Soil Chemistry and Ecology on a Restoration Trajectory of a Coastal Sandplain Forest, Punakaiki, New Zealand

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Abstract

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This research was carried out in order to better understand the interactive role of vegetation and soil biogeochemistry on an ecological restoration trajectory on the West Coast of New Zealand. The Punakaiki Coastal Restoration Project (PCRP) was developed to restore degraded land to a more natural vegetation, resembling the original sandplain forest that has largely disappeared. Ecological restoration at the site, in terms of practice and research, has mainly focused on plant establishment and faunal colonization. The present study investigated whether restoration of soils is an integral part of this process. The project aimed to understand whether ecological restoration significantly modifies soils and, *vice versa*, whether physio-chemical variability of soils significantly influences the restoration trajectory. This research is based on a combination of laboratory, glasshouse and field-based studies.

Incubation of native plant litters in soil was found to change soil chemical properties, including nitrogen (N) dynamics. It was found that two native species, *Kunzea robusta* and *Olearia paniculata*, may have the potential to ameliorate concerns associated with nitrate leaching and nitrous oxide production. Restored vegetation at the study site modified the dynamics of dissolved organic carbon (DOC) and mobile N in soil solution and increased rates of N mineralization. Interactions between vegetation and soil biota have significantly impacted these changes; changed soil conditions have also altered the composition of soil faunal communities. Study of soil pedogenesis revealed a formerly unknown spatial variability of the soil template. As soils have aged this has been reflected in a loss of soil total phosphorus (P), increase of occluded P and an increasing proportional importance of soil organic P. The dynamics of soil P fractionation on a short-term soil chronosequence across the site provided a better understanding of the response of soil biogeochemistry to the trajectory of ecological restoration on old and young soils. Key parameters were shown to be soil pH, organic matter, organic P and the variability of different P fractions.

A detailed comparison of remnants of New Zealand Flax and Nikau Palm, and abandoned agricultural grassland, provided an opportunity to investigate the effects of these different types of vegetation on soil development. Multiple variables were found to be significant, including differences in plant physiology, soil organisms, hydrological gradient of an alluvial fan, and guano deposition, all of which modified soil P fractionation and secondary iron/aluminium (Fe/Al) minerals. In a glasshouse experiment, soil dehydrogenase activity and biologically based P ($CaCl_2$-P, citrate-P and HCl-P) were significantly increased through interactions of earthworms and guano; the dynamic of soil P was modified by additional interactions with flax plants.

The relationships between soil chemistry, biodiversity and plants on the restoration trajectory at PCRP were synthesized using multivariate analysis. A conceptual model was developed, elucidating changes of soil physio-chemistry on the restoration trajectory. The success of the PCRP restoration and establishment of flora and fauna are strongly influenced by soil variability, but the developing plant communities also substantially modify soil physio-chemistry. The study illustrates that a preliminary investigation of site-specific soils should be an essential part of restoration practice.

Keywords: ecological restoration, litter, dissolved organic carbon, mineral nitrogen, soil leachates, phosphorus fractionation, iron/aluminium minerals, soil chronosequence, guano, earthworms.

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Chapter 1

Introduction and Literature Review

1.1 General introduction

Over 80% of New Zealand's biota is endemic due to more than 80M years and at least 2,000 km of evolutionary and geological isolation; it is one of the world's biodiversity hotspots (Cooper & Millener, 1993; Trewick, Paterson, & Campbell, 2007). New Zealand has a relatively short history of human colonization, in a global context, by Polynesians (ca. 800 years ago) and Europeans (ca. 200 years ago) (Anderson, 1991). Since then deforestation has been extensive, leading to significant loss of native vegetation cover from 75% to 20% of the land area (Atkinson & Cameron, 1993; McGlone, 1989).

With increasing recognition of native biodiversity, growing awareness of the losses of native vegetation and danger of exotic species invasion, more efforts are now devoted to reintroducing native plants to agricultural landscapes, restoring degraded ecosystems back to native vegetation, conserving native biota and re-connecting remnants to natural forests (Ewers et al., 2006; Walker et al, 2006; Walker, Price, & Rutledge, 2008). Conservation and restoration of native fauna and flora also aims to re-construct and re-provide ecosystem services (Benayas et al., 2009; Vilà et al., 2010). The successional trajectory of the restored ecosystem is particularly critical (Hobbs, Walker, & Walker, 2007; Prach & Walker, 2011). Vegetation, soil organisms and soil geochemistry are clearly interdependent, all contributing to the progress of ecological succession and success of restoration (Bardgett & Wardle, 2010; van der Putten et al., 2013). In restoration ecology, a 'restoration trajectory' has been referred to the hypothetical or projected process of ecosystem development (Hobbs & Norton, 1996).

This research was carried out in order to better understand the interactive role of vegetation and soil biogeochemistry in ecological restoration. The main body of the work is based on a case study of a 70 ha restoration of a sandplain forest on the West Coast of South Island, New Zealand. The first investigation is a laboratory study of the effects of native plants on soil nitrogen (N) dynamics through the processes of litter decomposition, using litter-soil incubation experiments. Then, the effects of forest restoration on the dynamics of dissolved organic carbon (DOC) and mobile nitrogen in soil leachates were monitored on the restoration trajectory at the Punakaiki Coastal Restoration Project (PCRP). The study develops with an investigation of the dynamics of soil phosphorus (P) and iron/aluminium (Fe/Al) minerals in the restoration trajectory, evaluating the importance of soil pedogenesis in forest restoration. Soil P and Fe/Al mineral dynamics are further investigated under different stands of vegetation at PCRP. Attempts to understand the contributions of nutrients from bird guano to the functioning of this system are further explored in an experimental glasshouse study of flax-earthworm-guano interactions on soil P dynamics. Finally, interpretation and discussion of my results drawn together in multivariate analysis in attempt to provide combined understanding and conceptual model of soil and plant variability in the restoration trajectory at PCRP.

The findings of this research will be valuable to elucidate the changes of soil biogeochemistry alongside the trajectory of coastal sandplain forest restoration and the importance of incorporating knowledge of soil pedogenesis into the study of ecological restoration.

1.2 Background and literature review

1.2.1 The Punakaiki Coastal Restoration Project (PCRP)

The Punakaiki Coastal Restoration Project (PCRP), located in Punakaiki, South Island, New Zealand, aims to restore lands that were once utilized for mining and agriculture to a more natural state. Current management of the restoration project involves a partnership between Rio Tinto, Conservation Volunteers New Zealand (CVNZ), the Department of Conservation (DoC) and Lincoln University. In 2009, the 80 ha property was gifted from Rio Tinto to DoC for stewardship, with funding provided for a restoration project. Conservation Volunteers is a non-governmental organization responsible for PCRP's management and implementation, in particular tree planting and volunteer inputs. The Lincoln University research team is responsible for ecological monitoring and research.

The vision for PCRP is to make a positive and lasting impact on the social, economic and environmental values of this unique location. The initial goal of the project was to restore the biodiversity of the Punakaiki area and build the ecological corridor between the mountains and sea. By the end of 2015, CVNZ volunteers had planted more than 140,000 native plants. In addition to restoring the land, the partnership formulated a proposal to develop the site for eco-tourism. From a research perspective, the Lincoln University’s role included the identification of measurable and credible indicators for determination of the success of the ecological restoration (Smith et al., 2016).

The PCRP project area

The PCRP site, within the Punakaiki Ecological District, encompasses 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 1.1, 1.2). Sandplain forest and wetland would have covered this area originally (Moskell, 2007b; as cited in Hahner et al., 2013). According to data collected from 1981-2010, the climate within this region of the West Coast is classified as warm and wet a mean annual precipitation of 2,200-2,600 mm, mean annual temperature of 12-13 °C, with 1,700 – 1,750 mean hours of sunshine (Hahner et al., 2013). The greater part of the property is on the western, seaward side of the State Highway (SH) 6, and adjoins the northern boundary of the Nikau Scenic Reserve (NSR); and the lesser part of the property is on the inland side of the road, to the northern end of the NSR (Figure 1.2).

Figure 1.1 Satellite imagery of the Barrytown flats and PCRP project area (sourced from: Google Earth and d-maps.com).

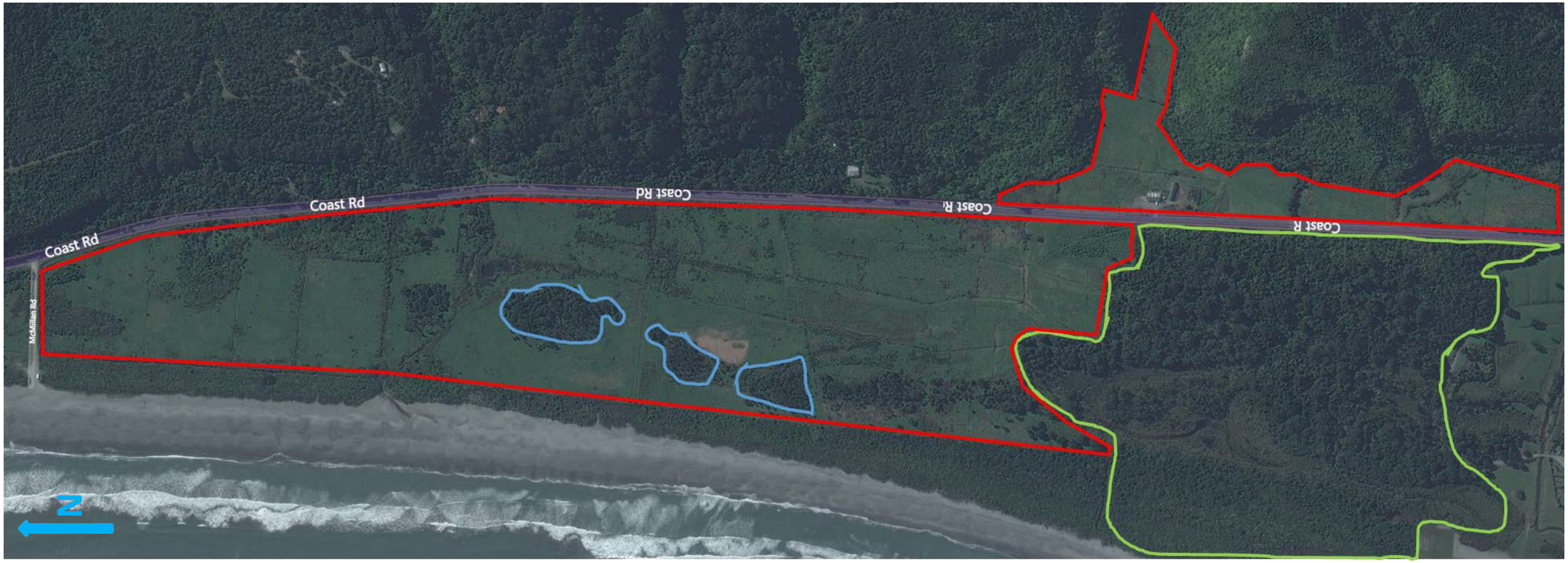


Figure 1.2 Aerial image of the PCRP site (sourced from Google Earth). The Nikau Scenic Reserve is highlighted in green, forest remnants are highlighted in blue, and the restoration areas are highlighted in red.

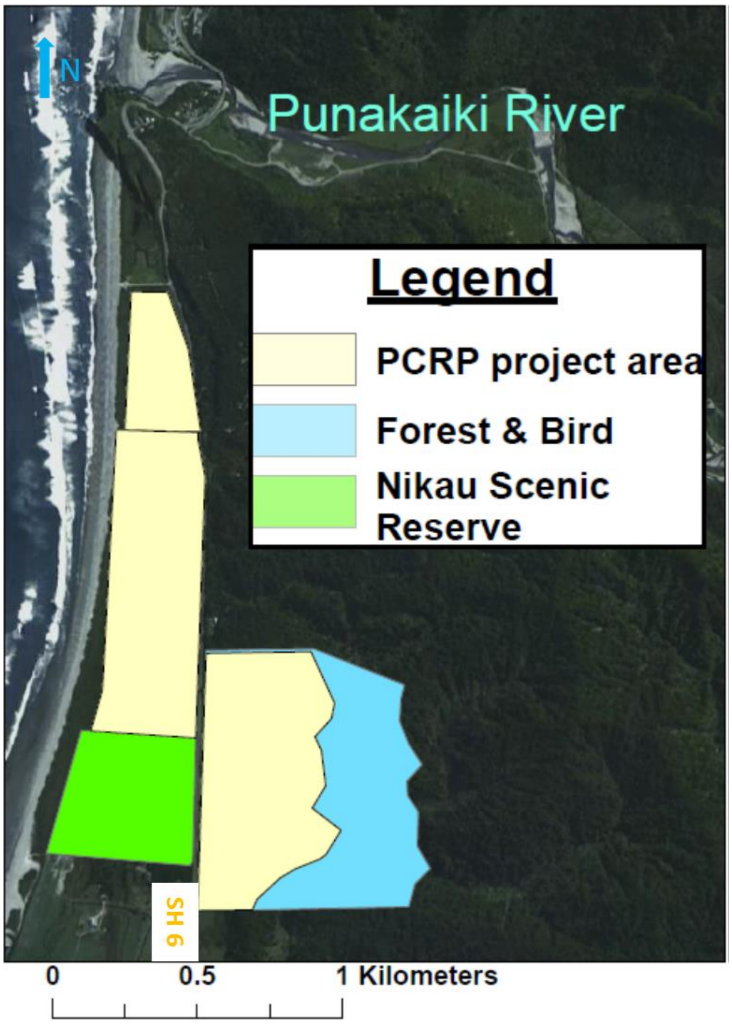


Figure 1.3 Diagram of the PCRP project area and nearby places of interest (Hahner et al., 2013).

An extensive amount of the land was logged sometime from the late 19th Century for timber harvesting, mined and then converted into farmland for cattle and sheep (James Washer, pers. comm., 2013). Pilot-scale mining and processing by Westland Ilmenite Limited (Wil, part of North Ltd.) occurred from 1966 to 1991. Most of ilmenite resources (90%) is located south of the Nikau Scenic Reserve, however further evaluation of ore quality and feasibility study concluded the project would not be cost-effective and viable using available technology. Rio Tinto acquired the land in 2000, and later gifted to the DoC for restoration purpose. Livestock was still present within restricted areas of the PCRP until about the middle of 2011 (Hahner et al., 2013). The understory vegetation of the few scattered forest remnants still reflect disturbance from livestock, but much of the native canopy is intact and understory vegetation clearly is recovering rapidly. The hillsides on the eastern side of the road had been logged, mined for gold, and cleared for livestock and was farmed until about 1970 (James Washer, pers. comm., 2013). These slopes are now covered with regenerating native bush.

PCRP is adjacent to the nesting ground and on the flight path of the Westland Petrel (*Procellaria westlandica*), which are listed as vulnerable on the IUCN Red List of Threatened Species of high risk of endangerment in the wild. This area is the only Westland Petrel breeding site in the world (Hahner et al., 2013). The land of the PCRP is situated directly below the flight path of these birds as they migrate between the ocean where they feed and their nesting sites in the hills. The PCRP project will support the wellbeing of this vulnerable species, and also provides a natural habitat for the blue penguin (*Eudyptula minor*) (Hahner et al., 2013).

Previous studies have been conducted in Punakaiki district, such as the Barrytown Flat Baseline Biological Survey 1985-1986 (Don, 1986; as cited in Hahner et al., 2013), the Soils of the Barrytown Flat, Westland (Wilms, 1985; as cited in Hahner et al., 2013), natural area assessment for the Grey District Council (e.g. Boffa-Miskell, 2006; as cited in Hahner et al., 2013) and most recently a report for the Punakaiki Coastal Restoration Project (Hahner et al., 2013). These studies have comprehensively reported overall environmental qualities, floral and faunal biodiversity, with geological and soil descriptions.

Soils at the PCRP

At the PCRP site, the coastal sand plain has formed as a prograding dune system, comprising marine and aeolian sand deposits which have accumulated in a coastal embayment. This sand plain consists of a series of relict shorelines (sand dunes or gravel ridges) with an intervening low lying sand plain and lagoon-swamp deposits (Figure 1.3). Different aged surfaces exist, with the youngest surfaces closer to the present day shoreline. Consequently, soils are developed on a range of surfaces, of variable age, a relationship known as a chronosequence. As summarized in Smith et al. (2016), soils at PCRP were developed from three major types of landforms: (i) well drained sand and gravel shorelines, ridges and plains; (ii) poorly drained and strongly gleyed alluvial fans whose parent material is heavy textured colluvium from Miocene silts and mudstones; and (iii) poorly to very poorly drained swales or lake swamp/lagoon features. Ilmenite, a titanium ore, is found associated with the low-lying parts of the landscape (sand plain) while the aeolian-deposited sand dunes comprise quartz sand (Brathwaite & Pirajno, 1993). The oldest shorelines abuts a postglacial marine cliff, cut into Miocene marine sediments (silts, mudstones) of the Blue Bottom Group. The marine cliff represents the mid-Holocene (approx. the last 5–6 ka) high sea stand. A series of marine terraces are preserved in the Miocene deposits, due to continuing tectonic uplift (Suggate, 1989). More detailed information of geomorphic evolution and soil development at the PCRP area is provided elsewhere (Smith et al., 2016).

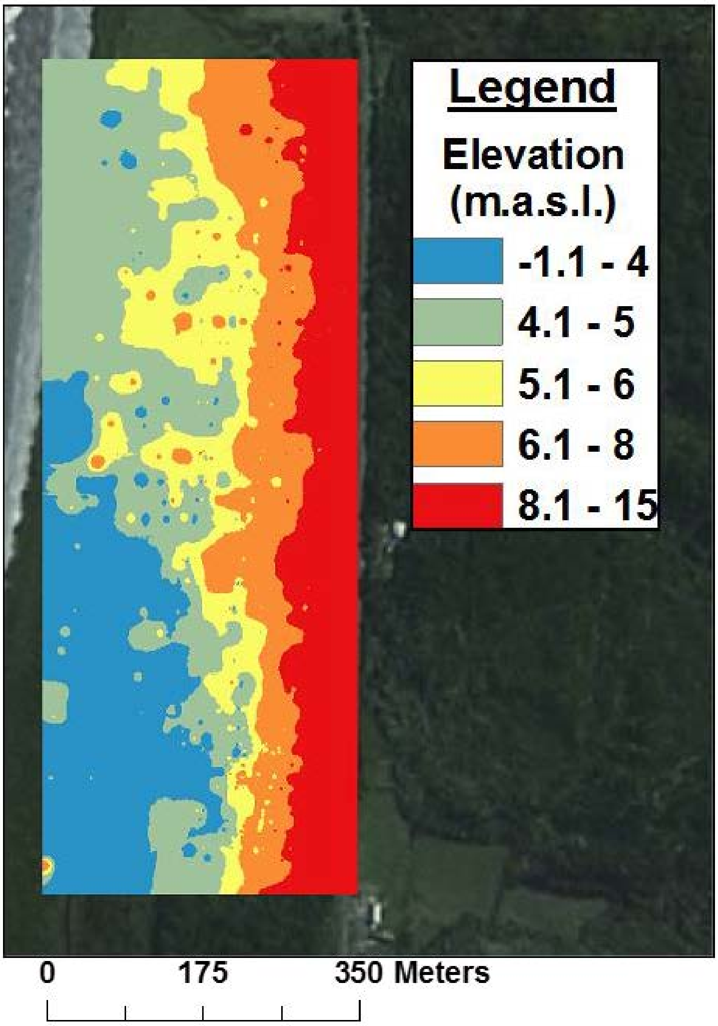


Figure 1.4 Digital elevation map of the PCRP study area illustrating the terraces, ridges and flats formed through coastal progradation (Hahner et al., 2013).

Vegetation at the PCRP

The Nikau Scenic Reserve (NSR) adjacent to the PCRP site was established in 1961, possessing an original intact sandplain forest, which extends about 20 hectare. The NSR shows a unique cross section of coastal sand-plain forest with assembly of shingle ridge low forest through to kahikatea (*Dacrycarpus dacrydioides*) and northern rata (*Metrosideros robusta*) forest, probably representing the original vegetation cover of surrounding areas. The NSR provides a point of reference for soils, and floral and faunal communities for the PCRP restoration. In addition, there are also remnant patches of vegetation within the PCRP site, including New Zealand Flax (*Phormium tenax*) and Nikau Palm (*Rhopalostylis sapida*) dominated stands, which provide the opportunity for further useful comparisons. The NSR and remnant forest stands also provide useful insights into temporal and spatial processes of vegetation change, in the context of the restoration effort (Hahner et al., 2013). In terms of the species selection for revegetation of PCRP, the Nikau Scenic Reserve provides the reference target plant community. Thirty five native woody species have been selected for revegetation, as shown in Appendix A (Table A.1). This shows that selection of species by the site manager (James Washer) has been largely based on soil moisture conditions, site exposure and shade conditions.

Unpublished studies have shown that *Myrsine salicina*, *Pittosporum eugenioides*, *Melicytus ramiflorus* and *Aristotelia serrata* are the most suitable pioneer species at the PCRP site. Progress with the restoration is shown in Figure 1.4.

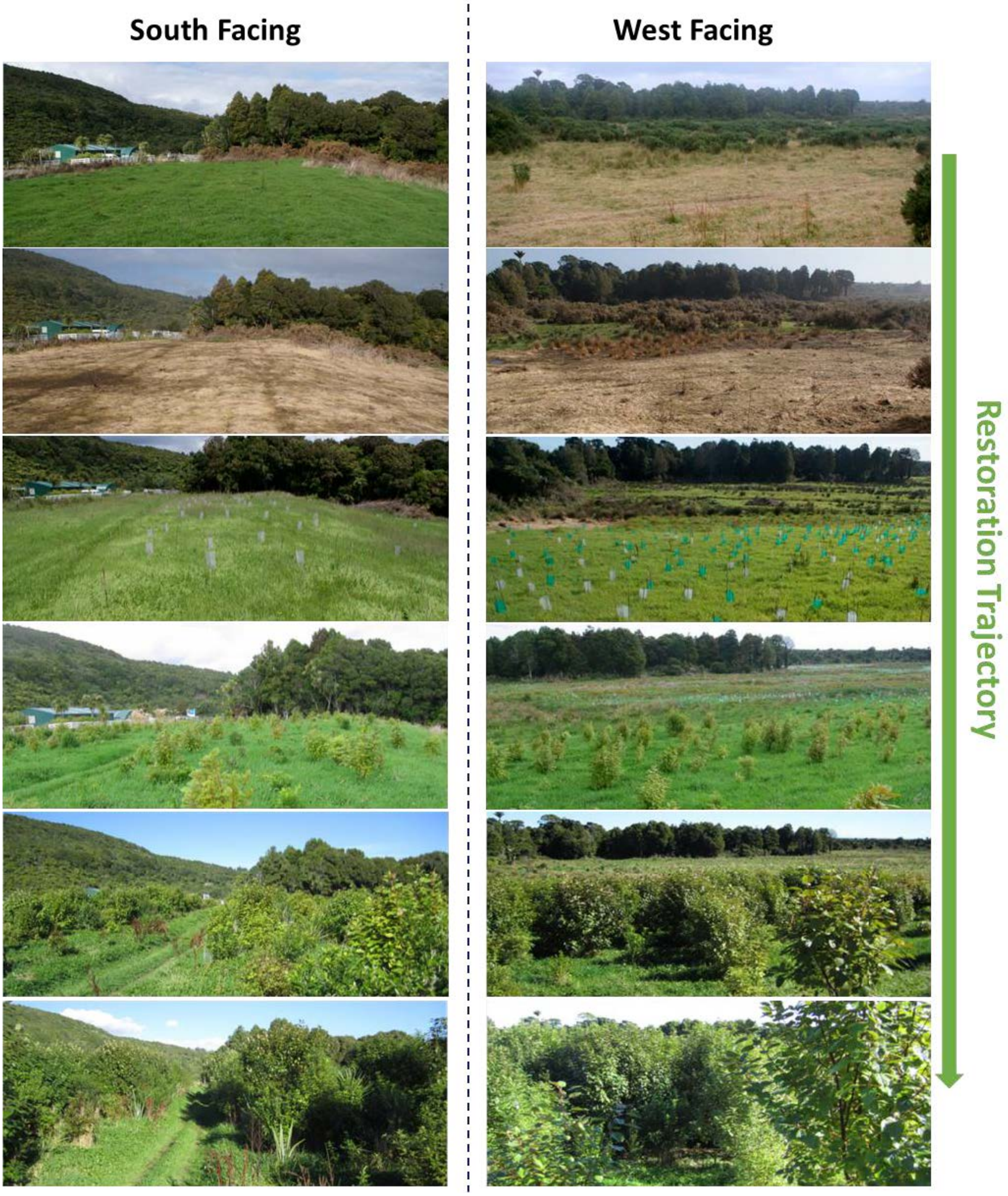


Figure 1.5 Development of restoration areas (42° 8'37"S; 171°19'51"E) from January 2009 until May 2013 (from top to bottom). Forest vegetation in the background of the upper photographs show Paparoa National Park (left) and Nikau Scenic Reserve (right). (Photographs by James Washer).

1.2.2 Ecological restoration

'Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed', as defined by the Society for Ecological Restoration (SER, 2004). In New Zealand, ecological restoration aims to restore native biodiversity and ecosystem (Saunders & Norton, 2001; Towns & Ballantine, 1993). How to judge the success of an ecological restoration has not really reached common ground (Perring et al., 2015; Petursdottir, Aradottir, & Benediktsson, 2013; Wortley, Hero, & Howes, 2013), but according to SER (2004) nine attributes should be considered as the criteria for evaluation of restored ecosystems (overall or partially) (Table 1.1). However, no study has measured all nine attributes (Ruiz-Jaen & Mitchell Aide, 2005). In addition considering ecological aspect, some extra attributes could be added according to specific goals of the restoration projects, such as cultural, social, aesthetic and economic perspectives (Wortley et al., 2013).

Table 1.1 Criteria for evaluating the success of ecological restoration (summarized from SER, 2004).

A restored ecosystem should:	(1) contain the species assemblage of a reference ecosystem;
	(2) consist of endemic species as much as practicable;
	(3) contain all functional groups (e.g. trophic levels) as necessary;
	(4) be capable of sustaining reproducing populations as necessary within the established physical environment;
	(5) be functioning normally in reference to its ecological stage;
	(6) fit in and allow abiotic and biotic exchanges with the larger surrounding landscape;
	(7) not be threatened by surrounding landscape;
	(8) be resilient under stress;
	(9) be self-sustaining and able to progress ecological succession towards its reference ecosystem.

In restoration ecology, a 'restoration trajectory' has been referred to the hypothetical or projected process of ecosystem development (Hobbs & Norton, 1996). On the course of long-term ecological restoration, the hypothetical or projected restored ecosystem would involve:

- recolonization by newly immigrated species, selection of adapted and adaptable species, and of species with slow growth;
- and (ii) accumulation of nutrients in soil and plants, changes in soil structures, processes of soil development, and reduction of soil toxicity where soil was contaminated (Bradshaw, 1983).

Since most studies have focused mainly on an ecological perspective, it has often been suggested that soil science should be included more in the study of ecological restoration (Bradshaw & Chadwick, 1980; Perring et al., 2015).Soil is the key part in the provision of ecosystem services that include the water purification, climate regulation, and also the role of a diverse soil biota in ecosystem functioning (Adhikari & Hartemink; 2016).

1.2.3 The role of plants in soil development

Vegetation is one of the factors that control the development of soils, alongside time, parent materials, climate, topography, and other biota (plants, animal and microbes) (McLaren & Cameron, 1996). Plants modify and mediate both the soil environment and soil quality (Berendse, 1998). Different plant species can alter soils in different ways (Binkley & Giardina, 1998), but particularly through plant litter inputs and rhizosphere processes that modify soil physical, chemical, and biological properties (McLaren & Cameron, 1996).

Plant litter

Plant litter inputs influence hydrological processes by providing a buffering zone that reduces the velocity of raindrops and surface water flow, as well as acting as mulch to mediate surface soil temperature and moisture (Li, Niu, & Xie, 2014; Ogée & Brunet, 2002). Decomposition of litter provides the major source of organic matter to soils, releasing nutrients and organic compounds for plant root uptake, and providing a resource for soil biota (soil invertebrate and soil microbes) (Hobbie, 2015). These organisms are critical for nutrient cycling, with obvious implications for a wide range of soil and environmental factors and processes, potentially improving the overall health of soils and ecosystems (van der Putten et al., 2013). Litter breakdown and decomposition occur through a range of processes that include leaching of soluble substances, mechanical breakdown and digestion by saprophagous soil animals, and enzymatic degradation of chemical compounds by saprotrophic microbes. Factors that influence rates and patterns of litter decomposition include: litter chemical composition, climate, soil nutrient availability (particularly mineral N), communities of soil organisms, and site-specific factors (Sayer, 2006).

