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Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence

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Abstract The aim of this study was to examine how shifts in soil nutrient availability along a soil chronosequence affected temperate rainforest vegetation. Soil nutrient availability, woody plant diversity, composition and structure, and woody species leaf and litter nutrient concentrations were quantified along the sequence through ecosystem progression and retrogression. In this super-wet, high leaching environment, the chronosequence exhibited rapid soil development and decline within 120,000 years. There were strong gradients of soil pH, N, P and C, and these had a profound effect on vegetation. N:P_{leaf} increased along the chronosequence as vegetation shifted from being N- to P- limited. However, high N:P_{leaf} ratios, which indicate P-limitation, were obtained on soils with both high and low soil P availability. This was because the high N-inputs from an N-fixing shrub caused vegetation to be P-limited in spite of high soil P availability. Woody species nutrient resorption increased with site age, as availability of N and P declined. Soil P declined 8-fold along the sequence and P resorption proficiency decreased from 0.07 to 0.01%, correspondingly. N resorption proficiency decreased from 1.54 to 0.26%, corresponding to shifts in mineralisable N. Woody plant species richness, vegetation cover and tree height increased through ecosystem progression and then declined. During retrogression, the forest became shorter, more open and less diverse, and there were compositional shifts towards stress-tolerant species. Conifers (of the

Podocarpaceae) were the only group to increase in richness along the sequence. Conifers maintained a lower N:P_{leaf} than other groups, suggesting superior acquisition of P on poor soils. In conclusion, there was evidence that P limitation and retrogressive forests developed on old soils, but N limitation on very young soils was not apparent because of inputs from an abundant N-fixing shrub.

Keywords Foliar nutrients · Nitrogen · Nutrient resorption · Primary succession · Retrogression

Introduction

Soil development has profound effects on the composition, structure and functioning of ecosystems (Jenny 1980; Wardle 2002). Availability of both N and P vary considerably during soil development as P is lost through leaching and adsorption, and N accumulates through fixation (Walker and Syers 1976; Crews et al. 1995). While much is known about nutrient availability during relatively short-term forest successions (<500 years), characterised by high availability of P and low availability of N (the progressive phase) (Walker and Moral 2003), comparatively few studies have explored how long-term P exhaustion affects community and ecosystem properties (the retrogressive phase) (e.g., Westman 1975; Walker et al. 1981; Crews et al. 1995). As a consequence, long-term P-limitation during soil development is poorly understood even though this knowledge is crucial in many regions with old, highly weathered soils e.g. Australia, Africa, and New Zealand.

Chronosequences provide a key opportunity for understanding how long-term nutrient limitation influences patterns of ecosystem development (e.g. Stevens and Walker 1970; Jenny 1980; Brubaker 1981; Pickett 1989; Wardle 2002). However, a very limited number of sequences exist that are appropriate for such work e.g. Cooloola dunes, Australia (Thompson 1981; Walker et al. 1981), the Mendocino marine terraces, California (West-

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man 1975) and the island archipelago of Hawaii (Chadwick et al. 1999). Some of the most influential work on long-term soil development was based on the Franz Josef glacial chronosequence in New Zealand, where large changes in soil P pools and decreasing availability of P occur over time (Stevens and Walker 1970; Walker and Syers 1976). A logical extension of that work is to link changes in N and P availability to vegetation processes and ecosystem properties (Wardle and Ghani 1995; Johnson et al. 2003) and contrast any patterns with those found along other sequences.

As soil nutrient availability declines, nutrient conservation within vegetation increases: this is manifest both as trait shifts within species (Eckstein et al. 1999; Aerts and Chapin 2000) and through compositional changes (Walker and del Moral 2003). At the leaf-level, such responses include longer leaf lifespans (e.g. Monk 1966), higher leaf mass per unit area (e.g. Wright et al. 2002), greater resorption of nutrients from leaves before abscission (e.g. Escudero et al. 1992) and lower nutrient concentrations in fresh leaves (Wright and Westoby 2003). Leaf N:P ratios have been used as a “tool” (sensu Koerselman and Meuleman 1996) for detecting whether vegetation is either N or P limited, with high leaf N:P ratios (>ca. 12.5) indicating P-limitation (Tessier and Raynal 2003). At the community-level, compositional shifts should favour taxa that acquire and retain nutrients most effectively (Grime 1979; Aerts and Chapin 2000). Open, short-stature forests often develop on impoverished soils (Westman 1975; Walker et al. 1981) with compositional shifts towards heath species and conifers (Wardle 1980; Bond 1989; Becker 2000). Diversity may decrease on very old soils if the pool of species that can tolerate nutrient stress diminishes. However, nutrient stress may instead alleviate competitive exclusion and thus promote diversity on older soils. Patterns of diversity through long-term ecosystem

development are therefore difficult to predict (Walker and del Moral 2003).

Here we explore how shifts in relative and absolute soil nutrient availability affect long-term vegetation development in a cool, temperate rainforest. We use nine sites distributed along the Franz Josef chronosequence that represent 120,000 years of soil development. At the leaf level, we test the utility of leaf N:P ratios as indicators of nutrient limitation by examining the correspondence between soil nutrient availability and foliar N:P ratios in both N-poor and P-poor soils. We test whether nutrient resorption from leaves is linked to soil nutrient availability, and, at the community level, we quantify how woody plant species diversity and forest composition, height and cover, shift with soil age and patterns of soil nutrient availability. Vitousek and Farrington (1995) demonstrated that there is a shift from N- to P-limitation through ecosystem development: we use our data to test whether this generalisation from Hawaii can be applied in New Zealand.

