4.1 (0.3) d
Total C/N initial	21 (0.3) b	20 (0.1) c	14 (0.5) e	28 (0.7) a	17 (0.2) d
Total C/N final	nd	nd	13 (0.1) c	27 (0.6) a	16 (0.08) b
Initial extractable NH_4^+-N (mg kg^{-1})	21 (0.3) a	24 (0.2) a	0.6 (0.03) b	1 (0.1) b	0.2 (0.1) c
Initial extractable NO_3^--N (mg kg^{-1})	3 (0.6) d	0.0 (0.0) e	35 (1) b	94 (1) a	8 (0.6) c
C mineralization (g kg^{-1})	49 (2) a	3.4 (0.1) d	8.3 (0.8) b	44 (1) a	4.3 (0.2) c
Net NH_4^+-N production (mg kg^{-1})	1220 (240)[x] a	16 (8) b	13 (6) b	1420 (120) a	3(1) b
Net NO_3^--N production (mg kg^{-1})	380 (54) b	150 (19) c	680 (47) a	550 (27) a	320 (13) b
Extractable C (mg kg^{-1}) initial	710 (40) a	146 (8) d	125 (7) e	560 (20) b	175 (6) c
Extractable C (mg kg^{-1}) final [y]	1020 (72) a	237 (6) c	249 (18) c	800 (74) b	179 (2) d
Microbial N (mg kg^{-1}) initial	953 (113) a	181 (30) c	315 (8) b	770 (15) a	150 (4) c
Microbial N (mg kg^{-1}) final[y]	245 (52) a	41 (5) c	92 (18) b	285 (14) a	41 (1) c

nd, not determined [x]After 210 days; [y]After 340 days;

after which net nitrification basically stopped (see Figure 2b). In spite of the initial similarity in NH_4^+-N production in the indigenous forest and pine LFH material, net nitrification in the forest sample was very low until day 84, after which it increased steadily until day 210.

The relationship between C mineralization rate and net mineral-N production rate at day 21 is shown in Figure 3. The mineral soil under indigenous forest had not gained mineral-N since the initial NH_4^+-N was nitrified over the 0–21 day period. There was a positive relationship ($r^2 = 0.90$ $P < 0.001$) between C mineralization rate and net mineral-N production rate for all the samples combined. There was also a positive relationship for the mineral soils alone ($r^2 = 0.77$ $P = 0.001$), but not for the LFH samples ($r^2 = 0.1$ $P = 0.5$) indicating that they were behaving differently from the mineral soils. The rates decreased during the incubation and the relationship in the mineral soils was weaker ($r^2 = 0.44$ $P < 0.001$) when all

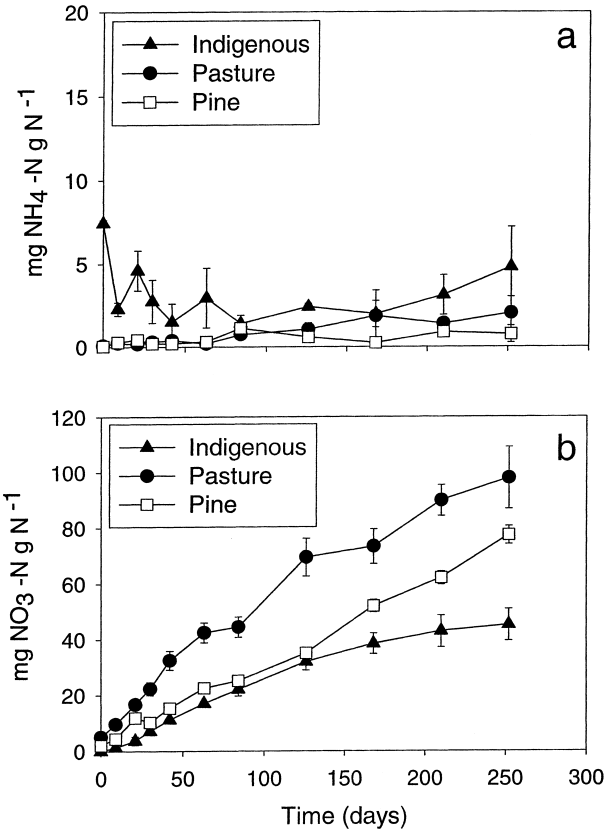

Figure 1. Cumulative mineral-N production in the mineral soil (0–10 cm) expressed per unit of initial total N for a) ammonium-N and b) nitrate-N. Error bars = 1 SE (n = 3).

sampling periods were included (Figure 4). The soil under pasture, however, had the greatest rates of C and N mineralization, showing that this mineral soil had the largest labile pools.

