RESEARCH ARTICLE

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Soil phosphorus dynamics along a short-term ecological restoration trajectory of a coastal sandplain forest in New Zealand

Hongtao Zhong^{1,2} I Carol Smith³ Brett Robinson⁴ Young-Nam Kim^{1,5} Kicholas Dickinson¹

¹Faculty of Agriculture and Life Sciences, Lincoln University, Canterbury, New Zealand

²School of Biological Sciences, The University of Western Australia, Perth, Western Australia, Australia

³Department of Soil and Physical Sciences, Lincoln University, Canterbury, New Zealand

⁴School of Physical and Chemical Sciences, University of Canterbury, Christchurch, New Zealand

⁵Department of Environmental Horticulture, University of Seoul, Seoul, South Korea

Correspondence

Hongtao Zhong, School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia. Email: hongtao.zhong@uwa.edu.au

Funding information

Closure & Legacy Management, Grant/Award Number: Punakaiki Coastal Restoration Project; Conservation Volunteers New Zealand, Grant/Award Number: 46061; Rio Tinto Services Ltd, Grant/Award Numbers: 46164, 46084

Abstract

We aim to understand the impact of ecological restoration on soil biogeochemistry, and the interrelationship between vegetation and soil phosphorus. In a study of two different-aged soils in coastal New Zealand, soils are described along a transition from abandoned agricultural pasture, through 6-year old restoration plots, towards forest fragments that have been largely undisturbed for 75 and 166 years. Soil biogeochemistry varied spatially along this restoration trajectory; there were profound changes in surface soil, but little impact on deeper soil horizons. In the early stages, soil organic matter accumulation and decomposition, and increasing demand of N from fast-growing plants corresponded with rapid nutrient mineralization. Loss of soil total P, an increase of occluded P, and the increasing importance of soil organic P as soils weathered and aged, supported conceptual models of longer-term soil pedogenesis. There was no evidence that the success of the establishment during ecological restoration markedly impacting soil P dynamics and biogeochemistry.

KEYWORDS

pedogenesis, phosphorus dynamics, restoration, soil biogeochemistry, soil chronosequence

1 | INTRODUCTION

It has often been suggested that more soil science should be included in the study of ecological restoration (Bradshaw, 1983; Perring et al., 2015) due to (Adhikari & Hartemink, 2016; Costantini et al., 2016). Nevertheless, soil development seldom receives detailed attention in restoration practice, beyond the necessity of addressing fertility and contamination constraints. Few studies have progressed towards an integrated understanding of the mutual interdependence between ecology and soil pedogenesis on degraded and damaged land undergoing restoration.

Vegetation development on degraded land is dependent on the characteristics of the soil template, with feedback to the physicochemistry of the soil provided by the biomass, life processes and activities of flora, fauna and microbes (Bradshaw & Chadwick, 1980). Numerous biotic and abiotic indicators of the transition towards ecosystem restoration have been proposed (Gann et al., 2019). Soil faunal communities (Frouz et al., 2009; Kooch, Tavakoli, & Akbarinia, 2018) and microbial indices (e.g., Hu et al., 2016; Ros, Hernandez, & Carlos, 2003) have provided useful descriptors of the restoration trajectory, with improved biomolecular methodologies enabling a contemporary focus on soil microbial assemblages and associated functional groupings (Banning et al., 2011; Harris, 2009; Strickland et al., 2017). Soil development is also facilitated through processes driven by vegetation and soil biota (Brady & Weil, 2008; Kelly, Chadwick, & Hilinski, 1998). Changes in soil biogeochemical processes along restoration gradients typically include measurements of soil organic matter, litter accumulation and decomposition, and physicochemical parameters such as soil pH, total carbon (C) and nitrogen (N), cation exchange capacity (CEC), and mobilization/immobilization of pollutants (e.g., Crouzeilles et al., 2016; Rowland, Prescott, Grayston, Quideau, & Bradfield, 2009; Wang, Kang, Cheng, Han, & Ji, 2016; Wortley, Hero, & Howes, 2013). The availability of soil phosphorus (P) plays a particularly critical role in agriculture and in the establishment of plants more generally (Menge, Hedin, & Pacala, 2012), but the dynamics of soil phosphorus has been considered as a 'slow variable' along the restoration gradient (Costantini et al., 2016) and has seldom been investigated in much detail.