Materials and methods

Site description

Repeated glacial advance and retreat across the narrow (<30 km) coastal strip of central western South Island, New Zealand, has created a series of schist outwash surfaces dating from >120,000 years ago to the present (Almond et al. 2001). Nine sites spanning the full range of soil ages were chosen between the Franz Josef glacier and the coast using Stevens' (1968) sites and additional terrace surfaces (Almond et al. 2001) (Table 1). The first seven sites have developed since the last glacial (<12,000 years). The two oldest sites were exposed during the last glacial and would have experienced ca. 60,000 years under cool climates (Moar and Suggate 1996) and also received modest depositions of loess (ca. 40 cm) (Almond 1996; Almond and Tonkin 1999). The current

Table 1 Site characteristics and soil ages along the Franz Josef chronosequence. An expanded version of this table is available electronically in ESM Appendix I

Site number	Approximate age (years)	Elevation (m)	Precipitation (mm) ^c	Landform ^a
1	<5	240	6,520	terrace slip
2	60 ^a	240	6,576	river terrace
3	130 ^a	220	6,188	river terrace
4	280 ^a	200	6,300	river terrace
5	500 ^a	200	6,278	outwash surface
6	5,000 ^a	245	6,427	kame terrace
7	12,000 ^a	265	3,706	kame terrace
8	40–80,000 ^b	225	3,623	moraine ^b
9 ^d	120,000 ^b	145	3,652	moraine

^aInformation from Stevens (1968)

^bData from Almond et al. (2001) and P.C. Almond and R.P. Suggate (personal communication, 2002); surface dates refer to the age of the glacial deposit and do not account for more recent loess overlay

^cPrecipitation was estimated for each site using elevation and geographic location from thin-plate splines fitted to data from nearby meteorological stations (Leathwick 2001; Leathwick et al. 2003). Site estimates were adjusted using the long-term mean (1966–1980) from a local climate station

^dThe landform at site 9 was described by Stevens (1968) and the surface age re-assessed by Almond et al. (2001) and P.C. Almond and R.P. Suggate (personal communication, 2002)

climate is wet temperate: mean annual temperature (1926–1975) at the valley mouth is 10.8°C (Hessell 1982) while precipitation is ca. 6.5 m for first six sites of the sequence, that are within the glacier valley, and ca. 3.5 m for the last three sites that lie between the valley mouth and the coast (Table 1). Forests in this region are formed by associations of broadleaved evergreen angiosperm and long-lived coniferous tree species (Wardle 1977, 1980, 1991).

Data collection

At each of the nine sites (Table 1), five 5 m radius plots were established in January 2002 for soil sampling and vegetation description. Five soil subsamples were collected from each plot with a 65 mm internal diameter corer; one core was taken at the centre of a plot and four additional cores 2 m from the centre in the four cardinal directions. Soil subsamples were pooled within plots for all analyses. FH horizons (organic horizon excluding surface litter) were also collected, but were only present at five sites and rarely exceeded 40 mm in depth. The upper 10 cm of mineral soil was collected in all plots and these are the data largely reported here. Prior to analyses, soil samples were stored in plastic bags, kept cool, and moist sieved (4 mm) to remove coarse organic debris and stones. Each sample was split into two subsamples. One subsample was adjusted to 60% water-holding capacity and used to measure mineral N pools, and net N and P mineralisation. From this, 10 g was weighed for 2 M KCl-extraction at day 0, and a further 10 g weighed into a 125-ml polypropylene container for incubation. Containers were fitted with polyethylene (30 µm) covers and put into plastic trays containing water. The trays and containers were put in polyethylene bags to maintain high humidity, and placed in an incubator at 25°C for 56 days before extraction in 100 ml 2 M KCl. This system allows for gas exchange. Day 0 mineral N and P was subtracted from day 56 values to give aerobic potentially mineralisable N and P. Anaerobic potentially mineralisable N was measured from 10 g moist soil in 10 ml water incubated for 7 days at 40°C. Nitrate-N, ammonium-N and phosphate-P were measured colorimetrically (QuikChem 8000; LaChat Instruments, Wisc., USA). The second soil subsample was dried at 30°C and used for measurement of gravimetric soil water content, pH (in water), total C and N (FP2000 CN analyser; LECO, Mich., USA), 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's P (all according to Blakemore et al. 1987). Results are expressed on an oven-dry (105°C) soil basis. Examination of the soil data revealed that one mineral sample (i.e. one plot within one site) was largely FH material (>40% C). This sample was excluded from analyses so $n=4$ at site 7.

Forest description data were collected in January 2002 using the relevé plot method of Allen (1992). The maximum height of all ground-rooted (i.e. not epiphytic), living woody and tree fern species with foliage overhanging plots was estimated. Non-woody species, which generally account for only a small proportion of cover in these forests, were not recorded. Visual assessment of cover for each species was recorded as one of six categories (1=<1%, 2=1–5%, 3=6–25%, 4=26–50%, 5=51–75%, 6=>76%) and the midpoint for each category used to calculate percentage cover. All woody species were recorded and assigned to one of four physiognomic groups: evergreen angiosperm, deciduous angiosperm, conifer, or tree fern.