C and N mineralization on a C and N basis

Because we wanted to assess qualitative differences in the C and N substrates across the three systems, we also expressed our results on an initial total C and N basis. Carbon mineralization (per unit C) differed significantly ($P < 0.001$) between the mineral soil samples, and followed the order pasture > pine > forest (Figure 5b). The high mineralization under pasture is consistent with the low lignin concentration in pasture litter (5%) and roots (10%), and a high content of labile soil C (A.K. Metherell pers. comm.). Carbon mineralization in the LFH material was higher in the indigenous forest than in the pine samples (Figure 5a). This was again consis-

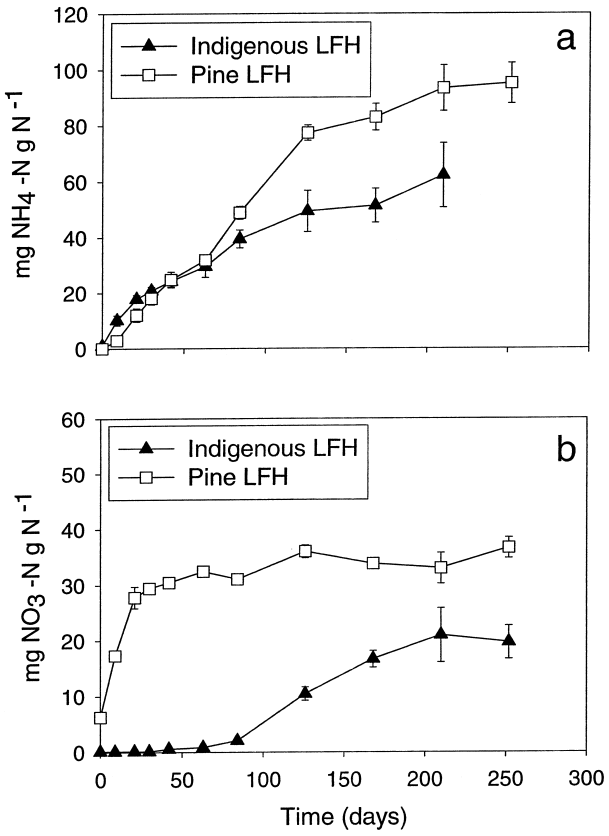

Figure 2. Cumulative net mineral-N production in LFH material expressed per unit of initial total N for a) ammonium-N and b) nitrate-N. Error bars = 1 SE (n = 3).

tent with the lower lignin concentrations (43%) in the indigenous forest LFH material, compared with that of *P. radiata* (50%).

The indigenous forest A horizon was the only topsoil to have a $\Delta^{14}C$ value (8 ‰) (Table 1) greatly below the atmospheric levels (149±5 ‰) at the time of sampling (Manning and Melhuish 2001), indicating retention of pre-bomb C in this particular topsoil. As expected, there were larger amounts of bomb C in all three soil surface horizons, where most fresh substrates are added, than in the deeper horizons. The low $\Delta^{14}C$ value in the indigenous forest A horizon suggests less 'new' C was incorporated there than in the other A horizons. There was a weak relationship ($r^2 = 0.55$, $P < 0.10$) between C mineralization on a total C basis after 210 days and $\Delta^{14}C$ values in FH material and the A horizons (Figure 6). The comparatively low values of both C mineralization and $\Delta^{14}C$ in the indigenous forest Ah horizon strongly suggest a smaller pool of labile 'new' compounds in the mineral soil due to microbial processing in the LFH layer and/or lower inputs of recent carbon in the Ah horizon. This supposition is consistent with C mineralization on a

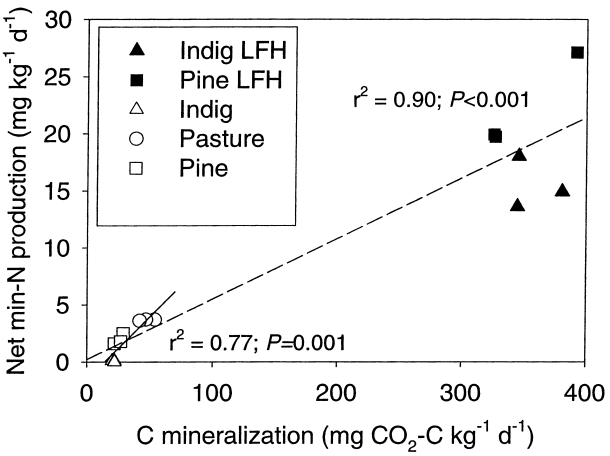

Figure 3. Relationship between net mineral-N production and C mineralization rates at day 21 for all replicates. The dashed line is the regression line for all samples; the solid line is for mineral soil samples.