Litter chemical composition is of course related to plant foliage that is highly variable in terms of structure and chemical composition (Schroth & Sinclair, 2003). During the initial stages of decomposition, four principal groups of soluble organic materials are released: sugars (mono-/oligo-saccharides), hydrocarbons (low-molecule weight), phenolics (hydrolyzed tannin) and glycerides, which can account for a considerable portion of total leaf litter mass loss (Uselman, Qualls, & Lilienfein, 2012). Apart from a substantial amount of organic C, all plant leaf litter contains essential nutrients including N, P, S, K, Ca, Mg, Mn, and Fe, but concentrations vary with species (Berg & McClaugherty, 2008). With regard to elemental outputs, for instance, Aponte et al. (2012) found that *Quercus* *canariensis* and *Q. suber* released nutrients in the order of K > Mg > C > P > Mn > S > N > Ca > Cu > Zn in a 2-year study. The proportion and concentration of these elements in the shed leaves would largely depend on species-specific translocation of nutrients back to living tissue of the plant prior to leaf senescence. This nutrient conservation mechanism is prevalent in infertile environments (Lim, Kim, & Nam, 2007); thus litter chemistry or litter quality is partly controlled at local level due to soil fertility. Climatic factor plays a significant role in litter decomposition on a regional scale (Berg & McMlaugherty, 2008).

Lignin and hemicellulose are the most recalcitrant components of litter (Wickings et al., 2012). Lignin content varies with plant species, ranging from 15 % to 40 % of litter mass (Berg & McMlaugherty, 2008). The degree of lignification of cellulose appears to be another important indicator of litter quality (Berg & McMlaugherty, 2008). These structural components and other fibres to a smaller extent, also reflect the mother plant. The types of lignin produced in the two main groups of seed plants are different: angiosperms contain similar levels of syringyl and guaiacyl types of lignin, and gymnosperms mainly have guaiacyl unit lignin (Ros et al., 2007). Deciduous species generally have higher lignin contents than evergreens and conifers, although much variation still exists in both groups. In summary, the chemical properties of litter or litter quality differ significantly with plant species, which affects litter decomposition and soil chemistry.

Significant differences in litter decomposition have been related to distinct substrate quality and varying C/N and N/P ratios, as well as litter Ca and Mn concentrations (Berg & McMlaugherty, 2008). These are often recognized to be the main rate-controlling factors. For example, the organic matter C/N ratio controls the mobilization or immobilization of substrate nitrogen (McLaren & Cameron, 1996), and soil N content is critical for the soil quality. However, different C/N ratios of organic materials have been considered to promote nitrogen mineralization; McLaren and Cameron (1996) suggested a ratio of 25 was critical, Heal et al. (1997) suggested 20, and Brady and Weil (2008) suggested 17. During vegetation succession, the amounts of mineralized nitrogen in the soil nutrient pool have been found to be 10-times more in comparison with pre-vegetated status within a few decades (Berendse, 1998). Other studies have indicated that calcium is one of the critical elements within the course of long-term plant-soil interactions. For instance, Reich et al. (2005) tested 14 temperate tree species at Poland and found out that higher foliage calcium (Ca) concentration was related to higher soil pH, abundance and biomass of earthworms, and forest floor turnover, but lower organic mass and total carbon in the O horizon on the forest floor. Manganese (Mn) also plays an important role in hemicellulose and lignin decomposition during the late stages, because it is key element for lignin enzymatic decomposition (Aponte et al., 2012).

The decomposer community plays another important role throughout the course of litter decomposition. Firstly, litter is fragmented or broken down by macro-organisms such as millipedes, earthworms, collembola and isopods. Secondly, coarse materials become finer materials, and increased surface area means more availability and access to micro-organisms (Gartner & Cardon, 2004). The quality and quantity of litter fall influence the nature of the soil faunal and microbial community, in terms of size, composition, function, and physiological properties (Sauvadet et al., 2016; Thoms et al., 2010; Wardle et al., 2006). The composition of the faunal and microbial community may, in reverse, influence the course of decomposition, and chemical changes in the litter during decomposition (Hunter et al., 2003; Wall et al., 2008; Bardgett & Wardle, 2010). With knowledge about the initial chemical composition of litter and the chemical changes during decomposition, it is possible to predict how mass-loss rates differ and change with time (Berg & McMlaugherty, 2008). Prescott (2005) found it is necessary to take into account the fate of faecal material produced by soil fauna within the overall study of litter decomposition in the context of nutrient cycling. Studies of litter decomposition rate have also focused on its significance to climate change due to elevated greenhouse gases emissions and atmospheric nitrogen deposition (Cornwell et al., 2008).

Soil pH had an overriding influence on litter decomposition and nutrient cycling through its effects on soil nutrient availability and the activity of decomposer communities (Berg & McMlaugherty, 2008). Bacteria and actinomycetes are generally dominant in alkaline conditions, whereas fungi dominate decomposition in acid environments (Allison et al., 2005; Frostegård et al., 1993). Therefore substrate pH may have a controlling effect, both directly on the microbes that participate in the decomposition processes, and on the solubility and thus the bioavailability of nutrients (Marschner & Rengel, 2012). Changing temperature and moisture create cycles such as wet-dry, hot-cold, and shrink-swell that also accelerate the physical breakdown of litter (Sayer, 2006). Obviously microbes are most active when they are in most suitable conditions of temperature and moisture (Berg & McMlaugherty, 2008).

Plant rhizosphere processes

Plant growth and production are dependent on how plants can adapt to local environments, particularly to their soil environment (Binkley & Giardina, 1998). This involves plant-soil interactions, and plant roots interacting with biotic and abiotic components of soil in the rhizosphere (York et al., 2016). Rhizosphere processes affect soils through exudation of organic compounds, water and nutrient uptake, nutrient mobilization/immobilization by roots and microbes, rhizosphere-mediated organic matter decomposition (e.g. leaf litter decomposition), and soil structure betterment by the root development (York et al., 2016). The feedback mechanisms between rhizosphere processes and litter decomposition are always large in magnitude (Pinton, Varanini, & Nannipieri, 2001).

The rhizosphere is a highly complex environment mediating all aspects of nutrient cycling through chemical, biological and physical processes (Hinsinger et al., 2009). Root hairs, which are single-celled extension structures with a high surface area, act as the most direct contact interface for interactive processes within rhizosphere soil (Bertin, Yang, & Weston, 2003). However, because this is such a complex microenvironment, conceptual and methodological difficulties of rhizosphere studies have been encountered. Problems include obtaining representative samples of rhizosphere soil, collecting root exudates and monitoring rhizo-microbial activities, as well as isolating major compositional differences between root and soil (Pinton et al., 2001; Schroth & Sinclair, 2003). However, development of analytic technologies, stable isotopes and radiolabelled tracers such as ^{13}C, ^{15}N, ^{32}P, ^{33}P, ^{35}S have helped scientists to understand nutrient flow and cycling in the rhizosphere both qualitatively and quantitatively (Neumann, George, & Plassard, 2009).

Root exudates mediate community development of soil fauna and microbes within the rhizosphere (Prashar, Kapoor, & Sachdeva, 2014; Shi, 2009) (Table 1.2). They are believed to have a critical function in regulation of plant growth metabolism (e.g. respiration), defence, nutrient acquisition, and rhizosphere biota community (Chen et al., 2006; Shi, 2009). Interactions between plants, soil and microbial communities are also important for exchange of energy and substances within the soil matrix, as well as creating an equilibrium between mobilization and immobilization of nutrients and bioavailability (Bertin et al., 2003; Lux & Rost, 2012). Chemical processes in the rhizosphere are important in regulating plant nutrient capture and uptake from soil (Neumann & Römheld, 2012), as well as protection from metal toxicity (George et al., 2012). Exudations of organic ligands are strong metal chelation to reduce their bioavailability to plant uptake (Hinsinger, 1998). Some groups of ligands act as phytosiderophores, which help root uptake of iron from calcareous soils; an example is mugineic acid produced by barley (Bertin et al., 2003). Rhizosphere processes may also provide protection from pathogenic activity and from counterparts through allelopathy (exudation of chemical compounds of one plant affects other plants) (Cardon & Whitbeck, 2007).

Rhizosphere processes also modify the dynamics of macronutrients, including carbon, nitrogen and phosphorus (Neumann & Römheld, 2012; York et al., 2016). One review study indicated 20-50 % of photosynthesis products are transferred to soil through root exudates and root turnover (Kuzyakov & Domanski, 2000). Schroth and Sinclair (2003) showed that carbon losses from the root into rhizosphere soil (whether as dissolved organic matter or through sloughed roots) is the momentum for many processes within the rhizosphere. In turn environmental changes in the rhizosphere modify soil nutrient availability. These include effects on soil pH, redox conditions, concentrations and mobility of ions, speciation and complexation of metals, and other interactions between root exudates and microbes (Hinsinger, 1998). Modification of pH generally plays a dominant role (Sattelmacher et al., 1993). For example, the balance of plant-available cationic (ammonium, NH_4^+) and anionic (nitrate,

NO_3^-) forms is mainly related to rhizosphere pH (Neumann & Römheld, 2012). Rhizosphere processes also involve symbiotic associations with nitrogen fixation bacteria (Prashar et al., 2014). Thus, nitrogen speciation and mobility is primarily determined in the rhizosphere. In addition, the rhizosphere normally has a higher P status than bulk soil, partially because P mobilization is closely related to activity of mycorrhizal fungi, including endo- and ecto- mycorrhizae (Hinsinger, 1998, 2001). These fungi mineralize or mobilize phosphorus from organic P, Fe-Al-OH fixed P and Ca-bound P via organic acid and hyphal invasion, making the element available for plant root uptake (Schaetzl & Thompson, 2015).

Table 1.2 Plant root exudates and their known functions in the rhizosphere (modified from Bertin et al., 2003; Shi, 2009).

Root exudates		Root exudates	
Class of compounds	Functions	Class of compounds	Functions
Aliphatic acids	Plant growth regulation	Phenolics	Plant growth regulation, allelopathy interactions, arbuscular mycorrhizal and actinorhizol interactions
Fatty acids	Plant growth regulation	carbohydrates	Lubrication, protection of plants against toxin, microbial growth stimulation
Sterols	Plant growth regulation	Amino acids and amides	Inhibit nematodes and root growth of different plant species, microbial growth stimulation, chemoattractants, iron scavengers
Hormones	Plant growth regulation	Vitamins	Microbial growth stimulation
Miscellaneous	Plant growth regulation, quorum quenching,	Enzymes and proteins	Plant defence, nod factor degradation

Physical processes induced by root penetration of soil and rhizosphere processes modify soil structure and increase soil porosity (e.g. oxygen content, water availability) (Hinsinger et al., 2009); whilst soil structure is influenced by root exudates which act as binding agents (Shi, 2009). Root exudates of polysaccharide gel (mucilage) bind soil aggregates, and also increase the root-soil interfaces area (Schroth & Sinclair, 2003). Propagation and distribution of rhizosphere microbes are influenced by roots systems and root exudates, resulting in microbial polysaccharide gels production, which provide an indirect contribution to soil structural stability (Prashar et al., 2014). Different plant rhizospheres modify and benefit soils differently through differential of root morphologies and rhizosphere plasticity (Carminati & Vetterlein, 2013), as well as through different exudation strategies (Jones, 1998). Different plant species also interact and compete with each other in the root zone (Faget et al., 2013). Overall, plant roots not only physically and nutritionally support of plant within the soil environment, but also feedback to the soil in answer to biotic and abiotic stresses (Bais et al., 2004; White et al., 2013).

1.2.4 Soil nitrogen

Nitrogen (N) is a fundamental component of many important plant compounds, for example amino acids (proteins and enzymes), nucleic acids (DNA and RNA), and chlorophyll (photosynthesis) (Brady & Weil, 2008). Plants usually contain 2.5-4.0% of N in dry biomass, varying between N-fixing and non-N-fixing plants, and with age of the plants (Brady & Weil, 2008). In non-agricultural terrestrial ecosystem, N inputs are mainly sourced from biological fixation (≅ 10-160 kg N ha^{-1} yr^{-1}) from atmospheric dinitrogen to ammonium-N, and to less extent by direct aerosol N deposition (1-12 kg N ha^{-1} yr^{-1}) (Boring et al., 1988; Galloway et al., 2008). In contrast, N is added to soil by fertilizer application and organic material amendment; animal urine and faeces return to the soil (85-90% of N ingested) can hugely increase enrichment in discrete patches in grazed pastures (Cameron, Di, & Moir, 2013).

Usually, soils contain about 0.1-0.6% N in the topsoil (0-15 cm), depending on soil type, vegetation cover and environment (Brady & Weil, 2008; McLaren & Cameron, 1996). Most of soil N (over 95%) is in organic form, with another 1-6% potentially fixed by clay minerals as NH_4^+, and only 1-2% of total soil N is in mineral form available for uptake by plants (as NH_4^+ and NO_3^-) (McLaren & Cameron, 1996). The N cycle is shown in Figure 1.5.

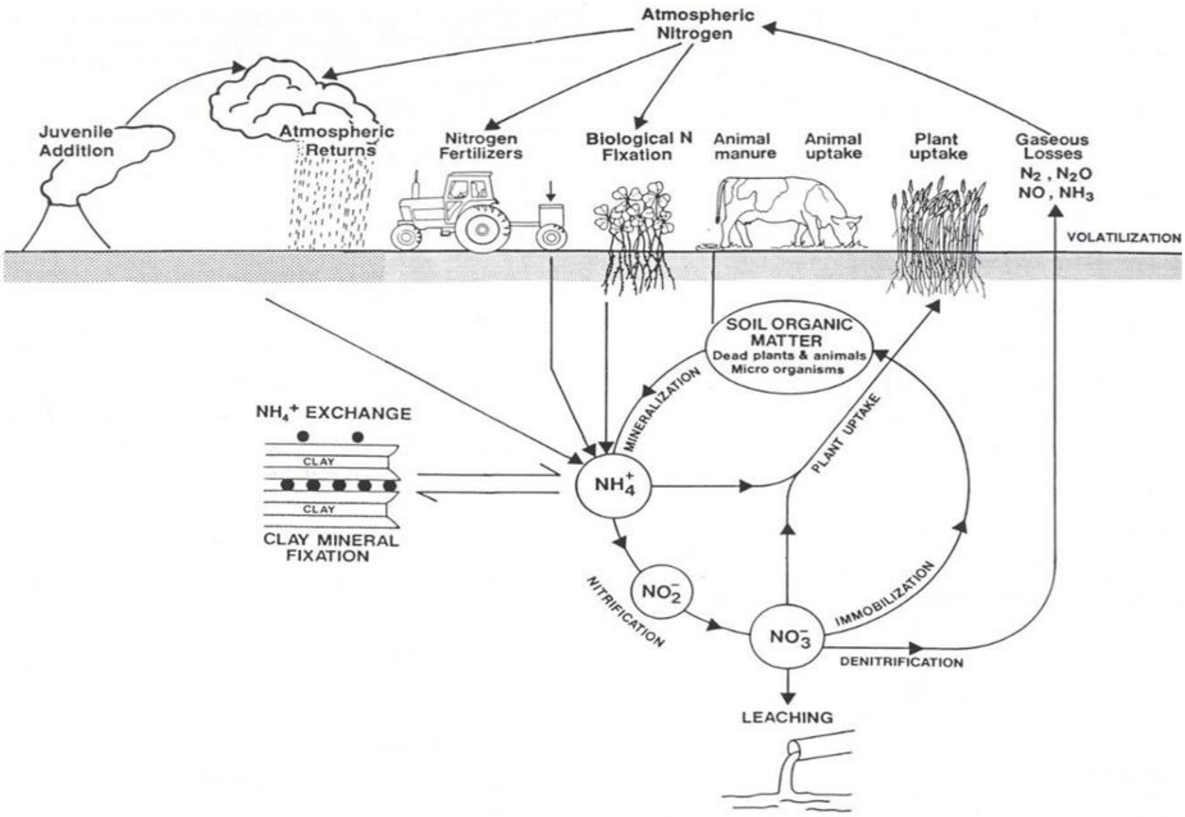


Figure 1.6 The nitrogen cycle (McLaren and Cameron, 1996, P 193, with permission).

The soil organic N pool can be mineralized. This mineralized NH_4^+-N which may be: (i) immobilized into soil microbial biomass; (ii) take up by plants; (iii) fixed in the interlayers of certain 2:1 clay minerals; (iv) volatilized via ammonia gas; or (v) oxidized to nitrite (NO_2^-) and subsequently to nitrate (NO_3^-) by the nitrifying bacteria via the nitrification processes. In turn, nitrate-N may be: (i) immobilized into soil microbial biomass; (ii) take up by plants; (iii) lost via leaching; or (iv) reduced and volatilized in gaseous forms of N_2O or N_2 by denitrifying bacteria via denitrification processes. Factors that control the dynamics of N in soil environment include pH, temperature, ammonium concentration, soil cation exchange capacity, soil moisture and plants in non-agricultural terrestrial ecosystems; with extra contributing factors such as fertilizer application, grazing animals and management regimes in agricultural ecosystems (Cameron et al., 2013).

1.2.5 Soil phosphorus

Phosphorus (P) is involved in the storage and transfer of energy in the form of ATP and ADP, and it is also a constituent of the two nucleic acids (DNA and RNA); therefore P is important in all stages of plant growth (Brady & Weil, 2008). Plants normally contain between 0.1% and 0.5% of P in dry biomass (McLaren & Cameron, 1996). Plant roots absorb P from soil solution in the form of orthophosphate (mainly $H_2PO_4^-$ in acid soil and HPO_4^{2-} in alkaline soil) (Shen et al., 2011). Most soil P is sourced from parent materials, mainly primary apatite minerals (e.g. fluorapatite, hydroxyapatite, carbonate apatite, and chlorapatite) (Brady & Weil, 2008). Total P concentrations range from 0.02% to 0.15% in New Zealand soils (McLaren & Cameron, 1996); but can be up to 0.3% in some soils overseas (Condron, Turner, & Cade-Menun, 2005). Although total P may seem high in soil, it is usually present in unavailable forms or outside the capture range of plant roots (Frossard et al., 2000). For this reason, management of soil P is of a particular concern in production land in order to meet plant demand (McLaren & Cameron, 1996).

Soil P exists in various forms in soils, including soluble P, labile P, organic P (including microbial biomass P), secondary mineral P, primary mineral P, and occluded P (Smeck, 1985). The nature of these forms depends on soil type, the extent of weathering and management regime (McLaren & Cameron, 1996). Processes involved in the dynamics of different P forms are (Brady & Weil, 2008):

(i) inorganic processes including physicochemical reactions, such as dissolution/precipitation and sorption/desorption;

(ii) biological processes initiated by plant root uptake and through assimilation of soluble P by soil microorganisms; and

(iii) recycling of P in food chains through mineralization and immobilization reactions.

The soil P cycle is shown in Figure 1.6. Following initial weathering of soil parent materials and primary P minerals, phosphates are released into soil solution. Mineralization of soil organic P can also replenish solution P to some extent (Tiessen, 2008). This solution P subsequently may follow different pathways that include:

(i) uptake by plants;

(ii) assimilation into soil microbial biomass becoming a part of soil organic P (immobilization);

(iii) binding to the surface of clay minerals (e.g. Fe/Al minerals in acid soils; Ca minerals in alkaline soils);

(iv) transformation or precipitation by secondary minerals; and

(v) loss via soil erosion or leaching.

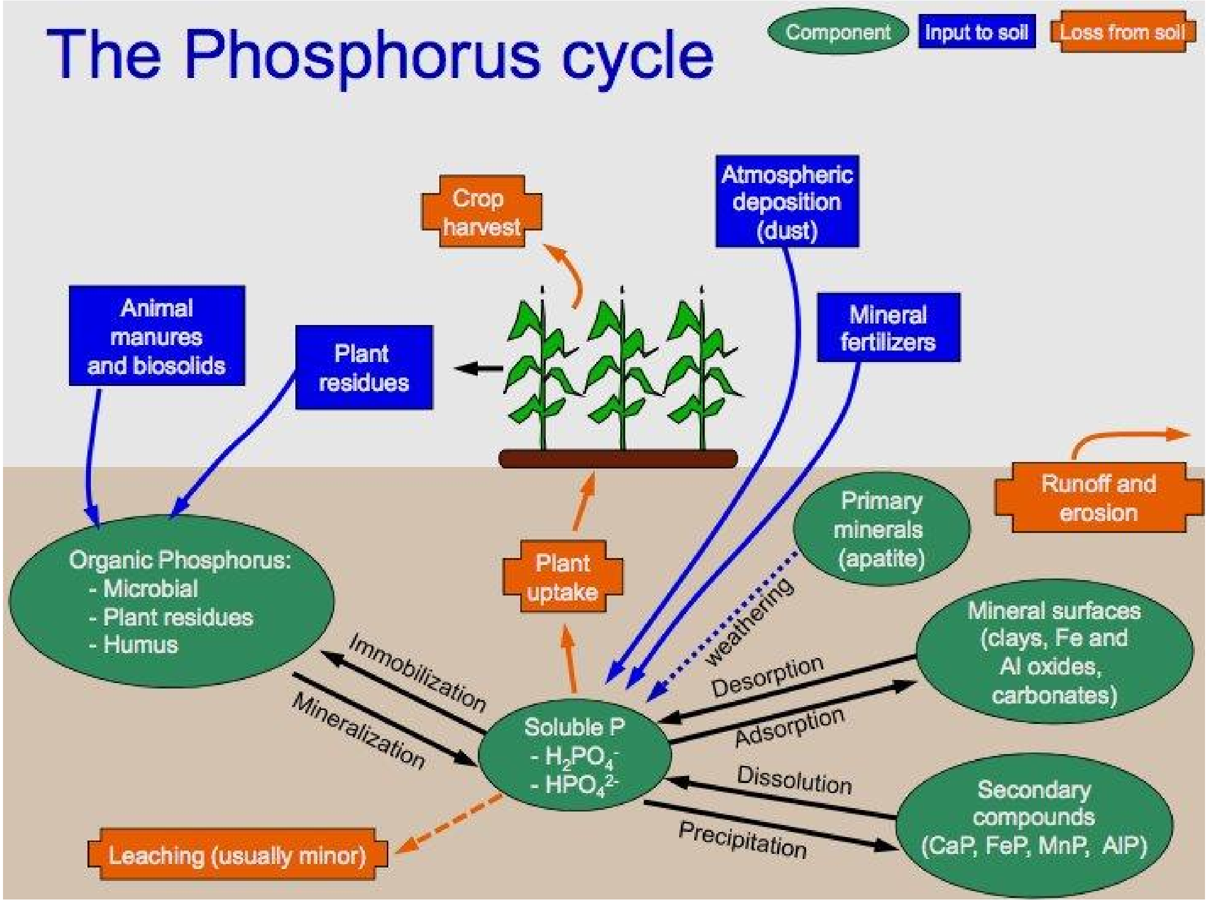


Figure 1.7 The phosphorus cycle (sourced from geography.hunter.cuny.edu).

Several environmental factors affect the availability of soil P to plant roots. Soil temperature affects soil microbial activities, and in turn affect organic P mineralization (Condron et al., 2005; Mackay & Barber, 1984). Soil compaction effects P uptake by plants by reducing pores spaces and availability of soil water and oxygen (Shierlaw & Alston, 1984). Soil redox potential can also affect P mobilization as Fe-bound P is released at potentials below 200 mV when Fe^{3+} is reduced to Fe^{2+} (Krairapanond, Jugsujinda, & Patrick, 1993). Soil pH significantly affects the physicochemical reactions of P via the prevalence of Ca/Mg related fixation at high pH>7, but Al/Fe related fixation at low pH<5.5 (Brady & Weil, 2008). Soils with higher clay or mineral contents tend to fix more P.

Phosphorus in soil and ecosystem development

In terrestrial ecosystems, for example forest ecosystems, N and P are the two critical nutrients that determine primary productivity, ecosystem functions and ecosystem succession (Peltzer et al., 2010; Vitousek et al., 2010). Unlike mostly atmospheric-sourced N in soils via biological fixation of dinitrogen and N deposition, release of P from soil parent materials weathering is the major source for terrestrial ecosystems (Vitousek et al., 2010). Using chronosequences appropriately can be a useful approach to study the dynamics of vegetation and soil development across timescales (Walker et al., 2010). In regard to different patterns of soil nutrients dynamics during long-term soil and ecosystem development, Walker and Syers's (1976) conceptual model was later updated by Turner and Condron (2013) who proposed that (Figure 1.7):

(i) an overall decrease of Total P because some weathered P was lost via leaching and runoff during soil development;

(ii) a gradual accumulation and prolonged importance of organic P (particularly increasing importance of soil microbial P as soils age (Turner et al., 2013));

(iii) a continual increase and eventual dominance of occluded P via irreversibly adsorbed or fixed Fe and Al sesquioxide clays;

(iv) a gradual decline and eventually depletion of weathering P inputs from primary P minerals (at this point onwards P input may be maintained by aerosol dust deposition (Chadwick et al., 1999; Eger, Almond, & Condron, 2013) or migration seabird guano (Roberts, Duncan, & Wilson, 2007)); and

(v) a final 'terminal steady state' ecosystem if no major disturbances occur (Wardle, Walker, & Bardgett, 2004); but this 'terminal steady state' may be extended because losses of P can be balanced by external P inputs to some degree (Turner & Condron, 2013).

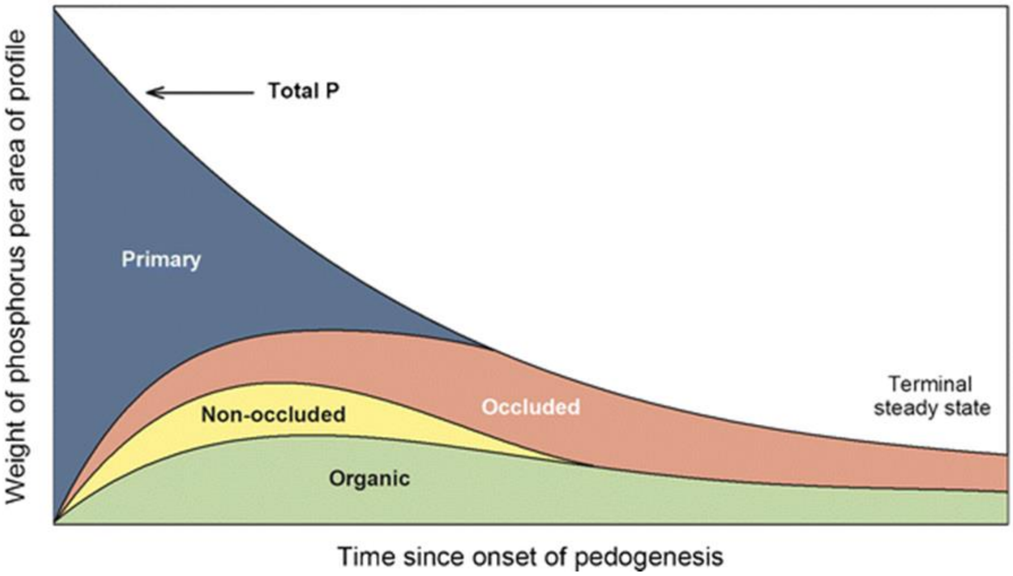


Figure 1.8 Conceptual model of changes in soil phosphorus fractions during long-term soil pedogenesis (sourced from Turner & Condron, 2013).

As weathered-P input declines, other essential nutrients (Ca^{2+}, Mg^{2+}, and K^{+}) also decline during soil and ecosystem development, resulting in a parallel soil pH decrease (Hedin, Vitousek, & Matson, 2003). However, fixed-N is absent in most soil parent materials, with some exceptions reported (Dahlgren, 1994; Morford, Houlton, & Dahlgren, 2016). In contrast to release of P and base cations by weathering in young soils, N supply mainly relies on biological fixation from atmospheric N_2 to NH_4-N (Vitousek & Farrington, 1997). Therefore, ecosystem succession and development is limited by soil N at the early stage, and plants with N-fixing symbioses tend to be favoured (Peltzer et al., 2010; Porder et al., 2007; Vitousek et al., 2010). Over time, and in the absence of other major disturbances, the quantity of N cycled in the system tends to increase, equilibrate with and then overtake that of P, so that with accompanying increasing substrate N:P ratio, eventually leads to P-limitation at a late stage of soil and ecosystem development (Peltzer et al., 2010; Vitousek et al., 2010).

1.2.6 The role of earthworms in soil

Worldwide there are 12 families and about 4,000 genera of earthworms (Megadrilacea, Oligochaeta) (Edwards, 2004). In New Zealand, 179 identified species of native earthworms exist in the family Megascolecidae; several new species have recently been found using DNA barcoding (Boyer, Blakemore, & Wratten, 2011; Buckley et al., 2015). However, since Europeans settlement at least 23 species of Lumbricidae earthworms have also been introduced to New Zealand (Kim, 2016). Most of New Zealand's native earthworms live under native vegetation, whilst introduced European earthworms are mainly distributed in disturbed and agricultural landscapes. Both native and exotic species can be found together in the borders or transitional zones between natural forest and production lands (Kim et al., 2015). European species are widely studied in the literature (Edwards, 2004); but little research has been carried out on the ecology of native New Zealand species or their benefits to soil function (Kim, 2016).