Leaf and litter N and P concentrations were measured for 30 species. Only a subset of these species was found at any one site, but collectively they accounted for ≥80% total woody species cover at each site. Fresh leaf samples were obtained from five randomly selected individuals of each species at each site. Fully expanded sunlit leaves were collected where possible. Canopy branches were sampled using orchard cutters or a shotgun. Freshly fallen leaf litter was also collected from the same individuals. Leaf and litter samples were dried (60°C, 48 h), weighed and ground prior to analysis of N and P concentrations using the acid digest and colorimetric methods of Blakemore et al. (1987). Litter nutrient data were used to

calculate resorption proficiency and efficiency (sensu Killingbeck 1996). Resorption proficiency is the concentration of nutrients in freshly fallen litter. Resorption efficiency is the proportion of fresh leaf nutrients resorbed prior to leaf fall; these data were calculated for each individual sampled. Efficiency and proficiency provide complementary insights into the process of resorption (Killingbeck 1996; Craine and Mack 1998; Van Heerwaarden et al. 2003) and so both have been presented here.

Data analysis

The optimum organisation of vegetation descriptions as a consequence of soil chemistry variables was based on DCCA (detrended canonical correspondence analysis). Fourteen soil variables and site age were entered as constraining variables. To determine which of these variables were most important in constraining compositional variation, canonical correspondence analysis (CCA), with forward selection, was used to extract the dominant five variables. As constraining variables are entered individually in this process, the arching effect that can occur when their number is large cannot arise (Palmer 1993). Soil variables were log transformed to normalise distributions, and default settings used except for down-weighting of rare species. The significance of the first axis in the DCCA and of each of the constraining variables in CCA was confirmed by unrestricted Monte Carlo tests with 199 permutations (Ter Braak and Šmilauer 1998).

Ordination was also used to optimally reduce the dimensionality in soil chemistry along the age sequence so that shifts could be correlated with shifts in leaf-level chemistry without using each soil variable individually. First axis sample scores from a DCA (detrended correspondence analysis) of the 14 soil variables were averaged for each site and used to represent the soil chemistry at that site/soil age.

Mean leaf and litter nutrient concentrations, and resorption efficiency, per site were calculated using cover-weighted values, to accommodate variation among sites in species composition. To reduce the possibility that patterns in leaf and litter chemistry, and resorption efficiency were artefacts of compositional shifts through the sequence, we tested whether the effect of site was independent of taxonomic family, using ANCOVA. As all the represented families were not present on all sites, a subset of data from nine families that spanned sites 3–8 were used for this analysis. Site means ($n=9$) were employed for all correlations to avoid pseudo-replication and data were transformed where necessary. Vegetation cover data were arcsin square-root transformed in all analyses. All ordinations were conducted in CANOCO for Windows 4.0 (Ter Braak and Šmilauer 1998). All other analyses were completed in SYSTAT version 7.0 (SPSS).

Results

Soil development

Soil pH declined sharply from ca. 6.8 to <3.9 within the first 280 years of soil development (Fig. 1a) and remained at ca. 3.8 for the rest of the sequence. This drop in soil pH was strongly correlated with changes in soil nutrients (Table 2). Only about 40% of total P remained after 5,000 years (Fig. 1b) and <15% remained at the oldest site. Inorganic P also declined with time but the rate of loss was even greater; <5% remained after 5,000 years (Fig. 1c). Organic P concentrations increased during the first 280 years from 0 to ca. 400 mg kg⁻¹ and declined thereafter to ca. 100 mg kg⁻¹ at the oldest site (Fig. 1d). Soil total N concentrations were low at <0.5% dry weight (d.w.) for

much of the sequence and rarely exceeded 0.75% d.w. (Fig. 1e). C and N concentrations were highly correlated (Table 2). Both increased through the first 500 years and remained relatively stable thereafter (Fig. 1e, f). Plant-available forms of N and P were assessed using aerobic mineralisable N, and the ratio of organic P to total C (Saggar et al 1998), respectively. Aerobic mineralisable N increased from <1 mg kg to a peak of ca. 115 mg kg during the first 60 years of soil development (Fig. 1g). Mineralisation remained moderately high (50–90 mg kg) through until 500 years and then declined to ca. 15 mg kg

at the oldest site (120,000 years) (Fig. 1g). Organic P: total C was highly variable at the youngest site (<5 years) but between the 60 and 120,000 year old sites, there was a gradual decline from ca. 5 to ca. 1 mg kg (Fig. 1h).

This complex gradient of soil nutrients was summarised using ordination. A DCA of the 14 soils variables was dominated by a single axis (Axis 1 eigenvalue 0.057, Axis 2 eigenvalue 0.002) that was most highly correlated with pH (−0.96), inorganic P (−0.93), total P (−0.87) and total N: total P (+0.82) ($df=42$, $P<0.0001$).