Walker and Syers (1976) proposed an early conceptual model of P dynamics during long-term soil and ecosystem development under natural conditions; during soil development there is: (a) a gradual decrease and eventual depletion of primary mineral P (mainly apatite P), (b) a continual increase and eventual dominance of occluded P, and (c) an overall decrease of total P. Surface runoff, leaching, and incorporation of P into biomass play a significant role. This model has been tested across long-term chronologies in different climatic zones, vegetation types, soil parent materials and different geomorphological sites in New Zealand and elsewhere (e.g., Chen et al., 2015; Crews et al., 1995; Eger, Almond, & Condron, 2011; Turner & Laliberté, 2015; Wardle, Walker, & Bardgett, 2004). Restoration studies that have given attention to soil phosphorus have invariably focussed on its effect on plant production and plant community assemblages (e.g., Chen, Condron, Davis, & Sherlock, 2000; Li et al., 2007; Oelmann et al., 2011), but not vice versa-on the effect of vegetation establishment on soil P.

In the present study, we question whether changes of soil P dynamics provide a useful measure of restoration progression. Is it possible to demonstrate that soils in restoration plots are being transitioned towards a reference of mature forest plots through the impact of developing vegetation? Our objectives were to investigate whether and how (a) restoration of vegetation modifies soil P in the direction of the target ecosystem; (b) an established conceptual model for soil P is applicable to succession along a shorter-term restoration trajectory; and (c) knowledge of pedogenesis could be used to inform practitioners concerned with restoration of biodiversity.

2 | MATERIALS AND METHODS

2.1 | Study site

The field study site is located in the Punakaiki Coastal Restoration Project (PCRP) area at Punakaiki, South Island, New Zealand. The PCRP involves a partnership between Rio Tinto, Conservation Volunteers New Zealand (CVNZ), the Department of Conservation (DOC) and Lincoln University. The PCRP study consists of a range of ecological (e.g., vegetation surveys, invertebrate [leaf litter and soil], herbivorous insects, mammalian pests) and edaphic (e.g., soil descriptions, soil biogeochemistry) components (see more details in Hahner et al., 2013). The present study covers the soil phosphorus dynamics component of the overall PCRP study.

The PCRP study site consists of a 114 ha of coastal land, within the Punakaiki Ecological District, encompassing the most northern part of the Barrytown Flats, is a strip of coastal sand plain between the foothills of the Paparoa Range and the Tasman Sea (Figure 1). According to data collected from 1981 to 2010, the climate within



FIGURE 1 Locations of the Punakaiki Coastal Restoration Project (PCRP) site, selected Transect 1 and 3, and the GPS coordinates for each plot (modified from Zhong, 2017); where M, mature forest plot; R, restoration plot; and U,unplanted grassland plot; SH6, State Highway 6 [Colour figure can be viewed at wileyonlinelibrary.com]

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this region of the West Coast is classified as warm and wet with a mean annual rainfall of 2,200–2,600 mm, mean annual temperature of $12^{\circ}C-13^{\circ}C$, and 1,700–1,750 mean hours of sunshine (Hahner et al., 2013).

Seven restoration monitoring transects were set up before the present study, and more details were provided in Smith et al. (2016). In the present study, Transects 1 and 3 were selected to represent a coastal sand dune chronosequence on this sand plain which has developed on a well-drained sand and gravel shoreline (Figure 1). The older Transect 1 (Mahinapua soil series) presented a greater expression of overall pedogenesis in the profiles than the younger Transect 3 (Karoro soil series) (Smith et al., 2016). In addition, each transect has three different stages of ecosystem development, consisting of a mature forest plot (M), a restoration plot (R), and an unplanted grassland plot (U). Mature forest plots (M1 and M3) are located in the Nikau Scenic Reserve (Figure 1). Restoration planting of a selection of native plants in plots R1 and R3 were initiated in August-October 2009 and January-April 2010, respectively (See the development of two restoration areas from January 2009 until May 2013 in Figure S1, Data S1). The unplanted grassland plots are not natural grassland, instead they used to be coastal sandplain forest and cleared for proposed ilmenite sand mining, however turned out to be uneconomic to mine. Therefore, the land was abandoned and occupied by invasive weeds until the PCRP established. The grassland consists of a mixture of introduced grasses, including ryegrass (Lolium perenne, Poaceae) and cocksfoot (Dactylis glomerata, Poaceae), with a substantial component of invasive weeds such as blackberry (Rubus spp., Rosaceae) and European gorse (Ulex europaeus, Fabaceae) but not well developed.

For each plot, a soil pit was dug for a soil profile description (Figure 2; also see detailed soil profile descriptions in the Data S2). It was thought that: (a) soils in restoration and unplanted plots on Transects 1 and 3, respectively, were similar before commencement of the PCRP trial; and (b) the corresponding mature forest soils on each transect provided a reference or targeting soil status for the restoration of native vegetation in the long term. Our assumption was that any measured changes in soil properties in restoration plots in comparison with unplanted plots at each transect would be primarily due to vegetation establishment and earlier land-use changes.