Earthworms are soil engineers, consumers, decomposers and modulators in ecosystem context (Edwards, 2004). They promote soil organic matter decomposition and subsequent nutrient cycling. As one of the key soil fauna in most habitats, earthworms have major effects on soil processes via feeding, digestion, excretion, burrowing and casting (Edwards & Bohlen, 1996), leading to changes of soil physical, chemical and biological properties (Brady & Weil, 2008). The effects of earthworms on soil properties differs between earthworm species, and between epegeic, endogeic and anecic ecological groups (Sheehan et al., 2006). Earthworms have significant effects on promoting soil organic C and N mineralization, as well as enhancing soil P availability (Amador, Görres, & Savin, 2003, 2006; James, 1991). Beneficial effects of earthworms on plant and crop production included increased soil nutrients availability for root uptake, improved soil aggregation and enhanced root growth (Brown, Edwards, & Brussaard, 2004; Laossi et al., 2010; van Groenigen et al., 2014).

1.2.7 The impact of bird guano on soil

Bird guano impacts soil by introducing substantial amounts of nutrients. The terms ‘guano’ and ‘droppings’ are both used in the literature for seabird or other birds respectively, but the word ‘guano’ is used in the present study. Bird guano contains multiple essential nutrients that may benefit plants when deposited on soil. Concentrations of N (8-21%) and P (0.12-16%) in guano are mainly dependent on the age of guano and the bird species (Otero et al., 2015; Szpak et al., 2012). Seabird guano has been reported to increase N in plant foliage around nesting colonies (Hawke & Newman, 2007). Guano-P has been estimated to remain for 4-15 years in soils around a colony, and to contribute a source of P to vegetation (Hawke, 2005). Excessive inputs of guano from high bird populations has also caused environmental issues, such as deterioration of nearby water body or damage to vegetation (Klimaszyk & Rzymski, 2016). In an extreme case, Antarctic ornithogenic soils formed under Adélie penguin (*Pygoscelis adeliae*) habitats have been highly influenced by penguin guano (Ball, Tellez, & Virginia, 2015; Emslie et al., 2014; Ugolini, 2013).

Biogenic sources of P, mainly from bird and bat guano accumulations account for 2-3% of world phosphate resources, which is small compared to sedimentary marine deposits (75%) and mineral phosphate deposits (15-20%) (Abouzeid, 2008). However, during the 20th century, guano resources in the Central Pacific Island of Nauru, formerly provided a substantial source of P fertilizer to Australia and New Zealand (Teaiwa, 2015); with negative environmental impacts on these island ecosystems (Manner, Thaman, & Hassall, 1984).

1.3 Study aim and objectives

This work aims to investigate the value of a combined knowledge of soil physio-chemical and biological properties to the trajectory of an ecological restoration at PCRP.

This research programme has the following objectives:

- Objective 1: To investigate whether and how plant leaf litter of different plant species modifies soil chemistry (Chapter 3).
- Objective 2: To investigate how ecological restoration modifies carbon and nitrogen dynamics at PCRP (Chapter 4).
- Objective 3: To investigate the dynamics of phosphorus and soil minerals in relation to a restoration trajectory on soil chronosequence at PCRP (Chapter 5).

- Objective 4: To investigate the dynamics of phosphorus and soil minerals under different stands of vegetation at PCRP (Chapter 6).
- Objective 5: To investigate the interactions between earthworm, flax and bird guano in a glasshouse pot experiment (Chapter 7).
- Objective 6: To evaluate the overall relationships between soil and plant variability along the restoration trajectory at PCRP (Chapter 8).

These objectives were investigated through a combination of laboratory, glasshouse and field studies.

1.4 Chapter descriptions

Chapter 2: General materials and methods

- This chapter provides details of the field study site, plants and soils used, plant and soil sampling in methodology, and protocols for analysis of plant and soil properties.

Chapter 3: Plant litter variability and soil N mobility (Soil Research, 2016, in press)

- This part of study aims to investigate the variability of native plant litter chemistry, and the effects of native plant litter on soil chemical properties. This was a study to evaluate the potential role of native plants to modify soils and ameliorate topical environmental concerns associated with agricultural land, in terms of nitrate leaching and GHG emissions.

Chapter 4: Ecological restoration and dynamics of DOC and mobile nitrogen in soil leachates

- Dissolved organic carbon and mobile nitrogen in soil solution are particularly important in nutrient cycling, ecosystem functioning and succession in terrestrial ecosystems. Little is known of the effects of forest ecosystem restoration on the dynamics of dissolved organic carbon and mobile nitrogen in soil. This chapter investigates the dynamics of dissolved organic carbon and mobile nitrogen in soil leachates on a restoration trajectory and their potential role in monitoring and assessing the progress of ecological restoration.

Chapter 5: The dynamics of soil P and soil minerals on the restoration trajectory

- Since Walker and Syers's (1976) conceptual P model was first proposed, transformation and dynamics of soil P during soil chronosequence and ecosystem development have been studied in many soils under different climatic zones and geomorphological sites. Many studies investigated the effects of afforestation on soil P dynamics, but little attention has been given to the effects of P on ecological restoration. Soil Fe/Al minerals, closely relating to soil P dynamics, also help to tell the story of soil development. This chapter investigates P dynamics and soil Fe/Al minerals on the restoration trajectory at PCRP. Understanding the importance of soil knowledge and pedogenesis in ecological restoration on different ages of soils is the challenge of this work.

Chapter 6: Soil phosphorus and mineral dynamics under different vegetation stands

- It is known that different plant species can modify soil biogeochemistry differently, including their effects on soil P and Fe/Al minerals. I investigate whether forms of soil P and Fe/Al minerals are different under flax and palm stands at PCRP. In this ecosystem, the role of external nutrient inputs from guano of birds should also be taken into consideration. This chapter evaluates the role of three plant stand variables on soil and ecosystem development.

Chapter 7: The interactions between earthworm, flax and guano on the P dynamics: a glasshouse pot trial

- This chapter reports an experimental study of interaction between plants, soil, earthworms and bird guano. This experiment simulates a scenario of soil beneath flax plants that receives bird guano and interacts with earthworms. Phosphorus-enriched bird guano from large coastal populations of seabirds in New Zealand are likely to have significant effects on coastal ecosystems. Earthworms are known to benefit soil processes and plant growth. However, little is known how their interactions will impact soil P dynamics.

Chapter 8: Analysis of wider dataset: PCRP restoration trajectory

- This chapter investigates the relationships between soil chemistry, biodiversity and plants on the restoration trajectory at PCRP through multivariate analysis.

Chapter 9: Synopsis and Conclusion: ecological restoration trajectory at PCRP

- This chapter synthesizes the overall findings of this research relating to the overall aim and six objectives.

Appendices

Appendix A includes: (i) Table A.1 outlines the selected restoration planting species and their planting scheme; and (ii) Table A.2 outlines the glossary of plant species abbreviations in the statistical analysis.

Appendix B includes supplementary data to accompany Chapter 3.

Appendix C provides three figures to show soil DOC, NH_4-N and NO_3-N concentrations of each plot in each transect and sampling event.

Appendix D includes: (i) Table D.1 provides the soil profile descriptions to accompany Chapter 5; and (ii) Table D.2 provides the soil profile descriptions to accompany Chapter 6.

Appendix E includes: Figure E.1 the correlation heat-plots of correlation of soil physicochemical variable within each plot type, for Ah and Bw soil to accompany Chapter 8.

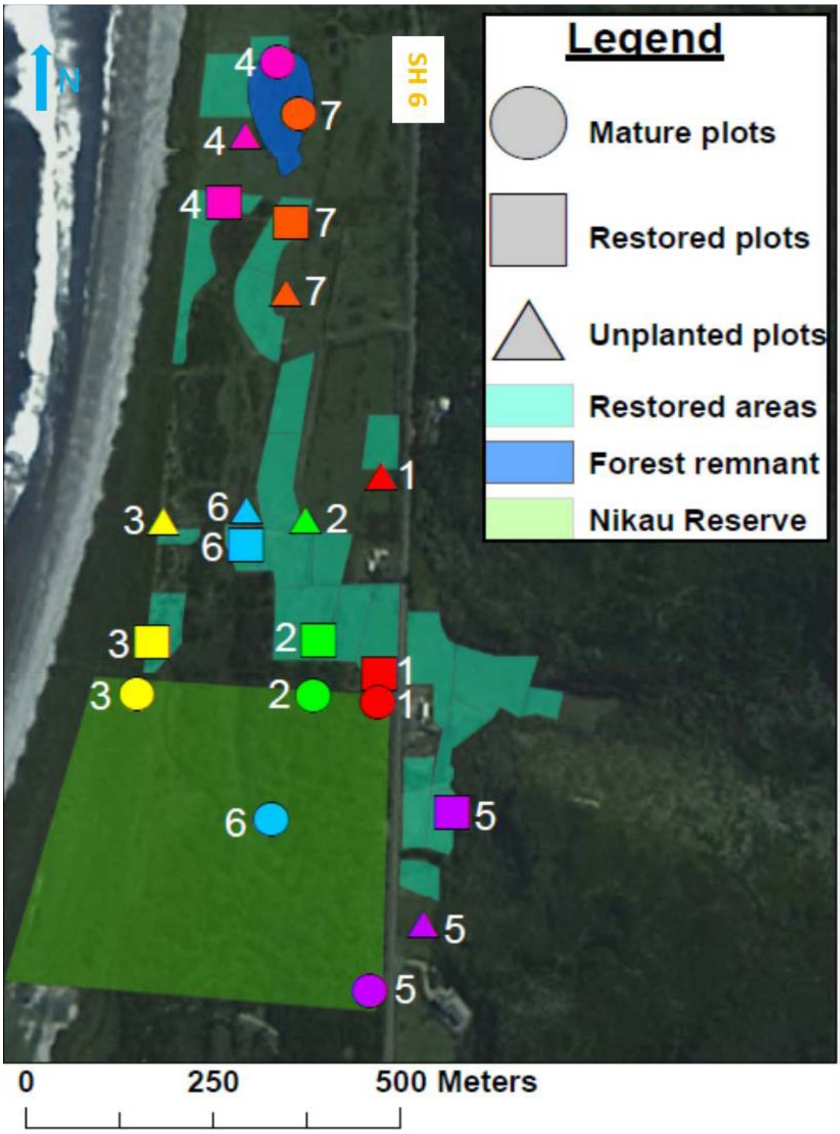
Appendix F introduces a published paper studied in the PCRP.

Chapter 2

General Materials and Methods

2.1 Study site: design of experimental plots

The field study site locates in the Punakaiki Coastal Restoration Project (PCRP) area (see Chapter 1). In terms of the experimental design, four monitoring transects were initially established in 2011 by N. Dickinson and M. Bowie, with three more transects added in July 2012 in order to make data from monitoring more statistically robust (Figure 2.1) (Hahner et al., 2013). These transects were aligned with dune ridges and run parallel with the coast line. Each transect consisted of three plots with each plot located on the same land surface in order to minimize confounding variables such as such as soil age and soil type. For each transect, one plot was located within Mature forest (NSR or remnant forest stands); one within a Restoration plot; and one within an Unplanted plot (abandoned agricultural grassland). A soil pit (about 1m × 1.5m × 2m) was dug in each of the 21 plots in order to describe soil profile. Soil types of the 21 plots are shown in Table 2.1. The author (myself) of this PhD study joined the PCRP project when soil survey of the project site was carried out in 2013. In the present part of the wider monitoring study, Transects 1, 2 and 4 were selected to investigate the effects of restoration practices on carbon and nitrogen dynamics in the soil leachates (Chapter 4). Transects 1 and 3 were selected to investigate soil phosphorus dynamics and soil minerals on restoration trajectories (Chapter 5). Remnant New Zealand Flax and Nikau Palm stands, and unplanted grassland were selected to investigate the effects of different vegetation on soil phosphorus dynamics and soil minerals (Chapter 6).



Restoration Plots	Starting Time
R1	Aug-Oct 2009
R2	May-Aug 2010
R3	Jan-Apr 2010
R4	Aug-Nov 2011
R5	Oct-Nov 2011
R6	Aug-Nov 2010
R7	May-Aug 2012

Figure 2.1 Distribution of the existing 7 transects in PCRP site (Hahner et al., 2013). Each numbered transect contains a plot of Mature Forest vegetation, a Restoration plot, and an area of agricultural grassland (not planted for restoration).

Table 2.1 Soil types present in each plot of each of the 7 transects at PCRP (modified from Smith et al., 2016).

Transect	Mature			Restored			Unplanted		
	Soil series	NZ soil classification(1)	USDA soil taxonomy(2)	Soil series	NZ soil classification(1)	USDA soil taxonomy(2)	Soil series	NZ soil classification(1)	USDA soil taxonomy(2)
1	Mahinapua	Sandy brown	Dystrudept	Mahinapua	Sandy brown	Dystrudept	Mahinapua	Sandy brown	Dystrudept
2	Kamaka	Orthic brown	Dystrudept	n.d.	n.d.	n.d.	Waiwero	Fluvial recent	Udifluent
3	Karoro	Orthic brown	Dystrudept	Karoro	Orthic brown	Dystrudept	Karoro	Orthic brown	Dystrudept
4	Kamaka	Orthic brown	Dystrudept	Kamaka	Orthic brown	Dystrudept	Kamaka-shallow	Orthic brown	Dystrudept
5	Kamaka	Orthic brown	Dystrudept	Kamaka	Orthic brown	Dystrudept	Kamaka	Orthic brown	Dystrudept
6	Kamaka-shallow	Orthic brown	Dystrudept	Kamaka-shallow	Orthic brown	Dystrudept	Kamaka-shallow	Orthic brown	Dystrudept
7	Kamaka	Orthic brown	Dystrudept	Kamaka-shallow	Orthic brown	Dystrudept	Kamaka-shallow	Orthic brown	Dystrudept

(1) Hewitt, 2010;
(2) Soil Survey Staff, 2014.

2.2 Materials

2.2.1 Plant leaf litter

Leaf litter was randomly collected from eight native and two exotic plant species commonly found on the Canterbury Plains. Necrotic leaves prior to abscission were sampled from a Lincoln University Dairy Farm (43°38’38’’S, 172°26’02’’E), where native plant plots had been established in 2008 (Franklin, 2014). Withered yellowing and necrotic litter of ryegrass was collected from the same area. *Pinus radiata* needle litter was collected from the Lincoln University campus. Three replicates per species of all plant leaf litter samples were collected and stored in paper bags prior to use in experimental work.

2.2.2 Litter incubation experiment soils

A Lowcliffe stony silt loam (mottled argillic pallic soil, Hewitt, 2010; udic Haplustalf, Soil Survey Staff, 2014), was collected from a dryland sheep paddock at the Gammack Estate (43°38’39’’S, 172°23’28’’E), near Lincoln University. This soil type is widely representative in the production agricultural landscape of the South Island, New Zealand (Molloy et al., 1998). This soil has slow permeability, medium nutrient content and low organic matter content. The surface 0-15 cm of the topsoil was used after discarding the mixed-grass turf. The soil was sieved through a 4 mm steel sieve, and stored for up to 3 months before use in laboratory incubation experiments.

2.2.3 Glasshouse pot trial soils

Topsoil (0-20 cm) of a silt loam [Sandy brown (Hewitt, 2000); Dystrudept (Soil Survey Staff, 2014)] were used from mature plot M1 at PCRP. The topsoil was collected after removing the surface litter layer. Soil was sieved through a 6 mm steel sieve, and stored for up to 3 weeks before used in a pot trial experiment.

2.3 Methods

2.3.1 Collection and analysis of plant and soil samples

Plant samples

Leaf litter samples were dried at 60 °C, crushed and ground though a 1 mm sieve (Restch centrifugal mill) then stored in air-tight polyethylene containers prior to analysis for chemical composition. Plant samples (both stem and root) were harvested from glasshouse experiments. Roots were gently separated and carefully washed from the soil. They were stored in paper bags and dried at 60 °C. Dry biomass was weighted afterward and they were prepared in the same way as litter samples.

Fresh soil samples

Fresh soils sampled from the litter incubation experiment, the glasshouse experiment and the field site, were sieved through a 2 mm brass sieve and stored in zip-lock polyethylene bags at 4 °C for less than 1 week prior to analysis.

Air-dried soil samples

A subsample of each soil, from the litter incubation experiment, the glasshouse experiment and the field site, were air dried (25°C for up to 1 week), and crushed using a rubber hammer or metal rod, then sieved through a 500 µm brass sieve, and stored in zip-lock polyethylene bags at room temperature prior to chemical analysis.

2.3.2 Quality control: analyses of soil biological and chemical properties

General analytical methods, and quality control and assurance follow those described in Lincoln University Laboratory Manual (Cresswell & Hassall, 2015). Specific details of methodology follow:

Soil microbial biomass carbon

Microbial Biomass Carbon (MBC) was measured by $CHCl_3$ fumigation and extraction as described in (Vance, Brookes & Jenkinson, 1987). Fumigation was performed in vacuum in an air-tight cabinet for 24 hours in the dark. A 5 g sample of fresh soil with visible roots removed was extracted in 20 ml 0.5M K_2SO_4 with and without fumigation. After 30 mins shaking in an end-over shaker (hereafter as shaker), soil extracts were then filtered (Whatman No. 42). Soluble organic carbon in extracts was analysed using a TOC-5000A with an auto sampler (Shimadzu, Japan). A conversion factor (K*c*) of 0.45 was applied to the results following (Wu et al., 1990).

Soil microbial biomass phosphorus

Microbial Biomass Phosphorus (MBP) was measured by $CHCl_3$ fumigation and extraction as described in (Brookes, Powlson, & Jenkinson, 1982). Fumigation was performed in vacuum in an air-tight cabinet for 24 hours in the dark. A 1 g soil sample (oven dry basis) with visible roots removed, was extracted with 20 ml 0.5M $NaHCO_3$ (pH=8.5) with and without fumigation. Soil extracts were shaken for 30 mins in a shaker and filtered through Whatman No. 42. Phosphate concentrations were determined by a UV160A spectrophotometer at 880 nm (Shimadu, Japan). A conversion factor (K*p*) of 0.4 was applied to the results following (Brookes et al., 1982).

Soil dehydrogenase activity

Soil Dehydrogenase Activity (DHA) was determined using a method involving reduction of triphenyltetrazolium chloride (TTC) to triphenylformazan (TPF), adjusted from Casida Jr, Klein and Santoro (1964) and Gong (1997). A sample (2 g) of fresh soil was incubated with 2 ml of 1% TTC–Tris buffer (pH=7.6) at 25 °C for 24 hrs in 25 ml falcon tubes in dark incubator. After extraction with 10 ml of methanol, the supernatant (centrifuge at 3000 rpm for 10 min) was measured by the absorbance at 485 nm through a UV 160A spectrophotometer (Shimadzu, Japan).

Soil mineral nitrogen

A fresh soil sample (4 g) was extracted with 40 ml 2M KCl in 50 ml falcon tubes and shaken for 1 hour in a shaker. Soil extracts were centrifuged at 2000 rpm for 10 mins, and then filtered (Whatman No. 41). Determination of mineral nitrogen (NH_4-N and NO_3-N) used a FIAstar 5000 triple channel analyser with SoFIA software version 1.30 (Foss Tector AB, Sweden) (Blakemore et al., 1987; Clough et al., 2001).

Soil $pH_{(water)}$ and electrical conductivity

Soil pH and electrical conductivity (EC) were measured in suspension with deionized (DI) water at a ratio of 5 g of air-dried soil to 25 ml of DI water using soil pH and EC probes (calibrated with pH 4 and 7 buffer solutions) (Mettler Toledo, Australia) (Blakemore et al., 1987).

Soil total organic matter and organic carbon

Soil total organic matter content was determined by loss on ignition (LOI) method. A 10 g of air-dried soil in a crucible was dried in 105°C for 12 hours, re-weighed when cool, placed into muffle furnace and hold at 550°C for 4 hours, and then re-weighed when cool. Soil organic carbon content was estimated by dividing the total organic matter (LOI) with a conversion factor of 1.72 (Blakemore et al., 1987).

Total carbon and nitrogen

Total C and N of dried plant leaf litter samples and soil samples were determined using the Dumas combustion method on CNS Elemental Analyser (LECO Elemental Analyser, NSW, Australia) (Blakemore et al., 1987). Results are expressed on an oven-dry (105°C) basis.

Elemental concentrations

Trace element contents were determined using ICP-OES (Varian 720 ES, Australia) following microwave digestion (Microwave digester, CEM MARS Xpress, USA) of the sample in 5M HNO_3 (Quality Control: International Plant Analysis Exchange, WEPAL Plant Material) (Blakemore et al., 1987). Results are expressed on an oven-dry (105°C) basis.

Olsen P

Olsen P was analysed on a 0.5M $NaHCO_3$ (pH=8.5) extraction at a ratio of 1 g to 20 ml of soil to extractant. Soil extracts were shaken for 30 mins in a shaker, then centrifuged at 2000 rpm for 10 mins and filtered (Whatman No. 42). Phosphate concentration in the extracts was determined using a Muphey-Riley colour reagent, with absorbance read at 880 nm on a UV160A spectrophotometer

(Shimadu, Japan) (Olsen et al., 1954; Blakemore et al., 1987). Results are expressed on an oven-dry (105°C) soil basis.

Soil extractable Fe and Al

Soil extractable Fe and Al were performed using three different extractions. Mineral contents in all extracts were determined using ICP-OES (Varian 720 ES, Australia) (Blakemore et al., 1987). Filtrates were stored in a freezer prior to analysis. Results are expressed on an oven-dry (105°C) soil basis. Three extractions include:

(1) A 0.5 g sub-sample of air-dried soil was extracted with 50 ml 0.2M acid oxalate reagent (ammonium oxalate and oxalic acid, adjust pH=3±0.5) in falcon tubes; soil extracts were shaken for 4 hours in a shaker, centrifuged at 2000 rpm for 10 mins and then filtered through Whatman No. 42; this extracted poorly crystalline minerals and mobile metal-organic complexes;

(2) A 1 g sub-sample of air-dried soil was extracted with 50 ml citrate-dithionite reagent (40 ml 0.3M tri-sodium citrate and 10 ml 1M sodium bicarbonate) in 100 ml centrifuge tubes with another 1 g of sodium dithionite added during water bath (≈100°C for 1 hour); soil extracts were centrifuged at 2000 rpm for 10 mins, then filtered through Whatman No. 42; this extracted Fe in secondary iron oxides and the fractions extracted by acid oxalate and pyrophosphate;

and (3) a 0.35 g sub-sample of air-dried soil was extracted with 35 ml of 0.1M sodium pyrophosphate solution in 50 ml high-speed centrifuge tubes (Thermo Scientific), shaken for 16 hours in a shaker; followed by 5 drops of 0.2% superfloc and shake vigorously on Vortex shaker; then centrifuged at 10,000 rpm for 30 mins and filtered through Whatman No. 42; this extracted Fe and Al in metal-organic complexes.

Soil phosphorus fractionation schemes

Two soil phosphorus fractionation schemes were employed in this study.

1. The first soil P fractionation scheme (non-sequential) adapted from Eger, Almond, & Condron. (2011) (used in Chapter 5 and 6), which includes:

(1) total phosphorus: P (tot) was estimated by NaOH fusion; a 0.1 g of air-dried soil in a nickel crucible added with 1.5 g NaOH pellets; heat to 400°C and hold for 10 mins, then increase heat to 800°C and hold for 15 mins in muffle furnace; remove the crucibles and place in a 250 ml beakers when cool; wash with approximately 60 ml hot DI water, and leave for 30 mins; wash the contents of the crucible into beakers and filter through Whatman No. 42 into 100 ml volumetric flask (rinse the beaker and filter paper carefully for several times); then add 3 ml concentrated H_2SO_4 (96-98%) to each flask, cool and make to volume with DI water (Smith & Bain, 1982);

(2) organic phosphorus: P (org) was estimated by subtracting the 0.5M H_2SO_4-extracted phosphorus after and before ignition; weigh 1 g of air-dried soil in a porcelain crucible and slowly heat to 505°C (1-2 hours) and hold for 1 hour in muffle furnace; transfer the contents of the crucible to 100 ml centrifuge tubes when cool; in a separate centrifuge tube, weigh 1 g of air-dried unignited soil; add 50 ml 0.5M 0.5M H_2SO_4 and shake for 16 hours in a shaker; centrifuged at 1500 rpm for 5 mins and filtered through Whatman No. 42 (Saunders & Williams, 1955);

(3) acid-extractable phosphorus: P (acid) equals to 0.5M H_2SO_4-extractable phosphorus on unignited soil described above in organic P methods;

(4) phosphorus attached to iron/aluminium oxides and mainly apatite phosphorus were estimated by sequential extractions with 0.1M NaOH for P (Fe/Al) and 1M HCl for P (Ca); a 1 g of air-dried soil extracts with 30 ml of 0.1M NaOH and shake for 16 hours in a shaker, centrifuged at 10,000 rpm for 10 mins, then filtered through Whatman No. 42; followed by a gentle wash with DI water, centrifuge and discard the supernatant; add 30 ml 1M HCl, shake, centrifuge and filter in the same manner; and these two fractions are considered as non-occluded phosphorus (Walker & Syers, 1976);

(5) inorganic phosphorus: P (in) was the difference between P (tot) and P (org);

(6) occluded phosphorus: P (occ) was the result of P (tot) - P (org) – P (Fe/Al) - P (Ca).

2. The second soil P fractionation scheme employed is used to extract soil biologically based phosphorus pools, which emulates mechanisms of plant and microbial phosphorus acquisition strategies (DeLuca et al., 2015). This methods is used in Chapter 7. Each P fraction was measured in parallel by shaking a 1 g of air-dried soil with 20 ml of each extractant for 3 h. Extracts were then centrifuged at 2280*g* for 30 min, and filtered through Whatman No. 42. Filtrates were stored in a fridge (4 °C) prior to analysis. They are:

(1) 0.01M $CaCl_2$ extractable P: $CaCl_2$-P represents soluble and weakly adsorbed inorganic P;

(2) 0.01M citrate extractable P: Citrate-P represents active inorganic P pool adsorbed to clay particles or weakly bound in inorganic precipitates;

(3) 1M HCl extractable P: HCl-P represents inorganic P pool that moderately bound to clay minerals or precipitate Fe, Al or Ca minerals.

Phosphate concentrations in all extracts were determined spectrophotometrically using a UV160A spectrophotometer at 880 nm (Shimadu, Japan) after reaction with molybdate blue (Murphy & Riley, 1962; Blakemore et al., 1987). Filtrates were stored in a fridge (4 °C) prior to analysis. Results are expressed on an oven-dry (105°C) basis.

Chapter 3

Plant Litter Variability and Soil N Mobility

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3.1 Introduction

Plant litter input and its decomposition modifies the physical, chemical and biological properties of soil, protecting soil from erosion (Li et al., 2014; Marshall et al., 1996), mediating soil temperature and water content (Judas, 1990; Ogée & Brunet, 2002) and providing a major source of organic matter nutrients to soil (Hobbie, 2015). Litter fall is also a determinate factor in the assemblages of invertebrates and microbial communities found in soil (Sayer, 2006). The value of litter has been viewed largely in terms of provisioning soil development and nutrient cycling, in turn contributing to ecosystem health (Bardgett & van der Putten, 2014). Much less attention has been given to the role of litter variability in containing the mineralisation of nutrients and limiting the release of fractions of nitrogen pollutants to the wider environment.

Litter decomposition processes are driven by multiple factors such as litter quality, substrate characteristics and soil decomposer communities (Berg & McClaugherty, 2008). Relatively small differences in chemical composition of foliar amendments are known to make large differences in N and P mineralization, accumulation and depletion in soil (Constantinides & Fownes, 1994; Kumar & Goh, 2003; Alamgir et al., 2012; Damon et al., 2014). Furthermore, amending soils with fresh plant material (including ryegrass) as green manure may enhance N_2O emissions (Baggs et al., 2000; Mitchell et al., 2013; Zhu et al., 2013). N_2O emissions have been correlated with CO_2 flux in various plant residues, but negatively correlated with the C/N ratio of residues and recalcitrant carbon compounds (Huang et al., 2004; Millar & Baggs, 2004; Yanni et al., 2011). It appears to be difficult to predict the magnitude and direction of N_2O emissions, but organic amendments stimulate microbial respiration, thus depleting O_2 and increasing anaerobic conditions for denitrification (Miller et al., 2008; Chen et al., 2013). It has been suggested that N_2O losses to the atmosphere could be reduced by applying different combinations of plant materials or N-fertiliser of different qualities and ages to soil (Millar & Baggs, 2004; Gentile et al., 2008).

Recycling organic wastes to soil has obvious benefits to sustainable soil management practices in agroecosystems, but research has largely focussed on agricultural and human wastes rather than natural vegetation. Organic amendments to soil potentially have some disadvantages in way of nitrogen losses to the wider environment both through enhanced nitrate (NO_3^-) leaching to water bodies and gaseous emissions of nitrous oxide (N_2O) (Thangarajan et al., 2013). In New Zealand, agriculture is now the largest anthropogenic source of NO_3^- and N_2O contributing 46.5% of total emissions of greenhouse gas (GHG) profile, the highest for any developed country (Thorburn et al., 2012). Tightening the N cycle is vital for the future of integrated soil fertility management of farmland (Yanni et al., 2011).