Fig. 1 Summary of mineral soil properties along the Franz Josef soil chronosequence. Data are means of five plots at each site with the exception of site 7 where $n=4$ (see Materials and methods). (Box plot symbols: horizontal lines are the median; shaded bars give 25 and 75% percentiles. See ESM Appendices I and II for further soil characteristics)

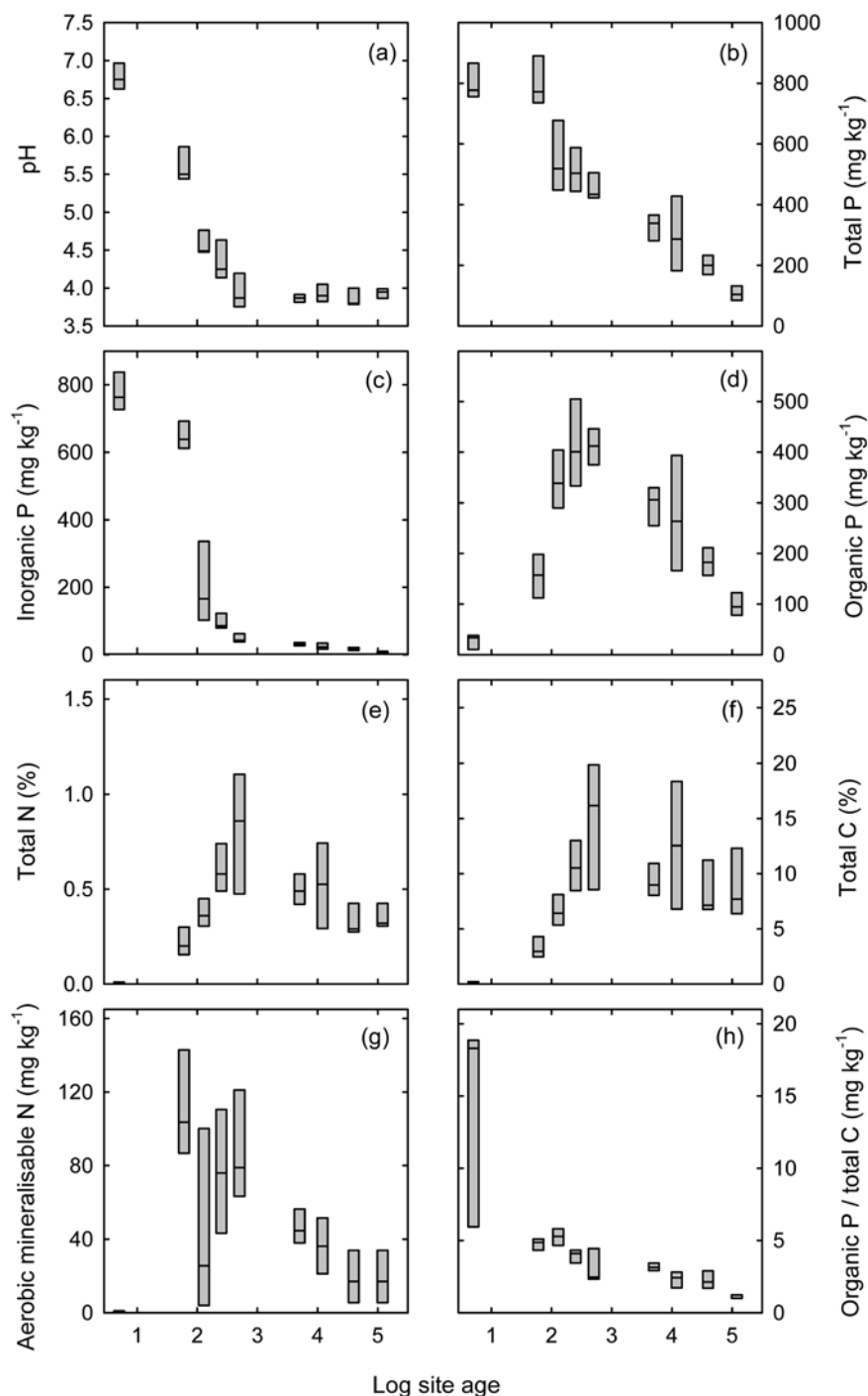


Table 2 Correlation coefficient matrix between 13 mineral soil measures^a and site age along the Franz Josef chronosequence, New Zealand. $n=9$ sites, based on means of 4/5 plots per site (see Materials and methods). Soil data were log transformed. Correlations are uncorrected because of the low statistical power ($df=7$) but those significant at $P<0.005$ are indicated in bold. Data are thus presented as an exploratory matrix to examine how soils vary in concert

	Site age	pH	Anaerobic mineralisable N	Total C	Total N	C:N	Olsen's P	Total P	Inorganic P	Organic P	N:P	Aerobic mineralisable N	C:P _{org}
pH	-0.85												
Anaerobic mineralisable N	0.66	-0.91											
Total C	0.68	-0.92	0.99										
Total N	0.59	-0.86	0.99	0.99									
C:N	-0.11	0.42	-0.72	-0.72	-0.81								
Olsen's P	0.59	-0.87	0.98	0.97	0.97	-0.76							
Total P	-0.95	0.73	-0.50	-0.52	-0.41	-0.08	-0.41						
Inorganic P	-0.96	0.91	-0.69	-0.71	-0.61	0.07	-0.61	0.93					
Organic P	0.29	-0.70	0.90	0.88	0.91	-0.83	0.92	-0.07	-0.35				
N:P	0.81	-0.95	0.97	0.98	0.95	-0.62	0.93	-0.68	-0.82	0.76			
Aerobic mineralisable N	0.27	-0.57	0.84	0.84	0.91	-0.97	0.86	-0.05	-0.24	0.90	0.74		
C:P _{org}	0.95	-0.77	0.58	0.62	0.53	-0.05	0.48	-0.95	-0.93	0.18	0.76	0.21	
Aerobic mineralisable P	0.84	-0.58	0.35	0.41	0.32	0.12	0.30	-0.80	-0.80	0.00	0.53	0.06	0.87