Approximate ages of each transect (dune) were estimated by counting tree rings in the largest forest trees, following standard methods described in Wells. Duncan, and Stewart (2001). It was assumed that the oldest tree would give a minimum age for dune stabilization, after which the only site disturbance would be associated with conversion to agricultural pasture. Although there was known to be some pilotscale ilmenite mining across the site (mainly south of the Nikau Scenic Reserve), there was no evidence of this in the soil profiles of excavated pits along transects being studied. It is unlikely that the trees were planted in the mature forest plots. It is thought that the approximate time required for tree colonization in this region is between 5 and 50 years (Wells, Yetton, Duncan, & Stewart, 1999). A limited number of randomly selected largest trees of kamahi (Weinmannia racemosa, Cunoniaceae) were selected at mature forest plots in each transect to take a tree core sample. This species were dominated by rata (Metrosideros robusta, Myrtaceae), but rata wood was too hard for coring. The cores were mounted and carefully sanded, and the number of rings were counted using a microscope. Although kamahi was not recommended for tree coring species due to its low tree ring



FIGURE 2 Soil profiles of dug pits in Transect 1 (top row) and 3 (bottom row) (from C. M. S. Smith et al., 2016), where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. Tape is metric in centimeters. Full profile descriptions are provided in Data S2 [Colour figure can be viewed at wileyonlinelibrary.com] clarity (Wells & Goff, 2006), the tree rings were sufficiently visible in the present study.

Profile soil samples were collected from each described soil horizon on the profile from existing excavated soil pits (collecting at least 200 g of moist soil from each horizon). At the same sampling event, field moist surface soil samples were collected at each plot (five replicates) using a stepping auger (diameter = 3.5 cm, depth = 10 cm). Surface soil samples within each plot were collected via walking away from each dug soil pit about 5-10 m five times at random directions. And, at each direction an approximately $2 \times 2 \text{ m}^2$ subplot was set and a stepping auger was stepped into the soil at least five times to collect surface soils to form one soil replicate. Therefore, there were five surface soil replicates at each plot across the study site. Both surface and profile soils were sampled, because it was thought that surface soils would have been modified in response to the current ecological restoration relatively faster and more evident than soils in deeper horizons, and the profile soils would be more likely to show the differences between old (Transect 1) and young (Transect 3) soils. Soil samples were sieved (< 2 mm) and stored in zip-lock polyethylene bags at 4°C for less than 1 week prior to analysis, with additional sub-samples being air dried (25°C for up to 1 week). Air-dried soils were crushed using a rubber hammer, sieved (500 µm brass sieve) and stored in ziplock polyethylene bags at room temperature.

2.2 | Soil analysis

Soil microbial biomass carbon (MBC) was measured by CHCl₃ fumigation and 0.5 M K₂SO₄ extraction on moist soils as described in Vance, Brookes, and Jenkinson (1987)). A conversion factor (Kc) of 0.45 was applied to the MBC results as described in Wu, Joergensen, Pommerening, Chaussod, and Brookes (1990). Soil microbial biomass phosphorus (MBP) was measured by CHCl₃ fumigation and 0.5 M NaHCO₃ (pH adjusted to 8.5) extraction on moist soils as described in Brookes, Powlson, and Jenkinson (1982). A conversion factor (Kp) of 0.4 was applied to the MBP results following Brookes et al. (1982). Following extraction in 2 M KCl on moist soil, determination of mineral nitrogen (NH₄-N and NO₃-N) used a FIAstar 5,000 triple channel analyser with SoFIA software version 1.30 (Foss Tector AB, Sweden; Clough, Stevens, Laughlin, Sherlock, & Cameron, 2001). Soil pH and electrical conductivity (EC) were measured using pH and EC probes (Mettler Toledo, Australia). Soil total organic matter (% SOM) was measured as loss on ignition in a muffle furnace at 500°C. Soil organic carbon (% SOC) was estimated by dividing the total organic matter with a conversion factor of 1.72 (Blakemore et al., 1987).