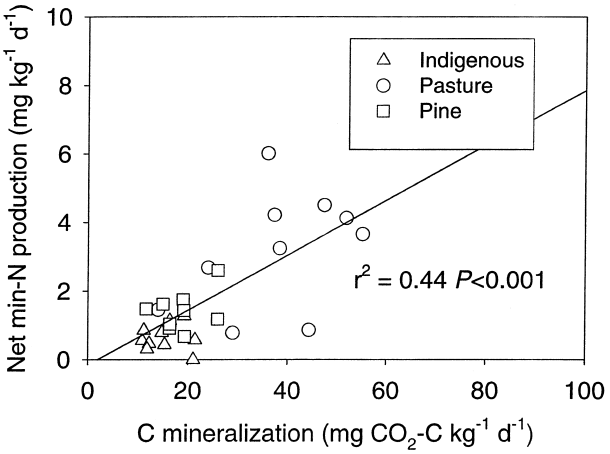

Figure 4. Relationship between net mineral-N production and C mineralization rates for mineral soils on days 0, 9, 21, 30, 42, 63, 84, 126, 168, 210 and 252. The solid line is the regression line for all samples.

total C basis being greater in the indigenous forest than pine LFH material (Figure 5).

On a total N basis, the pasture soil had the greatest net NO_3^--N production, and the indigenous forest sample the least ($P = 0.001$) (Figure 1). The order of net mineralization plus nitrification, a measure of the proportion of labile N, was: pasture > pine > forest. The N fixed by the white clover is the likely source of the labile N. Some of this labile material or other labile metabolites from the previous pasture appear to have persisted in the mineral soil under pine.

Total net NH_4^+-N production on a total N basis increased steadily for the first 100 days in both LFH samples, and was then higher in the pine than in the indig-

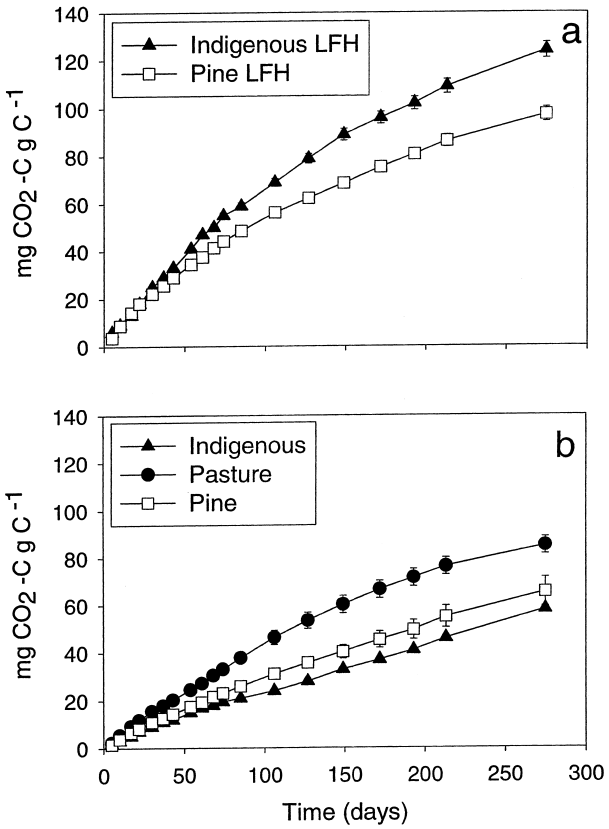

Figure 5. Cumulative CO_2-C production expressed per unit of initial total C for a) LFH material and b) 0–10 cm mineral soil. Error bars = 1 SE (n = 6).

enous forest samples; this arose primarily from lower NH_4^+-N production in the indigenous forest samples between 63 and 126 days (Figure 2a). After 210 days, when large amounts of N had accumulated (Figure 2), the rates of net NH_4^+-N production in both samples were very low.

