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N and P in New Zealand soil chronosequences and relationships with foliar N and P

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Abstract. The growth of forest species in soil development chronosequences becomes increasingly phosphorus (P)-limited with time, as P is weathered, eroded and leached from soil. Foliar nitrogen (N) concentrations also tend to decrease with soil age when vegetation may be limited in both N and P. Here we report on soil development in temperate rain forests along three New Zealand chronosequences that have minimal pollution and disturbance from human activities, at Franz Josef, Waitutu and Central Volcanic Plateau, and on factors influencing soil net N mineralization (aerobic; 56 days) and foliar N and P concentrations. Except in very young soils (< 500 years), at least 85% of total-P in mineral soil (0–10 cm) was transformed to organic-P. In each chronosequence, total-P declined with time, and foliar N:P ratios (mass) generally increased from 8 to 15–18, suggesting P was more limiting than N in the oldest soils of the chronosequence. There was a negative relationship between net N mineralization and C:N ratio for mineral soil. For the FH (organic) layer, net N mineralization had the strongest relationships with total-N concentration (positively) and C:organic-P ratio (negatively); however, relationships varied with forest group, suggesting that other factors were also important. Foliar P of kamahi (*Weinmannia racemosa* Linn. f.), a dominant canopy species, was related to soil organic-P, suggesting mineralization was an important process for tree nutrition.Foliar N was positively related to N concentration in the FH layer, but was not significantly related to any measured property in mineral soil, possibly because of the wide range of soils. The consistent declines in both soil and foliar P across the contrasting chronosequences strongly suggest that vegetation becomes progressively P-limited during long-term ecosystem development.

Introduction

Human activities (e.g., fertilizer addition, atmospheric N deposition) have altered both the N and P status of soils throughout large areas of the world, obscuring relationships between soil nutrient status and the original vegetation. In unpolluted regions, however, it is still possible to examine these relationships, and determine whether vegetation is limited by N and/or P availability in soils. Studies from soil chronosequences in such unpolluted regions (e.g., Hawaii, New Zealand) have indicated vegetation becomes progressively

P-limited when soils age, as P becomes occluded in soils, and eroded and leached from them (Walker and Syers 1976; Vitousek et al. 1995, Wardle et al. 2004). On younger soils, vegetation may be limited by N; this can also occur in rainforests on older soils where drainage is restricted and soil redox potentials are low, thus increasing denitrification, slowing decomposition and making P more soluble (Miller et al. 2001; Schuur and Matson 2001). In some humid temperate ecosystems organic-N may also be lost by leaching (Perakis and Hedin 2002; Hedin et al. 2003). An indication of this N limitation on older soils comes from foliar N concentrations, which tend to decrease with increasing soil age. Therefore, both N and P may limit forest growth on older soils (Vitousek et al. 1995; Tanner et al. 1998; Richardson et al. 2004).

To understand how and when N limitation arises in old-growth forest ecosystems, it is necessary to identify which factors control N mineralization. This is because most plant-available N in unpolluted ecosystems is derived from heterotrophic mineralization of organic-N in organic and mineral soil horizons. It is generally understood that heterotrophic N mineralization is controlled by many factors including climate, litter quality (e.g., N content, lignin:N ratio, tannin:N ratio) soil C:N ratio, pH, drainage condition, and texture (Pastor et al. 1984; Reich et al. 1997; Scott and Binkley 1997). However, it is also increasingly recognized that P can limit microbial processes and may also influence N mineralization (Pastor et al. 1984; Saggar et al. 2000; White and Reddy 2000; Cleveland et al. 2002; Matzek and Vitousek 2003; Stevenson 2004).

In this paper, we bring together data from three well-preserved chronosequences in old-growth forests in New Zealand, and also examine the organic horizons under single indigenous species in six soils of increasing age at other sites. We address the following questions: (i) how do soil N and P pools change with soil age; (ii) do rates of net N mineralization correlate most strongly with soil P or other soil properties; and (iii) are leaf N and P concentrations in kamahi (*Weinmannia racemosa* Linn. f.), a dominant canopy tree species, correlated with soil N and P, respectively, or entirely with soil P (i.e. providing evidence that vegetation becomes N limited because of P, not N). Each of these questions is addressed at the broad scale, across all chronosequences, and also within each chronosequence in relation to unique site characteristics.

Materials and methods

General description of the forests

All the sequences are in temperate rainforest dominated by evergreen angiosperms with a conifer component (largely of the Podocarpaceae) that frequently forms an emergent canopy, and is generally more abundant on older soils. Conifer species included rimu (*Dacrydium cupressinum* (Sol. ex G. Forst.)), totara (*Podocarpus totara* D. Don ex Lambert), and matai

(*Prumnopitys taxifolia* (Sol. ex D. Don) de Laub.) (Podocarpaceae), which were present as large trees in old-growth stands, but had few saplings or small trees in the understorey. The angiosperm kamahi, which is a widespread and representative dominant canopy tree in New Zealand's forests (Wardle 1991), occurred at most sites.

Site descriptions and sampling procedures

Leaf and soil samples were collected for chemical analyses. Because we used data from several existing studies, plot sizes and subsamples differ at each chronosequence. Generally soil samples were collected with a 2.5-cm-diameter Hoffer tube, and at all sites the FH (organic horizon, excluding surface litter) horizon was separated from the mineral soil sample (0–10 cm, which generally included A, AB or AE horizons and the top of B or E horizons). Several samples were collected from each site (as detailed on a site-by-site basis below), and mixed together to form a composite sample that was then subsampled for chemical analysis. Soils were stored for about a week at 4 °C in plastic bags whilst awaiting chemical analyses.

Foliar samples of young, fully open leaves of kamahi from the sunlit canopy were collected from all sites when present using a shotgun and/or orchard clippers. They were air-dried in the field, and later oven-dried at 70 °C. The site details are as follows:

Volcanic chronosequence

Permanent plots (210 by 20 m) were established in 1957–1962 (McKelvey et al. 1958) in a range of unlogged forests on the central North Island Volcanic Plateau, New Zealand, (38S; 176E) (Tables 1 and 2). The soils underlying the plots were all formed in rhyolitic tephra layers (i.e., of volcanic origin). About 8 of the 15 plots selected here were on well-drained Pumice Soils (Hewitt 1998) within 40–50 km of the epicentre of the Taupo Pumice eruption (c. 1750 BP), and the topsoils were formed in Taupo Pumice. The remaining seven plots were on Allophanic Soils formed in older rhyolitic tephras (c. 7000–14,000 BP). Soil textures ranged from sandy loam in younger soils closer to the epicentre, to silt loam in older soils further from the epicentre. Climates are uniformly humid with mean annual rainfalls of 1600–2400 mm. Mean annual temperatures ranged from 10 to 13 °C (New Zealand Meteorological Service 1985). On each of the 15 Volcanic Plateau plots, 20 subsamples of FH material and mineral soil (0–10 cm depth) were taken 10 m apart on a 200 m transect within each plot in April 2001 or April 2002.