This study aims to investigate:

(i) the variability of leaf litter chemistry between New Zealand native plant species; and

(ii) how native plant litters modify marginal farmland soil chemistry and potentially contribute to the amelioration of significant environment concerns around nitrate leaching and greenhouse gas emissions.

We question whether native plant litters could play a role in nitrogen management within intensive agricultural landscape matrices.

3.2 Materials and methods

3.2.1 Plant material and soil collection

Leaf litter was randomly collected from eight native and two exotic plant species commonly found on the Canterbury Plains (Table 3.1). Necrotic leaves were sampled prior to abscission from a restoration plot at Lincoln University Dairy Farm (43°38’38’’S 172°26’02’’E), where native vegetation had been established in 2008 (Franklin, 2014). Withered yellowing and necrotic litter of ryegrass (*Lolium perenne*), was collected from the same area. Pine (*Pinus radiata*) needle litter was collected from trees on the Lincoln University campus. Three replicates per species of all plant leaf litter samples were collected and stored in paper bags. They were dried at 60 °C, ground though a 1 mm sieve and stored in air-tight polyethylene containers prior to analysis for chemical composition.

Table 3.1 Plant species of the present study (source of preferred names for native species: www.nzflora.landcareresearch.co.nz), and their carbon to nitrogen ratios and acid detergent fibre (ADF) contents; data are mean values ± standard errors (n=3). All species are New Zealand native plants, apart from ryegrass and pine.

	Species	Family	Common name	C/N ratio	ADF (%)
Native dicots	*Sophora microphylla* Aiton (1789)	Fabaceae	kowhai	14.1 (3.3)^{c}	26.5 (2)^{e}
	Kunzea robusta de Lange et Toelken (2014)	Myrtaceae	kānuka	25.9 (0.6)^{c}	27.1 (2.9)^{e}
	Coprosma robusta Raoul (1844)	Rubiaceae	karamu	60.5 (4.7)^{b}	29.4 (0.5)^{de}
	Olearia paniculata (J.R.Forst. & G.Forst.) Druce (1917)	Compositae	akiraho	68.1 (3.8)^{b}	33.4 (0.3)^{cd}
	Dodonaea viscosa Jacq. (1760)	Sapindaceae	akeakea	30.4 (6)^{c}	36.8 (1.2)^{c}
Native monocots	*Carex secta* Sol. ex Boott. (1853)	Cyperaceae	pukio	65.1 (8.7)^{b}	46.7 (1.5)^{b}
	Cortaderia richardii Endl. (1836)	Poaceae	toetoe	58.4 (6.1)^{b}	47.7 (0.8)^{b}
	Phormium tenax J.R. & G.Forst. (1776)	Xanthorrhoeaceae	flax	101.8 (19.3)^{a}	56.5 (0.6)^{a}
Exotic species	*Lolium perenne*	Poaceae	perennial ryegrass	18.5 (0.3)^{c}	25.7 (1)^{e}
	Pinus radiata	Pinaceae	radiata pine	69.0 (12.5)^{b}	57.6 (1.7)^{a}

Lowcliffe stony silt loam (mottled argillic pallic soil, Hewitt, 2010; udic Haplustalf, Soil Survey Staff, 2014), was collected from a dryland sheep paddock at the Gammack Estate (43°38’39’’S 172°23’28’’E), situated near to Lincoln University. This soil type is widely represented in the production agricultural landscape of South Island (Molloy et al., 1998). This soil has slow permeability, medium nutrient content and low organic matter (Table 3.2). Surface topsoil (0-15 cm) was used after discarding the mixed-grass turf. The soil was sieved to 4 mm, and stored for up to 3 months before use in incubation experiments.

Table 3.2 Selected soil chemical and physical properties of the soil used in this study (modified from Kim et al., 2015). Data in columns are means (n=3) with standard errors in parenthesis.

Texture	silt loam
pH (1:5 W)	5.4 (<0.01)
Organic Matter (%)	7.5 (0.1)
Total N (%)	0.3 (<0.01)
C/N Ratio	12.2 (0.3)
NH_4-N (mg kg^{-1})	2.9 (0.5)
NO_3-N (mg kg^{-1})	88.1 (0.6)
Olsen P (mg kg^{-1})	34.4 (0.1)
Total P (mg kg^{-1})	341 (-)

3.2.2 Incubation experiment

To investigate the effects of leaf litter decomposition on soil chemistry, three separate litter-soil incubation experiments were carried out. In the first incubation experiment, 0.5 g, 1 g, and 1.5 g litter samples of the eight native species were mixed with 100 g of soil, and control without litter addition was included. In the second incubation experiment, 1.5 g of litter of 10 species (eight native and two exotic) was mixed with 100 g of soil, with an additional control without litter addition. In the third experiment, we conducted an additional litter-soil incubation experiment with only one species, *Oearia paniculata*, using 3 g of leaf material to 200 g of soil (same litter to soil ratio maintained) with three treatments: fresh green foliage, leaf litter and control (no litter addition). Since the three incubation experiments were conducted separately, we tested soil pH, mobile nitrogen, and available phosphorus at the start of each incubation experiment.

Three incubation experiments were conducted using 400 ml (6.5 cm diameter) screw-top-polyethylene incubator chambers, maintained at 16 °C, with a simulated 10/14 hours day/night rotation. Water contents of the litter-soil mixtures were maintained by weight, watering to 60% of soil field capacity (Shelton et al., 2000). Each incubator chamber was secured by a piece of nylon mesh with a rubber band to prevent contamination. Conditions were identical in three incubation experiments except that, in the second and third incubation experiments, small drainage holes had been drilled in the base of the chambers; these holes were sealed with air-tight duct tape immediately prior to gas sampling. The first and second incubation experiments were carried out over 31 days with gas samples taken on Day 30 in 290ml headspace. The third incubation experiment lasted 33 days and gas samples were taken on day 0, 2, 4, 8, 16, and 32, in 180ml headspace. Gas was sampled with a 15-mins interval (t_0, t_{15} and t_{30}) sampling scheme, using an air-tight glass syringe. Samples (10 ml) of gas were extracted through an air-tight septa located in the lid of the chamber, and then were injected into pre-evacuated 6 ml Exetainer glass vials (Labco Ltd., High Wycombe, UK). Soil samples were taken from the incubation chambers one day after gas sampling was completed in each incubation experiment, and stored in zip-lock polyethylene bags at 4 °C for less than 1 week prior to analysis.

3.2.3 Chemical analysis

Total carbon and nitrogen of leaf litter were analysed by an Elementar Vario-Max CN Elementary Analyser (Elementar GmbH, Germany). Trace element content was determined using ICP-OES (Varian 720 ES, Australia) following microwave digestion (Microwave digester, CEM MARS Xpress, USA) of the sample in 5M HNO_3 (International Plant Analysis Exchange, WEPAL Plant Material). Acid detergent fibre was determined gravimetrically as the residue remaining after extraction with a cetyl-trimethylammonium bromide, sulphuric acid solution (AOAC, 1990). This fibrous content represents the least decomposable portion of plant litter, including lignin, cellulose, insoluble forms of protein and minerals (ash).

Fresh soil samples were sieved (2 mm), and gravimetric water content was determined following drying at 105 °C. Further sub-samples were extracted with 2M KCl to determine mobile nitrogen (ammonium-N and nitrate-N) using a FIAstar 5000 triple channel analyser with SoFIA software version 1.30 (Foss Tector AB, Sweden) (Blakemore et al., 1987; Clough et al., 2001). Soil pH was determined on 1:5 (*w*/*v*) soil/water ratio on the air-dry soil (Mettler Toledo, Australia). Olsen P was determined on a 0.5M $NaHCO_3$ extraction using a UV160A spectrophotometer (Shimadu, Japan) (Olsen et al., 1954; Blakemore et al., 1987).

Gas samples were analysed using gas chromatography (SRI 8610 GC; SRI Instruments, CA, USA). Carbon dioxide (CO_2) and nitrous oxide (N_2O) were determined by flame ionization and ^{63}Ni electron capture detectors respectively, linked to an auto sampler (Gilson 222 XL; Gilson Inc., WI, USA) (Mosier & Mack 1980). Nitrous oxide and carbon dioxide production were calculated following equations described previously (Franklin, 2014).

3.2.4 Statistical analysis

Data were analysed using Minitab (Minitab Inc., State College, Pennsylvania, USA), performing one-way ANOVA with the Fisher's least-significance-difference post-host test and principal component analysis.

3.3 Results

3.3.1 Litter chemistry

Leaf litter of native plants showed a large variation in both fibre content and C/N ratio (Table 1). Fibre content of native monocots and pine needle litters was significantly higher than native dicots. C/N ratios ranged from 14 to 102, and were highest in native flax (*P. tenax*). Concentrations of macronutrients in the litter differed significantly between species and between the three plant groupings (Figure 3.1). Nitrogen was significantly higher in the N-fixing legume *S. microphylla* compared to other species. In the mid-range, *K. robusta* and *D. viscosa* had N concentrations similar to ryegrass, while other species had lower N concentrations. Phosphorus concentrations in *S. microphylla* and ryegrass litters were significantly higher than other native species. Potassium in *L. perenne* was significantly higher than all other species. Other macronutrients showed considerable variabilities between litters.

Trace element concentrations varied between species (Figure 3.2). Iron concentrations were significantly lower in native species, and Mn was high in *C. secta*. Native monocots contained less B, Zn and Cu, but more Mo. Principal Components Analysis of macro and micro nutrients (Figure 3.3) showed that 40% of the data variation as explained by the first principal component was due to a combination of P, S, and Cu. Some 35% of the data variation, illustrated by the second principal component, was positively correlated with Ca and B but negatively correlated with Mo. Ryegrass was largely separated by K, P, and S contents.

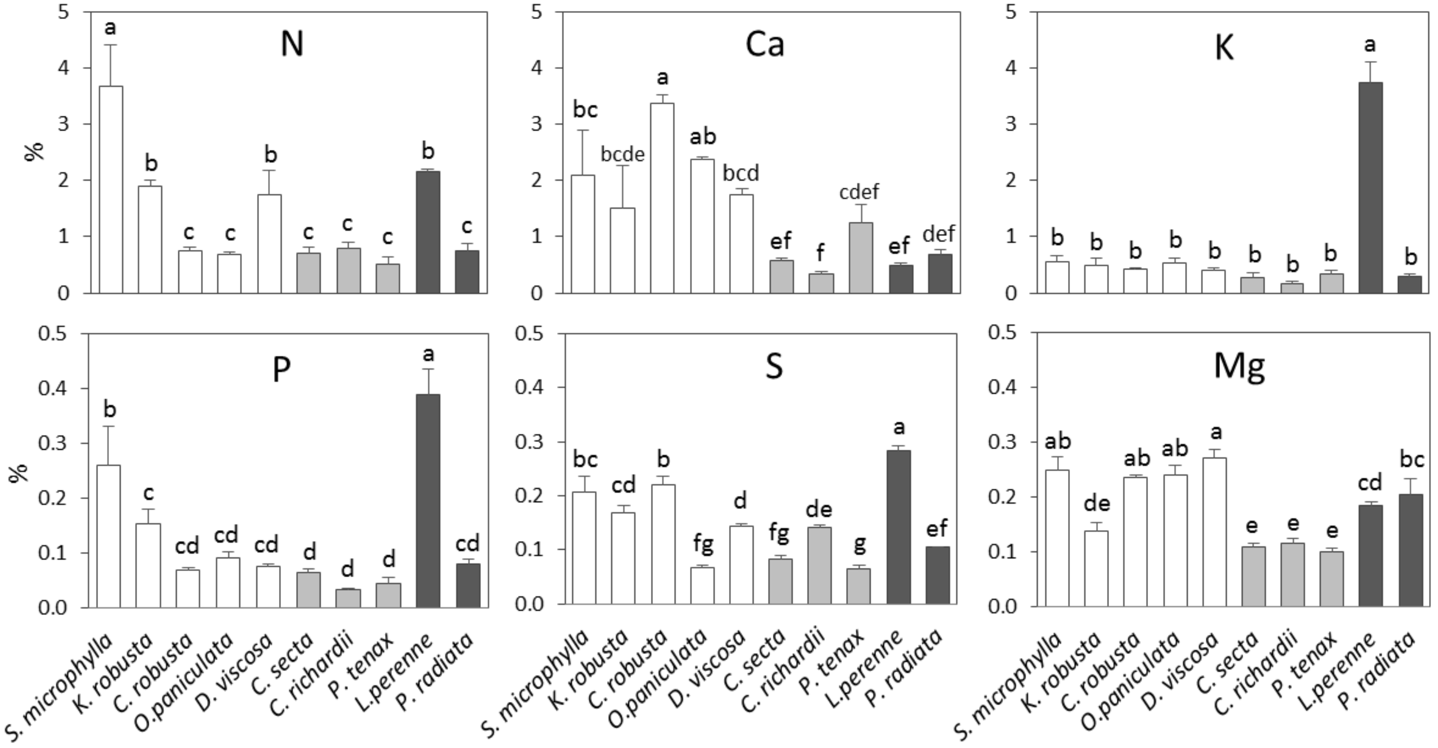


Figure 3.1 Macronutrient concentrations from foliage samples (□, native dicotyledons; ▨, native monocotyledons; ■, exotic species). Data are mean values ± standard errors (n=3). One-way ANOVAs with Fisher's test were run separately for each plant species and concentrations (p<0.05).

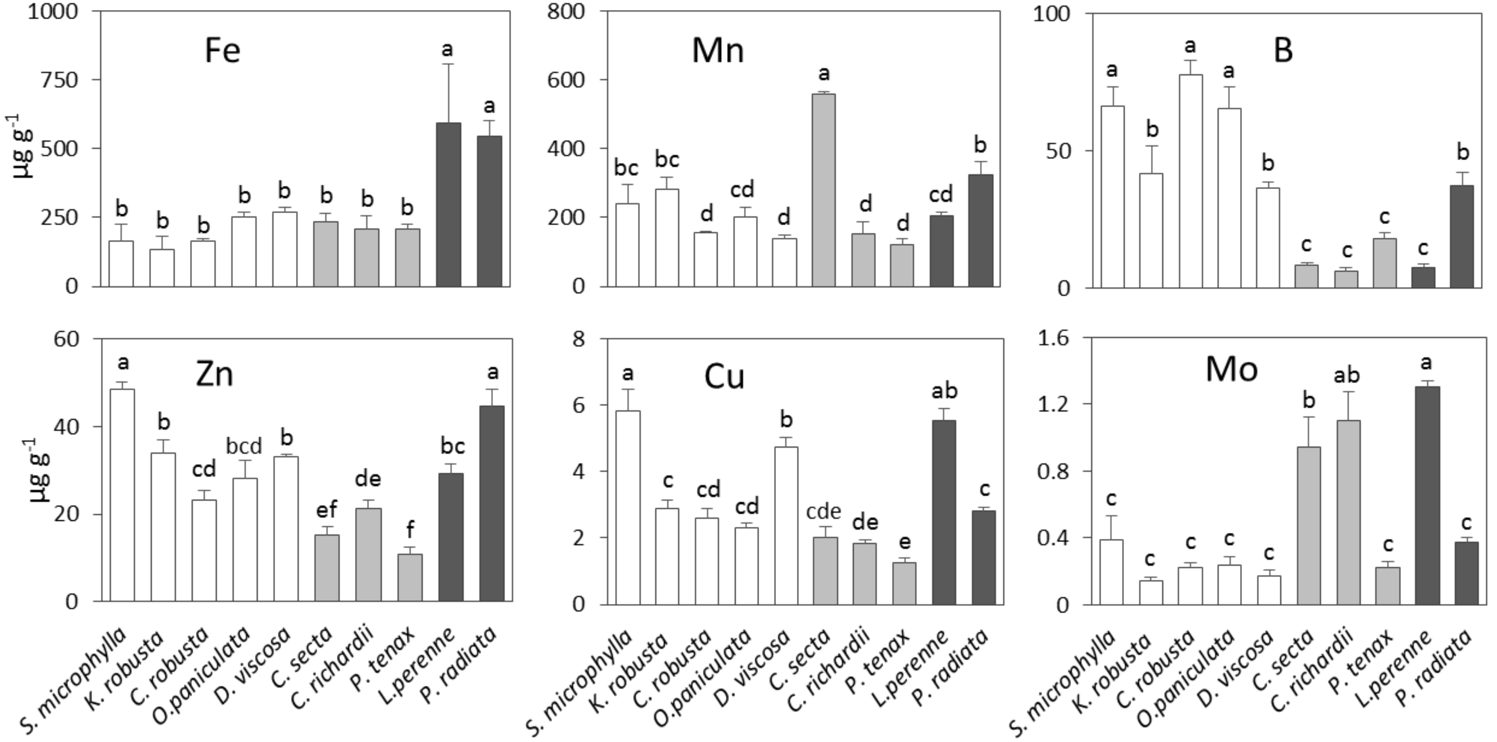
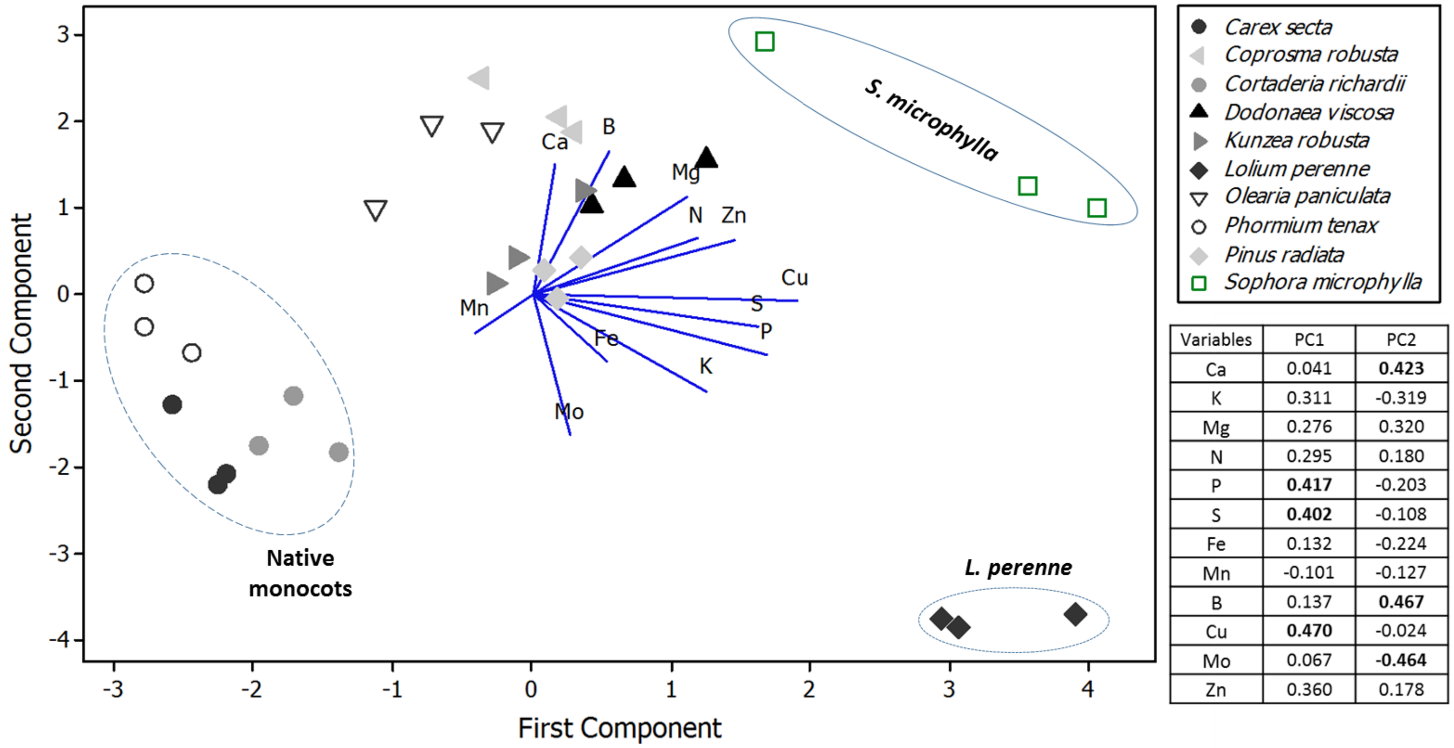


Figure 3.2 Trace element concentrations from foliage samples (☐, native dicotyledons; ▨, native monocotyledons; ■, exotic species). Data are mean values ± standard errors (n=3). One-way ANOVAs with Fisher's test were run separately for each plant species and concentrations ($p<0.05$).



Variables	PC1	PC2
Ca	0.041	**0.423**
K	0.311	-0.319
Mg	0.276	0.320
N	0.295	0.180
P	**0.417**	-0.203
S	**0.402**	-0.108
Fe	0.132	-0.224
Mn	-0.101	-0.127
B	0.137	**0.467**
Cu	**0.470**	-0.024
Mo	0.067	**-0.464**
Zn	0.360	0.178

Figure 3.3 Principal component analysis of foliar nutrient concentrations amongst 10 species. Points represent individual plants (n=3). The relative loading of the variables onto the axes is tabled. The first two components describe around 40% and 35% of data variation respectively.

3.3.2 Soil and litter incubation

Amendment of soil with native plant litter modified soil pH, mobile species of N and available P compared to the control soil (Table 3.3). In the first incubation experiment, soil pH increased in proportion to the amount of litter added. The amount of NH_4^+ in soil varied considerably between the different plant litter amendments and with different amounts of litter. Mineralization of NH_4^+ substantially increased with addition of three of the native dicot litters (*C. robusta, O. paniculata* and *D. viscosa*) and one monocot litter (*C. secta*). The range of NH_4^+ concentrations was significantly different between the first and second incubation experiments (0-10 mg kg^{-1} compared to 20-35 mg kg^{-1} respectively), including the controls. In the first incubation experiment, soil NO_3^- concentration was significantly less than the control in all treatments, falling lower with increasing amounts of litter. Most litters, except N-rich ryegrass and *S. microphylla* litter, appeared to sequester nitrate. Plant-available P, measured as Olsen P, was slightly reduced in the presence of litter compared to control, and with increasing amounts of litter. There was no statistical difference between first and second incubation experiments with regard to plant available P.

Table 3.3 Selected soil chemical characteristics from 30-day litter-soil incubation experiments. Data in columns are means (n=3) with standard errors in parenthesis.

	First Incubation Experiment												Second Incubation Experiment			
	pH (1:5 W)			NH$_4$-N (mg kg^{-1})			NO$_3$-N (mg kg^{-1})			Olsen P (mg kg^{-1})			NH$_4$-N (mg kg^{-1})	NO$_3$-N (mg kg^{-1})	Olsen P (mg kg^{-1})	pH (1:5 W)
Treatments	0.5 g	1 g	1.5 g	0.5 g	1 g	1.5 g	0.5 g	1 g	1.5 g	0.5 g	1 g	1.5 g	1.5 g			
Control	4.9 (<0.01)^{e}	4.9 (<0.01)^{h}	4.9 (<0.01)^{g}	1.9 (0.4)^{ab}	1.9 (0.4)^{d}	1.9 (0.4)^{d}	155 (6)^{a}	155 (6)^{a}	155 (6)^{a}	37 (<0.1)^{a}	37 (<0.1)^{a}	37 (<0.1)^{a}	4.7 (<0.01)^{h}	28 (1)^{e}	99 (3)^{b}	34 (<0.1)^{b}
S. microphylla	5.1 (0.1)^{b}	5.6 (<0.01)^{bc}	6.0 (<0.01)^{a}	1.7 (0.3)^{ab}	0.3 (0.1)^{e}	0.3 (0.5)^{e}	122 (6)^{b}	103 (5)^{b}	81 (6)^{b}	29 (<0.1)^{f}	27 (<0.1)^{e}	25 (1)^{e}	5.3 (<0.01)^{e}	29 (2)^{cde}	109 (3)^{a}	34 (1)^{b}
K. robusta	5.0 (<0.01)^{d}	5.6 (<0.01)^{b}	6.0 (<0.01)^{a}	1.4 (<0.01)^{ab}	0.1 (<0.01)^{e}	3.6 (0.5)^{c}	86 (4)^{c}	76 (9)^{c}	34 (4)^{c}	33 (<0.1)^{b}	31 (1)^{b}	29 (1)^{b}	5.4 (<0.01)^{c}	35 (<0.1)^{a}	2 (<0.1)^{de}	29 (<0.1)^{d}
C. robusta	5.2 (<0.01)^{ab}	5.6 (<0.01)^{c}	5.7 (<0.01)^{c}	1.5 (0.1)^{ab}	8.7 (0.5)^{a}	9 (0.7)^{a}	77 (2)^{cd}	47 (8)^{d}	3 (1)^{fg}	29 (<0.1)^{f}	25 (<0.1)^{f}	25 (<0.1)^{e}	5.5 (<0.01)^{b}	23 (<0.1)^{f}	1 (<0.1)^{e}	25 (<0.1)^{h}
O. paniculata	5.2 (<0.01)^{a}	5.5 (<0.01)^{d}	5.7 (<0.01)^{c}	1.2 (0.1)^{ab}	6.4 (0.1)^{c}	7.9 (0.4)^{ab}	75 (5)^{cd}	38 (5)^{de}	26 (7)^{cd}	31 (<0.1)^{e}	28 (<0.1)^{d}	27 (<0.1)^{d}	5.5 (<0.01)^{b}	29 (1)^{de}	1 (<0.1)^{e}	28 (<0.1)^{ef}
D. viscosa	5.1 (<0.01)^{cd}	5.4 (<0.01)^{e}	5.5 (<0.01)^{e}	1.2 (0.1)^{b}	7.5 (0.1)^{b}	8.9 (0.3)^{a}	87 (3)^{c}	47 (2)^{d}	15 (1)^{de}	31 (<0.1)^{e}	27 (<0.1)^{de}	28 (<0.1)^{c}	5.3 (<0.01)^{d}	32 (<0.1)^{abcd}	2 (1)^{de}	29 (<0.1)^{de}
C. secta	4.9 (<0.01)^{e}	5.1 (<0.01)^{g}	5.4 (<0.01)^{f}	1.5 (0.2)^{ab}	7.1 (0.2)^{b}	7.5 (0.5)^{b}	109 (9)^{b}	78 (10)^{c}	13 (1)^{ef}	32 (<0.1)^{b}	31 (<0.1)^{b}	28 (<0.1)^{c}	5.2 (<0.01)^{f}	32 (1)^{abc}	2 (<0.1)^{de}	27 (<0.1)^{fg}
C. richardii	4.8 (<0.01)^{f}	5.3 (<0.01)^{f}	5.6 (<0.01)^{d}	2 (0.5)^{a}	0.02 (<0.01)^{e}	0.5 (0.3)^{e}	116 (6)^{b}	80 (12)^{c}	2 (<0.1)^{fg}	32 (<0.1)^{d}	29 (<0.1)^{c}	28 (<0.1)^{c}	5.1 (<0.01)^{g}	29 (2)^{bcde}	1 (<0.1)^{e}	27 (<0.1)^{fg}
P. tenax	5.1 (<0.01)^{bc}	5.7 (<0.01)^{a}	5.8 (<0.01)^{b}	1.3 (0.2)^{ab}	0.2 (0.2)^{e}	<0.01^{e}	69 (1)^{d}	20 (4)^{e}	2 (<0.1)^{fg}	33 (<0.1)^{b}	31 (<0.1)^{b}	29 (<0.1)^{b}	5.2 (<0.01)^{ef}	27 (2)^{e}	1 (<0.1)^{e}	27 (<0.1)^{gh}
L. perenne	-	-	-	-	-	-	-	-	-	-	-	-	5.6 (<0.01)^{a}	32 (1)^{ab}	40 (2)^{c}	44 (1)^{a}
P. radiata	-	-	-	-	-	-	-	-	-	-	-	-	5.2 (<0.01)^{ef}	30 (2)^{bcde}	6 (2)^{d}	32 (<0.1)^{c}

3.3.3 Gaseous emissions

After a lag phase following wetting, increasing the amount of litter increased the organic matter available for microbial decomposition, consequently increasing respiration, as reflected in overall increased CO_2 emissions (Figure 3.4). Nitrous oxide emissions were lower at the highest level of litter amendment. Carbon dioxide emissions were 10 times higher in the second incubation experiment following the drilling of drainage holes, and CO_2 production was recorded with all litter amendments apart from *D. viscosa*, and differences in the production of N_2O were evident between species (Figure 3.5). Five species amendments led to an absence of N_2O gas production. *Pinus radiata* stimulated the highest N_2O emissions. The additional incubation experiment with *O. paniculata* showed significant differences in CO_2 and N_2O fluxes between treatments (Figure 3.6). Both green foliage and leaf litter amendments enhanced CO_2 production more than the control, but released less N_2O.