^a As FH samples were only available from a subset of plots, these data were not included in the analysis but are available in ESM Appendix II

Shifts in nutrient limitation

N:P_{leaf} varied between 9.2 and 16.0 (Fig. 2) and was positively correlated with site age ($r=0.76$; $P<0.02$; ratio data arcsin square root-transformed). This correlation generally corresponded to a shift from N- to P-limitation with time. However, the high N:P_{leaf} at the 60-year-old site indicated that P-limitation also occurred on young, P-rich soils (Figs. 1b, 2). An abundant N-fixing shrub, *Coriaria arborea*, increased N availability on young soils (Fig. 1g) and produced a similar mean N:P_{leaf} of 13.4 at the 60-year-old site as the mean at the 60,000-year-old site, where the cause of high N:P_{leaf} was low soil P concentrations (Fig. 1b).

The relationship between site age and N:P_{leaf} was further examined by physiognomic groups. As this comparison could only be made where all groups co-existed, this analysis was constrained to the three most abundant groups, i.e. evergreen angiosperms, conifers, and tree ferns (ESM Appendix III) and excluded the first and last sites. Mean conifer N:P_{leaf} was significantly lower than that of evergreen angiosperms and tree ferns across all sites (ANCOVA; $F_{2,89}=7.71$, $P<0.001$; Bonferroni post hoc tests $P<0.001$; ratio data arc-sin square-root transformed).

The nutrient content of both fresh leaves and litter declined with increasing soil age, most notably for foliar P between the 280- and 120,000-year-old sites (Fig. 3a,b). Leaf and litter N concentrations were highest at the 60-year-old site (Fig. 3a), accounting in part for the high N:P_{leaf} at this site (see above; Fig. 2). Shifts in leaf and litter chemistry among sites were independent of family (ANCOVA; effect of family n.s. in all cases). Fresh leaf nutrient concentrations and nutrient resorption proficiency were both negatively correlated with axis 1 of the soil variables DCA, i.e. with the changes in soil nutrients (Pearson's correlation; $r>-0.63$; $df=7$; $P<0.07$ in all instances); likewise, resorption efficiency was positively

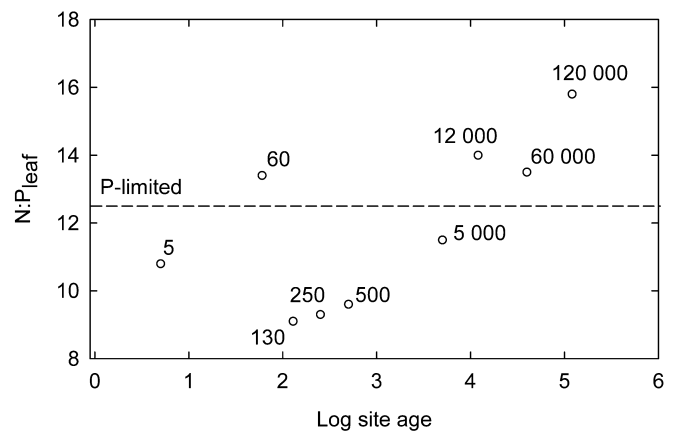


Fig. 2 Shifts in foliar N:P_{leaf} along the chronosequence. Leaf nutrient data were cover-weighted and the mean for each site is labelled with approximate site age in years. The dotted line indicates an N:P_{leaf} of 12.5, above which vegetation is thought to be P-limited (Tessier and Raynal 2003)

correlated with this axis (Pearson's correlation; $r \geq 0.69$; $df=8$; $P < 0.04$ in both instances).

N and P resorption efficiencies increased with soil development (Fig. 3c) and did not indicate that N limitation was greater on younger soils. P resorption efficiency increased from ca. 45% at the youngest site to almost 75% on the oldest site while both the absolute N efficiency and the increase with site age was more modest, from ca. 35% to ca. 55% (Fig. 3c).

Forest diversity, structure and composition

Forest diversity and structure shifted strongly with soil age, having clear progressive (5 to 5,000 year-old soils) and retrogressive (12,000 to 120,000-year-old soils)

phases (Fig. 4). Woody species richness was at a maximum on 5,000 year-old soil with a mean of 17 species per plot (Fig. 4a), declining to ca. 60% of this maximum on the oldest soil. Forest canopy height reached a maximum of 32 m at 12,000 years and declined during retrogression to ca. 10 m at the oldest site (Fig. 4b).