The soil P fractionation scheme (non-sequential) followed Eger et al. (2011), which includes (a) soil total P: P (tot); (b) organic P: P (org); (c) acid-extractable P: P (acid); (d) iron (Fe) or aluminium (Al) bound P: P (Fe/Al), (e) calcium (Ca) bound P: P (Ca); and (f) occluded P: P (occ). Detailed P fractionation methods are provided in Table 1. The main reason of applying non-sequential P fractionation was to allow a fair comparison with Eger et al. (2011), a coastal sand

TABLE 1 Soil P fractionation scheme

P fractions	Extractions	References
Total P	NaOH fusion (400°C and hold for 10 mins and 800°C hold for15 mins) in a nickel crucible	Smith and Bain (1982)
Organic P	Subtracting the 0.5 M H_2SO_4 -extracted phosphorus after and before ignition (slowly heat to 505°C [1-2 hours] and hold for 1 hour)	Saunders and Williams (1955)
Acid-extractable P	0.5 M H ₂ SO ₄ -extractable phosphorus on unignited soil described above in organic P method	Walker and Syers (1976)
Fe- or Al-bound P and ca-bound P	Sequential extractions with 0.1 M NaOH for P (Fe/Al) and followed by 1 M HCl for P (ca)	Walker and Syers (1976)
Occluded P	Equals to: P (tot) - P (org) - P (Fe/Al) - P (ca)	Eger et al. (2011)

dune chronosequence under same climate zone. The P fate of P (org), P (Fe/Al), P (Ca) and P (occ) are directly related to pedogenesis (Walker & Syers, 1976), in contrast to Hedley, Stewart, and Chauhan (1982) which focuses more on the availability of soil P. Filtrates were stored in a fridge (4° C) prior to analysis. Phosphate concentrations in all extracts were determined spectrophotometrically using a UV160A spectrophotometer at 880 nm (Shimadu, Japan) after reaction with molybdate blue (Blakemore et al., 1987; Murphy & Riley, 1962). Results are expressed on dry soil basis.

Extractable Fe and Al were extracted separately for different mineral forms, using (a) 0.2 M acid oxalate (Fe_o and Al_o) to extract poorly crystalline minerals and mobile metal-organic complexes, and (b) citrate-dithionite reagent (0.3 M tri-sodium citrate and 1 M sodium bicarbonate) (Fe_d and Al_d) to extract secondary iron oxides and the fractions extracted by acid oxalate and pyrophosphate (Eger et al., 2011). Extractable Fe and Al concentrations in all extracts were determined using ICP-OES (Varian 720 ES, Australia). Filtrates were stored in a freezer prior to analysis. Results are expressed on dry soil basis.

2.3 | Statistical analysis

Data analyses used MINITAB version 17 (Minitab Inc., State College, PA), performing one-way analysis of variance (ANOVA) with the Fisher's least-significance-difference post-host test, Pearson correlation analyses for key soil parameters with P fractions, and principal component analysis (PCA). Non-parametric Mann–Whitney tests used for profile soil properties comparisons between plots.

3 | RESULTS

3.1 | Properties of surface soil

Transect age estimation from tree cores showed that the age of Transect 1 could be as recent as 166 years ago, and Transect 3 as recent as 75 years ago (Table 2). This is the likely the time of first establishment of woody plants on these parts of this pro-grading shoreline. The forest canopy has probably remained intact since this time, although some stock access to the forest was evident in a somewhat depleted understorey at the beginning of the present study.

In the surface soil (0–10 cm), pH was higher (0.2–0.5 units) in both the restoration and unplanted plots compared with mature forest plots (Table 3). Microbial C:P ratio, total C, total N, C:N ratio and N:P ratio were consistently higher in M3 compared to the other plots. This is due to extremely high fine soil organic matter in the M3 Ah-horizon (Data S2). Soil EC, ammonium-N and nitrate-N, and MBC were consistently higher in the younger transect (Table 3). Virtually all measured soil P fractions were lower in the mature forest plots (Table 4). The concentrations of P (tot) and P (org) were higher in the younger Transect 3 in parallel compared with the older Transect 1. Acid-extractable P, P (Ca) and P (Fe/Al) and were all significantly lower in mature forest plots in both transects.

Organic P (ca. 50% to 60% of Total P) and occluded P (ca, 20% to 40% of Total P) consistently accounted for the two largest soil P fraction in most plots (Figure 3). Soil P fractionations were non-sequentially extracted in the present study, resulting that the sum of different proportions of P (org), P (acid), P (Fe/AI) and P (Ca), P (occ) as fractions of P (tot) at each plot can be higher than 100%.

PCA of surface soil properties of Transects 1 and 3 showed mature forest plots (M1 and M3) were separated by high soil MBC and EC, but they were low in soil P (acid), P (Ca), P (tot) and pH

	NZ soil classification ^a	USDA soil taxonomy ^b	Number of tree rings	Estimated transect age
Transect 1	Sandy brown	Dystrudept	116	166
Transect 3	Orthic brown	Dystrudept	25	75

TABLE 2Soil types and results ofsoil ages estimation at transects 1 and 3.The estimated transect age given in thecolumn 4 is based on the assumption thatforest take 50 years to initiate

^aHewitt (2010).