Franz Josef chronosequence

Seven sites were selected along the Franz Josef chronosequence on the west coast of the South Island, New Zealand (43.23 S; 170.11 E) (Richardson et al. 2004). The ages of the terraces were from 130 to 120,000 years. The two

Table 1. Age of volcanic ash or terrace and some properties of the organic (FH) horizons.

Site	Age BP	*n*	Total C (g/kg)	Total N (g/kg)	C:N	Total P (g/kg)	C:organic-P	pH (water)	Net N mineralization (mg/kg)
Volcanic Plateau									
2	1750	1	451	18	25.3	736	660	4.0	647
3	1750	1	397	16	24.2	656	634	4.5	551
6	1750	1	384	17	22.6	706	607	3.9	504
7a	1750	1	390	16	25.1	647	662	3.9	500
7b	1750	1	360	15	23.4	767	450	4.6	677
23	1750	1	450	19	23.2	663	723	3.8	358
24	1750	1	388	20	19.6	833	493	4.1	596
38	1750	1	454	17	26.1	673	722	4.0	449
1	7000	1	396	20	19.5	628	671	4.0	607
41	7000	1	306	16	18.8	611	527	4.3	595
39	8000	1	499	14	35.1	390	1349	3.7	116
31	14,000	1	424	18	23.1	707	639	3.5	451
32	14,000	1	413	15	27.2	476	920	3.7	184
29	14,000	1	445	18	24.1	576	837	3.8	385
30	14,000	1	431	18	24.6	410	1109	4.0	220

Franz Josef									
5000BP	5000	5	374 (10)	14 (0.4)	27.7 (0.8)	673 (25)	616 (24)	3.7 (0.0)	213 (32)
12,000BP	12,000	5	377 (18)	11 (0.8)	34.0 (1.2)	504 (14)	751 (84)	3.9 (0.1)	120 (29)
40,000BP	40,000	2	312 (0)	8 (0.1)	41.2 (0.5)	380 (10)	909 (22)	3.9 (0.0)	70
120,000BP	120,000	1	235	6	37.3	228	1146	4.2	63
Waitutu									
Terrace EW	79,000	9	432 (17)	10 (0.2)	42.1 (1.3)	390 (87)	989 (19)	4.1 (0.0)	109 (26)
Terrace MP	79,000	20	485 (12)	12 (0.3)	40.5 (0.4)	392 (44)	1286 (11)	4.1 (0.0)	96 (15)
Terrace EC	99,000	20	490 (11)	12 (0.4)	41.2 (0.8)	372 (55)	1316 (12)	4.3 (0.1)	158 (18)
Terrace WC	121,000	17	475 (12)	13 (0.5)	37.9 (1.0)	371 (51)	1319 (10)	3.9 (0.1)	109 (18)
Terrace 6W	291,000	24	499 (11)	12 (0.5)	43.2 (1.4)	278 (52)	1749 (7)	4.0 (0.0)	38 (10)
Terrace 6C	291,000	23	420 (13)	9 (0.4)	46.4 (1.6)	242 (58)	1793 (7)	4.0 (0.0)	43 (10)
Single species									
Mt Beech	12,000	4	397 (11)	10 (0.5)	38.5 (2.5)	535 (53)	923 (87)	3.6 (0.1)	156 (32)
Red Beech	c22,000	4	493 (16)	15 (0.5)	32.0 (1.4)	866 (89)	771 (84)	3.8 (0.2)	293 (39)
Silver Beech	c22,000	4	463 (32)	15 (1.1)	31.3 (1.4)	461 (57)	1223 (92)	3.7 (0.1)	283 (45)
Yellow Silver Pine	> 150,000	4	368 (39)	8 (0.3)	46.6 (3.7)	264 (11)	1610 (109)	4.3 (0.1)	35 (3)
Rimu	> 150,000	4	486 (7)	12 (0.5)	42.3 (2.1)	355 (15)	1634 (72)	4.1 (0.3)	33 (4)
Kauri	> 200,000	4	523 (2)	11 (0.5)	45.9 (2.3)	315 (9)	1975 (50)	3.9 (0.1)	47 (4)

SE in parentheses; Volcanic site numbers were those used by McKelvey et al. (1958); The young sites at Franz Josef and Waitutu had no or thin FH horizons.

Table 2. Some properties of mineral soil 0–10 cm.

Site	*n*	Total C (g/kg)	Total N (g/kg)	C:N	Olsen-P (mg/kg)	Total P (mg/kg)	Organic P (mg/kg)	pH (water)	Net N mineralization (mg/kg)
Volcanic Plateau									
2	1	55	2.9	18.9	3	203	190	4.4	53
3	1	85	4.5	19.1	3	331	311	4.7	51
6	1	75	3.8	19.4	4	310	285	4.5	52
7a	1	80	4.9	16.2	7	653	589	5.0	109
7b	1	74	4.6	16.0	7	598	507	5.3	76
23	1	66	3.5	18.8	3	244	225	4.6	61
24	1	73	4.4	16.6	4	339	312	4.6	97
38	1	74	3.4	22.0	3	235	220	4.4	38
1	1	70	3.6	19.1	2	305	286	4.7	70
39	1	109	4.2	25.8	2	153	144	4.2	19
31	1	93	4.4	21.3	3	309	284	4.4	65
32	1	87	3.8	22.7	2	219	206	4.4	34
29	1	91	4.4	21.0	2	234	218	4.4	75
30	1	89	3.9	23.0	2	157	142	4.5	42
Franz Josef									
130BP	5	66 (7)	3.7 (0.4)	17.8 (0.3)	7 (0)	554 (55)	345 (31)	4.6 (0.1)	47 (23)
280BP	5	107 (12)	6.1 (0.8)	17.8 (0.6)	14 (2)	514 (36)	415 (43)	4.4 (0.1)	77 (18)
530BP	5	146 (29)	8.0 (1.6)	18.2 (0.2)	10 (1)	458 (29)	409 (29)	4.0 (0.1)	90 (13)