There were distinct changes in forest composition with soil age although 20 of the 45 species recorded were common on at least five of the nine sites (ESM Appendix III). The DCCA ordination of vegetation composition was dominated by a single axis with sites organised according to age and shifts in soil pH and nutrient pools (Table 3). Conifer cover increased with soil age from <1% of total cover (130 years) to 45% (120,000 years) and was correlated with axis 1 of the DCCA ($r=0.93$; $df=8$; $P < 0.001$). Evergreen angiosperms accounted for over 55%

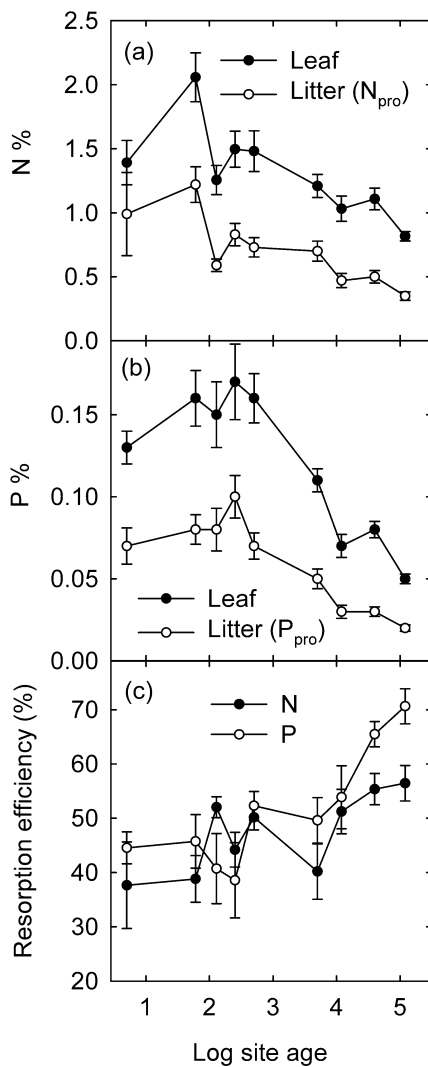


Fig. 3 Shifts in leaf chemistry along the soil chronosequence: **a** leaf and litter N concentration; **b** leaf and litter P concentration; **c** resorption efficiency (the proportion of nutrients resorbed before leaf fall). Litter nutrient concentration data in panels *a* and *b* represent resorption proficiency (N_{pro} and P_{pro}) (sensu Killingbeck 1996). Data are cover-weighted averages using all species sampled from each site (see Materials and methods). Vertical bars are 1 SE

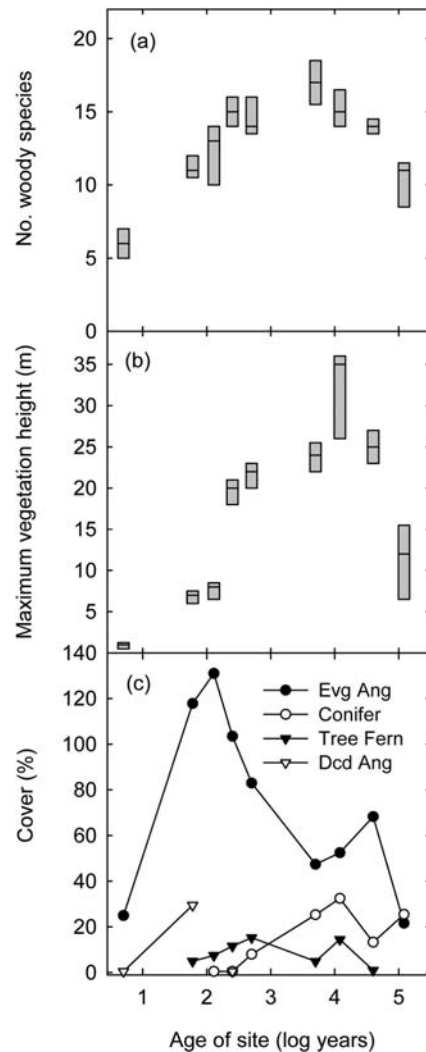


Fig. 4 Vegetation development along the Franz Josef soil chronosequence: **a** mean woody species richness per plot; **b** mean maximum vegetation height (m) per plot; **c** mean % cover per site for each of the four physiognomic groups. *Evg Ang* evergreen angiosperms, *Dcd Ang* deciduous angiosperms. Each box is derived from five replicate plots. (Box plot symbols: horizontal lines are the median; shaded bars give 25 and 75% percentiles)

Table 3 Correlation coefficients between soil chemistry variables and site age, and sample scores from the first two axes from a DCCA of woody species compositional variation. Correlations significant at $P < 0.05$ after Bonferroni correction are given in bold. Site means employed in correlation ($n=9$; $df=7$). Variables marked with* were selected by stepwise CCA (unrestricted Monte Carlo permutation tests, all significant at $P=0.001$)

	DCCA Axis 1 (Eigenvalue=0.712)	DCCA Axis 2 (Eigenvalue=0.088)
*Total P	-0.969	-0.134
Inorganic P	-0.937	-0.272
*pH	-0.933	-0.269
C:N	-0.391	-0.116
Aerobic mineralisable N	-0.176	0.273
Organic P	0.281	0.347
Olsen's P	0.555	0.563
*Total N	0.580	0.497
*Anaerobic mineralisable N	0.738	0.377
Total C	0.775	0.417
Aerobic mineralisable P	0.807	0.099
C:P _{org}	0.814	-0.062
N:P	0.932	0.106
*Site age	0.942	0.111

of forest cover on all sites, but proportional cover declined with site age (correlation with axis 1 of DCCA: $r=-0.77$; $df=8$; $P=0.015$). Although deciduous angiosperms initially accounted for 15% of total cover at the 60-year-old site, they were generally rare or absent along the rest of the chronosequence (correlation with axis 1 of DCCA: $r=-0.85$, $df=8$; $P=0.004$) (Fig. 4c). Tree ferns contributed 5–10% of total plant cover across all sites with the exception of the oldest and youngest sites, where they were absent (correlation with DCCA axis 1 n.s.). Axis 2 accounted for very little compositional variation and was not correlated with cover of a physiognomic group or with soil variables (Table 3).