^bSoil Survey Staff (2014).

TABLE 3	Selected surface so	il chemical and	d biochemica	l properties	(0-10 cm)	ł
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Plots	pH (H ₂ O)	EC (mS cm ⁻¹)	NH ₄ -N (mg kg ⁻¹)	NO ₃ -N (mg kg ⁻¹)	MBC (mg kg ⁻¹)	MBP (mg kg ⁻¹)	Microbial C: P molar ratio	TC (mg g ⁻¹)	TN (mg g ⁻¹)	C:N ratio	N:P ratio
M1	4.83 (0.21) ^c	0.12 (0.01) ^b	2.6 (1.0) ^b	0.8 (0.2) ^b	671 (186) ^b	5.8 (1.7) ^a	47 (6) ^b	35.8	2.3	15.93	5.8
R1	5.44 (0.04) ^a	0.04 (<0.01) ^c	2.0 (1.2) ^b	0.7 (0.2) ^b	294 (35) ^b	2.1 (0.5) ^b	67 (14) ^b	28.0	2.7	10.22	4.5
U1	5.46 (0.12) ^a	0.03 (<0.01) ^c	0.8 (0.3) ^b	2.0 (1.1) ^b	342 (70) ^b	1.6 (0.2) ^b	92 (25) ^b	43.1	3.5	12.41	5.8
M3	5.01 (0.13) ^{bc}	0.18 (0.01) ^a	13.7 (8.4) ^a	1.4 (0.5) ^b	1985 (354) ^a	2.5 (0.4) ^b	385 (141) ^a	282.4	16.3	17.33	12.5
R3	5.52 (0.13) ^a	0.11 (0.02) ^b	2.8 (0.7) ^b	7.7 (2.2) ^a	382 (74) ^b	5.9 (1.0) ^a	30 (10) ^c	29.5	3.0	9.78	5.0
U3	5.22 (0.06) ^{ab}	0.05 (<0.01) ^c	5.1 (0.9) ^{ab}	3.0 (0.9) ^b	364 (17) ^b	5.6 (0.6) ^a	27 (4) ^c	68.1	6.2	11.07	4.8

Note: Data in columns are means (n = 5) with SEs in parenthesis. The same letters indicate no significant difference (p < .05). Where '1' plots are the older transect and '3' plots are the younger transect; where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. TC, TN, C:N ratio and N:P ratio were modified from Smith et al. (2016), which were measured in 2012.

Abbreviations: EC, electrical conductivity; MBC, microbial biomass carbon; MBP, microbial biomass phosphorus; TC, total carbon; TN, total nitrogen.

Plots	P (tot)	P (org) (mg kg ⁻¹)	P (acid) (mg kg ⁻¹)	P (ca) (mg kg ⁻¹)	P (Fe/Al) (mg kg ⁻¹)	P (occ)
M1	400 (78) ^b	247 (71) ^b	29 (5) ^b	23 (3) ^b	5 (1) ^d	125 (14) ^a
R1	551 (16) ^{ab}	310 (21) ^{ab}	100 (11) ^a	73 (7) ^a	20 (2) ^{cd}	149 (29) ^a
U1	540 (50) ^{ab}	204 (8) ^b	103 (15) ^a	58 (3) ^a	50 (19) ^{ab}	227 (36) ^a
M3	456 (32) ^b	275 (40) ^b	40 (3) ^b	32 (4) ^b	24 (3) ^{cd}	125 (34) ^a
R3	658 (60) ^a	394 (21) ^a	117 (12) ^a	69 (9) ^a	67 (7) ^a	128 (49) ^a
U3	546 (117) ^{ab}	252 (24) ^b	87 (12) ^a	67 (10) ^a	36 (2) ^{bc}	191 (104) ^a

 TABLE 4
 Surface soil (0–10 cm)

 phosphorus fractions and Fe and Al
 minerals

Note: Data in columns are means (n = 5) with SEs in parenthesis. The same letters indicate no significant difference (p < .05). Where '1' plots are the older transect and '3' plots are the younger transect; where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot.

Abbreviations: P (tot), total phosphorus; P (org), organic phosphorus; P (acid), acid-soluble phosphorus; P (Ca), primary apatite P; P (Fe/Al), secondary mineral P; P (occ), occluded phosphorus.

(Figure 4). A second PCA component was positively correlated with soil Fe and Al minerals, but to a lesser extent negatively correlated with soil MBP and P (Fe/Al).