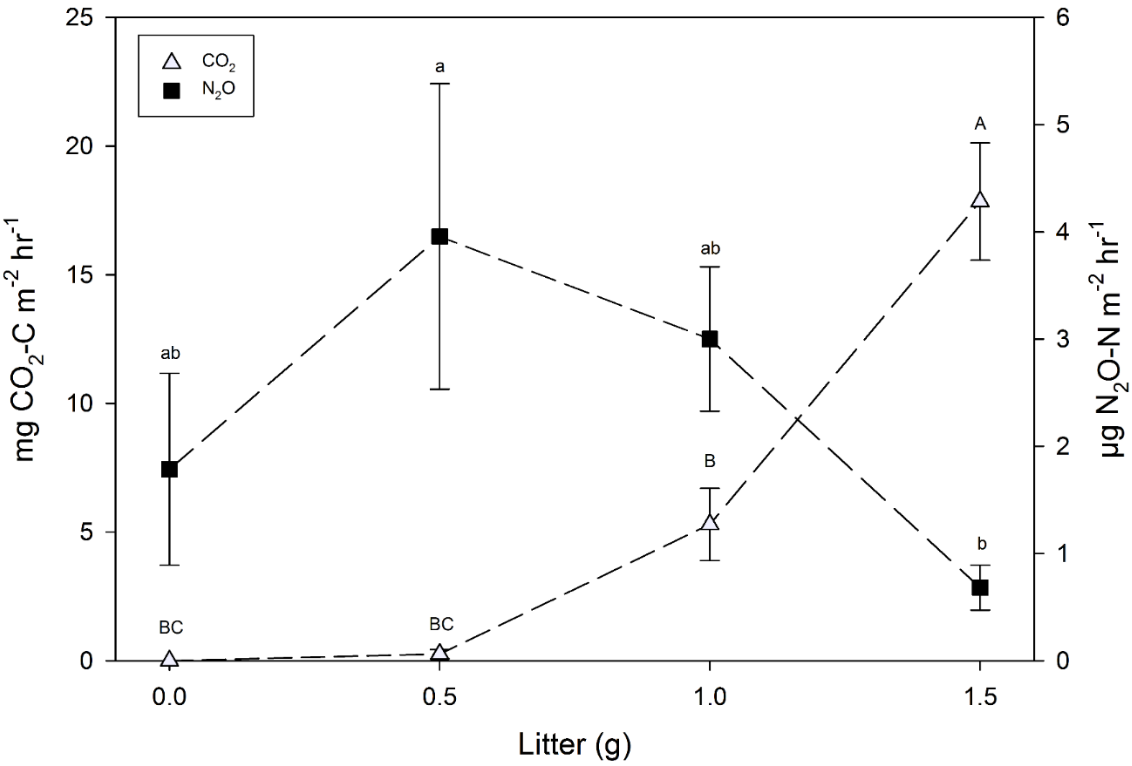


Figure 3.4 Overall soil △ CO_2 and ■ N_2O production of first-run soil incubation experiment at day 30, with 0 g, 0.5 g, 1 g and 1.5 g litter. Data of the 8 native species are combined and shown as mean values ± standard errors ($p<0.05$). Capitalised letters indicate significances for CO_2 production, lower case letters indicate significances for N_2O production. Zero values indicate likely headspace dilution or inhibitory effects of litter on gas emissions.

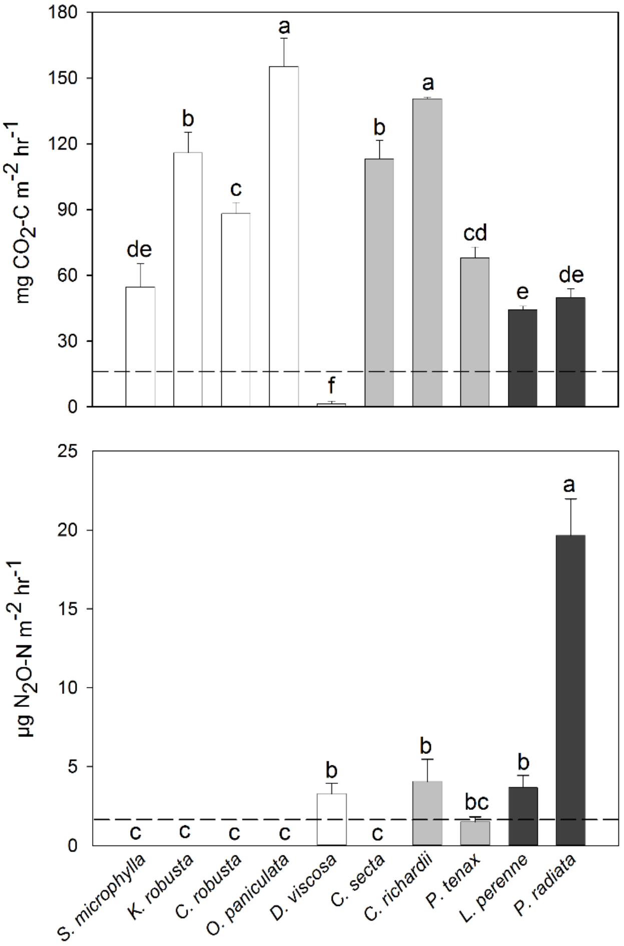


Figure 3.5 Soil CO_2 and N_2O production from second-run of litter-soil incubation experiment at day 30, using 1.5 g of litter (□, native dicotyledons; ▨, native monocotyledons; ■, exotic species); where dash lines indicate control treatments. Data are mean values ± standard errors (n=3). One-way ANOVAs with Fisher's test were run separately for CO_2 and N_2O production ($p<0.05$). Zero values indicate likely headspace dilution or inhibitory effects of litter on gas emissions.

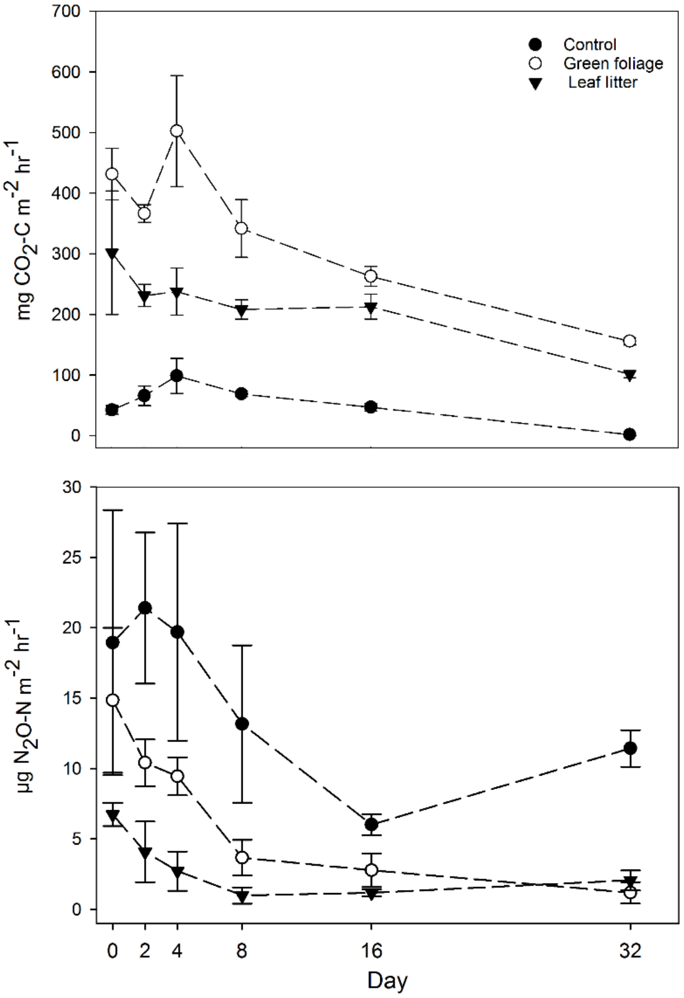


Figure 3.6 N_2O and CO_2 fluxes of *Olearia paniculata* litter-soil incubation using 1.5 g of litter. Data are mean values ± standard errors (n=3). One-way ANOVA with Fisher's test showed N_2O flux ($P<0.001$) and CO_2 flux ($P<0.001$) differences between treatments.

3.4 Discussion

3.4.1 Variation of litter chemistry

Plant litter quality and chemistry is highly variable in C/N ratios, fibre and nutrient contents. In turn this influences the progression of leaf litter decomposition and nutrient cycling, with onward implications for soil and environmental processes (Aponte et al., 2012; Berg & McClaugherty, 2008). Although C/N ratio has long been considered a primary factor in organic matter decomposition, fibre content such as recalcitrant lignin also controls the later stages of decomposition (Berg & McClaugherty, 2008; McLaren & Cameron, 1996). Our own earlier work showed that foliage from a range of native plants, compared to ryegrass, contained less nitrogen and higher but variable concentrations of a range of trace elements and tannins (Dickinson et al., 2015; Hahner et al., 2014). Uptake of nutrients from soil and leaf senescence strategies before shedding are species specific (Lim et al., 2007; Morgan & Connolly, 2013), although the amount of re-adsorption of nutrients prior to leaf shedding is entirely unknown in New Zealand native plant species.

The results of the present study, like those of Hahner et al. (2014), showed ryegrass is particularly efficient at sequestering the major nutrients, N, P, S and K, in both green and senescent foliage. Dickinson (1984) demonstrated that turf-forming grasses (including ryegrass) are far less conservative than herbaceous and woody plants in nutrient retention following senescence, relying on a growth strategy of rapid acquisition from soil rather than reabsorption prior to leaf shedding. Contrasting to this, in the present study, N contents in leaf litter of *P. tenax*, *C. richardii*, *O. paniculata* and *C. robusta* were significantly lower than in green foliage (see Table B.1 in Appendix B). The N-fixing shrub *S. microphylla* produces litter with a high N content; Berg & McMlaugherty (2008) similarly found that leaf litter of N-fixing species could have almost 10 times more nitrogen than N-poor species such as pine needle litter. The long leaf fibres of *P. tenax* provided the highest Ca concentration and fibre content among native monocots (Table 3.1, Figure 3.1). *K. robusta* is an early successional species on poor soils, with known symbiotic mycorrhizal associations to help acquire soil P (Davis et al., 2013; Smith et al., 2011), explaining relatively high P concentration compared to most other native species.

Widespread deficiencies of Cu, Co, Zn, Se, I, B, Mo, Mn and Fe in plants and animals in New Zealand are well described: 20-30% of farms are micronutrient deficient; fertilizers and supplements are routinely provided to both crops and livestock (Condron et al., 2000; Grace, 1992; Will, 1990). Molybdenum was high (c. 2 mg kg^{-1}) in green leaf material of *P. tenax* (Hahner et al., 2014), but low (c. 0.15 mg kg^{-1}) in its litter (Figure 3.2). Ryegrass contained high concentrations of Fe, Cu, Mo and Zn. Multivariate analysis separated pasture ryegrass and native monocots from other species. Herbaceous and woody plants were separated by the second principal component of calcium and boron (Figure 3.3), generally agreeing with the findings of Hahner et al. (2014).

3.4.2 Changes to soil chemistry

Soil pH increases were positively correlated with basic cation concentrations of leaf litter, in particular with Ca. This correlation has similarly been reported in other studies (Clarholm & Skyllberg, 2013; Marschner & Noble, 2000; Reich et al., 2005). Aponte et al. (2012) found that addition of litter to soil increased available K, Mg and Ca. However, in the present study, all of the 0.5 g litter treatments resulted in a lower pH than the original soil (Table 3.3). This may have been due to the small pH elevating effect from the relatively small amount of litter containing basic cations being negated by the acidifying effect of CO_2 produced from microbial respiration, or due to organic acid release from litter decomposition. Only minor changes in soil properties had occurred during storage between incubation experiments (data no shown).

A major limitation in the first incubation experiment was that the incubation chamber was a closed non-leaching system, with no possibility of losing basic cations or anions from the system. In the second incubation experiment drainage holes were drilled to allow for this, but in fact, no leachates were drained from the chambers while soil was maintained below full water holding capacity. The holes would of course have allowed increased aeration of the soil during incubation. In a study of the effects of water content on N_2O emissions, however, Zhu et al. (2013) thought that closed non-leaching chambers provide an effective experimental system in the laboratory, although they acknowledged it is uncertain how transferable these findings would be to the field condition.

In the present study, *S. microphylla* litter with a relatively low C/N ratio of 14 did not promote the mineralization of N as increasing amounts of litter were added to the soil (Table 3.3). Different C/N ratios of organic materials have been considered to promote nitrogen mineralization; McLaren and Cameron (1996) suggested a ratio of 25 was critical, Heal et al. (1997) suggested 20, and Brady and Weil (2008) suggested 17. It is known that temporary nitrate depression can occur when organic materials are first incorporated into soil, until the substrate C/N ratio falls to 20 (Brady & Weil, 2008). Nevertheless, Cabrera et al. (2005) and Ros (2012) considered that net mineralization of N is related more strongly with dissolved organic carbon or the water-soluble faction of organic matter. In the present study, *Phormium tenax* and *Pinus radiata* both had high fibre content, but *P. radiata* had relatively lower C/N ratio. This resulted in nitrate depression in both species treatments with minimal N mineralization in the *P. tenax* treatment (Table 3.3). Clearly it is important to take both fibre contents (e.g. lignin content) and C/N ratios of organic residues into consideration when evaluating N mobility associated with organic amendments (Brady & Weil, 2008).

Soil P availability is regulated by multiple factors, such as soil P fractionation, pH, redox potential, equilibrium criteria, plant and soil organisms, and chelating agents (Brady & Weil, 2008; McLaren & Cameron, 1996). Decreased soil available P after litter-soil incubation may have been due to adsorption of added litter P by soil organic factions, and to a lesser extent P associated surface absorption sites. The organic fraction of phosphorus may first be released by microbial decomposition, but at the same time also partially immobilized by microorganisms through assimilation into microbial biomass. Organic phosphorus is also gradually fixed by soil Fe/Al in acidic soils or Ca/Mg in alkaline soils, thus becoming temporally unavailable for plant uptake. Similar results were obtained by Singh and Jones (1976), Hedley et al. (1982), and by Varinderpal-Singh et al. (2006). In contrast, Randhawa et al. (2005) demonstrated that the application of green manure on agricultural soils increased soil exchangeable P through enhancement of organic P mineralization.

3.4.3 Litter amendments influence GHG emissions

All negative gas production rates were adjusted to zero for data analysis, since the gas sampling schemes we conducted were unlikely to indicate real negative gas productions. Possible reasons for the negative production rates recorded were: (i) N_2O or CO_2 did not have sufficient time to refill, leading to headspace dilution by N_2, O_2 and H_2O (vapour); (ii) reduced N_2O or CO_2 diffusivity due to different specific surfaces of ground leaf litter with different fibre contents; and (iii) less available NH_4^+ for nitrification processes due to potential adsorption onto ground leaf litter. Other soil amendments, such as biochar, have been reported to offer temporary sorption sites for N_2O or CO_2 gases and NH_4^+ (Clough et al., 2010; Cornelissen et al., 2013). However, apart from these potential physical effects on gas emissions by added litters, chemical and biological effects that may potentially play a role cannot be ignored.

Incorporation of organic residues to soil obviously increases soil microbial biomass, in turn raising microbial respiration and subsequent greenhouse gases emissions, although this flux may only last days or weeks (Blagodatskaya & Kuzyakov, 2008; Kuzyakov & Bol, 2006). In the first incubation experiment of the present study, CO_2 production was increased by litter amendments, while N_2O was suppressed (Figure 3.4). In the second incubation experiment, *D. viscosa* was particularly resistant to decomposition with low CO_2 production but positive N_2O production, even though its C/N ratio around 30 and fibre content of 35% were low compared to native monocots (Table 3.1, Figure 3.5). This is unlikely to have been an experimental error, as CO_2 and N_2O concentrations were measured from the same gas sample vial. It is likely there was insufficient mineralizable carbon to generate measurable quantities of CO_2 and N_2O at later stages of incubation. Mineralizable C availability from organic substrate does appear to have a critical role in soil gas production processes (Huang et al., 2004; Mitchell et al., 2013; Thangarajan et al., 2013).

Nitrous oxide can be derived from both nitrification and denitrification (Cameron et al., 2013; Thangarajan et al., 2013), and it has been suggested that providing more NO_3^- to denitrifying bacteria increases N_2O emissions (Bolan et al., 2004; Cameron et al., 2013; Muhammad et al., 2011). In the first incubation experiment of the present study, lower nitrate-N concentrations at the 1.0 g and 1.5 g treatments might partially explain lower N_2O production with increased litter amendments (Table 3.3, Figure 3.4). In the additional incubation experiment, *O. paniculata* gas fluxes (Figure 6) showed that green foliage treatment with lower C/N ratio (see Table B.2 in Appendix B) produced more CO_2 but suppressed overall N_2O production compared to control. Franklin et al. (2014) found *K. robusta* with a low leaf C/N ratio had an inhibitory effect on denitrification. In the present study, some native plant litter-soil mixtures similarly led to negative N_2O production estimates (Figure 3.5). This was due to N_2O concentrations at t_1 or t_2 being lower than at t_0, which would have been due to an inhibitory effect on the nitrifier or denitrifier denitrification processes. Contrary to this interpretation, however, Zhu et al. (2013) noted that crop residues with higher C/N ratio led to increased N_2O that indicated enhanced denitrification.

3.4.4 Agricultural context in New Zealand

The Canterbury Plains of the South Island of New Zealand has been extensively converted to agriculture, and native vegetation has been marginalized (Winterbourn & Knox, 2008). In less than 200 years since European colonization, conservation of biodiversity has been largely based on land separation, rather than land sharing. More recent reconciliation of agricultural production with biodiversity, coupled with an awareness of biodiversity losses, has meant that native plants are now being substantially restored to agricultural landscapes. This partial rewilding of farmland may also help to mitigate the environmental impact of agriculture and critically build resilience into the agricultural economy (Dickinson et al. 2015). Over 80% of New Zealand's native plant species are endemic and not found elsewhere, and it has been found there is a high variation of foliage chemistry among New Zealand native plants (Dickinson et al., 2015; Franklin, 2014; Hahner et al., 2014; Lambert et al., 1989). The findings of the present work suggest that restoring biodiversity to agricultural landscapes may provide benefits to both conservation and the environment.

3.5 Conclusions

Differences between native plant litter in terms of C/N ratio, acid detergent fibre, macronutrient and trace element content have a notable impact on soil chemistry, markedly different to the effects of litters from the two exotic species. When small amounts of litter are incorporated into soil there is a substantial impact on soil pH, reflecting the addition of Ca, and the acidifying effect following decomposition and microbial respiration. Leaf litter chemistry and fibre content are likely to have significant influence on the decomposability of litter, thereby also directly determining CO_2 emissions. At the same time, native plant litter clearly inhibits the release of N_2O from soil. The present paper has shown that litter incorporated into soil from native plants modifies soil characteristics and may help to ameliorate concerns associated with nitrate leaching and GHG emissions. Native plants embedded in intensive agricultural landscapes may play a small but significant role in tightening the N cycle and improving integrated soil fertility management.

Chapter 4

Ecological Restoration and Dynamics of DOC and Mobile Nitrogen in Soil Leachates

4.1 Introduction

Carbon and nitrogen cycles connect the living and non-living parts of the environment, for example through photosynthesis and biological nitrogen fixation (Bardgett & Wardle, 2010). These two cycles are inseparably linked. It has been estimated that up to 20% of carbon fixed by photosynthesis is invested into soil via plant root exudation; potentially 5% of this investment is stored as soil organic matter (Hütsch, Augustin, & Merbach, 2002; Nguyen, 2009). Biological nitrogen fixation is the largest source of nitrogen input into terrestrial ecosystems (Sullivan et al., 2014). Nitrogen is a critical nutrient for plants and is involved in many physiological functions, particularly as a primary constituent for proteins and nucleic acids (Brady & Weil, 2008). Plants uptake nitrogen as nitrate and ammonium. However, nitrate is prone to leach out from the plant-soil interface, potentially reaching surface water bodies or aquifers, which may cause further environmental issues (McLaren & Cameron, 1996).

Dissolved organic carbon (DOC) is defined as the fraction of total organic carbon in soil-dissolved organic matter (DOM) solution that passes through a 0.45μm micro filter (Zsolnay, 2003). DOC is the main constituent of soil-dissolved organic matter, although it only accounts for a minor part of soil organic matter. Its mobility, activity, lability and accessibility in the soil matrix contribute significantly to soil biodiversity, nutrient cycling, ecosystem functioning and development (Kalbitz et al., 2000). Since 1990s, extensive research has been devoted to study the dynamics and controls of DOM in forest ecosystems both under controlled laboratory and field conditions (Kalbitz et al., 2000; Bolan et al., 2011). However, conflicting results have been found under field conditions compared to those findings from laboratory studies (Kalbitz et al., 2000, Michalzik et al., 2001).

The dynamics of soil DOM (including DOC) is regulated by biotic and abiotic factors, including the organic matter pool, decomposer communities, soil pH, metal oxides and clay contents; and environmental factors including moisture, temperature, precipitation and water fluxes (Kalbitz et al., 2000; Bolan et al., 2011). There are questions that remain to be answered, in terms of the effects of changes in size and composition of litter or humus resources on the DOM release, as well as the relative importance of biotic and abiotic factors on temporary and long-term DOM controls under field conditions (Bolan et al., 2011). Soil DOM concentrations have been found to vary considerably under different vegetation types and land uses, such as forest, grassland and arable soils (Chantigny, 2003; Kawahigashi, Sumida & Yamamoto, 2003). It has been suggested that the responses of soil C and N pools to grassland-to-forest conversion (mainly to *Pinus* Spp. plantation) vary dramatically, with either increases or decreases; depending on the species involved, biotic and soil conditions, and management history of the site (Guo & Gifford, 2002; Berthrong et al., 2009). Research has indicated that land afforestation induces increases of dissolved organic carbon and nitrogen fluxes (Laik et al., 2009; Rosenqvist et al., 2010).

The aim of the present study is to investigate whether soil DOC and mobile nitrogen will change on a restoration trajectory in this coastal sand plain area. My hypothesis is that soil DOC and mobile N could reflect changes of vegetation development and associated biotic factors. This chapter has two objectives:

(1) to investigate the modification of dissolved organic carbon and mobile nitrogen in soil leachates on the restoration trajectory; and

(2) to investigate if dissolved organic carbon and mobile nitrogen could play a role in monitoring of the course of the ecological restoration trajectory.

4.2 Materials and methods

In this chapter, Transect 1 (Karoro soil series well drained soils developed on sand), Transect 2 (Waiwero soil series) and Transect 4 (Kamaka soil series alluvial fans over sand plain) were selected (Figure 4.1). The reasons of selecting these three transects, sitting on three types of soils, are:

(i) previous visual inspection of all dug soil pits in PCRP site indicated these were the only three complete transects in which it was feasible to install soil leachate samplers; others had high gravel contents in the profiles;

(ii) the three transects are located on north and south parts of PCRP site that could potentially represent a better overall picture of the site; and

(iii) this comparison could potentially reveal the relative importance of vegetation and soil types on variation of soil C and N dynamics in the restoration trajectory.

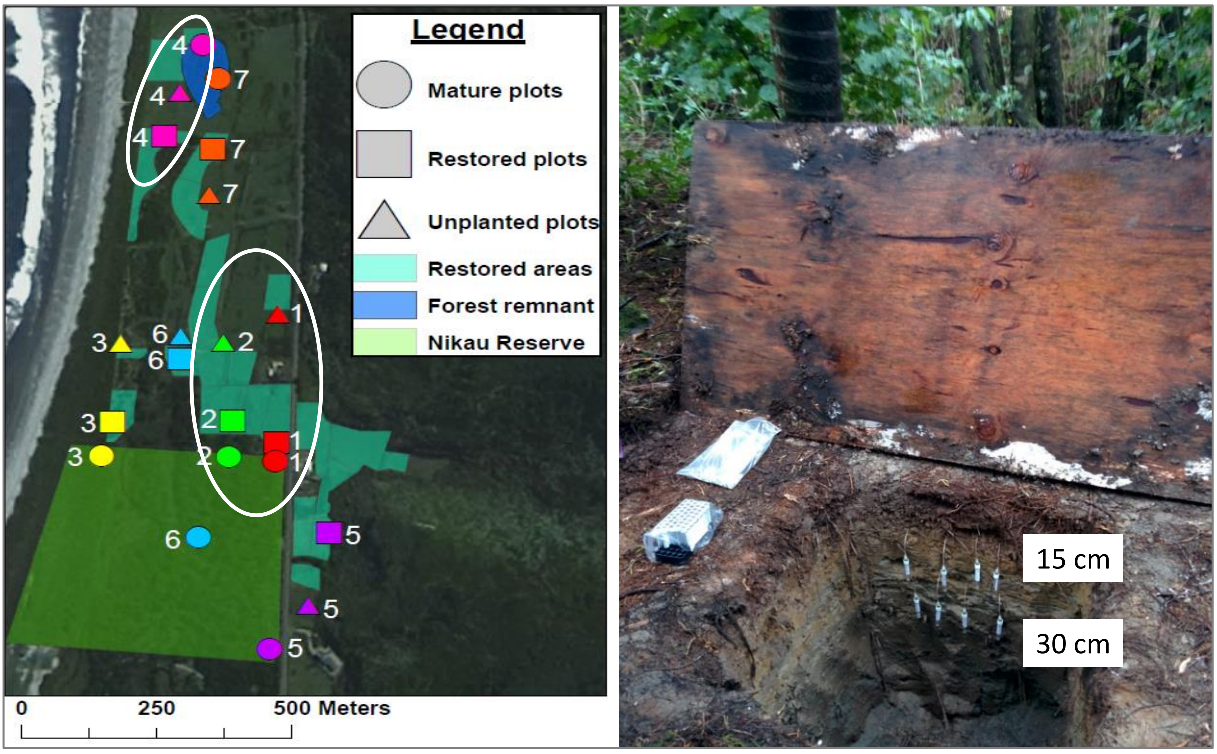


Figure 4.1 Outline of experiment design. Left: locations of selected transects. Right: layout of Rhizon Vacuum Samplers in the soil profile.

Each transect has three different stages of ecosystem development, including a Mature Forest (M) plot, Restoration (R) plot, and Unplanted (U) plot. For each plot, a soil pit (approx. 1 m^2 and 1-2 m deep) was dug for soil profile description. This was carried out with the support and advice of Dr. Carol Smith. Related site characteristics are listed in Table 4.1.

Rhizon Vacuum Samplers (10 cm porous polymer tube 2.5 mm OD, glassfibre strenthener, PE/PVC tubing 12 cm and male luer, Eijkelkamp Agrisearch Equipment, Netherlands) were installed in the sides of existing soil pits to extract 5-10 ml of interstitial soil leachate without significantly disturbing the structure, chemistry or biology of the soil. Rhizon Vacuum Samplers were permanently installed in soil pits, allocated in 4 replicates in 15 cm and 30 cm depth respectively. On every sampling event, surface soil samples were collected in 5 replicates using a stepping corer. There were four sampling events during 2014-2015, including 2014.08.05/06 (winter), 2014.11.12/13 (spring), 2015.01.14/15 (summer), and 2015.11.10/11 (spring), with 45, 33, 32, and 39 soil leachate samples collected in each sampling event respectively.

Soil leachate samples were then stored at 20 °C before dissolved organic carbon (DOC) and mobile nitrogen (ammonium-N and nitrate-N) analyses. Following filtering through 0.45 µm micro filter, DOC concentrations were analysed by a total organic carbon analyser, fitted with an auto sampler (TOC-5000A, Shimadzu, Japan). Ammonium-N and nitrate-N concentrations were determined by flow injection analysis on a FIAstar 5000 triple channel analyser (Foss Tector AB, Sweden).

The Shannon's diversity index was calculated for each plot with the formula below (Magurran, 2004):

$$H' = -\sum_i \mathrm{pi} * \ln(\mathrm{pi})$$

H' = Shannon's diversity index;
pi = relative abundance of species "i"; calculated with the formula pi = $\frac{ni}{\sum_i ni}$, where ni is the midpoint of cover range.

Treatment of soil samples and analyses of soil properties follow the same protocols described in the Chapter 2 (General Materials and Methods), including measurements of soil pH, 2M KCl extraction of mineral nitrogen, microbial biomass carbon, Olsen P. Statistical analyses were performed using Minitab (Minitab Inc., State College, Pennsylvania, USA), using one-way ANOVA with the Fisher's least-significance-difference post-host test.

4.3 Results

4.3.1 Study site features and properties of surface soil

Mature Forest (M) plots had marginally different depths of litter cover, and R1 had started to accumulate surface litter (Table 4.1). Results of the Shannon Index of Diversity showed that M plots has the highest native plant diversity, followed by the Restoration plots. Restoration plots had higher soil and leaf litter invertebrate diversity than U plots, and was closer to the corresponding M plots.

Table 4.1 Selected study sites characteristics from Transect 1, 2 and 4 of Mature (M), Restoration (R) and Unplanted (U) plots.