Discussion

Soil development

Phosphorus limitation appears to be the major driver of vegetation dynamics along much of the Franz Josef chronosequence. Total soil P declined 8-fold from ca. 800 mg kg⁻¹ to ca. 100 mg kg⁻¹ over 120,000 years (Fig. 1). Total soil N increased through the first 500 years of ecosystem development to ca. 0.8% dry weight where it stabilised for the remainder of the sequence (Fig. 1). These results suggest that nutrient limitation shifted through time from N limitation on young soils (<500 years) to P limitation on older soils (>500 years), supporting the patterns reported from other long-term chronosequences such as Hawaii (Crews et al. 1995). The rapid development of podzolised, P-poor soils at Franz Josef clearly

indicates the extreme rates of weathering and leaching in this very wet, temperate region. In addition to precipitation, acid soils and leaf litter exacerbate rates of soil P loss (Brady and Weil 1996). A river terrace chronosequence further south in New Zealand, that receives comparable annual precipitation (ca. 6.4 m), developed P-poor podzols (3 mg/kg Olsen's P) after just 1,400 years (Smith and Lee 1984), supporting the pattern reported here. Rapid weathering and loss of soil P in just 120,000 years contrasts with the patterns reported from other chronosequences such as the Mendocino marine terrace sequence in California (Westman 1975; Northup et al. 1995), or the Cooloola dune sequence, Australia (Walker et al. 1981; Thompson 1992), where comparable soil P loss has occurred over ca. 400,000 years and >700,000 years, respectively. In addition to rates of weathering, parent material and nutrient subsidies are likely to account for differences among chronosequences in the rates of P decline.

We expected that P limitation would be more significant than N limitation as soil N concentrations were not unusually low along the sequence (Brady and Weil 1996). Soil N typically increases through early succession, as reported here (Walker and del Moral 2003), but changes in N availability through retrogression are less clear. Soil total N did not vary through retrogression along the Mendocino chronosequence (Northup et al. 1995). Likewise, at Franz Josef, soil total N concentrations stabilised around 500 years (Fig. 1e) and mineralisable N declined only slowly after 500 years. Nitrogen inputs to older soils are likely to be small and largely atmospheric in origin, as low soil P probably limits the activity of free-living, prokaryotic N-fixers (Matzek and Vitousek 2003). Furthermore, exclusion of shade-intolerant N-fixing plants must significantly reduce N inputs once tall forest develops.

Nutrient limitation

Although N:P_{leaf} increased with soil age, this ratio was a poor indicator of soil nutrient availability. High N:P_{leaf} was obtained from leaves on both young and old sites, in spite of these soils having very different N and P concentrations. On young soils, the high N:P_{leaf} was almost certainly a consequence of N-addition by a dominant N-fixing shrub which mitigated N-limitation on a young soil (Bellingham et al. 2001). On the older soils, the high N:P_{leaf} reflected low soil P concentrations. While a high N:P_{leaf} correctly suggested P limitation in both instances, the contrasting mechanisms responsible at different stages of the chronosequence impair the utility of N:P_{leaf} as an indicator of soil nutrient status (cf. Tessier and Raynal 2003). The soil nutrient concentrations (Fig. 1), the relatively high leaf N concentrations on young soils (ca. 1.5%) and strong increases in P resorption proficiency and efficiency along the chronosequence (Fig. 3), together suggest that vegetation at Franz Josef is largely P-limited. In a recent review of N:P_{leaf} values, Tessier and Raynal (2003) summarised that values greater

than 12.5 indicated P-limitation. At Franz Josef, P-limitation was associated with $N:P_{\text{leaf}}$ values as low as 10. This uncertainty is probably a consequence of few data from old, weathered soils in the literature (Tessier and Raynal 2003).

Leaf and litter nutrient concentrations

The ranges of resorption efficiency and proficiency values reported here correspond with published reviews of efficiency (Aerts and Chapin 2000) and proficiency (Craine and Mack 1998) data. However, mean leaf N (0.8% d.w.) and P (0.05% d.w.) concentrations at the oldest site were unusually low on a global basis (Aerts and Chapin 2000), but were comparable with leaf nutrient concentrations from retrogressive forest at Cooloola, Australia (Walker et al. 1981) and nutrient-poor soils in Hawaii (Vitousek et al. 1995). The significant correlations between nutrient resorption and the first DCA ordination axis of soil chemistry data clearly indicated that both resorption efficiency and proficiency were generally coupled to soil nutrient availability. Aerts and Chapin (2000) concluded that there was no relationship between soil nutrient availability and leaf-level resorption processes. This conclusion was reached, in part, by testing for differences between plant functional groups that typically occur on soils of different fertility, i.e. deciduous and evergreen species. Here, we examined the average leaf within a community along a strong gradient of nutrient availability and observed that both resorption and nutrient availability can be strongly linked, a pattern also reported by Herbert and Fownes (1999) from the Hawaiian chronosequence.