Gross NH_4^+-N production and nitrification

Gross nitrification occurred immediately in both the LFH material and mineral soil from under pine and in the mineral soil under pasture (Table 4), indicating that nitrifiers were present and that heterotrophic competition for NH_4^+-N was relatively low. In contrast, gross nitrification was not detected until day 21 (Table 4) in either LFH or mineral soil samples from under indigenous forest, and remained low in the LFH material through day 84 (Table 4). Gross rates of NH_4^+-N and NO_3^--N production and consumption were similar ($P > 0.10$) in the pine and pasture mineral soils (Tables 4 and 5), and gross consumption rates of NH_4^+-N did not differ sig-

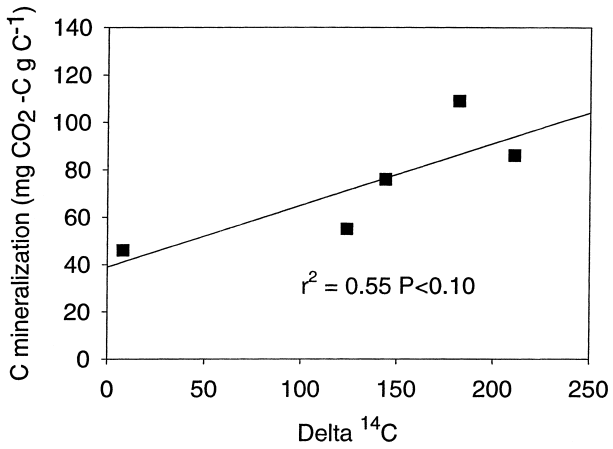

Figure 6. Relationship between cumulative C mineralization (210 d) and $\Delta^{14}C$ value. The solid line is the regression line.

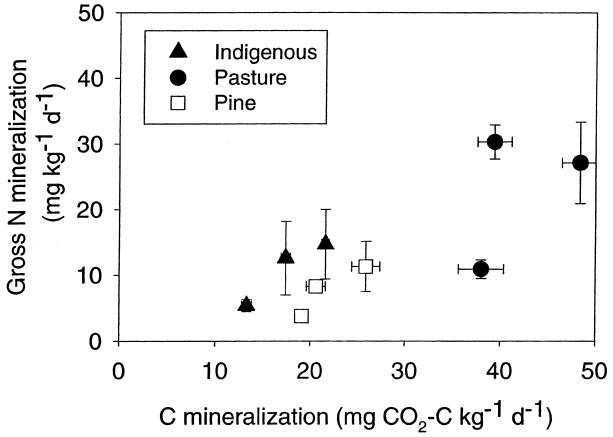

Figure 7. Relationship between gross NH_4^+-N production and C mineralization rates at days 21, 42, and 84 for mineral soil. Error bars = 1 SE.

nificantly with time in either soil. For the mineral soil samples, there was a weak relationship between gross NH_4^+-N production and C mineralization rates ($r^2 = 0.57$, $P < 0.05$) (Figure 7). The relationship was not as good as that obtained for a study of one mineral soil (Hart et al. 1994a) and of three soils under pine (Scott et al. 1998), possibly because the soil under indigenous forest appeared to produce more NH_4^+-N per unit of C mineralized than did the soil under pine.

The pasture mineral soil had low NH_4^+-N concentrations with very short mean residence times, and high NO_3^--N concentrations that turned over much more slowly (Table 6). In contrast, mean residence times of NO_3^--N in the indigenous forest mineral soil were comparatively low, indicating faster turnover of its soil NO_3^--N

Table 4. Gross NH_4^+-N production and gross nitrification. Values are means with SE given in parentheses (n = 3).

	Day 0	Day 21	Day 42	Day 84
Gross NH_4^+-N production (g N kg N^{-1} day^{-1})				
LFH				
Indigenous Forest	6.8 (0.7)	5.0 (0.6)	8.2 (1.7)	2.0 (3.3)
Pine	4.5 (0.6)	9.7 (0.9)	7.9 (2.1)	12.8 (0.6)
0–10 cm				
Indigenous Forest	6.3 (0.8)	4.4 (1.5)	3.8 (1.7)	1.6 (0.3)
Pasture	2.6 (0.3)	3.9 (1.0)	4.4 (0.4)	1.6 (0.2)
Pine	3.0 (0.7)	2.8 (1.0)	2.0 (0.2)	0.9 (0.1)
Gross nitrification (g N kg N^{-1} day^{-1})				
LFH				
Indigenous Forest	0.0 (0.0)	0.4 (0.5)	1.0 (0.8)	1.5 (2.1)
Pine	6.6 (0.2)	8.3 (2.0)	7.0 (1.2)	8.1 (0.4)
0–10 cm				
Indigenous Forest	0.0 (0.0)	3.1 (3.3)	8.2 (0.7)	8.2 (1.3)
Pasture	3.3 (0.3)	3.8 (0.9)	2.0 (1.4)	6.4 (2.4)
Pine	3.1 (0.2)	2.0 (1.0)	4.7 (0.7)	4.7 (0.9)

pool. Mean residence times of NH_4^+-N were greater in LFH material than in 0–10 cm soil in both the indigenous forest and pine samples (Table 6).