Site	GPS coordinates	Vegetation type	Litter depth (cm) (1)	Shannon index of diversity (1)	
				Plant (2)	Invertebrate (3)
M1	42° 8'38.39"S; 171°19'50.36"E	Mature forest	≈ 8 cm leaf litter	2.29	2.00
M2	42° 8'37.53"S; 171°19'46.07"E	Mature forest	≈ 6 cm leaf litter	2.47	1.49
M4	42° 8'09.38"S; 171°19'45.73"E	Mature forest	≈ 5 cm leaf litter	2.27	1.64
R1	42° 8'37.11"S; 171°19'50.54"E	Restoration Aug-Oct 2009	1-2 cm leaf litter	1.98	1.45
R2	42° 8'35.45"S; 171°19'46.65"E	Restoration May-Aug 2010	leaf-grass litter	1.65	1.23
R4	42° 8'16.10"S; 171°19'41.10"E	Restoration Aug-Nov 2011	leaf-grass litter	1.79	0.56
U1	42° 8'28.29"S; 171°19'50.98"E	Mixed grasses	-	-	1.00
U2	42° 8'29.60"S; 171°19'46.30"E	Mixed grasses	-	-	0.86
U4	42° 8'12.20"S; 171°19'43.30"E	Mixed grasses	-	-	0.84

(1) Modified from Hahner et al. (2013);
(2) Plant diversity accounts only for native species;
(3) Invertebrate diversity includes leaf litter and surface soil invertebrates, and both native and introduced species.

Soil pH was significantly lower in two of the M plots, compared to R and U plots (Table 4.2). R4 had the highest NH_4-N concentration, while M2 had the lowest NH_4-N (p<0.05). M plots with lower soil pH had lower NO_3-N concentration in soil, compared to R and U plots. Soil MBC was significantly higher in some the M plots (two of three). M4 had much higher Olsen P, which it was only marginally different in the other plots.

Table 4.2 Selected year-round surface soil (0-10 cm) properties from Transect 1, 2 and 4. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (*p*<0.05). MBC: Microbial Biomass Carbon.

Site	pH (1:5 H_2O)	Mobile N (mg/kg)		MBC (mg/kg)	Olsen P (mg/kg)
		NH_4-N	NO_3-N		
M1	4.55 (0.1)^{d}	4.1 (1.2)^{bcd}	0.7 (0.1)^{c}	479 (70)^{b}	24.5 (1.8)^{b}
M2	4.26 (<0.01)^{e}	1.5 (0.3)^{d}	0.4 (0.1)^{c}	873 (103)^{a}	10.1 (0.9)^{de}
M4	5.57 (0.1)^{a}	3.6 (0.7)^{bcd}	5.5 (1.7)^{a}	274 (41)^{cd}	79.4 (3.6)^{a}
R1	5.37 (<0.01)^{ab}	2.0 (0.6)^{cd}	1.6 (0.5)^{bc}	219 (35)^{cd}	8.2 (0.4)^{e}
R2	5.05 (0.1)^{c}	4.1 (0.5)^{bcd}	1.9 (0.6)^{bc}	284 (70)^{c}	25.5 (0.5)^{b}
R4	5.27 (<0.01)^{b}	8.0 (2.3)^{a}	3.5 (0.3)^{b}	250 (31)^{cd}	18.9 (0.4)^{c}
U1	5.51 (0.1)^{a}	2.1 (0.8)^{cd}	2.2 (0.5)^{bc}	204 (25)^{cd}	13.2 (0.1)^{d}
U2	5.41 (<0.01)^{ab}	6.6 (0.6)^{ab}	1.9 (0.2)^{bc}	164 (50)^{cd}	11.8 (0.3)^{de}
U4	5.26 (0.1)^{b}	5.0 (1.0)^{abc}	0.7 (0.1)^{c}	122 (19)^{d}	25.2 (0.7)^{b}

4.3.2 Properties of upper two horizons in the profile soils

In the upper two soil horizons of the selected transects, soil texture were mostly sandy and loamy (Table 4.3). Overall, R plots had higher pH in both Ah and Bw horizons, compared to M and U plots (Figure 4.2). Total C, Total N and soil C/N ratios were higher in the Ah horizon for M plots relative to R and U plots. Unusually, some of the soil organic carbon were higher than soil total carbon, because of different sampling times (2012 and 2014-2015 measurements). Higher concentrations of Al and Fe in Bw horizon soils than Ah horizon soils were evident in M plots (Figure 4.3). Concentrations of Na, Mg and K were significantly higher in M4 in both Ah and Bw horizons.

Table 4.3 Soil horizons and texture from Transect 1, 2 and 4 (modified from Smith et al., 2016, as described in 2012).

Sites	Depth (cm)	Horizons	Texture
M1	0 - 15	Ah	Silt loam
M2		Ah	Loamy silt
M4		Ah	Loamy silt
R1		Ah	Fine sandy loam
R2		Ah	Silt loam
R4		Ah	Silt loam
U1		Ah	Silt loam with fine sand
U2		Ah	Fine sandy loam
U4		Ah	Sandy loam
M1	15 - 30	Bw1	Sandy loam
M2		Bw	Loamy silt
M4		Bw	Silt loam
R1		Bw	Sandy loam
R2		Bw	Sandy loam
R4		Bw(g)	Loamy sand
U1		Bw(g)1	Sandy loam
U2		Bw(f)1	Sandy loam
U4		Bw(f)	Medium sand

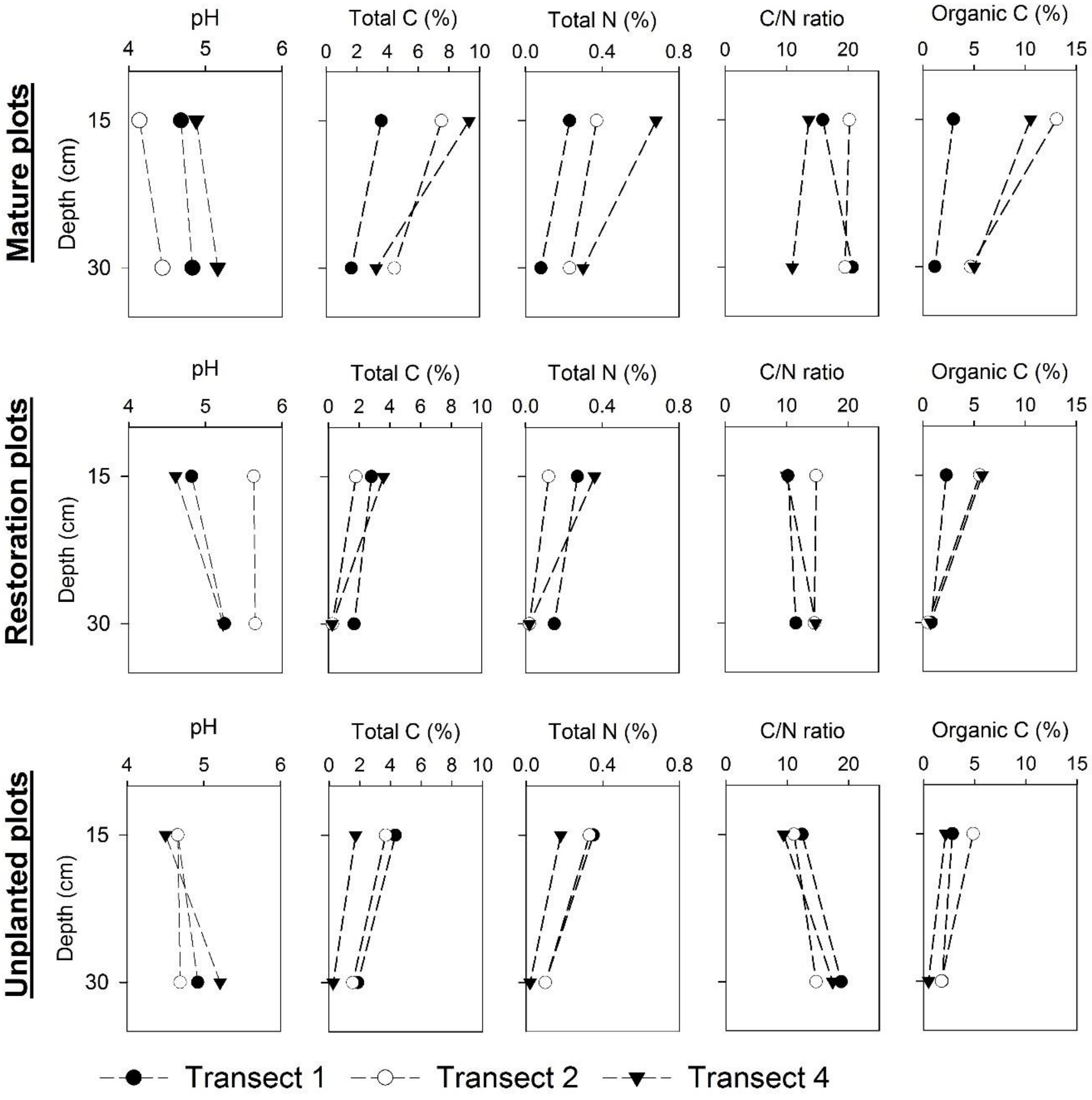


Figure 4.2 Selected soil properties for Ah and Bw horizons from Transect 1, 2 and 4. Soil pH and organic C content were measured in 2014-2015 in the present study, while soil Total C, Total N, and C/N ratios were modified from Smith et al. (2016), as measured in 2012.

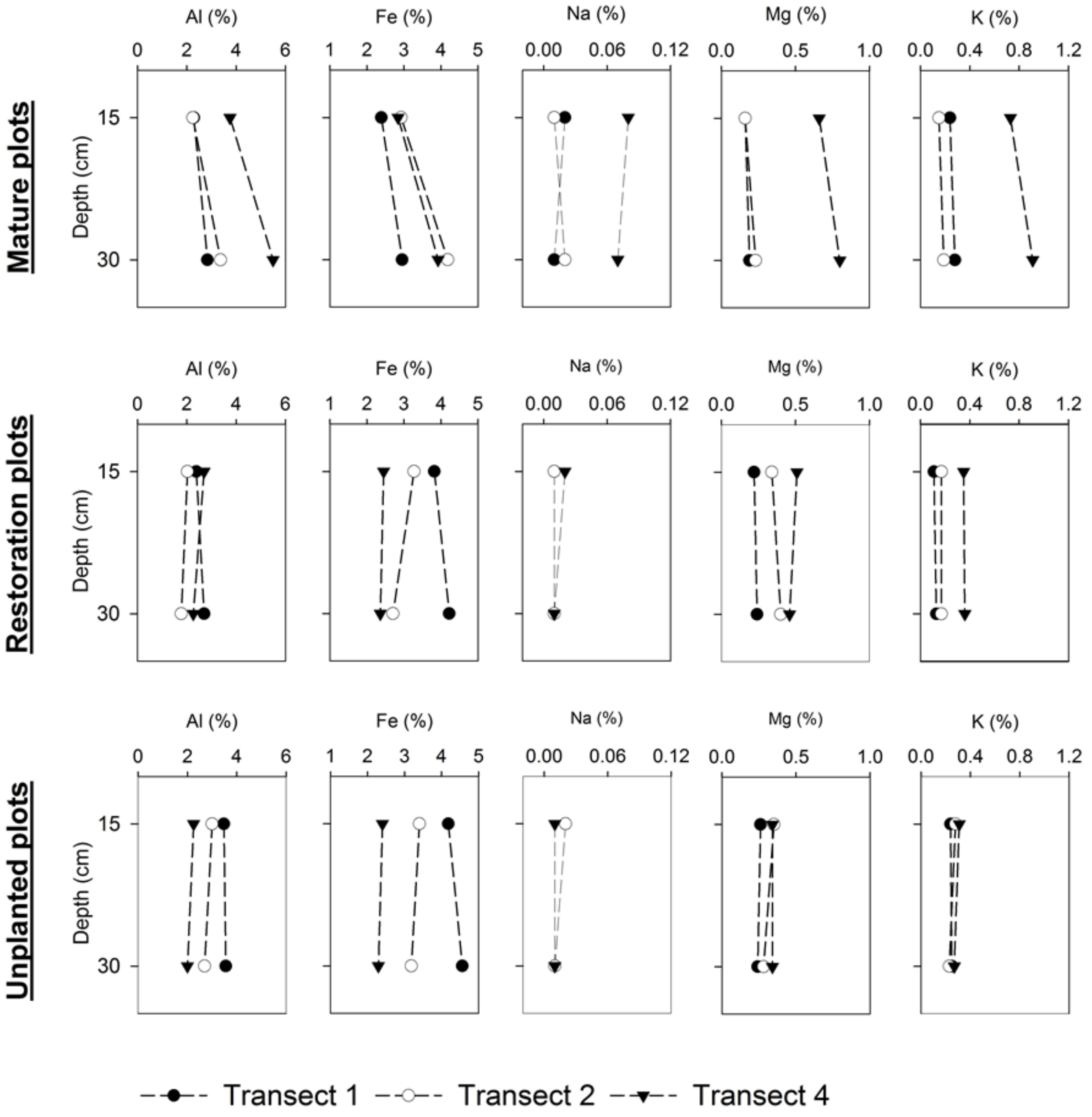


Figure 4.3 Soil Al, Fe, Na, Mg, and K concentrations in Ah and Bw horizons from Transect 1, 2 and 4. (Data were modified from Smith et al. (2016), as measured in 2012).

4.3.3 Dissolved organic C and mobile N dynamics in soil leachate

Due to field site heterogeneity and changing weather conditions, I could not always collect soil leachate samples from all 4 replicates at plots, and I have also excluded values from a few flooded soil plots from the data analyses. This led to missing values at some soil plots, hence lower replication. Details of soil DOC, NH_4-N and NO_3-N concentrations of each plot in each transects and sampling event are showed in the Appendix C (Figure C.1, C.2 and C.3).

A summary of statistical analyses is shown in Table 4.4. These indicated that variation of soil DOC concentrations were more controlled by different sampling events, while NH_4-N and NO_3-N in soil leachate were more mediated by different vegetation types. However, different Transects (1, 2 and 4) had the least influences on the variation of soil DOC and mobile nitrogen dynamics.

Table 4.4 Summary of p values from one-way ANOVA with the Fisher's least-significance-difference tests comparing DOC, NH_4-N and NO_3-N between different sampling events, treatments (mature forest, restoration and unplanted plots) and transects (Transect 1, 2 and 4) on 15 cm and 30 cm separately.

Depth	Factor	DOC	NH_4-N	NO_3-N
15 cm	Sampling events	<0.001	0.231	0.04
	Treatments	0.477	0.001	<0.001
	Transects	0.628	0.199	0.033
30 cm	Sampling events	<0.001	<0.001	0.054
	Treatments	0.755	0.003	<0.001
	Transects	0.445	0.151	0.238

The results on a mature, restoration and unplanted basis at different sampling times are presented in Figure 4.4. Dissolved organic carbon concentrations were significantly higher in winter ($p<0.001$); but there were no significant differences in mobile-N concentrations between sampling events, apart from NH_4-N concentration at 30-cm depth. Mobile nitrogen concentrations had larger variation on Restoration plots.

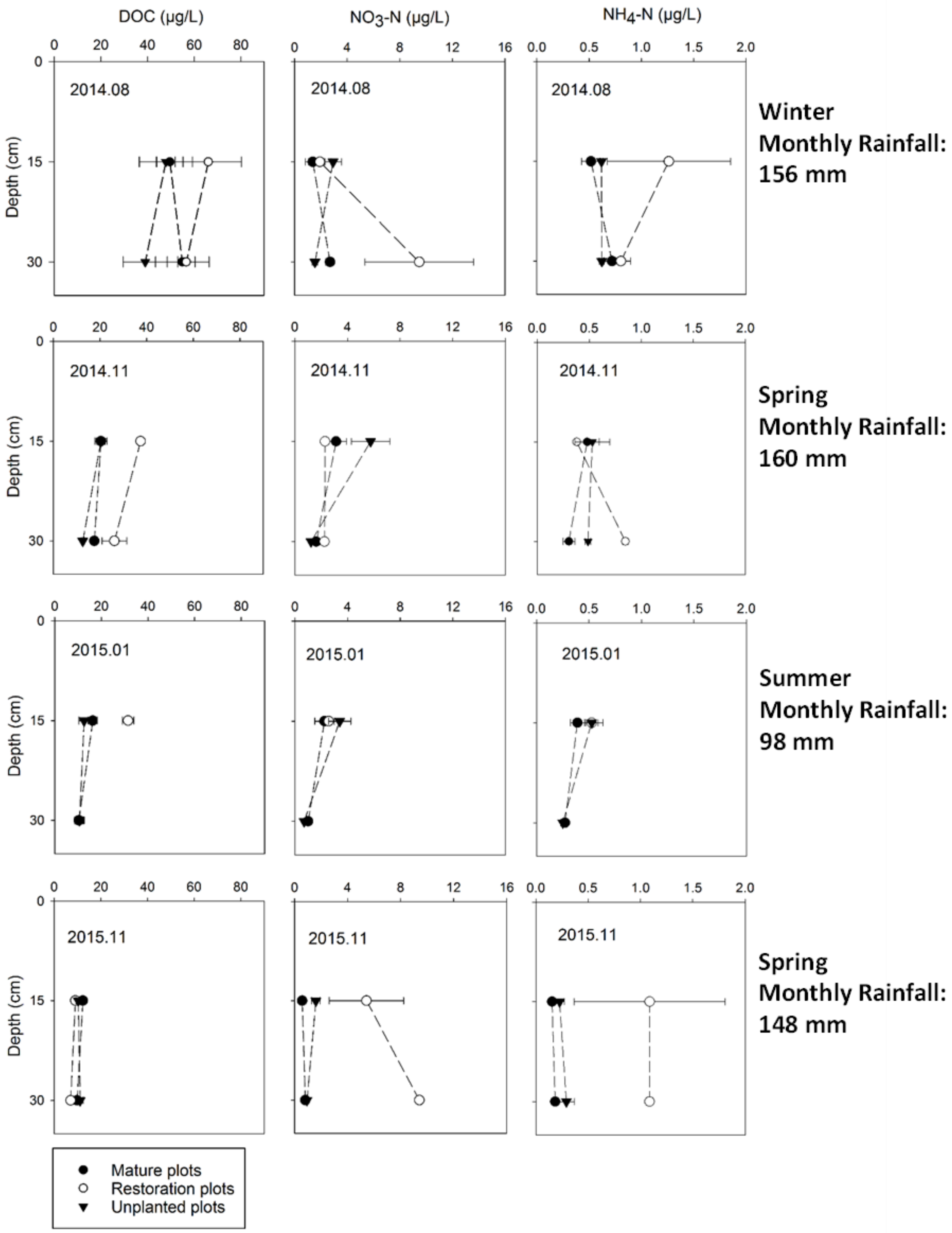


Figure 4.4 Variations of dissolved organic carbon and mobile nitrogen concentrations shown in mature forest, restoration, and unplanted plots at four sampling events at 15 cm and 30 cm depth. Missing error bars indicate insufficient soil leachate samples at that soil plots on that time. (Monthly rainfall data are sourced from National Institute of Water and Atmospheric Research (NIWA), New Zealand).

The overall DOC and mobile nitrogen concentrations are shown in Figure 4.5. Dissolved organic carbon concentrations were not significantly higher in restoration plots compared to mature forest and unplanted plots; and differences of DOC between 15- and 30-cm were not significant among mature, restoration and unplanted plots. Nitrate-N concentrations in restoration plots were significantly higher ($p<0.05$) only at 30 cm depth. Restoration plots had significantly higher ($p<0.05$) ammonium-N concentrations compared to mature forest and unplanted plots, despite a relatively high variation on 15 cm depth.

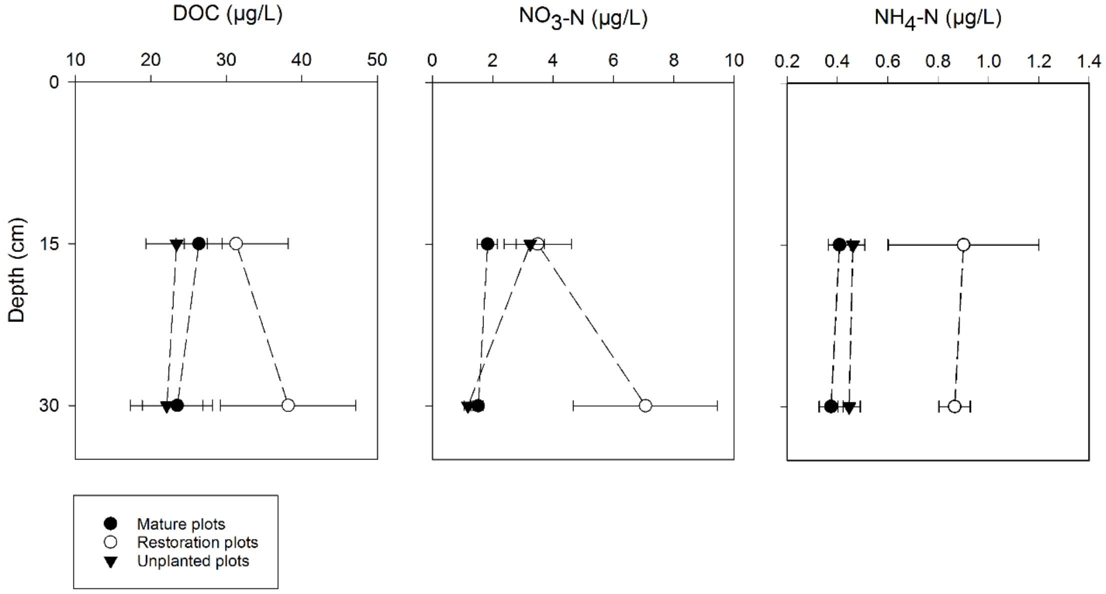


Figure 4.5 Overall dissolved organic carbon and mobile nitrogen concentration at Mature Forest, Restoration, and Unplanted plots (15 cm and 30 cm).

4.4 Discussion

4.4.1 Soil chemistry on the restoration trajectory

Modification of soil biology and chemistry by ecological restoration has been shown in these findings. Restoration plots had soil chemical and biological properties that significantly different from Mature Forest and Unplanted soils. Soil pH, microbial biomass carbon, mineral nitrogen and invertebrate richness are known to be parameters that respond to plant restoration relatively fast (Harris, 2009; Banning et al., 2011). This could be explained by plant leaf litter accumulation and subsequent decomposition at the Restoration plots starting to influence soil properties (in particular in R1, the oldest restoration). Mo et al. (2016) reported that soil pH, soil organic matter, N, and P in the surface 10 cm had been modified after 8-years of subtropical forest restoration. It has been suggested that plant community changes can give rise to soil biota changes (Wardle et al., 2004a; Kardol & Wardle, 2010). Although, Korboulewsky et al. (2016) illustrated that increasing soil fauna diversity was more related to specific tree species rather than tree species richness. In the present study, soil available P was similar in Restoration and Unplanted plots. It is possible that soil available P is less responsive to plant restoration in the short term. An earlier study found that the bicarbonate-extractable P fraction (inorganic and organic P species), which is comparable to Olsen P in the present study, showed only slight decreases between 19-yr radiata pine afforestation and unplanted grassland soils (Chen et al., 2000).

Transect 4, which was located in the northern part of the PCRP site (Figure 4.1), was previously reported to have livestock presented until about the middle of 2011 (Hahner et al., 2013). Some degree of animal excreta sourced N and P might have been left in the soils, and this would help to explain the high soil available N and available P in M4 soils. Soil pH was high in M4 and this could be possibly due to receiving relative large amount of marine spray containing high basic cations (Whipkey et al., 2000), followed by subsequent stem flow and deposition on soils, as it is located closer to current shoreline compared to other two mature forest plots. Significant gains of Na from marine spray was evident in coastal chronosequences study in Eger et al. (2011), and inputs of Na, Mg, and K in M4 were previously reported at the present site by Smith et al. (2016) (Figure 4.2). However, it was difficult to quantify the influence of marine aerosols deposition on soils in the present study.

In this 4-7 years restoration study, soil organic carbon in the Ah horizons started to build up in the restoration plots, compared to the unplanted plots, and can be attributed to continuous plant litter inputs. This is similar to results measured in restoration soils previously (Smith et al., 2016). Elsewhere, in a 16-year rehabilitation of Jarrah forest in a post-bauxite mining landscape, George et al. (2010) found that soil C in the top 20 cm was restored towards the original native forest. In the present study, additional mineralizable carbon and nitrogen sourced from plant leaf litter invested by newly restored plants has resulted in relatively higher soil available ammonium-N and subsequent nitrate-N in restoration plots. Lower soil pH at M1 and M2 plots might not favour nitrification to proceed, thus resulting in lower nitrate-N concentrations (Clough et al., 2004). Restoration and Unplanted grassland soils have faster soil C and N turnover rates, as reflected in lower soil C/N ratios in the topsoil (Figure 4.2). In contrast, in European temperate forests, older mature forest soils have been found to stabilize litter decomposition rates and nitrogen mineralization (Trap et al., 2011). Given that mature forests have reduced growth rates and they are more likely to rely on internal nutrient cycling rate, it has been argued that forests present a relatively conservative pattern of nitrogen utilization (Davidson et al., 1992).

4.4.2 DOC and mobile N in soil water

Seasonal changes of dissolved organic matter in soil solution are strongly influenced by rainfall, temperature and vegetation (Kawahigashi et al., 2003). In the present study, high rainfall in the winter sampling event might have contributed to higher DOC fluxes, but had no noticeable effects on mobile

N concentrations. On the other hand, different ages of restoration led to high variations in DOC and mobile N (comparing to M and U plots). Mature Forest plots have thicker litter cover and larger soil microbial communities but lower DOC than the Restoration plots. This differs to the expectation that larger pools of litter or humus, with higher microbial activity, will promote higher dissolved organic matter concentrations in soil solution (Kalbitz et al. 2000; Chantigny, 2003).

Previous studies of the relationship between soil pH and dissolved organic matter (DOM) have seldom been conducted under field conditions. Some laboratory studies have suggested DOM solubility is promoted by higher soil pH, because of the stimulation of microbial activities, but this often is supported in the field-scale study due to site spatial variability of soil properties and longer timescale (Andersson et al., 2000; Kalbitz et al. 2000). It has also been cautioned that soil dissolved organic matter concentrations previously measured as water or hot-water extraction in the laboratory may be different from real dissolved organic carbon transported through soil profile measured in soil leachates (Fröberg et al., 2011).

In the present study, the sandy soils in the soil profiles could explain why DOC concentrations did not decrease significantly from 15 cm to 30 cm depth. Other studies have shown that stabilization of dissolved organic matter in mineral soils via adsorption or precipitation can significantly reduce its concentration (Kalbitz and Kaiser, 2008); and this reduction could be up to three quarters of the initial DOC concentration (Camino-Serrano et al., 2014). Kaiser and Kalbitz (2012) indicated that a proportion of dissolved soil organic matter could be prone to pass through the soil matrix without adsorption or precipitation under sites dominated by preferential flows. Therefore, a relatively low adsorption capacity of DOC in the soil matrix of the present study would have resulted in similar concentrations in 30 cm depth compared to 15 cm depth, but this could further lead to losses of DOC to deeper soils and groundwater or to nearby streams.

Factors that contributed to a significantly higher ammonium-N concentration in soil leachates at restoration plots could have been:

(i) nitrogen mineralization promoted by the newly developed plants were reflected in increased microbial biomass carbon in surface soil and lower soil C/N ratio in Bw horizon in restoration plots compared to unplanted plots;

(ii) plant litter input quantity and quality, and subsequent decomposition may have been modified by plants used for restoration (Gessner et al., 2010); and

(iii) litter decomposition and soil bioturbation induced by increased leaf litter and soil invertebrate diversity in restoration plots compared to unplanted plots (Hättenschwiler, Tiunov, & Scheu, 2005; García-Palacios et al., 2013).

Soil nutrient mineralization would be substantially promoted by rapidly growing plants to meet the demand for growing plant uptake; but meanwhile leading to increasing nitrogen losses. Russell and Raich (2012) found that this promotion varies between different plant species or vegetation types. With regard to the rise of nitrate-N concentrations at 30 cm for the restoration plots, similar result have been reported previously by Jones et al. (2008), where slight increases of nitrate-N concentration with soil depth was measured.

Apart from the above biotic and abiotic factors that may contribute to the different soil chemical properties between Restoration, Mature and Unplanted plots, other operational practices could also make some contribution. It is worth noting that former mixed grass cover were herbicide sprayed to facilitate later restoration plantings. Therefore, these dead grass inputs may provide a kick start for organic matter inputs to soils, providing a substantial quantity of C and N with relatively low C/N ratio. In consequence, this could have contributed to higher DOC concentrations in soil leachates in Restoration soils, as well as higher mobile N in some plots. Also, soil disturbance caused by tree plantings might have changed soil properties. However, the question is whether or not the effects of these sources on DOC and mobile N were still taking place after 5 years. Previous studies have found that land use or management practice changes influence soil organic matter quality and microbial decomposition of organic matter and in turn the release of dissolved organic carbon and nitrogen (Kalbitz et al. 2000; Kawahigashi et al., 2003); but Chantigny (2003) suggested effects of such changes on soil C and N dynamics are usually short term.