5000BP	5	94 (8)	5.0 (0.4)	18.8 (0.3)	9 (1)	327 (21)	295 (18)	3.9 (0.0)	47 (5)
12,000BP	5	123 (24)	5.1 (0.9)	24.1 (0.6)	8 (1)	293 (50)	274 (59)	3.9 (0.1)	36 (6)
40,000BP	5	86 (14)	3.4 (0.4)	25.4 (0.5)	10 (1)	201 (16)	184 (14)	3.9 (0.1)	19 (7)
12,0000BP	5	90 (14)	3.6 (0.3)	24.8 (1.8)	5 (1)	108 (11)	99 (10)	3.9 (0.0)	14 (4)
Waitutu									
Alluvium SB	24	46 (2)	2.3 (0.1)	20.6 (0.8)	nd	1142 (63)	434 (35)	5.1 (0.0)	24 (4)
Alluvium WS	2	35 (6)	1.6 (0.2)	21.0 (1.3)	11 (4)	681 (24)	227 (10)	5.3 (0.1)	52
Alluvium EW	2	38 (4)	2.3 (0.3)	16.7 (0.6)	11 (1)	675 (13)	367 (10)	5.6 (0.0)	55
Alluvium EC	2	83 (4)	3.9 (0.3)	21.6 (0.8)	4 (0)	511 (44)	431 (10)	5.3 (0.0)	21
Alluvium WW	2	79 (2)	2.9 (0.0)	27.0 (0.3)	3 (0)	261 (13)	224 (10)	4.8 (0.0)	7
Alluvium WWA	23	100 (9)	4.2 (0.4)	26.0 (1.1)	nd	572 (75)	406 (68)	4.7 (0.0)	16 (5)
Terrace EW	20	148 (6)	4.8 (0.2)	35.1 (0.4)	nd	219 (10)	199 (8)	3.9 (0.0)	17 (3)
Terrace MP	16	141 (8)	4.0 (0.3)	37.6 (1.3)	nd	154 (14)	139 (13)	4.0 (0.0)	12 (4)
Terrace EC	10	172 (7)	4.3 (0.2)	40.7 (1.4)	nd	147 (11)	142 (12)	4.0 (0.0)	11 (3)
Terrace WC	11	166 (5)	4.9 (0.2)	36.9 (1.5)	nd	203 (12)	185 (11)	4.0 (0.0)	14 (2)
Terrace 6W	7	204 (17)	5.8 (0.6)	37.2 (1.8)	nd	231 (12)	227 (11)	4.1 (0.1)	14 (4)
Terrace 6C	15	133 (9)	3.7 (0.3)	36.4 (0.9)	nd	161 (11)	147 (9)	4.0 (0.0)	13 (3)

SE in parentheses; nd = not determined.

youngest soils were Recent Soils, there was one Brown Soil (530 years), and four Podzols were formed in quartzo-feldspathic loess (topsoil ages were 5000 to 20,000 years). Soil textures ranged from sandy loam to silt loam (loess). The climate is wet temperate, with a mean annual temperature of 11 °C and a mean annual precipitation ranging from around 3600–6600 mm between the coastal plains and the glacier terminal, respectively. At each of the seven sites, five 5-m-radius plots were established in summer 2002 (Richardson et al. 2004). Five subsamples of mineral soil (0–10 cm) were collected from each plot with a 6.5-cm-diameter corer; one core was taken at the centre of a plot and four additional cores 2 m from the centre in each of four compass directions. Soil subsamples within plots were pooled for all analyses and stored at 4 °C. FH horizons were also collected, when present.

Waitutu chronosequence

The Waitutu sites were in Fiordland National Park in the south-west of South Island, New Zealand (46.12 S; 167.05 E). The area is characterized by a series of at least 13 marine terraces on soft Tertiary rock, the youngest of which is a Holocene raised beach close to sea level, and the oldest of which lies 12 km inland and is estimated to be at least 900,000 years old (Ward 1988). Terraces 2–4 correspond to the three sea-level peaks of the last interglacial, and have been dated at 79,000, 99,000 and 121,000 years, respectively. Terrace 6 is dated at 291,000 years (Ward 1988). The terrace sequence is intersected by two large rivers, bordered by narrow alluvial terraces. The youngest soils that were sampled consisted of recently deposited alluvium. Samples were also collected from terraces 2, 3, 4 and 6. The alluvial surfaces have Recent Soils, often lacking a FH layer, while the soils from terraces 2–4 are poorly drained Podzols formed in quartzo-feldspathic loess. Terrace 6 has Organic Soils as well as Podzols. All of the soils have a sandy loam to silt loam texture. Mean annual temperatures are around 10 °C, and mean annual precipitation is around 1800 mm.

We drew data from two studies on the Waitutu terrace sequence. The first set of samples came from eight large plots (100×150 m), established in 2001/2002, that were representative of the predominant vegetation growing on all the terrace types described above. Composite samples were collected at 20-m intervals on a grid within each of the plots, each consisting of three cores of mineral soil (0–10 cm) collected at the apices of a triangle with 1.75 m sides; 5–24 replicates of soil were collected. When present, FH material was also collected. Since the upper-terrace mineral soils were poorly drained, some had >250 g C/kg; these particular samples have not been included in our analyses because they are classed as organic soils. The second set of samples came from four 20 × 20 m plots on the alluvial surfaces, and formed part of a fertilizer trial. The no-fertilizer plots were sampled. A total of 15 subsamples were randomly taken from within each plot in March 2002, and combined. There were two replicates of soil from each plot.

Single species

Five soils were sampled from under single indigenous species within 20 km of Reefton (42.07 S; 171.52 E), South Island, New Zealand, and a further soil under kauri in the North Island (35.39 S; 173.33 E). The ages of the surfaces ranged from 12,000 to >200,000 years. Four composite samples of FH material only were collected at each site. The species were mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook f.) Poole), red beech (*Nothofagus.fusca* (Hook.f.) Oerst.), silver beech (*Nothofagus menziesii* (Hook.f.) Oerst.), yellow silver pine (*Lepidothamnus intermedius* (Kirk) Quinn), rimu and kauri (*Agathis australis* (D. Don) Lindl.). Each forest was a mature, closed canopy forest and sampling occurred on a stable landscape position (i.e., no significant recent erosion). Foliar data were not available for these species, and were not able to be included in the statistical analyses.