In the indigenous forest LFH material, initial NH_4^+-N consumption rates were lower than gross NH_4^+-N production rates, suggesting that microbial metabolism was not limited by NH_4^+-N availability (Tables 4 and 5). The high rates of net NO_3^--N production in the pine LFH sample also suggest high N availability in this material as well (Figure 2a).

General discussion

The pasture soil had a high N status, had the highest initial microbial C and N values, (Table 3; Figure 8b) and mineralized C and N rapidly. These data are consistent with high amounts of labile C and N materials that would have been added to the soil by grasses, legumes and grazing animals, and then processed by the biological populations. The mean residence time of NH_4^+-N increased during the incubation (Table 6) as substrate (C) availability declined, and microbial biomass decreased (Figure 8b). The rapid decrease in the microbial biomass pool in the pasture soil from day 0 suggests that, in spite of the high amount of labile soil C, the microorganisms may have been C limited for cell maintenance and replacement. Since there was a high concentration of NO_3^--N in the soil, they do not appear to have been N limited.

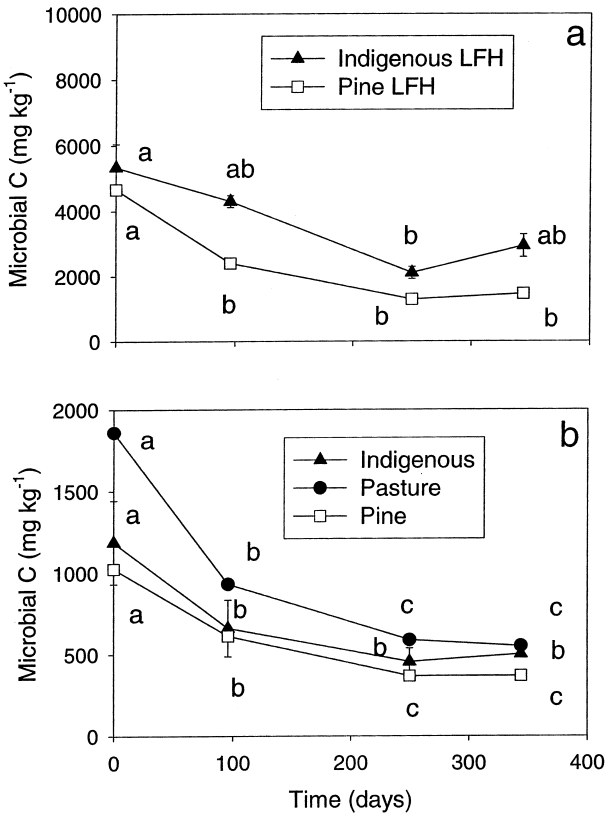

Figure 8. Changes in microbial biomass C with time for a) LFH material and b) 0–10 cm mineral soil. Error bars = 1 SE (n = 3). For each system, values on each point not marked with the same letter differ significantly ($P < 0.05$) from each other.

Carbon mineralization and net NO_3^--N production in the mineral soil under pine were significantly lower than under pasture, and probably reflect a change in substrate availability associated with the land-use change from pasture to pine. Soil organic matter under pine had a higher C/N ratio, and probably contained a greater proportion of lignin and recalcitrant materials than under pasture. The gross cycling of N was, however, similar in the pine and pasture mineral soils (Tables 4 and 5), with rapid accumulation of NO_3^--N from day 0 (Figure 1b). The pine catchment has a particularly high N status for a soil under *P. radiata* in New Zealand (Scott et al. 1998), probably because of both N deposition and of N fixation by the previous pasture.

During our incubation of the indigenous forest mineral soil, the mineralization of C and N, and the partitioning of NH_4^+-N between nitrifiers and heterotrophic microorganisms, followed broadly similar trends to those found by Hart et al. (1994a) and Chen and Stark (2000) in other ecosystems. Hart et al. (1994a) concluded that N turnover was influenced by declining C availability, whereas Chen and Stark

Table 5. Gross NH_4^+-N and gross NO_3^--N consumption. Values are means with SE given in parentheses (n = 3).