4.4.3 Roles of DOC and mobile N in ecological restoration

Vegetation development and recolonization of fauna are generally used to evaluate the progresses and success of an ecological restoration (Ruiz-Jaen & Mitchell Aide, 2005). However, the question in this study was whether monitoring of carbon and nitrogen status in the soil could indicate soil improvement and may be valuable for better management of the ecological restoration. It has been suggested that the flux and composition of soil dissolved organic matter are sensitive indicators of changing vegetation types and environmental conditions (Kawahigashi et al., 2003; Bolan et al., 2011). Wang et al. (2010) indicated that a better understanding of plant-induced soil N changes during early stages of vegetation restoration is critical for the advancement of restoration practices. Bush (2008) found that soil C and N increase during the early- and mid-successional stages, but decrease and stabilize from the mid- to late-successional stages. However, one concern is that such an increase of dissolved organic carbon under early vegetation development could be a readily available carbon source for anaerobic soil microbes, thereby inducing the reduction of nitrate to release the potent greenhouse gas nitrous oxide (N_2O) (Bolan et al., 2011). The dynamics of soil DOM, including adsorption/desorption and precipitation/dissolution processes, as well as microbial processing, through the soil profile are important from a pedological point of view (Bolan et al., 2011; Kaiser and Kalbitz, 2012). However, DOC and mobile N are highly variable, and predictive modelling requires monitoring data from a longer time sequence than was available in the present study.

4.5 Conclusion

The intent of this study was not to provide a complete answer to which biotic or abiotic factors are controlling DOC and dissolved N in soil solution on a costal sand plain forest restoration trajectory. Instead, the objectives were to investigate if these parameters varied predictively. Modification of soil properties, dissolved organic carbon and dissolved nitrogen in soil leachates by ecological restoration practices have been found in the present study. Differences in the restoration trajectory have indicated that early-stage development of restored vegetation is an important factor contributing soil carbon and nitrogen dynamics, but differences are variable between plots of the same vegetation type. The time that could be spent at the site was limited in the present study, which restricted the opportunity to collect a larger quantity and more regular samples. The main findings of this part of the research are:

(1) Early-stage restoration has started to lower surface soil pH due to the decomposition of newly-accumulated litter, and has promoted soil carbon and nitrogen mobilization likely to be due to increased microbial activity and diversity of litter-soil invertebrates.

(2) Ammonium-N concentrations in soil leachates were significantly higher in restoration plots. Fast-growing newly restored vegetation has clearly influenced the dynamics of soil leachate DOC concentrations, possibly with more being released in restoration plots.

(3) It was suggested that DOC and mobile N in soil leachates might be controlled by preferential flow during wet season, in particular making it less likely that DOC could react with clay minerals when transported through the soil matrix.

(4) DOC and mobile N in soil leachates appears to indicate the progress of the course of ecological restoration, as reflected in accelerated C and N cycling.

(5) DOC and mobile N appear to be significantly modified during restoration but, due to high variability and additional factors, these measurements have a limited role to play in monitoring the trajectory.

Chapter 5

The Dynamics of Soil P and Soil Minerals in the Restoration Trajectory

5.1 Introduction

Walker and Syers's conceptual model (1976) proposed that during soil and ecosystem development, there is: (i) a gradual decrease and eventual depletion of primary mineral P (mainly apatite P); (ii) a continual increase and eventual dominance of occluded P; and (iii) an overall decrease of Total P during soil development (due to e.g. surface runoff or leaching of P, incorporation of P into biomass).

Since this conceptual soil-ecosystem-phosphorus model was proposed, it has been tested in different climatic zones (tropical, temperate, arid and boreal), different vegetation (rain forest and grassland), different soil parent materials (e.g. quartz sand, schist, limestone and basalt), and different geomorphological sites (e.g. volcanic islands, glacial moraine and costal sand dunes) (Chen et al., 2015; Crews et al., 1995; Eger et al., 2011; Wardle et al., 2004b). Examples of studied chronosequences were summarized in Table 5.1.

Studies have also investigated the relationship between ecosystem succession and soil development, as well as the transition of ecosystem nutrient limitation (from an N-limiting to a P-limiting ecosystem) with regard to long-term soil chronosequences (e,g, Crews et al., 1995; Parfitt et al., 2005; Peltzer et al., 2010). However, a modelling study conducted in Menge et al. (2012) showed that, in all timescales the transitions between N and P limitation critically depends on limits to the capacity of symbiotic N fixation; rather than only on a terminal state of P limitation that prevails in highly-developed ecosystems. On the other hand, Kitayama (2005) indicated that such a terminal state may not be necessarily reached in a hyper-diverse tropical rainforest, since hyper-diverse ecosystems are more capable of adapting to P-limitation via more diverse P-acquisition strategies (e.g. mycorrhizal symbiosis, carboxylate release from cluster roots).

In terms of the effects of vegetation on the dynamics of soil P, previous studies have been mainly focused on monoculture forest afforestation (Chen et al., 2000), in the production landscapes (Li et al., 2007), or multi-species re-vegetation in experimental grasslands (Oelmann et al., 2011). However, the effects of ecological restoration on soil P dynamics in the field has rarely been studied. Ecological restoration practices on soil may expedite soil development via a range of processes involving vegetation and soil organisms. There would appear to be potential benefits associated with incorporating more soil science into the study of restoration ecology, as proposed long ago by

Bradshaw and Chadwick (1980), and recently re-emphasized by Moorhead (2015) and Perring et al. (2015).

The hypothesis is that a restoration trajectory should reveal how far soils in restoration plots have been restored compared to unplanted plots; and whether soils in restoration plots are being restored toward a reference of mature forest plots. This chapter aims to investigate:

(1) the effects of soil age on the phosphorus dynamics and soil minerals dynamics on a soil chronosequence at PCRP;

(2) whether there are differences in the phosphorus dynamics and soil minerals dynamics on the restoration trajectory at PCRP; and

(3) if the success and trajectory of the ecological restoration differs during different stages of soil development.

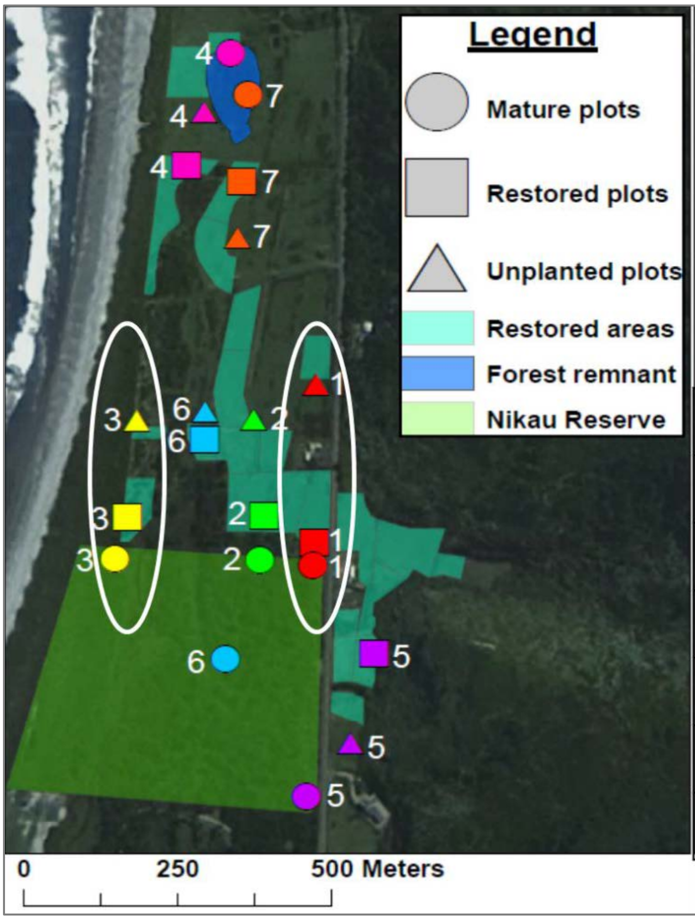
Table 5.1 Characteristics of chronosequences that had been studied or tested.

Chronosequence	Coordinates	Mean temp. (°C)		Mean annual rainfall (mm)	Cause of chronosequence	Parent material	Duration of chronosequence (years)	References
		January	July					
Cooloola, Australia	27°30'S; 153°30'E	25	16	1400-1700	Sand dunes of varying age caused by aeolian sand deposition	Sand derived from quartz grains	> 600,000	Walker et al. (2001); Chen et al. (2015)
Franz Josef, New Zealand	43°25'S; 170°10'E	15	7	3800-6000	Surfaces of varying ages caused by glacial retreat	Chlorite schist, biotite schist, gneiss	< 5 - > 120,000	Richardson et al. (2004)
Haast, New Zealand	43°43'S; 169°04'E	14.5	7.5	3455	Surfaces of varying age caused by aeolian sand deposition	Sand derived from quartz grains, with remainder feldspar, mica and chlorite	370 - 6500	Eger et al. (2011); Roberts et al., 2015
Hawaiian archipelago	12-22°N; 155-160°W	14	17.5	2500	Surfaces of varying ages caused by volcanic lava flow	Basalt tephra	300 - 4.1×10^6	Crews et al. (1995); Vitousek & Farrington (1997)
San Francisco Volcanic Field, USA	35°14'-35°32' N; 111°25'-112°08'W	11.5 (mean annual temp.)		1300	Surfaces of varying ages caused by volcanic lava flow	Basalt tephra	930 - 3×10^6	Selmants & Hart (2010)

5.2 Materials and methods

In this chapter, Transect 1 and 3 were selected to represent a chronosequence on this sand plain which has developed on a well-drained sand and gravel shoreline (Figure 5.1). 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). Restoration plots R1 and R3 were initiated in Aug-Oct of 2009 and Jan-April of 2010, respectively.

For each plot, a soil pit was dug for a soil profile description (Figure 5.2; also see detailed soil profile descriptions in the Appendix D.1). It was thought that: (i) soils in restoration and unplanted plots in Transect 1 and 3 were similar before commencement of the PCRP trial; and (ii) 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. My assumption was that any measured changes in soil properties in restoration plots in comparison with unplanted plots would be primarily due to vegetation or land-use changes.



Site	GPS coordinates
M1	42° 8'38.39"S; 171°19'50.36"E
R1	42° 8'37.11"S; 171°19'50.54"E
U1	42° 8'35.75"S; 171°19'37.68"E
M3	42° 8'38.00"S; 171°19'36.02"E
R3	42° 8'28.29"S; 171°19'50.98"E
U3	42° 8'29.68"S; 171°19'38.59"E

Figure 5.1 Locations of selected Transect 1 and 3 on PCRP site.

Approximate ages of each dune (transect) were estimated by tree coring and age estimation following standard methods described by Wells, Duncan and Stewart (2001). It is assumed that the oldest tree will give a minimum age for dune stabilization if there has been no site disturbance, which is thought to be the case. The approximate time required for tree colonization in South Westland, New Zealand is estimated to be between 5 to 50 yrs (Wells et al., 1999). In order to protect native trees, a limited number of randomly selected largest trees of kamahi (*Weinmannia racemosa*, Cunoniaceae) were selected at each transect in order to take a tree core sample. This species dominated with Northern rata (*Metrosideros robusta*, Myrtaceae), but rata wood was suggested to be too hard to take coring sample (J. Washer, pers.comm). 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 clarity (Wells and Goff, 2006), the tree rings were sufficiently visible to allow them to be counted in the present study.

Field moist surface soil samples were collected at each plot (5 replicates) using a stepping auger (diameter=3.5 cm, depth=10 cm). At the same sampling event, 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). 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 than soils in deeper horizons, and 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).

Treatment of soil samples and analyses of soil properties followed the same protocols previously described in Chapter 2 (General Materials and Methods). Soil moisture content, 2M KCl-extractable nitrogen, microbial biomass carbon and microbial biomass phosphorus were determined on fresh soil within one week. Soil pH, electrical conductivity (EC), soil organic carbon, the first soil phosphorus (P) fractionation scheme, and soil extractable Fe and Al were determined on air-dried soils.

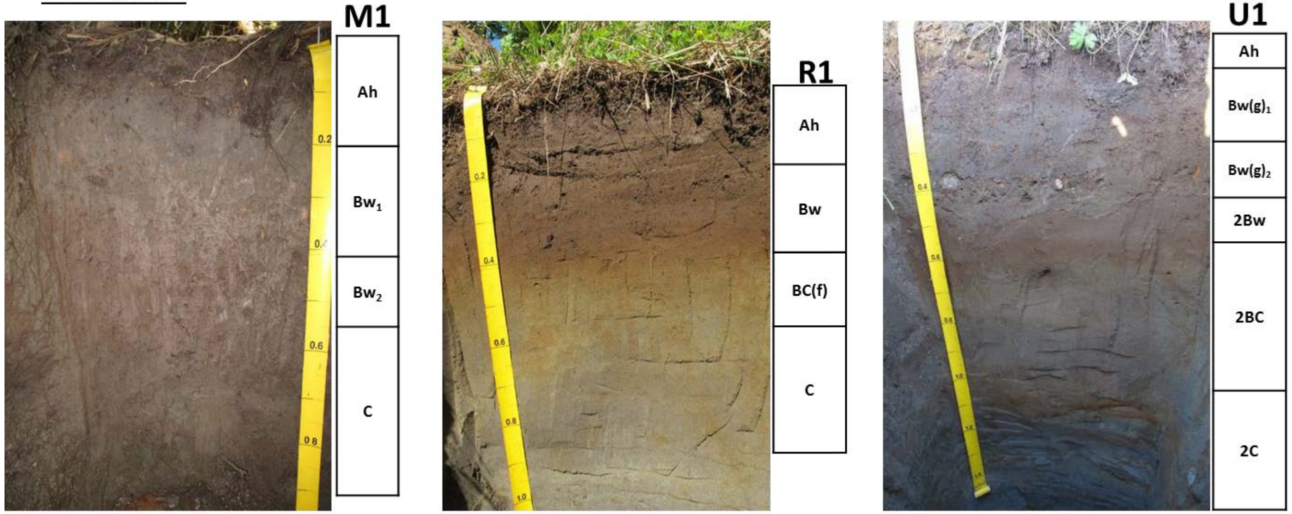
The first soil P fractionation scheme (non-sequential) followed Eger et al. (2011), including (1) total soil P: P (tot); (2) organic P: P (org) was the result of subtracting P (acid) from the 0.5M H_2SO_4-extractable P after ignition, (3) acid-extractable P: P (acid) was the 0.5M H_2SO_4-extracted phosphorus, (4) Fe/Al-bound P: P (Fe/Al) and Ca-bound P: P (Ca), (5) inorganic P: P (in) was the difference between P (tot) and P (org); and (6) occluded P: P (occ) was calculated as P (tot) - P (org) – P (Fe/Al) - P (Ca).

Extractable Fe and Al were extracted separately using acid oxalate (Fe_o and Al_o), citrate-dithionite (Fe_d and Al_d) and pyrophosphate (Fe_p and Al_p) for different forms.

The area-based soil properties (g m^{-2}) were calculated using the concentrations and soil volume density data (Blakemore et al. 1987). This gives the estimation of total stocks of soil P and allow comparison of P stocks between different soil ages and plots. There was insufficient soil (fine sand) remaining after passing through the 500 µm from M3 Bw and C horizons for P fractionation. To allow a fair comparison between M3 and other plots, area-based total amounts of P were calculated only down to 30 cm depth.

Data were analysed using Minitab (Minitab Inc., State College, Pennsylvania, USA), performing one-way ANOVA with the Fisher's least-significance-difference post-host test, Pearson correlation analyses for key soil parameters with P fractions, and non-parametric Mann-Whitney test for profile soil property comparisons between Transect 1 and 3.

Transect 1



Transect 3

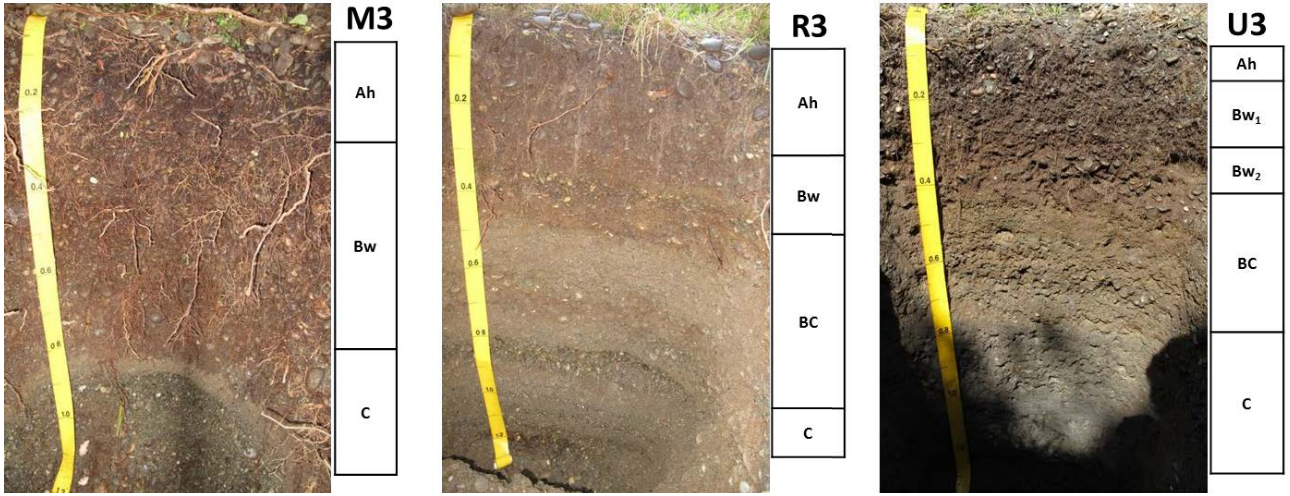


Figure 5.2 Soil profiles of dug pits in Transect 1 (top row) and 3 (bottom row) (from Smith et al., 2016). Full profile descriptions are provided in Appendix D.1 (Table D.1).

5.3 Results

5.3.1 Site characteristics and properties of surface soil

Transect age estimation from tree cores showed that the age of Transect 1 could start as recently as 166-yr ago, and the age of Transect 3 could be as recently as 75-yr ago (Table 5.2).

Table 5.2 Soil types and results of soil ages estimation at Transect 1 and 3.

	NZ soil classification (1)	USDA soil taxonomy (2)	Number of tree rings	Estimated transect age
Transect 1	Sandy brown	Dystrudept	116	166
Transect 3	Orthic brown	Dystrudept	25	75

1) Hewitt, 2010;
(2) Soil Survey Staff, 2014.

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 5.3). Soil pH was generally higher in the younger Transect 3 compared with the older Transect 1 (U3 was an exception). Soil EC, ammonium-N and nitrate-N, and MBC were consistently higher in the Transect 3 compared with Transect 1. Microbial biomass P produced significantly variable data, with higher MBP in restoration and unplanted plots in the Transect 3 compared with Transect 1. 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. Soils in Transect 3 were found to have marginally higher Na, Mg, and K concentrations.

Virtually all measured soil P fractions were lower in the Mature Forest stands (Table 5.4), except for P (occ) and P (org) in unplanted plots. The concentrations of P (tot), P (org), and P (in) were higher in the younger Transect 3 in parallel compared with the older Transect 1. Acid-extractable P, P (Fe/Al) and P (Ca) were all found to be significantly low in mature forest plots in both Transect 1 and 3 compared with the restoration and unplanted plots. There was no significant difference observed in P (occ) concentrations among all plots.

Soil P fractionations were non-sequentially extracted in the present study, meaning that the sum of different proportions of P (org), P (occ), P (acid), P (Fe/Al) and P (Ca) as fractions of P (tot) at each plot was higher than 100% (Figure 5.3), Organic P consistently accounted for the largest soil P faction amongst most plots (ca. 50% to 60% of Total P). Occluded P took the second largest part of soil P fraction (ca. 20% to 40% of Total P). Soil P (acid), P (Fe/Al) and P (Ca) factions were consistently low in mature forest plots (less than 7% of Total P), compared with restoration and unplanted plots.

Concentrations of acid oxalate extractable and citrate-dithionite extractable Al and Fe in the surface soils were consistently highest in R1 compared to other plots (Table 5.5). Total Al and Fe concentrations were found to be consistently lower in mature plots at both transects, compared to restoration and unplanted plots. Overall, total Al and Fe concentrations were lower in Transect 3 than Transect 1.

Principal component analysis of surface soil properties of Transects 1 and 3 (Figure 5.4) showed the first and second components shared similar loadings of data variations, with 27% and 25% respectively. Mature plots (M1 and M3) were allocated to the left due to the first component, which was mainly driven by high soil MBC and electrical conductivity, but low in soil acid extractable-P, Ca-mineral P, Total P and pH. However, the second component was positively correlated with soil Fe and Al minerals, but to a lesser extent negatively correlated with soil MBP and Fe/Al-bound P.

Table 5.3 Selected surface soil chemical and biochemical properties (0-10 cm). Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (*p*<0.05). Where MBC: microbial biomass carbon; MBP: microbial biomass phosphorus.

Sites	pH (H$_2$0)	EC (dS/m)	NH$_4$-N (mg/kg)	NO$_3$-N (mg/kg)	MBC (mg/kg)	MBP (mg/kg)	Microbial C:P molar ratio	TC (%)$^{(1)}$	TN (%)$^{(1)}$	TP (%)$^{(1)}$	C:N ratio$^{(1)}$	N:P ratio$^{(1)}$	Na (%)$^{(1)}$	Mg (%)$^{(1)}$	K (%)$^{(1)}$
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}	3.58	0.23	0.04	15.93	5.75	0.02	0.16	0.24
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}	2.80	0.27	0.06	10.22	4.5	0.01	0.22	0.11
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}	4.31	0.35	0.06	12.41	5.83	0.02	0.26	0.24
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}	28.24	1.63	0.13	17.33	12.54	0.08	0.36	0.27
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}	2.95	0.30	0.05	9.78	5	0.01	0.44	0.25
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}	6.81	0.62	0.13	11.07	4.77	0.02	0.31	0.34

(1) Modified from Smith et al. (2016), which were measured in 2012.

Table 5.4 Surface soil (0-10 cm) phosphorus fractionation. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (p<0.05). Total phosphorus: P (tot); organic phosphorus: P (org); inorganic phosphorus: P (in); acid-soluble phosphorus: P (acid); primary apatite P: P (Ca); secondary mineral P: P (Fe/Al); and occluded phosphorus: P (occ).

Sites	P (tot)	P (org)	P (in)	P (acid)	P (Ca)	P (Fe/Al)	P (occ)
				(mg/kg)			
M1	400 (78)^{b}	247 (71)^{b}	153 (15)^{b}	29 (5)^{b}	23 (3)^{b}	5 (1)^{d}	125 (14)^{a}
R1	551 (16)^{ab}	310 (21)^{ab}	242 (23)^{ab}	100 (11)^{a}	73 (7)^{a}	20 (2)^{cd}	149 (29)^{a}
U1	540 (50)^{ab}	204 (8)^{b}	336 (50)^{a}	103 (15)^{a}	58 (3)^{a}	50 (19)^{ab}	227 (36)^{a}
M3	456 (32)^{b}	275 (40)^{b}	180 (35)^{ab}	40 (3)^{b}	32 (4)^{b}	24 (3)^{cd}	125 (34)^{a}
R3	658 (60)^{a}	394 (21)^{a}	364 (48)^{ab}	117 (12)^{a}	69 (9)^{a}	67 (7)^{a}	128 (49)^{a}
U3	546 (117)^{ab}	252 (24)^{b}	294 (107)^{ab}	87 (12)^{a}	67 (10)^{a}	36 (2)^{bc}	191 (104)^{a}

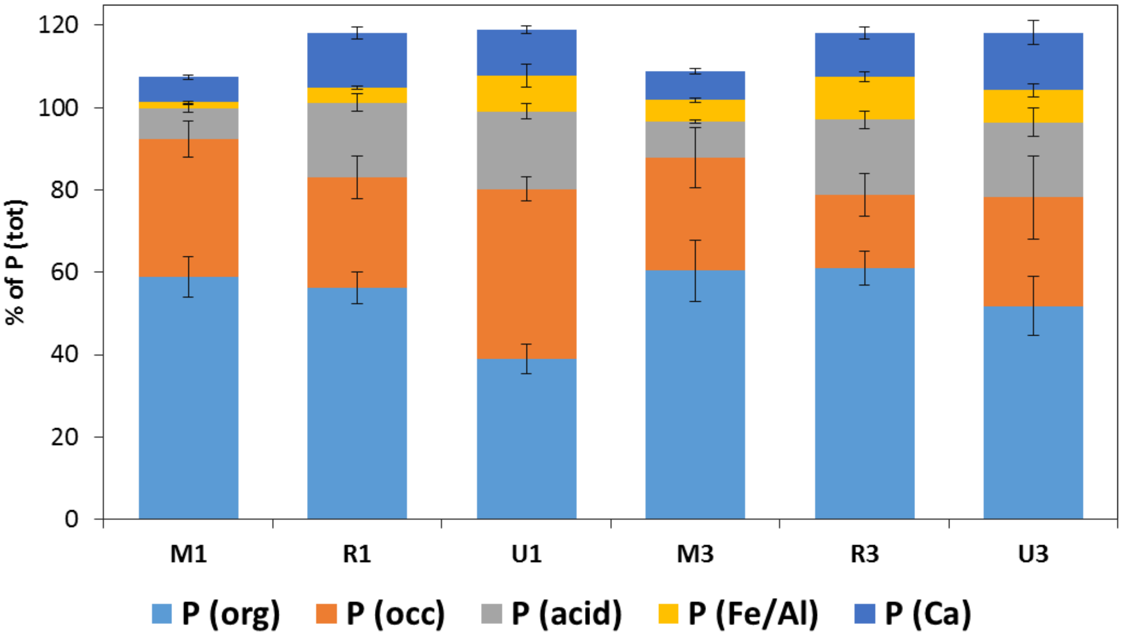
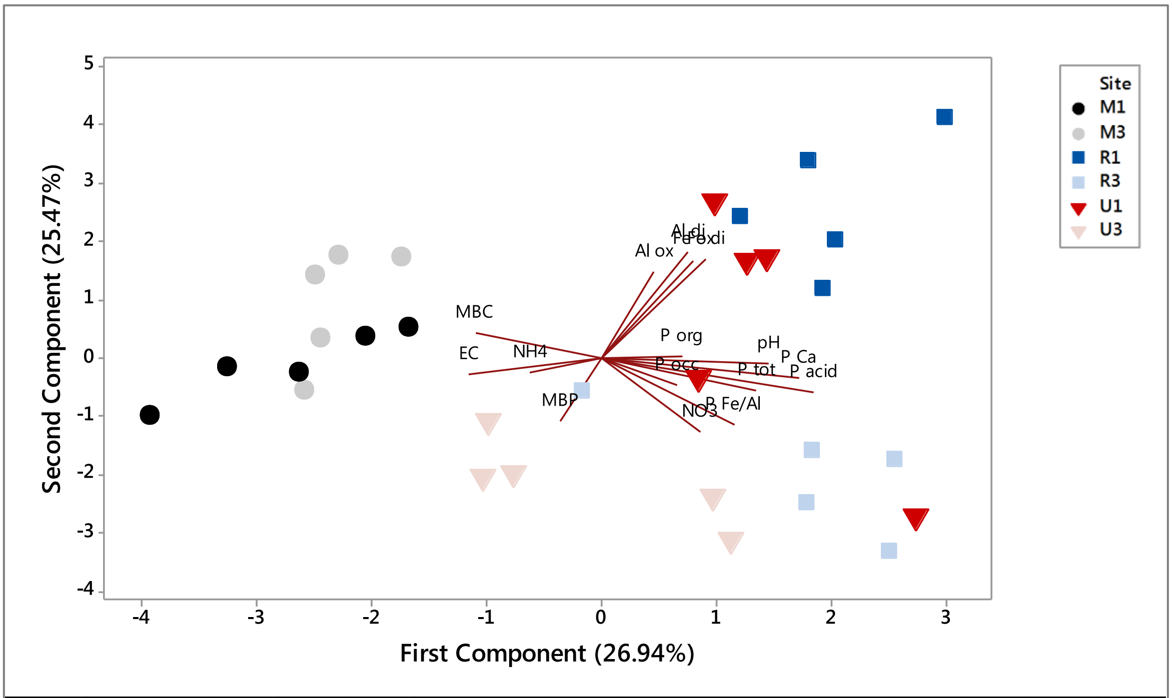


Figure 5.3 Proportion of organic P, occluded P, acid-extractable P, Fe/Al bound P and Ca bound P of Total P in surface soils at Transect 1 and 3. Data are mean values ± standard error (n=5).

Table 5.5 Surface soil (0-10 cm) soil Fe and Al minerals. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (p<0.05). Al_o, Fe_o and Si_o are oxalate-extractable iron and aluminium; Al_d, Fe_d and Si_d are citrate/dithionite-extractable iron and aluminium.