3.2 | Properties of soil profiles

In the older Transect 1, soil pH (4.5–5.3) tended to be similar through the profile, but increased with depth (from 5.3 to 6.2) in younger Transect 3 (Figure 5). M3 and U3 Ah horizons had significantly higher EC. Apart from an exceptionally high SOC content (ca. 25%) in M3 Ah, the rest of profile soils had between 0.2% and 5% of SOC, decreasing with soil depth. Soil MBC concentration was highest in M3 Ah, and



FIGURE 3 Proportion of organic P (\blacksquare), acid-extractable P (\blacksquare), Fe/Al-bound P (\blacksquare), Ca-bound P (\blacksquare) and occluded P (\blacksquare) of Total P in surface soils (0–10 cm) at Transect 1 (older) and 3 (younger). Where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. Data are mean values ± *SE* (*n* = 5) [Colour figure can be viewed at wileyonlinelibrary.com]

decreased with soil depth in the rest of profile soils. R1 had more than double of MBC, compared to R3. NH_4 -N concentration was exceptionally high in M3 Ah. NO₃-N was significantly high in the Ahhorizons of R3 plot.

The depth trend of P (tot) showed a general increase in the M1 profile, but P (tot) tended to decrease in the top two horizons in Transect 3 (Figure 6). Soil P (org) generally showed a decreasing trend with depth in both transects. The proportional significances of P (org) to P (tot) were clearly evident in all Ah-horizons in both transects (Figure 7). Conversely, P (acid) generally showed increasing concentrations with depth and accounted for up to 90% of P (tot) in the bottom C-horizons (Figures 6 and 7). Secondary mineral P (Fe/AI) presented its importance with a general increase trend with depth in Transect 1, while a reverse pattern was presented in the Transect 3. Primary mineral P (Ca) became a more important faction with depth in both transects. Soil P (occ) were mostly higher in Transect 1 than in Transect 3.

The area-based soil P stocks on soil profiles, Mann–Whitney test results of significant difference between Transect 1 and 3 on profile soil chemical properties, and the results of Pearson Correlation analyses were given in the Tables S1–S3, Data S1.

4 | DISCUSSION

4.1 | Soil phosphorus dynamics

Along the restoration trajectory, the proportional importance of soil organic P, MBP, Fe/Al-bound P, and Ca-bound P fractions to total P in the restored plots were moving away from the unplanted plots. After only 6 years, both surface soils and lower soil profiles moved slightly but surely towards the P status in the mature forest



Variables	рН	EC	NH ₄ -N	NO3-N	MBC	MBP	P tot	P org	P acid	P Fe/Al	P Ca	P occ	Feo	Al	Fe _d	Al _d
PC1	0.34	-0.27	-0.14	0.20	-0.25	-0.08	0.31	0.16	0.43	0.27	0.40	0.15	0.19	0.11	0.21	0.17
PC2	-0.02	-0.07	-0.06	-0.32	0.10	-0.27	-0.14	0.01	-0.15	-0.28	-0.08	-0.12	0.41	0.36	0.41	0.44

FIGURE 4 Principal component analysis of soil properties in surface soils at Transect 1 (older) and 3 (younger). Where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot [Colour figure can be viewed at wileyonlinelibrary.com]





FIGURE 5 Selected profile soil chemical properties in Mature (\bullet), Restored (\bigcirc) and Unplanted (\blacktriangledown) plots at Transect 1 and 3. Where '1' plots are the older transect and '3' plots are the younger transect; where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. EC and MBC stand for electrical conductivity and microbial biomass carbon, respectively

plots. From a soil development perspective, soil P fractions in the present study mainly agree with the conceptual model of Walker and Syers (1976), as the younger less-weathered soils in Transect 3 had overall larger soil total P pools than the older more-weathered soils in Transect 1. Similar results of soil P factions on soil chronosequences and ecosystem development had been reported in many longer-term studies (e.g., Chen et al., 2015; Crews et al., 1995; Eger et al., 2011; Izquierdo, Houlton, & van Huysen, 2013; Parfitt et al., 2005). In the present study, the concentration of P (org) and proportional importance of P (org) to P (tot) had been significantly increased by restoration of native woody and perennial plants, compared to abandoned and unrestored exotic grassland (Table 4 and Figure 3). In northwest Russia, a similar pattern of soil inorganic and organic P transformations was observed in a 40-year Pinus sylvestris natural revegetation site (Celi, Cerli, Turner, Santoni, & Bonifacio, 2013). It was believed that soil organic P fraction was mainly driven by the development of vegetation cover. This position can be justified by the contribution of vegetation restoration on soil P dynamics being mostly defined in the upper two horizon soils, rather than at greater depths (Figure 6). Zhou et al. (2013) suggested that soil P fractionation was more governed by changes of soil pH, microbial activity and vegetation cover in a short-term young soil chronosequence. In the present study, the restoration of native plant species at the oldest restoration site (R1) had substantially promoted the weathering of soil minerals. Further study of effects of the effects of vegetation restoration and composition on soil microbial P dynamics would be worthwhile.