	Day 0	Day 21	Day 42	Day 84
Gross NH_4^+-N consumption (g N kg N^{-1} day^{-1})				
LFH				
Indigenous Forest	2.8 (0.2)	3.9 (0.4)	5.1 (0.1)	3.0 (0.5)
Pine	4.2 (0.4)	7.2 (0.5)	4.4 (0.1)	8.2 (0.3)
0–10 cm				
Indigenous Forest	13.9 (1.3)	4.1 (0.8)	3.2.(0.6)	3.2 (0.2)
Pasture	3.0 (0.3)	3.5 (0.8)	3.9 (0.4)	2.5 (0.5)
Pine	2.2 (0.1)	2.6 (0.4)	2.0 (0.2)	2.4 (0.1)
Gross NO_3^--N consumption (g N kg N^{-1} day^{-1})				
LFH				
Indigenous Forest	0.2 (0.0)	0.5 (0.5)	1.2 (0.7)	1.4 (1.9)
Pine	5.6 (0.1)	12.4 (0.1)	11.7 (1.3)	6.5 (0.3)
0–10 cm				
Indigenous Forest	0.0 (0.0)	1.1 (2.7)	6.4 (0.2)	5.9 (1.1)
Pasture	3.4 (0.2)	3.5 (0.4)	8.6 (1.0)	4.5 (0.5)
Pine	3.0 (0.1)	6.0 (0.2)	7.0 (0.6)	4.2 (0.5)

(2000) data led to conflicting conclusions as to whether heterotrophic organisms were C or N limited for cell maintenance and replacement. The reduction in C mineralization rates and microbial C with time in all samples (Figures 5 and 8) suggests increasing C limitation. This was not reflected in extractable C concentrations that generally increased during incubations (Table 3) and, as found in other ecosystems (Ross et al. 1996), did not provide a good indication of the availability of biodegradable C. On the other hand, NO_3^--N in the indigenous forest mineral soil was increasingly used by heterotrophs from day 0 (Table 5), suggesting they were somewhat N limited. Overall, it appears that microbial metabolism may have been limited by either C or N at different stages of the incubation.

Several workers have suggested that nitrifying bacteria are poor competitors for NH_4^+-N and are only able to get sufficient NH_4^+-N after C becomes limiting (see Chen and Stark (2000)). Our results for the indigenous forest samples, however, could suggest that gross nitrification rates increased at the same time as heterotrophs were switching to NO_3^--N as a source of N (Tables 4 and 5), and that the nitrifiers were able to compete against heterotrophs for NH_4^+-N. A better alternative explanation is the presence of adjacent microsites favoring either NH_4^+-N production or N immobilization, allowing high rates of nitrification and NO_3^--N immobilization to occur concurrently (Jackson et al. 1989; Chen and Stark 2000).

Land-use comparisons

Previous work in adjacent grassland and cropland sites suggested that qualitative differences in C inputs influenced the relationship between C mineralization and

Table 6. Mean residence time (days) of mineral-N pools during the incubation. SE in parentheses; n = 3.

	Ammonium			Nitrate		
	Day 21	Day 42	Day 84	Day 21	Day 42	Day 84
LFH						
Indigenous Forest	3.7 (0.7)	3.1 (0.4)	7.5 (1.7)	0.1 (0.0)	0.3 (0.03)	0.6 (0.01)
Pine	1.2 (0.2)	3.7 (1.0)	3.8 (0.1)	3.9 (1.2)	4.6 (0.8)	3.9 (0.2)
0–10 cm						
Indigenous Forest	1.6 (0.3)	0.3 (0.1)	1.1 (0.6)	1.0 (0.0)	1.4 (0.03)	2.9 (0.7)
Pasture	0.06 (0.01)	0.09 (0.04)	0.5 (0.1)	4.7 (0.8)	7.5 (0.0)	8.4 (1.9)
Pine	0.2 (0.02)	0.2 (0.00)	1.2 (0.2)	4.2 (1.2)	3.3 (0.2)	4.7 (0.7)

NH_4^+-N production (Schimel 1986). While differences in C inputs would have been important in our three ecosystems, there were also differences in N inputs arising from N fixation by legumes in the pasture and probably, to a lesser extent, from dry deposition of N on the trees. The soil under pine would probably also have retained N accumulated from legumes 23–40 years ago, when it was under pasture. The presence of this < 40-year-old pool of labile N in the soils under pasture and pine could explain their rapid net production of NO_3^--N. Although net nitrification did not initially occur in the indigenous forest soil, nitrate-N was leached to stream water in the indigenous forest catchment (Parfitt et al. 2003). Possibly, in the field, N is nitrified in microsites, and the NO_3^--N produced is translocated to lower soil layers, enabling leaching to take place (Hart et al. 1993; Parfitt et al. 2001). The amounts of NO_3^--N leached, estimated from the concentrations and the water yield in 1996, were 5 kg N ha^{-1} yr^{-1} for indigenous forest, 21 kg N ha^{-1} yr^{-1} for pine, and 20 kg N ha^{-1} yr^{-1} for pasture; losses of dissolved organic N were less than one tenth of these values (Parfitt et al. 2003).