Analytical procedures

All soil samples were sieved moist through a 5-mm sieve to remove coarse organic debris and stones, and split into two subsamples. One was stored for up to 7 days at 4 °C before measurement of mineral-N (ammonium-N plus nitrate-N) and mineralizable N. The other samples were dried at 30 °C before analysis for C, N and P. Water contents were obtained by drying FH samples at 80 °C, and mineral soil at 105 °C.

We measured net N mineralization by incubating FH material and mineral soil at 60% of water-holding capacity in 125-ml polypropylene cups for 56 days at 25 °C (Scott et al. 1998). Mineral-N was determined at 0 and 56 days by extracting the samples with 2 M KCl, shaking for 1 h, then filtering. The solid to solution ratios (w:v) were 1:25 for FH material and 1:10 for mineral soil. Extractable ammonium-N and nitrate-N were measured colorimetrically with a Lachat Quickchem FIA800 analyser. Net N mineralization was calculated as the difference in mineral-N values at 0 and 56 days.

The subsamples dried at 30 °C were used for measurement of gravimetric soil water content, pH (in water; 1:2.5 w/v), total C and N (LECO FP2000 CN analyser), and total P (ignition and dissolution in 0.5 M sulphuric acid), inorganic-P (dissolution in 0.5 M sulphuric acid), organic-P (difference between total and inorganic pools) and Olsen-P (bicarbonate extractable) using a Lachat Quickchem FIA800 analyser. Results are expressed on an oven-dry (105 °C) soil basis. Foliar N and P were determined in Kjeldahl extracts. All methods are well-established soil test procedures for New Zealand soils, including acid soils (Landcare Research 2004).

Statistical analyses

Our aims were to determine which factors influenced the rate of supply of N and P to plants, using the nitrogen mineralization rate and Olsen-P concentrations as indicators of N and P supply in the soil, and foliar N and P as integrated measures of availability to the plant. Our analyses consisted of a series of regression analyses using N mineralization rate, Olsen-P and foliar N and P as response variables. We found it necessary to log transform the N mineralization rates before analysis, to ensure the residual errors from the regression analyses were approximately normally distributed, but no transformation was required for the other explanatory variables.

The data were collected in a nested design, with surfaces of different ages sampled within each of three sites. A characteristic of the dataset is that each sample was a composite of many subsamples, and so presumably represented closely the soil in a sampling area, but we had relatively few samples for statistical analyses. Therefore, our regression analyses were based on fitting regression lines to each site and comparing the variation explained by the regression lines against the residual variation

$$\log(\text{N mineralization})_j = \alpha_i + \beta_i \text{N}_{ij} + \varepsilon_{ij}$$

Here the regression of N mineralization rate on soil N was fitted as a general linear model in which a separate line was fitted for each site (intercept and slope for site i are α_i and β_i respectively) and ε_{ij} is the residual variation left unexplained by the regression lines ($\varepsilon_{ij} \sim \text{N}(0, \sigma^2)$). To test whether the inclusion of different slopes for different sites was justifiable on statistical grounds, an alternative model was fitted which had only a single slope for all sites, and the two models were compared with a *F*-test (Crawley 2002). Using a similar approach, we tested whether the inclusion of intercepts for each site was justifiable on statistical grounds, and whether other soil variables were significant determinants of N mineralization rates. If two explanatory variables are closely correlated with one another then either one could be significantly related to the mineralization rate when considered alone, but a model containing both terms would have little extra explanatory power. Therefore, we explored the extent of correlations by generating a table of correlation coefficients (without consideration of site differences), and made all our statistical tests conservatively, by testing the significance of additional terms after all other terms were included. Our procedure was based on standard model simplification methods described by Crawley (2002), and models were fitted using glm routine in Splus 6.0 (Insightful Corporation).

We used the Akaike information criterion (AIC) to rank alternative models (Hilborn and Mangel 1997; Burnham and Anderson 2002). Information is not a particularly tangible concept, but it might be thought of as the precision of estimates obtained from the model. The AIC balances the smaller residual sum of squares (i.e., better information) resulting from adding a term to the model against the extra variability introduced (i.e., information absorbed) by estimating an extra parameter. The AIC has a formal basis in information theory, but in normal distribution models like ours the change in the AIC on adding one parameter is approximately equal to

$$\text{(Proportional drop in residual sum of squares)} \times \text{(sample size)} + 2$$

That is, the information absorbed from the sample to estimate an extra parameter is equivalent to two AIC units.

The difference between this approach and a hypothesis test is that AIC focuses on whether an extra term improves the estimates, whereas an hypothesis test focuses on whether the sample provides evidence that an extra term is needed. Using $p < 0.05$ as the evidence required to add a term generally leads to smaller models than minimizing the AIC, which means small differences in AIC can be attributed to sampling variability. The few models with the smallest AIC must still be assessed for biological plausibility and consistency.

The value of AIC is that it ranks all models even if they have different sets of parameters, whereas a hypothesis test can compare two models only if one has extra parameters not in the other. We have given the AIC for a wide range of models in a single table (see Table 3), clearly showing which variables are the important ones.

Results

Soil chronosequences

The C:N ratios of the samples ranged from 18.8 to 46.6 for the FH material and from 16.0 to 40.7 for mineral soil (Tables 1 and 2), and they generally increased with increasing soil age. The pH values were mainly in the range 3.5 to 4.3 for the FH material, and 3.9 to 4.7 for mineral soil; some of the youngest soils, however, had higher pH values. The Olsen-P values ranged from 2 mg/kg in the oldest volcanic soils to 14 mg/kg in the 280-year-old soil at Franz Josef (Table 2). The total-P concentration of both FH (organic) horizons and mineral soils tended to decrease with time, while the C:organic-P ratio tended to increase (Figures 1 and 2).

Net N mineralization tended to decline with age of the FH horizons; the youngest soils, however, did not have FH horizons. Some of the youngest mineral soils had low net N mineralization values (Table 2 and Figure 2) but in soils older than about 1000 years net N mineralization generally decreased with increasing soil age. The amount of nitrate-N produced during incubation of FH material was generally < 5% of the total mineral-N present (ammonium-N plus nitrate-N), but in five of the volcanic samples it ranged from 11 to 42% (data not shown): the C:N ratios of these particular samples (1, 6, 7b, 24, 41) ranged from 23 to 19. For the mineral soils, nitrate-N ranged from 0 to 100% of the total mineral-N released (Figure 3). Generally, there was no nitrification when C:N ratios were > 23, and 100% nitrification when C:N ratios were < 17.