Contrasting results were reported relating grassland afforestation studies in inland dry mountainous areas of New Zealand, where there were lower organic P concentration in the topsoil of pine stands compared with adjacent grassland (Chen et al., 2000; Condron, Cornforth, Davis, & Newman, 1996; Davis & Lang, 1991). This was thought to be due to enhanced mineralization of soil organic P under the trees. A number of variables could explain the differences between studies, including (a) different degrees of organic material decomposition because of the different ages of restoration or afforestation (De Schrijver et al., 2012; Zhang, Shi, Wen, & Yu, 2016); (b) multi-species restoration versus single species afforestation (Oelmann et al., 2011) and revegetation of arbuscular mycorrhizal fungi dominated versus ectomycorrhizal fungi dominated plant mixtures (Rosling et al., 2016) resulting in different strategies of P utilisation and P dynamics; and (c) different environmental conditions (dry versus wet climate) (Chen, Condron, & Xu, 2008). Extrapolation of the results of the present study site would suggest that organic P pool in restoration soils will eventually approach the level in the mature forest soil and become stabilised.



FIGURE 6 Profile soil phosphorus fractionations in Mature (\bullet), Restored (\bigcirc) and Unplanted (\triangledown) plots at Transect 1 and 3. Where '1' plots are the older transect and '3' plots are the younger transect; where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. Data were not available in M3 Bw and C-horizons, and R3 C-horizon, due to the high pebble and gravel contents

FIGURE 7 Proportion of organic P (), acidextractable P (), Fe/Al-bound P (), Ca-bound P () and occluded P () of Total P in soil profiles at Transect 1 (top row) and 3 (bottom row). Where M, mature forest plot; R, restoration plot; and U, unplanted grassland plot. Data were not available in M3 Bw and C-horizons, and R3 C-horizon, because they had high pebble and gravel contents, so there was insufficient soil (fine sand) remaining after passing through the 2 mm sieve for analysis of soil P fractionation [Colour figure can be viewed at wileyonlinelibrary.com]



Although soil occluded P fractions were not significantly different between plots, this could be because of the relatively short gap in soil ages between transects; there remains a small indication occluded P become slightly more important as soils age (from older Transect 1 to younger Transect 3). Nevertheless, occluded P fractions were proportionally less important in restoration plots, compared to mature and unplanted plots at both transects (Figure 3). This is partially attributed to promoted P transformation by restored vegetation, as reflected in increased importance of organic P. Elsewhere, similar results were obtained in a 300-year post-landslide tropical forest development at Puerto Rico (Frizano, Johnson, Vann, & Scatena, 2002). The authors attributed this to the potential release of P from occluded pool by soil biota. In South China, Zhang et al. (2016) found an increase in occluded P fraction at a mid-way (90-year old) forest successional stage, but a decrease to the late (ca. 400-year old) successional stage. They thought increased organic acid production (rhizosphere processes and microbial activities) in mid-succession promoted the release of inorganic P into soil solution but that, in the favourable pH environment of tropical soils, this might be quickly precipitated by Al and Fe and become occluded.

Lower in the soil profiles of the present study, total soil P concentrations (ca. 518-865 mg kg⁻¹ on a 75-year terrace) in the A-horizon at the younger Transect 3 were similar to the youngest site at a comparable study on Franz Josef Schist outwash glacial chronosequence in the same region (ca. 554 mg kg $^{-1}$ on a 130-year terrace) (Parfitt et al., 2005). However, concentrations were higher than on another study at the Haast sand dune chronosequence (ca. 220 mg kg⁻¹ on a 370-year terrace) (Eger et al., 2011). These differences could be attributed to soils developing from different parent materials or to different degrees of weathering. The presence of ilmenite sand in the present study site could contribute to relatively larger soil P pool; inclusion of primary apatite P in the ilmenite sand has been reported previously (Cescas, Tyner, & Syers, 1970; Syers, Williams, & Walker, 1968). The difference was particularly evident at the deeper horizons (2Bw, 2BC and 2C) of U1, showing sharp increases of P (Ca) concentrations, as well as P (acid) (Figure 6). This potential change of parent material (from Bw to 2Bw, see profile description in Data S2) also led to a relatively low stock of primary mineral P in the upper horizons at U1 profile (Table S1, Data S1). However, overall losses of soil P stocks in the upper soil horizons in the present study were less evident in comparison to Eger et al. (2011) although under similar humid climate, which may firstly due to different time-scale of soil chronosequence. Secondly, differences in soil P stocks may be in part related to the variation of soil density among plots (Crews et al., 1995). Nevertheless, the presence of primary apatite P (Ca) in the upper soil horizons indicates a relatively young soil development stage at the present study site, but it is projected that their concentrations and relative importance will continue to decrease as both the soils and ecosystem age.