Since all catchments started as indigenous forest, our results clearly show the effects of change in land use on N cycling processes in the one soil type. In the indigenous forest, the loss of 5 kg N ha^{-1} y^{-1} was about the same rate as the atmospheric additions, and the inputs and outputs appear to have been in balance. Although the soil under pasture would have gained N from fixation by white clover, pasture growth in New Zealand is usually N limited for most months of the year (Carran 1979; Haynes and Williams 1993) because of competition with soil microorganisms for mineral N (Jackson et al. 1989). Both cattle and sheep grazed the pasture from month to month, on a farm-management rotation. Urine-affected patches in soils under pasture are enriched in N, and with high rainfall (usually in winter), NO_3^--N is leached mainly from these patches (Haynes and Williams 1993). The pine trees were 22 years old and were past the stage of maximum N accumulation in their biomass (Dyck et al. 1987). We would speculate that net mineral-N production in this soil exceeded the demand by both pine trees and soil microorganisms, leading to increased NO_3^--N leaching as the pine trees became mature (Cooper et al. 1987; Parfitt et al. 2003). The leaching losses under pine are consis-

tent with our incubation data that show the influence of previous pasture on the N cycle in the pine catchment.

Conclusions

Our incubations show that rates of C and N mineralization during decomposition were higher under pasture and pine than indigenous forest. There was a clear influence of previous land use, in particular the influence of the previous (grazed) grass-legume pasture, on N cycling in the pine plantation. Future studies of the N cycle need to take account of the competition between plants and microorganisms, and the influence of grazing animals.

Acknowledgements

We acknowledge the field support provided by Peter Beets (Forest Research), and M.W. Gradwell (Soil Bureau) and A.K. Metherell (AgResearch) for data. We also thank Ray Webster and Troy Baisden (Landcare Research) and the three reviewers for helpful advice. This project was funded by the Foundation for Research, Science and Technology, New Zealand; contract C09X0016.

References

Beets P.N. and Brownlie R.K. 1987. Puruki experimental catchment: site, climate, forest management, and research. N. Z. J. For. Sci. 17: 137–160.

Brooks P.D., Stark J.M., McInteer B.B. and Preston T. 1989. A diffusion method to prepare KCl extracts for ^{15}N analysis. Soil Sci. Soc. Am. J. 53: 1707–1711.

Carran R.A. 1979. Soil nitrogen and pasture management. Proc. New Zealand Grassland Assoc. 40: 44–50.

Chen J. and Stark J.M. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush - crested wheatgrass soil. Soil Biol. Biochem. 32: 47–57.

Compton J.E. and Boone R.D. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81: 2314–2330.

Conant R.T., Paustian K. and Elliott E.T. 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecol. Appl. 11: 343–355.

Cooper A.B. 1986. Suppression of nitrate formation within an exotic conifer plantation. Plant Soil 93: 383–394.

Cooper A.B., Hewitt J.E. and Cooke J.G. 1987. Land use impacts on streamwater nitrogen and phosphorus. N. Z. J. For. Sci. 17: 179–192.

Dyck W.J., Mees C.A. and Hodgkiss P.D. 1987. Nitrogen availability and comparison to uptake in two New Zealand *Pinus radiata* forests. N. Z. J. For. Sci. 17: 338–352.

Ellis A.J. and Mahon W.A.J. 1977. Chemistry and Geothermal Systems. Academic Press, New York.

Hart S.C. and Firestone M.K. 1991. Forest floor-mineral soil interactions in the internal nitrogen cycle of an old-growth forest. Biogeochem. 12: 103–127.

Hart S.C., Firestone M.K., Paul E.A. and Smith J.L. 1993. Flow and fate of soil nitrogen in an annual grassland and a young mixed-conifer forest. Soil Biol. Biochem. 25: 431–442.

Hart S.C., Nason G.E., Myrold D.D. and Perry D.A. 1994a. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology 75: 880–891.

Hart S.C., Stark J.M., Davidson E.A. and Firestone M.K. 1994b. Nitrogen mineralization, immobilization, and nitrification. In: Weaver R.W., Angle J.S. and Bottomley P.S. (eds), Methods of Soil Analysis Part 2. Microbiological and Biochemical Properties. 3rd edn. Soil Sci. Soc. Am., Madison, pp. 985–1018.