Table 3. Statistical comparisons of relationships between measures of plant available nutrients (net N mineralization rates and Olsen-P concentrations), foliar N and P concentrations of kamahi and nutrient concentrations (total N concentration, organic-P concentration, total-P concentration, C:N and C:organic-Pratios) in the soil FH and mineral layers.

	N mineralization		Olsen-P	Foliar-N	Foliar-P	
	FH layer	Mineral soil	Mineral soil	FH layer	FH layer	Mineral soil
Null model	58	38	34	35	19	9
Intercept for each site	23	36	19	6	10	12
+N (1 slope)	19	35	21	**0**	5	9
(site × slope)	24	33	15	6	7	14
+C:N (1 slope)	14	**0**	8	7	7	4
(site × slope)	17	4	12	13	11	9
+organic-P (1 slope)	16	25	13	8	3	2
(site × slope)	15	37	17	14	2	10
+total-P (1 slope)	17	11	**0**	8	2	6
(site × slope)	16	9	1	15	1	15
+C:organic-P (1 slope)	6	16	11	10	8	8
(site × slope)	7	10	8	13	**0**	13
+N + C:organic-P (1 slope)	**0**	13	11	0	3	0
(site × slope)	2	5	14	28	20	38
+N + organic-P (1 slope)	17	28	25	0	4	5
(site × slope)	21	20	9	24	17	36
+N + total-P (1 slope)	18	14	2	0	5	4
(site × slope)	21	20	14	24	16	42
+C:N + organic-P (1 slope)	15	4	11	11	6	5
(site × slope)	21	7	9	27	21	35
+C:N + C:organic-P (1 slope)	18	3	11	8	10	8
(site × slope)	19	12	25	26	24	37
+C:N + total-P (1 slope)	15	1	4	3	4	8
(site × slope)	21	10	11	19	41	112

A series of alternative regression models were compared using the small-sample Akaike Information Criterion ($\mathrm{AIC_c}$). The model with the lowest $\mathrm{AIC_c}$ is most strongly supported by the available data, and the differences in $\mathrm{AIC_c}$ between it and all other models are presented (i.e., the best model has $\Delta\mathrm{AIC_c} = 0$). Models with an extra parameter have had two $\mathrm{AIC_c}$ units added; following Occam's Razor the simplest model with $\mathrm{AIC_c} = 0$, and consistent with biological plausibility, is preferred. Models for which $\Delta\mathrm{AIC_c} < 2$ are almost as well supported by the data as the best model, while $\Delta\mathrm{AIC_c} > 4$ provides strong evidence that a particular model is inferior. For each response variable, we fitted a separate regression line for each site (i.e., 'Site × slope' with 3 parameters) and compared the model with one fitted with a single slope common to all sites ('1 slope' with 1 parameter).

Relationships between net N mineralization and other soil properties

The net N mineralization rate of the FH layers was, on average, almost seven times that of the corresponding mineral layer (303 vs. 43 mg/kg). Much of the variance (68%) in the mineralization rate in the FH layer was explained by site differences, whereas only 12% of the variance in the net N

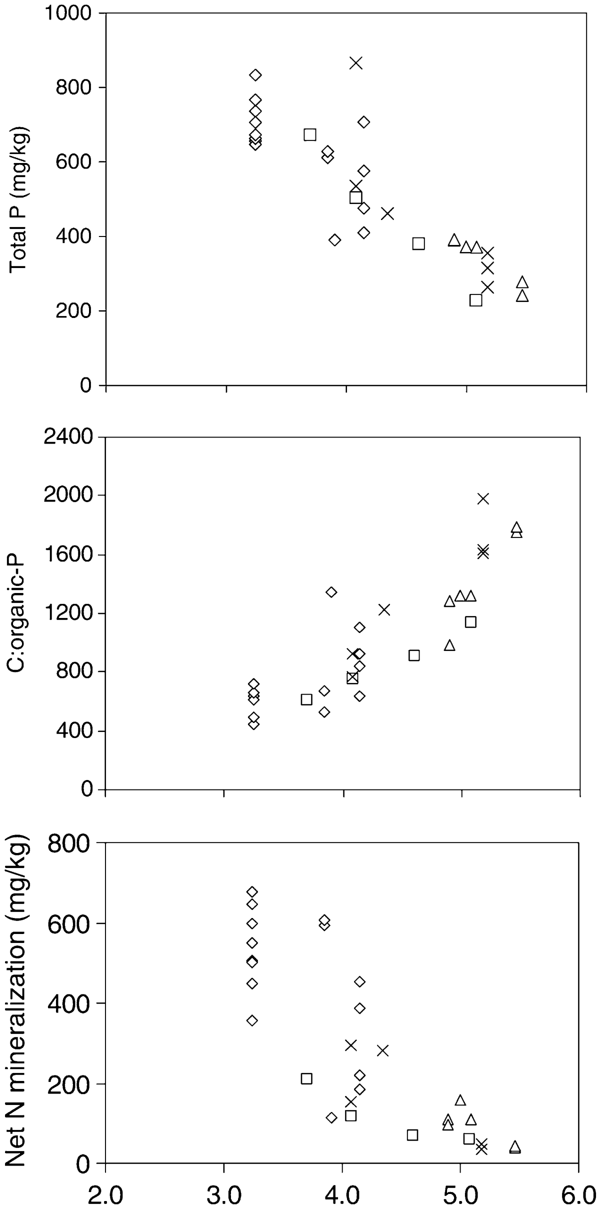

Figure 1. Relationships between total P, C:organic-P ratio, and net N mineralization of the FH (organic) horizons and site age. The young sites at Franz Josef and Waitutu had no (or thin) FH horizons.