4.2 | The importance of soil biogeochemistry in the ecological restoration

Different impacts of ecological restoration on soils developed from different parent materials have been reported previously (Abella, Crouse, Covington, & Springer, 2015). In the present study, soils with two different development stages have clearly responded differently to the ecological restoration in terms of soil pH, mineral nitrogen, microbial biomass C and P dynamics. Differences between unplanted grassland, restoration site and mature forest plots also help to elucidate the effects of ecological restoration on soil development pathways. With a clearer understanding of these changes over an extended time-period, prediction of future soil development would provide insights into the rate of re-supply of ecosystem services (Moorhead, 2015; Prach & Walker, 2011).

This work has relevance to current global changes to increase tree planting to mitigate climate change (Bastin et al., 2019; O'Connell, Ruan, & Silver, 2018). Soil nutrient transformation is likely to have particularly critical implications when ecological restoration is undertaken on large-scale across landscapes. In much longer-term soil chronosequences, we know that soil nutrient dynamics is transformed from being N-limited in the early stages to being P-limited at later stages of ecosystem development, eventually leading to ecosystem retrogression if no major disturbance occurs (Peltzer et al., 2010). This results in old regressive forest ecosystems (Wardle et al., 2004). However, landscapes typically consist of a mosaic of different stages of soil development, as reflected in newly developed versus highly weathered soils in the present study. Of course vegetation composition also changes along long-term soil chronosequences. Many previous studies have indicated that plant community changes are mainly driven by soil nutrient dynamics that accompany long-term soil development (Crews et al., 1995; Richardson, Peltzer, Allen, McGlone, & Parfitt, 2004; Turner, Wells, Andersen, & Condron, 2012). Pioneer N-fixing species are critical in the early stages, while plants adjusted to P-poor soils perform well in the late stages. It has been suggested that mixed species planting may facilitate vegetation restoration by providing a combination of N-fixing, P demanding and P-mobilising species, the latter require N to promote growth (Hinsinger et al., 2011; Vance, 2001). Selecting appropriate native plant species assemblages that complement soil nutrient status and soil development potential could make a substantial impact on restoration practice and outcomes in the future.

5 | CONCLUSIONS

- Soil biogeochemistry, including soil P dynamics, varied along a trajectory of ecological restoration on the short-term soil chronosequence and had been modified by restoration planting. In some cases, but not always, this was strongly directional towards the forest soil characteristics.
- Dynamics of soil organic matter (accumulation and decomposition) and increasing demand of N from fast-growing plants early in the restoration was associated with rapid nutrient mineralization.
- 3. Earlier conceptual models fit this short-term restoration trajectory, with a loss of total P, an increase of occluded P and increasing importance of soil organic P as soils age. Progressive changes of P fractions in soil are probably directional soil development trends in these restored ecosystems.
- 4. There was no evidence that the success of establishment of plants varied across the site, but vegetation establishment markedly impacted soil biogeochemistry. This knowledge makes a valuable contribution to our understanding of restoration biogeochemistry, but requires further advancement before it will be useful to practitioners.

ACKNOWLEDGMENTS

The authors thank Closure & Legacy Management, Rio Tinto Services Ltd., and Punakaiki Coastal Restoration Project (PCRP) for their sponsorship of this work. We thank the financial support of Rio Tinto Services Ltd. (grant numbers 46084, 46164) and Conservation Volunteers New Zealand (grant number 46061). The authors thank Mike Bowie and James Washer for assistance in the field.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study Data are available from the figshare repository: https://doi.org/10.6084/m9.figshare.12994289.v1.

ORCID

Hongtao Zhong b https://orcid.org/0000-0003-0674-0010 Young-Nam Kim b https://orcid.org/0000-0002-9745-6551

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SUPPORTING INFORMATION

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How to cite this article: Zhong H, Smith C, Robinson B, Kim Y-N, Dickinson N. Soil phosphorus dynamics along a short-term ecological restoration trajectory of a coastal sandplain forest in New Zealand. *Land Degrad Dev*. 2021;32: 1250–1261. https://doi.org/10.1002/ldr.3782