Forest progression and retrogression

Forest progression and soil total N accumulation were not coupled beyond 500 years (Figs. 1, 4). There was a delay between maximum soil total N (500 years), peak species richness (5,000 years) and maximum forest height (12,000 years). At 5,000 years, the species pool still contains plant species from earlier stages, but also supports species of nutrient-poor soils that dominate older sites (ESM Appendix III). One of these, *Dacrydium cupressinum* (Podocarpaceae) nearly always forms an emergent canopy (Wardle 1991), and the later dominance by this species accounts for the late peak in forest height (Fig. 4b).

Conifers were the only plant group to increase in species richness along the chronosequence (Fig. 4c). A comparative analysis of $N:P_{\text{leaf}}$ indicated that this group was less phosphorus-limited than evergreen angiosperms or tree ferns. Enright and Ogden (1995) considered that southern conifer nutrient-use was not distinguishable from angiosperms of the same environments, but clear evidence to the contrary is reported here. This nutrient-use specialisation by conifers supports the concept that the abundance of conifers on infertile soils is in part a

consequence of specialised adaptations (Becker 2000). The mechanisms by which conifers achieve this adaptation are unclear, but more effective mycorrhizal symbionts may be important (Baylis et al. 1963; Russell et al. 2002).

Both the patterns and the magnitude of change in plant species richness over long time scales are likely to depend on soil drainage (Peet 1992), nutrient subsidies that offset retrogression (Chadwick et al. 1999), the size of the species pool available (e.g. islands vs continental systems; Kitayama and Muller-Dombois 1995; Watson 2002) and the strength of competitive exclusion under changing soil nutrient conditions (Grime 1979). Extremely low soil P concentrations of the oldest soils at Franz Josef may preclude many plant species present on younger soils and their absence is not fully compensated for by an increase in species that can tolerate P-poor conditions. At Franz Josef, woody species richness declined through retrogression to 60% of the maximum, yet this change was modest compared with the Cooloola dune chronosequence in Australia where tree species diversity at the oldest site was just 22% of the sequence maximum (Walker et al. 1981). Declines in woody species richness along the Cooloola sequence were representative of shifts in total plant diversity: total plant species richness declined to 59% of the maximum, and an even greater loss of richness (<30% of the maximum) was reported from the Mendocino marine terrace sequence in California (Westman 1975). While it is clear that plant diversity can decline through retrogression, it is difficult to compare the magnitude of this change between systems where different measures of diversity have been made. For example, the Franz Josef forests support a rich epiphytic flora, and had this component been included in the study here, the decline in diversity would have been of a far greater magnitude.

Does retrogression occur on old soils?

The strong gradients of soil nutrient availability and pH were associated with large changes in plant community structure and composition (Fig. 4). There was a clear progressive succession through the first seven sites (ca. 12,000 years), and clear retrogression at the last two sites. Retrogression at these sites is most likely driven by declines in soil P availability, together with pH, but could be partly confounded by climatic and glacial disturbance. However, the loess deposits at these sites were small (ca. 40 cm) and have endured a very long period of weathering. The forest currently supported on these soils almost certainly represents the retrogression that would occur in the absence of catastrophic disturbance, as a consequence of P depletion. Although palaeoclimatic shifts will have influenced the pace of soil and ecosystem development, the sequence of events that we interpret here are unlikely to have been affected (Pickett 1988; Kitayama and Mueller-Dombois 1995). Other environmental changes along the sequence (e.g. valley bottom vs maritime microclimates) certainly influence aspects of the ecosystem development reported here, but the large-scale pattern

of vegetation change could not be caused by these alone. In particular, whilst precipitation was higher at the younger sites, it is counter-intuitive to ascribe changes in soil nutrients to rainfall: soil N increased among sites receiving similar precipitation (5–500 years) and soil P declined with site age in spite of older sites receiving less precipitation. Similar sequences to retrogressive forest have been reported from other chronosequences in California (Westman 1975; Jenny 1980) and Australia (Walker et al 1981), supporting our conclusion that the species-poor, short-stature, open forest on our oldest sites is a consequence of soil age.

Conclusion

In conclusion, we have demonstrated how a strong gradient of soil nutrient availability along a glacial chronosequence is associated with the progression and retrogression of a temperate rainforest. The sequence of events in this chronosequence has occurred ca. 35 times as rapidly as Hawaii (Crews et al. 1995) and approximately eight times more than Cooloola, Australia (Thompson 1992). Insignificant nutrient deposition in a pristine, maritime environment (Miller 1961; Verhoeven et al. 1987; Meurk et al. 1994); the super-wet, temperate climate; the phosphorus-poor substrate (McLaren and Cameron 1996); and a flora rich in slow-growing, long-lived species with few N-fixers (Wardle 1991), together account for the rapid ecosystem development and decline reported here. There was evidence from species composition and nutrient resorption processes of P limitation on old soils that supported forests with retrogressive properties. Attention to P limitation as a structuring force in plant communities is long overdue as a generalised concept; with the exception of excessively degraded systems, e.g. Australia (Beadle 1966), the significance of P worldwide remains undetermined.

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