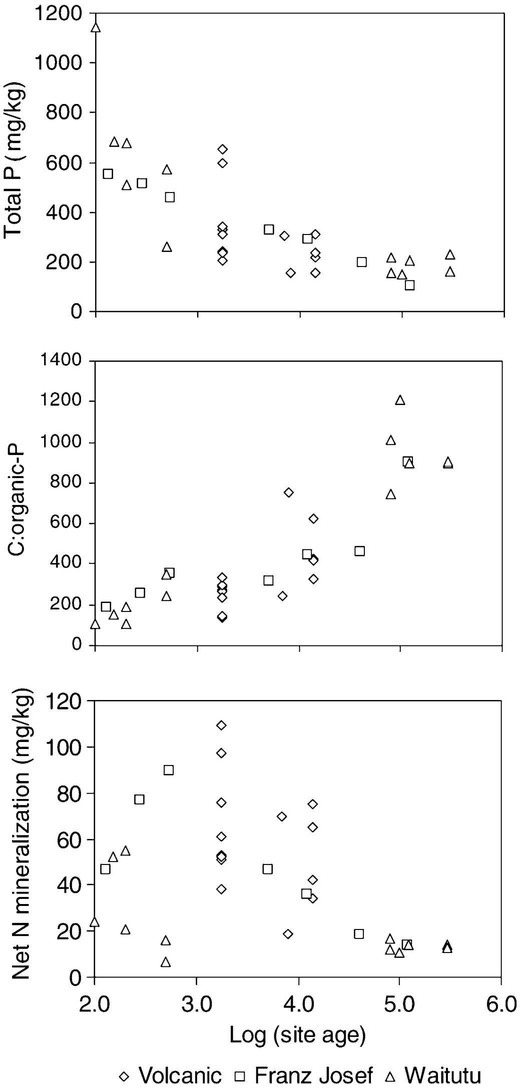

Figure 2. Relationships between total P, C:organic-P ratio, and net N mineralization of 0–10 cm mineral soils and site age.

mineralization of the mineral soil could be attributed to sites. For the FH layer, the best-fitting model included both N and C:organic-P (Table 3 and Figure 4); the slope of the regression relationships was invariant (Table 4), but the intercepts varied significantly among site. For the mineral soil, the best-fitting model included only the C:N ratio (Figure 3); the slope of the

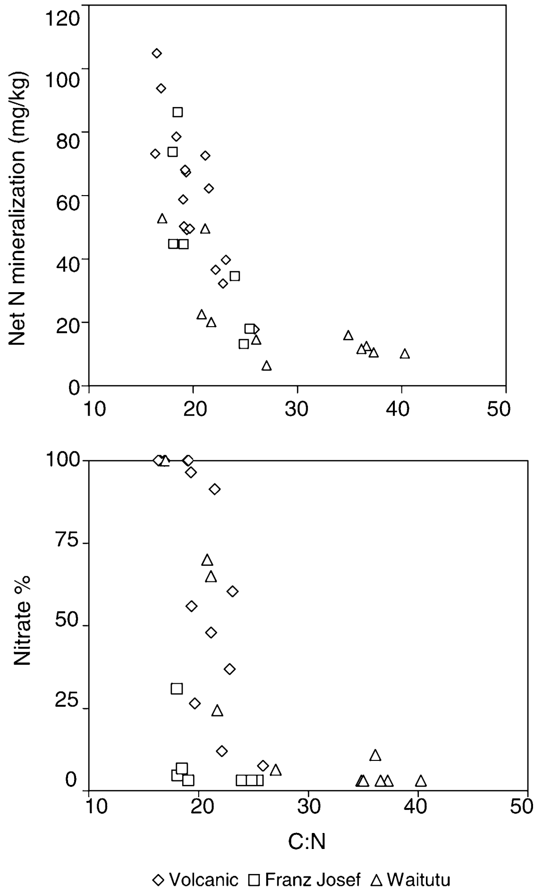

Figure 3. Relationships between net N mineralization and nitrate production (% of total mineral-N present after 56 days) and the C:N ratio of 0–10 cm mineral soils.

regression relationships was invariant, but the intercepts again varied significantly among sites (Table 4).

Relationships between Olsen-P and other soil chemical properties

Olsen-P is one measure of plant-available P in mineral soil because the Olsen (bicarbonate at pH 8.5) extraction removes readily available P from soil surfaces. In our mineral soil, 44% of the variance in Olsen-P could be attributed to site. Only a very small fraction of the total P pool was extracted by bicarbonate solution (1.7 ± 0.2%). Instead, most of the P in the soil was in an organic form (92 ± 0.5% in the FH layer, 85 ± 3% in the mineral layer). The strongest determinant of Olsen-P concentrations was total-P (Table 3).

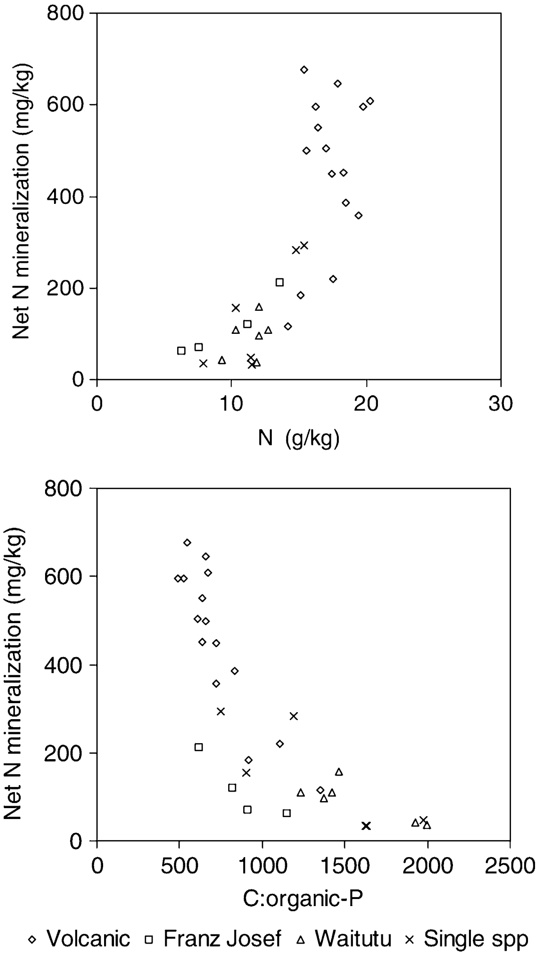

Figure 4. Relationships between net N mineralization and total N and the C:organic-P ratio of the FH (organic) horizons.