Haynes R.J. and Williams P.H. 1993. Nutrient cycling and soil fertility in the grazed pasture system. Adv. Agron. 49: 119–199.

Jackson L.E., Schimel J.P. and Firestone M.K. 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in annual grassland. Soil Biol. Biochem. 21: 409–415.

Kaye J.P. and Hart S.C. 1997. Competition for nitrogen between plants and soil microorganisms. Trends Ecol. Evol. 12: 139–143.

Kirkham D. and Bartholomew W.V. 1954. Equations for following nutrient transformation in soil, utilizing tracer data. Soil Sci. Soc. Am. Proc. 18: 33–34.

MAF 1999. A national exotic forest description as at April 1998. Ministry of Agriculture and Forestry, Wellington, New Zealand, ISSN: 1170-5191.

McMurtrie R.E., Medlyn B.E. and Dewar R.C. 2001. Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years. Tree Physiol. 21: 831–839.

Atmospheric ^{14}C record for Wellington. Online TRENDS. A compendium of data on global change. Manning M.R. and Melhuish W.H. 2001., cdiac.esd.ornl.gov.

MfE 1997. Climate change: the New Zealand response II. New Zealand's second communication under the Framework Convention for Climate Change. Ministry for the Environment, Wellington, New Zealand, 191 pp.

O'Connor M.B., Prime P.N., and Wilkinson R.C. 1979. Nitrogen fixation in pasture IV. Central North Island pumice-land, Wairakei. N. Z. J. Exp. Ag. 7: 15–17.

Nadelhoffer K.J., Emmett B.A., Gundersen P., Kjonaas O.J., Koopmans C.J., Schleppi P. et al. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145–147.

Neill C., Piccolo M.C., Melillo J.M., Steudler P.A. and Cerri C.C. 1999. Nitrogen dynamics in Amazon forest and pasture soil measured by ^{15}N pool dilution. Soil Biol. Biochem. 31: 567–572.

Nichol S.E., Harvey M.J. and Boyd I.S. 1997. Ten years of rainfall chemistry in New Zealand. Clean Air 31: 30–37.

Parfitt R.L., Salt G.J. and Saggar S. 2001. Post-harvest residue decomposition and nitrogen dynamics in *Pinus radiata* plantations of different N status. Forest Ecol. Manag. 154: 55–67.

Parfitt R.L., Salt G.J. and Hill L.F. 2003. Clear-cutting reduces nitrate leaching in a pine plantation of high natural N status. ForestEcol. Manag 170: 43–53.

Rastetter E.B., McKane R.B., Shaver G.R. and Melillo J.M. 1992. Changes in C-storage by terrestrial ecosystems - how C-N interactions restrict responses to CO_2 and temperature. Water Air Soil Poll. 64: 327–344.

Ross D.J. and Tate K.R. 1993. Microbial carbon and nitrogen in litter and soil of a southern beech (*Nothofagus*) forest: comparison of measurement procedures. Soil Biol. Biochem. 25: 467–475.

Ross D.J., Tate K.R. and Feltham C.W. 1996. Microbial biomass, and C and N mineralization in litter and mineral soil in adjacent montane ecosystems in a southern beech *Nothofagus* forest and a tussock grassland. Soil Biol. Biochem. 28: 1613–1620.

Ross D.J., Tate K.R., Scott N.A. and Feltham C.W. 1999. Land-use change: effects on soil carbon, nitrogen and phosphorus pools and fluxes in three adjacent ecosystems. Soil Biol. Biochem. 31: 803–813.

Rowland A.P. and Roberts J.D. 1994. Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods. Comm. Soil Sci. Plant Anal. 25: 269–277.

Schimel D.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochem. 2: 345–357.

Scott N.A., Parfitt R.L., Ross D.J. and Salt G.J. 1998. Carbon and nitrogen transformations in New Zealand plantation forest soils from sites with different N status. Can. J. For. Res. 28: 967–976.

SYSTAT 1992. SYSTAT for Windows: Statistics, Version. SYSTAT Inc., Evanston, IL, USA, 750 pp.

Tate K.R., Ross D.J., O'Brien B.J. and Kelliher F.M. 1993. Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. Soil Biol. Biochem. 25: 1601–1612.

Widmer P., Brookes P.C. and Parry L.C. 1989. Microbial biomass nitrogen measurement in soils containing large amounts of inorganic nitrogen. Soil Biol. Biochem. 21: 865–867.