Analysis of foliar N and P concentrations in kamahi

Foliar concentrations of N (Table 5) were related to total-N in the FH layers, but for the mineral soils, there was no general relationship with any of the measured properties (Table 3). The slope of the relationship between foliar N and total-N in the FH material was invariant across the sites (Tables 3 and 4). There was no evidence to support the hypothesis that soil P had any additional effect on foliar N. Foliar concentrations of P were closely related to organic-P and total-P in the FH layers, and to organic-P, but not Olsen-P (data not shown), in the mineral soil (Tables 3 and 4); in the FH material, however, organic-P generally accounted for >90% of total-P. Foliar P concentrations

Table 4. Parameter estimates (mean ± SEM) obtained from the best-fitting regression models identified in Table 3 (in bold).

	Variable	Net N mineralization		Olsen-P	Foliar N	Foliar P	
		FH	Mineral	Mineral	FH	FH	Mineral
Intercept	Volcanic Plateau	5.6 ± 0.5	7.3 ± 0.4	0.4 ± 1.1	0.66 ± 0.11	na	0.06 ± 0.01
	Franz Josef	4.7 ± 0.4	7.1 ± 0.4	6.0 ± 1.3	0.68 ± 0.07	na	0.06 ± 0.01
	Waitutu	5.4 ± 0.6	6.8 ± 0.4	3.9 ± 1.5	0.44 ± 0.07	na	0.07 ± 0.01
Slope	N	0.69 ± 0.3	na	na	0.19 ± 0.06	na	0.061 ± 0.024
	C:N	na	−0.16 ± 0.02	na	na	na	na
	Total-P	na	na	0.011 ± 0.003	na	na	na
	C:organic-P	−11.9 ± 2.4	na	na	na	na	−0.40 ± 0.14
	Volcanic C:Po	na	na	na	na	−0.10 ± 0.09	na
	Franz Josef C:Po	na	na	na	na	−0.81 ± 0.17	na
	Waitutu C:Po	na	na	na	na	0.04 ± 0.11	na

na = not applicable.

Table 5. Foliar concentrations of N and P in kamahi.

Site	*n*	N (g/kg)	(SE)	P (g/kg)	(SE)	N:P	(SE)
Volcanic Plateau							
2	1	9.1		0.62		14.6	
3	1	8.6		0.69		12.5	
23	1	10.6		0.69		15.4	
24	1	10.8		0.73		14.9	
38	1	8.3		0.62		13.5	
1	1	10.9		0.78		13.9	
41	1	10.3		0.77		13.3	
39	1	9.4		0.60		15.6	
31	1	10.1		0.78		13.0	
32	1	10.7		0.82		13.1	
29	1	10.5		0.71		14.9	
30	1	10.5		0.60		17.6	
Franz Josef							
130BP	5	7.4	(0.8)	0.66	(0.05)	11.3	(1.4)
280BP	5	10.0	(0.4)	0.93	(0.08)	11.2	(1.3)
530BP	5	9.3	(0.4)	1.01	(0.08)	9.4	(0.9)
5000BP	5	9.8	(0.3)	0.79	(0.05)	12.7	(1.0)
12,000BP	4	8.5	(0.3)	0.61	(0.03)	14.2	(0.7)
40,000BP	5	8.6	(0.2)	0.70	(0.05)	12.5	(0.8)
120,000BP	5	7.9	(0.6)	0.45	(0.03)	17.5	(1.1)
Waitutu							
Alluvium SB	3	8.2	(0.2)	1.20	(0.26)	7.5	(1.5)
Alluvium EW	4	8.1	(0.4)	1.13	(0.16)	7.7	(1.3)
Alluvium EC	4	7.4	(0.4)	0.72	(0.05)	10.3	(0.2)
Alluvium WW	4	7.9	(0.4)	0.68	(0.03)	11.8	(0.9)
Terrace EW	3	6.4	(0.2)	0.50	(0.03)	13.1	(0.7)
Terrace MP	6	7.1	(0.4)	0.57	(0.08)	13.3	(1.3)
Terrace WC	9	6.0	(0.2)	0.48	(0.05)	13.1	(0.8)
Terrace 6	5	6.9	(0.2)	0.47	(0.05)	15.0	(1.0)

SE in parentheses.

were also closely related to both soil N concentrations and the ratio of C:organic-P in both the FH material and mineral soil (Table 3).

Discussion

Soil chronosequences

New Zealand rainforests generally have a temperate climate, and rainfall exceeds evapotranspiration in most months. Our data show that soil P concentrations generally declined with time as P is weathered, eroded and leached from the soils. Over half the P may be lost in several 1000 years. The ratio of soil C:organic-P also widened, suggesting plants may have greater difficulty competing with the soil microbial biomass for P in the older than in the younger soils (Saggar et al. 1998). The pool of labile (mineralizable) N also declined with time after about 1000 years, although the soils that are younger than 1000 years had a range of labile N values. The likely source of N in young soils is the N-fixing early-colonizing shrub *Coriaria arborea* Lindsay (Walker et al. 2003).

Net N mineralization

For the FH (organic) layer, net N mineralization was related most strongly to total-N concentration and C:organic-P ratio, with 68% of the variance explained by site. This suggests other factors also affected net N mineralization in these FH layers in the different sites. The lignin:N ratio in litter can influence net N mineralization in forest soils (Scott and Binkley 1997; Ferrari 1999), including those in New Zealand (Wardle et al. 2002), and, although not measured here, may also have been important in our FH material. Moreover, browsing mammals can indirectly affect litter decomposition, N and P release, and soil C and N storage through their selective grazing on different plant species. They could, therefore, have influenced nutrient mineralization and uptake (Harrison and Bardgett 2004) at our sites, although the direction of change may, as at other New Zealand sites (Wardle et al. 2001), have been inconsistent under the different forest species.

For all the mineral soils, there was a negative relationship between net N mineralization and soil C:N ratio, although the soil age, parent material, and forest species varied widely. This relationship often holds for a small range of forests or pastures on soils of similar age (Pastor et al. 1984; Andersson et al. 2002; Parfitt et al. 2005). However, it rarely holds for a wide range of forests on soils of different age and texture (Scott and Binkley 1997; Reich et al. 1997), possibly because clay-associated organic matter, with a narrow C:N ratio, generally has a greater rate of net N mineralization than less decomposed organic matter associated with silt or sand (Parfitt and Salt 2001).

The inverse relationships between nitrification of the mineral-N produced on incubation and the C:N ratio of both FH material and mineral soil were similar to those found in other forest ecosystems (Goodale and Aber 2001; Ross et al. 2004). Although differences in plant species at some of our sites may have had an influence on nitrate-N formation (Satti et al. 2003; Lovett et al. 2004), our results agree with those found elsewhere (Ollinger et al. 2002), with nitrate-N generally not found when soil C:N ratios were >23.

In old-growth forests with different plant species and soils, Pastor et al. (1984) found that soil net N mineralization was correlated negatively and highly significantly with the litter C:P ratio. This ratio may influence P mineralization and P availability (Sagger et al. 1998), and was high at many of our sites. As discussed earlier, P can limit microbial processes, and heterotrophic N mineralization may therefore have also been limited by low concentrations of labile P in most of our FH layers and the oldest mineral soils in the Franz Joseph, and particularly Waitutu, sequences.

Foliar N and P

The volcanic soils generally supported the highest foliar N concentrations, possibly because some of these forests receive additions of volcanic ammonium-N (5 kgN/ha/year) by wet and dry deposition (Parfitt et al. 2001, 2003). These additions may also raise the N status of the soils (Matzec and Vitousek 2003). Foliar N was similar at sites of different age on the Volcanic Plateau, but generally decreased with increasing age of the sites at Franz Josef and Waitutu.

There was a positive relationship between foliar N and soil N concentration in the FH layers; however, foliar N showed no general relationship with any of the measured properties in the mineral soil. In the oldest soils, most of the feeding roots are in the FH layer, which can be up to 20 cm deep, and we would speculate that most N uptake occurs in this layer (Silvester 1978, 2000). Some of the oldest soils at Waitutu also had poor drainage that could cause slower decomposition of soil organic matter and loss of N by denitrification (Schuur and Matson 2001). In young alluvial soils, however, there was no FH (organic) horizon, either because of recent flooding or because of mixing by insects and mammals. Therefore, in these soils the N supplied to trees would come largely from mineral soil. Overall, the lack of a significant relationship between foliar N and N in mineral soil might be explained by the wide range of soils in the data-set, including those with volcanic N additions, those with different amounts of FH material and the alluvial soils with low total N.

Foliar P values were >1.0 g/kg on three of the youngest soils, including two in the Waitutu chronosequence. These particular Waitutu soils had very high total-P (675, 1142 mg/kg) and high inorganic-P (300, 700 mg/kg) concentrations. At the Franz Josef chronosequence, two very young soils (<100 years old) had total-P concentrations of about 800 mg/kg (Richardson et al. 2004); in such soils, the P is mainly in the mineral apatite (Walker and Syers 1976). Most of the young soils at Franz Josef and Waitutu had Olsen-P values of about 10 mg/kg, which would arise from a pool of labile inorganic-P that has probably weathered from apatite. The high foliar P concentrations (>0.9 g/kg) at these particular sites are consistent with these Olsen-P values.

Foliar P values were 0.6 g/kg or less in some of the oldest soils in each group and foliar N:P ratios (mass) generally increased from about 8 to 15–18 with age. Where the ratios increase from about 10 to 14, the limitation shifts from N to P for slow growing plants (Sterner and Elser 2002; Williamson et al. 2004), and our measured values cover this range. Foliar P was related to soil organic-P, suggesting mineralization was an important process supplying P to plants (Saggar et al. 1998). Except in the very young soils, at least 85% of the total-P in the mineral soil had been transformed to organic-P. These older soils have low concentrations of labile (Olsen) P; they also have active aluminium (allophane and Al-humus complexes) that can sorb P (Miller et al. 2001), and the P supply to plants is therefore likely to arise mainly from mineralization of organic-P. In these P-limited ecosystems, plants with mycorrhizae capable of producing chelates to solubilize P or enzymes to mineralize organic P could enhance productivity.

In these New Zealand chronosequences, soil organic-P increased rapidly with time, as a result of the decomposers processing forest litter and roots, whose quantity and quality are in turn influenced by N nutrition and pH (Richardson et al. 2004). In the oldest soils at Waitutu, the ratio of fungal to bacterial biomass increased, as did the fungal-feeding to bacterial-feeding nematode densities (Williamson et al. 2004). The oldest soils, however, had considerable contents of total-N, which, except for soil under kauri (Silvester 2000), was mainly in the 0–100 cm mineral soil (Stevens 1968). Nevertheless, these old soils had both N and P limitations, resulting in litter-fall with wide C:N (120) and C:P ratios (2000) (Richardson et al. 2004). With such wide ratios, resource quality is low, populations of soil organisms are reduced (Williamson et al. 2004), and N and P are likely to be largely immobilized by decomposers (Silvester 2000). These soils were also generally wetter and more podzolized, and supported forests that were shorter, more open and less diverse than those at younger sites (Richardson et al. 2004). The restricted N nutrition in these old-growth forests, however, cannot be ascribed to a single cause, but could arise from factors such as microbial immobilization, P limitation of the microbes, and poor drainage (Schuur and Matson 2001).

Conclusions

The pool of labile N, as measured by net N mineralization, in New Zealand forest soils generally decreased with time for soils older than about 1000 years. Soil P concentrations also tended to decrease with time, and over half the total P may be lost over several 1000 years. At least 85% of the P was transformed to organic-P in all except the youngest soils. Foliar P in kamahi generally decreased as organic-P decreased, and foliar N:P ratios suggested P was more limiting than N in the oldest soils. Soil C:N ratios became wider with time as P availability decreased. Net N mineralization in the FH layer was partly related to both C:organic-P ratio and N concentration. Foliar N generally decreased over time at Franz Josef and Waitutu, but not in the Volcanic chronosequence, possibly because of atmospheric inputs of volcanic ammonium-N.

Consistent declines in both soil and foliar P across a range of contrasting soil sequences strongly suggest that, in the absence of major disturbance, vegetation becomes progressively P-limited during long-term ecosystem development (Wardle et al. 2004). These findings have several implications for managing nutrients and ecosystem productivity on highly weathered soils found on old, stable landscape positions. For example, low P availability in agroecosystems could limit the possible benefits of nitrogen additions. Similarly, sustainable forestry programmes must consider long-term availability of P, as well as N, for maintaining long-term productivity. In areas with high atmospheric N deposition and N-enriched ecosystems, the addition of P may enhance N uptake and reduce N leaching to surface and ground waters. Finally, attempts to increase C sequestration on highly weathered soils may be greatly enhanced by P additions, leading to increased ecosystem biomass, organic C inputs to the soil and soil C storage.

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