Sites	Al_o	Fe_o	Si_o	Al_d	Fe_d	Si_d	Al	Fe
	(%)						(%)$^{(1)}$	(%)$^{(1)}$
M1	0.25 (0.08)^{bc}	0.53 (0.08)^{cd}	0.01 (<0.01)^{d}	0.18 (0.03)^{cd}	0.52 (0.12)^{bc}	0.09 (0.02)^{b}	2.28	2.39
R1	0.44 (0.05)^{a}	1.24 (0.13)^{a}	0.01 (<0.01)^{bc}	0.46 (0.06)^{a}	1.78 (0.22)^{a}	0.05 (<0.01)^{b}	2.38	3.82
U1	0.25 (0.02)^{bc}	0.92 (0.14)^{b}	0.01 (<0.01)^{bc}	0.31 (0.05)^{b}	1.39 (0.30)^{a}	0.05 (<0.01)^{b}	3.47	4.18
M3	0.30 (0.03)^{b}	0.88 (0.07)^{b}	0.01 (<0.01)^{c}	0.26 (0.04)^{bc}	0.89 (0.09)^{b}	0.16 (0.03)^{a}	1.44	1.83
R3	0.24 (0.03)^{bc}	0.74 (0.07)^{bc}	0.02 (<0.01)^{a}	0.17 (0.02)^{cd}	0.69 (0.07)^{bc}	0.09 (0.01)^{b}	1.80	2.08
U3	0.13 (0.01)^{c}	0.37 (0.02)^{d}	0.01 (<0.01)^{b}	0.09 (0.01)^{d}	0.33 (0.04)^{c}	0.07 (0.01)^{b}	1.87	2.14

$^{(1)}$ Modified from Smith et al. (2016), which were measured in 2012.



Variables	pH	EC	NH_4-N	NO_3-N	MBC	MBP	P tot	P org	P acid	P Fe/Al	P Ca	P occ	Fe_o	Al_o	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 5.4 Principal component analysis of soil properties in surface soils at Transect 1 and 3.

5.3.2 Properties of profile soil

In the older Transect 1, soil pH in M and R plots tended to stabilize between 5.0-5.3, while pH was distributed between 4.7-5.1 in the U plots (Figure 5.5). In the younger Transect 3, pH increased with depth from 5.3 to 6.2. Soil pH was significantly different between Transect 1 and 3 ($p<0.0001$) (Table 5.6). M3 and U3 Ah horizons had significantly higher EC, with 0.29 and 0.19 dS m^{-1} respectively, compared to other horizons ($p=0.6824$). Apart from an exceptionally high content (ca. 25 %) in M3 Ah, the rest of profile soils had between 0.2 to 5 % of SOC which decreased with soil depth ($p=0.6366$). Soil MBC concentration was highest in M3 Ah (ca. 860 mg kg^{-1}), and decreased with soil depth in the rest of profile soils ($p=0.7976$). R1 had more than double of MBC, compared to R3 (ca. 127 and 42 mg kg^{-1} respectively). In Transect 1, NH_4-N concentrations were reasonable through all three profiles (ranging from 4 to 7 mg kg^{-1}) ($p=0.0004$). However, NH_4-N concentration was exceptionally high in U3 Ah (ca. 140 mg kg^{-1}). Nitrate-N (NO_3-N) was significantly high in the Ah horizons of both unplanted plots (around 35 mg kg^{-1} in U1 Ah and U3 Ah) ($p=0.018$).

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 5.6). Soil P (tot) was significantly different between Transect 1 and 3 ($p=0.0001$) (Table 5.6). Soil P (org) generally showed a decreasing trend with depth in both transects (from up to around 620 mg kg^{-1} in the M3 Ah to 10 mg kg^{-1} in the C horizons), except for R1 C horizon ($p=0.8876$). The proportional significances of P (org) to P (tot) were clearly evident in all Ah horizons in both transects (ranging from 50% to 80% of Total P) (Figure 5.7). Conversely, P (acid) generally showed increasing concentrations with depth and accounted for up to 90% of P (tot) in the bottom C horizons ($p=0.0265$) (Figure 5.6, 5.7). Secondary mineral P (Fe/Al) presented its importance with a general increase trend with depth in Transect 1, while a reverse pattern was presented in the Transect 3 ($p<0.0001$). The proportional importance of P (Fe/Al) was more evident in Transect 1 than Transect 3 (except for the top two horizons at U3). However, primary mineral P (Ca) became a more important faction with depth in both transects ($p=0.1520$). Soil P (occ) were usually higher in Transect 1 (ca. 80 mg kg^{-1} or more) than in Transect 3 (ca. 80 mg kg^{-1} or less), apart from R1 C horizon ($p<0.0001$).

Although overall losses of soil P stocks in the upper 30 cm were not evident from the younger Transect 3 to the older Transect 1 in the present study, higher stocks of soil P (occ) and secondary mineral P (Fe/Al) were presented in older Transect 1 than the younger Transect 3 (Table 5.7).

The results of Pearson correlation analyses showed that soil EC and P (org) were positively correlated with soil organic carbon content (Table 5.8). Soil P (tot) was positively correlated with P (acid), P (Fe/Al), and P (Ca). Among soil inorganic P fractions, including P (acid), P (Fe/Al), and P (Ca), they were positively correlated with each other.

In Transect 1, profile depth trends of extractable Al and Fe were similar in all three extractions (Figure 5.8, top row). Unplanted plots had significantly higher concentration of dithionite - and pyrophosphate-extractable Al and Fe in Ah and Bw horizons, compared to Mature plots. In Transect 3, extractable Al and Fe showed distinct separations in the Ah horizon in all three extractions (Figure 5.8, bottom row). Soil Al_o, Al_d and Al_p were significantly different between Transect 1 and 3 ($p<0.05$), while Fe_o, Fe_d and Fe_p were not significantly different between transects ($p>0.05$) (Table 5.6).

Except for U1 2Bw and M3 Ah, the rest of soil horizons at both transects did not present inorganic forms of Al (Table 5.9). The older Transect 1 soils had a higher allophane content when compared to the younger Transect 3. M3 Ah horizon had the highest amorphous Fe content, while crystalline Fe was absent. Amorphous and crystalline Fe were well distributed on the soil profiles at both transects. In terms of Fe_o/Fe_d ratios, M3 Ah was the only horizons higher than 1. Ratios of Fe_p/Fe_o and Al_p/Al_o are mostly above 1 among soil horizons.

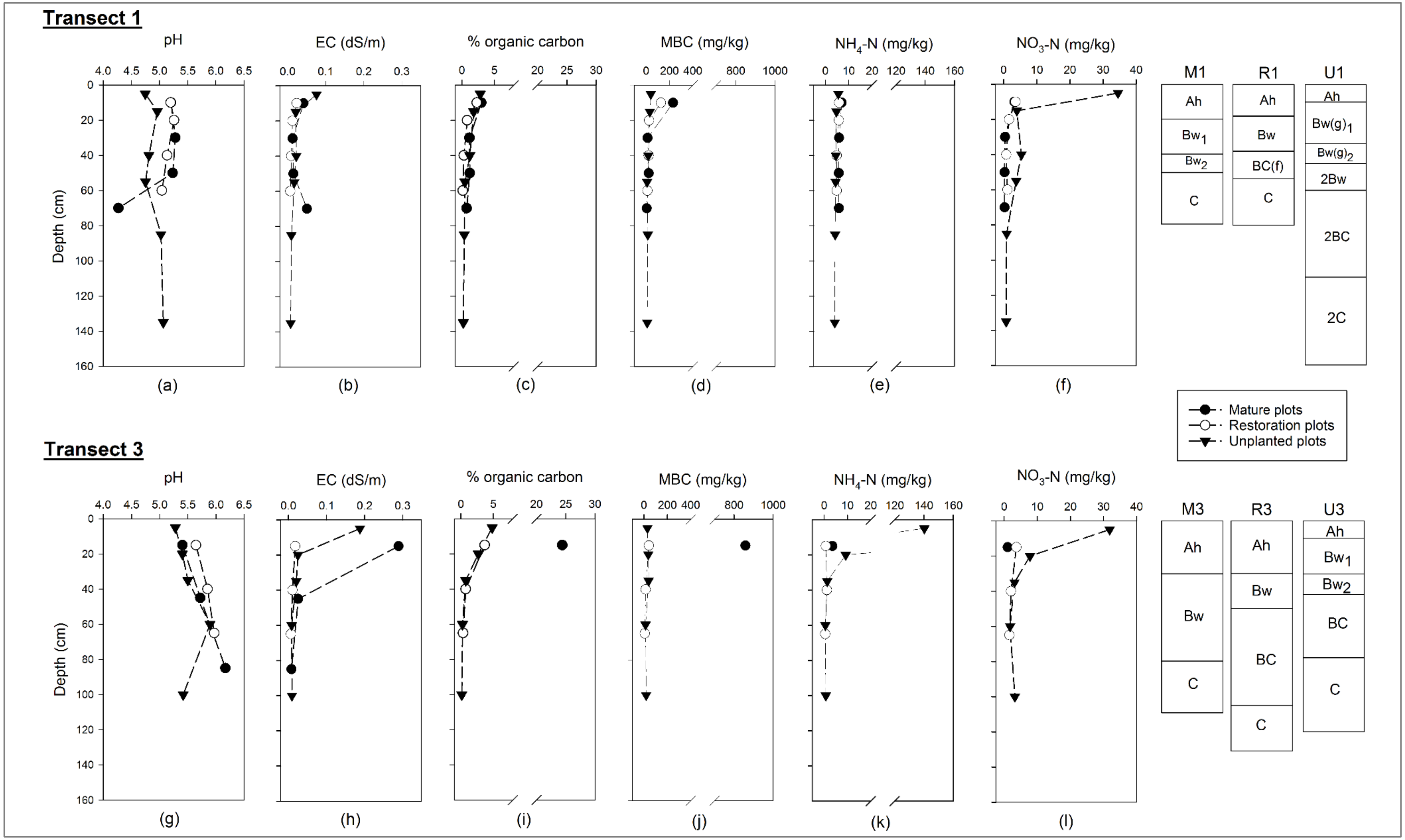


Figure 5.5 Selected profile soil chemical properties in Transect 1 [top row (a) to (f)] and 3 [bottom row (g) to (l)]. EC and MBC stand for electrical conductivity and microbial biomass carbon respectively.

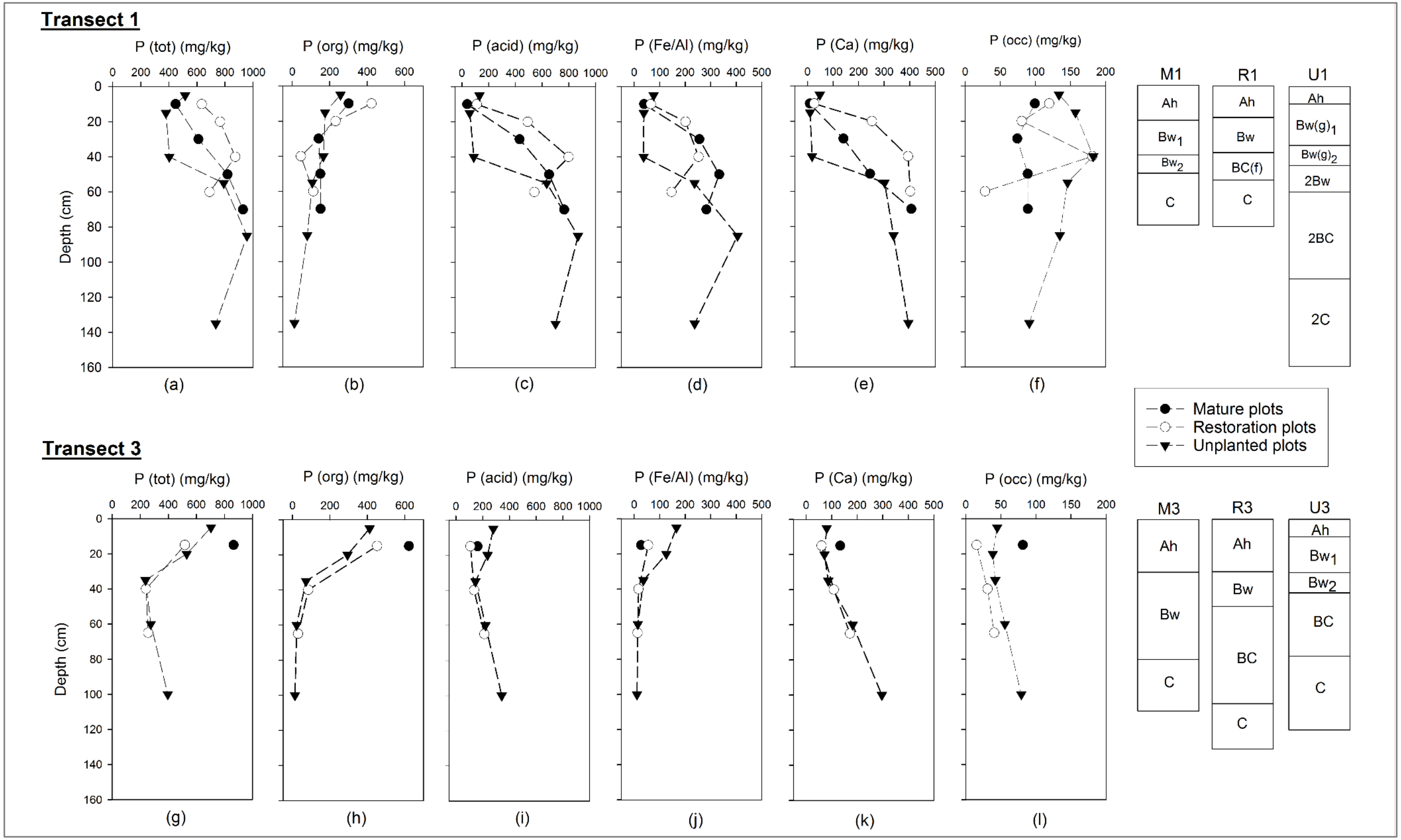


Figure 5.6 Profile soil phosphorus fractionations in Transect 1 [top row (a) to (f)] and 3 [bottom row (g) to (l)]. Data were not available in M3 Bw and C horizons, and R3 C horizon, due to the high pebble and gravel contents.

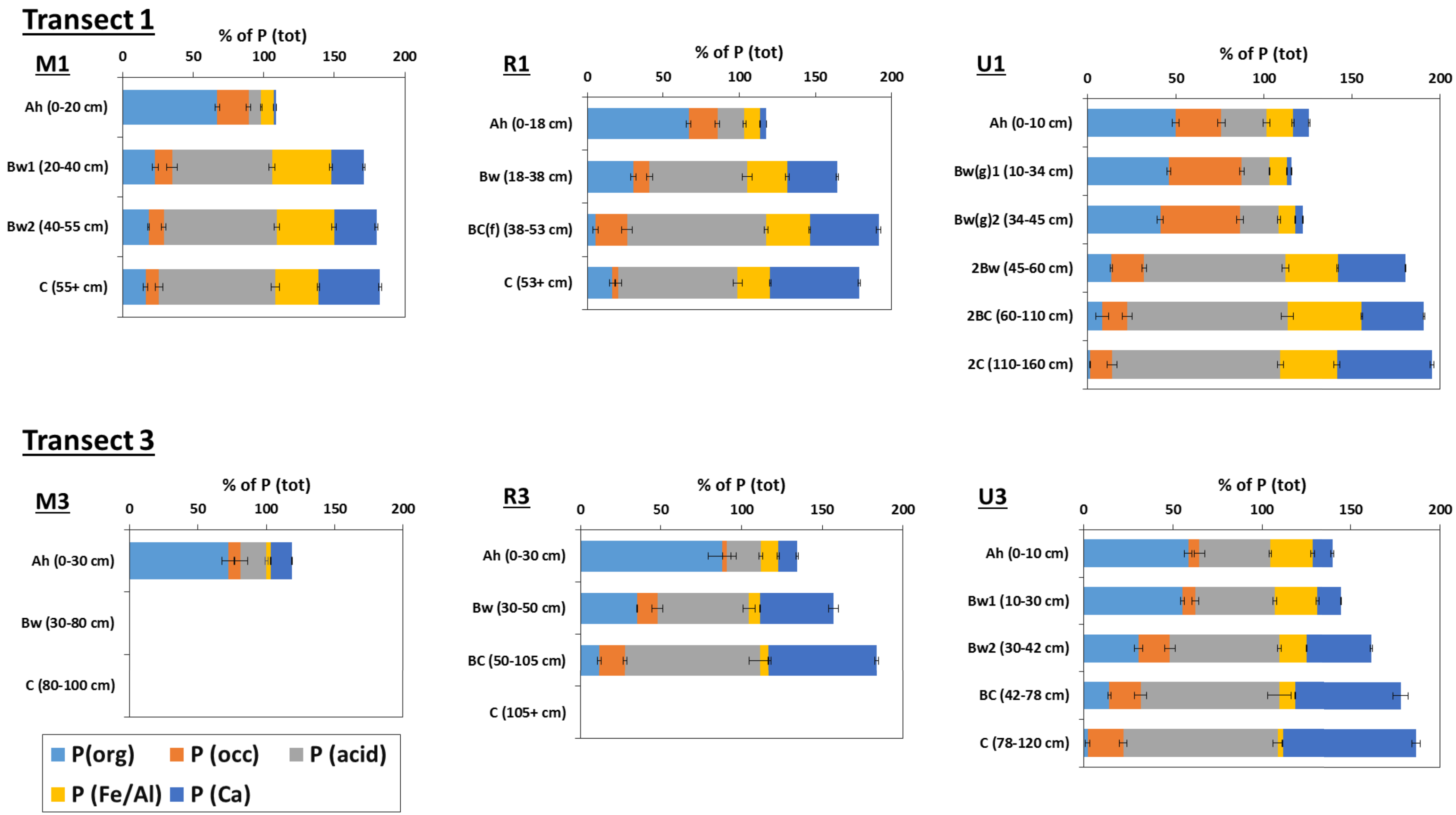


Figure 5.7 Proportion of organic P, occluded P, Fe/Al bound P and Ca bound P of Total P in soil profiles at Transect 1 (top row) and 3 (bottom row). Data were not available in M3 Bw and C horizons, and R3 C horizon, due to the high pebble and gravel contents.

Table 5.6 Mann-Whitney test results of significant difference between Transect 1 and 3 on selected profile soil chemical properties. * indicates $p < 0.05$ and ** $p < 0.01$; ns means not significant.

	pH	EC	NH_4-N	NO_3-N	MBC	% SOC	P (tot)
P value	<0.0001**	ns	0.0004**	0.0180*	ns	ns	0.0001**
	P (org)	P (acid)	P (Fe/Al)	P (Ca)	P (occ)	Al_o	Fe_o
P value	ns	0.0265*	<0.0001**	ns	<0.0001**	0.0018**	ns
	Si_o	Al_d	Fe_d	Si_d	Al_p	Fe_p	Si_p
P value	ns	0.0015**	ns	ns	0.0024**	ns	0.0028**

Table 5.7 Area-based stocks of soil phosphorus fractions in the top 30 cm at Transect 1 and 3. Total phosphorus: P (tot); organic phosphorus: P (org); inorganic phosphorus: P (in); acid-soluble phosphorus: P (acid); primary apatite P: P (Ca); secondary mineral P: P (Fe/Al); and occluded phosphorus: P (occ).

Site	Horizon	Depth (cm)	P (tot)	P (org)	P (occ)	P (acid)	P (Fe/Al)	P (Ca)
			(g m^{-2})					
M1	Ah	0 - 20	119.4	80.2	26.4	10.7	10.4	2.4
	Bw1	20 - 30	84.7	19.5	10.3	59.9	35.4	19.5
Profile mass to 30 cm			**204.1**	**99.7**	**36.7**	**70.6**	**45.8**	**21.9**
R1	Ah	0 - 18	154.7	103.2	29.2	27.4	16.0	6.3
	Bw	18 - 30	137.9	41.7	14.5	88.8	36.2	45.5
Profile mass to 30 cm			**292.7**	**144.9**	**43.7**	**116.1**	**52.2**	**51.8**
U1	Ah	1 - 10	70.3	35.1	18.2	18.0	10.4	6.6
	Bw(g)1	10 - 30	107.2	49.4	44.4	16.7	10.7	2.8
Profile mass to 30 cm			**177.6**	**84.5**	**62.6**	**34.7**	**21.1**	**9.3**
M3	Ah	0 - 30	142.8	79.0	13.4	26.7	4.5	22.1
Profile mass to 30 cm			**142.8**	**79.0**	**13.4**	**26.7**	**4.5**	**22.1**
R3	Ah	0 - 30	193.8	112.8	5.8	40.6	20.6	22.7
Profile mass to 30 cm			**193.8**	**112.8**	**5.8**	**40.6**	**20.6**	**22.7**
U3	Ah	0 - 10	80.0	46.9	5.1	31.8	18.9	9.2
	Bw1	10 - 30	153.2	84.9	11.1	68.3	36.5	20.7
Profile mass to 30 cm			**233.2**	**131.7**	**16.2**	**100.1**	**55.3**	**29.9**

Table 5.8 Pearson correlation coefficients among key chemical properties and concentrations of phosphorus factions in profile soils at Transect 1 and 3. * indicates *p* < 0.05 and ** *p* < 0.01 (n=69); ns means not significant.

Correlation coefficient (r)	pH	EC	SOC %	P (tot)	P (org)	P (acid)	P (Fe/Al)	P (Ca)
EC	ns							
SOC %	ns	0.898**						
P (tot)	-0.583**	ns	ns					
P (org)	ns	0.724**	0.749**	ns				
P (acid)	-0.423*	ns	ns	0.758**	-0.439*			
P (Fe/Al)	-0.494*	ns	ns	0.808**	ns	0.896**		
P (Ca)	ns	ns	ns	0.588**	-0.524*	0.905**	0.638**	
P (occ)	-0.622**	ns	ns	ns	ns	ns	ns	ns

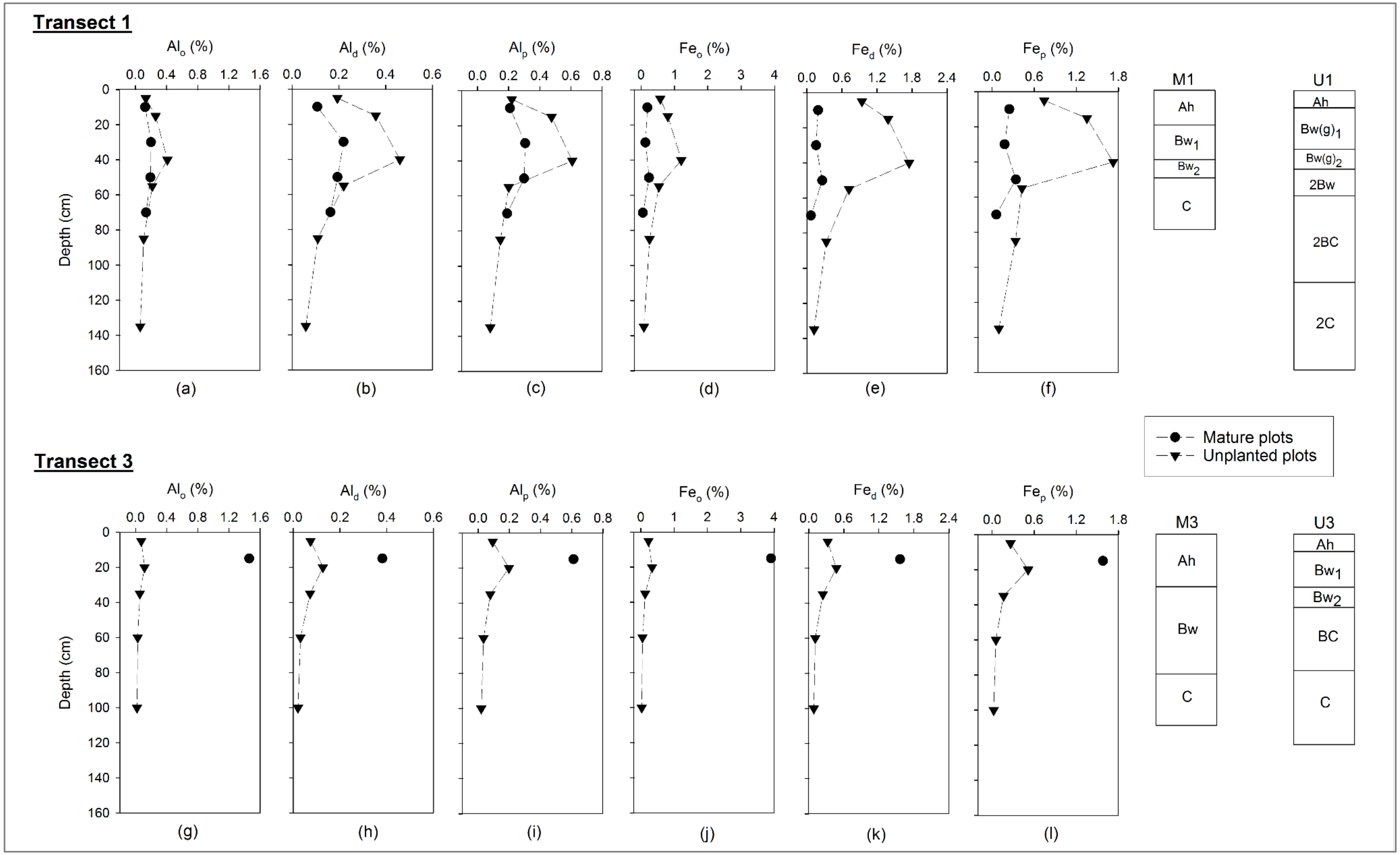


Figure 5.8 Profile soil mineral analyses of mature and unplanted plots in Transect 1 [top row (a) to (f)] and 3 [bottom row (g) to (l)]. Al_o and Fe_o, are oxalate-extractable aluminium and iron; Al_d and Fe_d are citrate/dithionite-extractable aluminium and iron; and Al_p and Fe_p are pyrophosphate-extractable aluminium and iron. Data were not available in M3 Bw and C horizons, and R3 C horizon, due to the high pebble and gravel contents.

Table 5.9 Analyses of clay Al and Fe factions on Transect 1 & 3. Data were not available in M3 Bw and C horizons, and R3 C horizon, due to the high pebble and gravel contents.

Site	Horizon	Depth (cm)	Non-organic Al (%) (1)	Allophane % (2)	Amorphous Fe (%) (3)	Crystalline Fe % (4)	Fe_o/Fe_d (5)	Fe_p/Fe_o (6)	Al_p/Al_o(6)
M1	Ah	0-20	0.0	0.020	0.188	0.009	0.977	1.314	1.668
	Bw1	20-40	0.0	0.010	0.131	0.029	0.836	1.373	1.542
	Bw2	40-55	0.0	0.014	0.240	0.025	0.909	1.413	1.563
	C	55+	0.0	0.000	0.053	0.019	0.750	1.135	1.382
U1	Ah	0-10	0.0	0.006	0.574	0.371	0.607	1.296	1.660
	$Bw(g)_1$	10-34	0.0	0.023	0.802	0.589	0.579	1.690	1.840
	$Bw(g)_2$	34-45	0.0	0.199	1.203	0.547	0.690	1.436	1.480
	2Bw	46-60	0.016	0.108	0.536	0.186	0.752	0.795	0.928
	2BC	60-110	0.0	0.036	0.255	0.080	0.773	1.310	1.393
	2C	110-160	0.0	0.022	0.083	0.042	0.668	1.176	1.349
M3	Ah	0-30	0.847	0.0	3.905	0.000	2.492	0.415	0.431
	Bw	30-80	-	-	-	-	-	-	-
	C	80-100+	-	-	-	-	-	-	-
U3	Ah	0-10	0.0	0.010	0.231	0.095	0.712	1.143	1.255
	Bw_1	10-30	0.0	0.011	0.339	0.136	0.726	1.543	1.734
	Bw_2	30-42	0.0	0.001	0.132	0.112	0.562	1.239	1.408
	BC	42-78	0.0	0.012	0.052	0.060	0.466	1.042	1.229
	C	78-120	0.0	0.012	0.031	0.058	0.356	0.731	1.059

(1) non-organic bound Al is calculated by $Al_o - Al_p$ (Parfitt and Henmi, 1982);

(2) percentage of allophane is calculated by $100 * Si_o / \{23.4 - (5.1[(Al_o - Al_p)/Si_o]\}$ (Laffan et al., 1989);

(3) amorphous bound Fe is the Fe_o (Parfitt and Childs, 1982);

(4) crystalline bound Fe is estimated by $Fe_d - Fe_o$ representing free iron oxides in crystalline bonds (Harrison et al., 1990);

(5) Fe_o/Fe_d is the activity ratio indicating the degree of ageing or crystalline of free iron oxides (Cornell and Schwertmann, 2003);

(6) Eger et al. (2011).

5.4 Discussion

5.4.1 Surface soil chemistry

Differences of surface soil chemistry were shown on a relatively short timescale on the soil chronosequence and restoration trajectory. The younger Transect 3 soils usually showed greater chemical and biological activity with higher Soil MBC and mineral nitrogen, compared with the older Transect 1. Soil pH was more acidic with soil age, and reached a plateau in the mid-later stage of soil chronosequence. This was mainly due to the acid production (organic and inorganic acids) following the decomposition of accumulated organic materials. Similar patterns of soil chemistry, in particular soil pH, had been shown in previous long-term soil chronosequence studies in a similar climate at the Haast chronosequence (Eger et al., 2011); as well as in a million-year timescale chronosequence study in tropical island forest ecosystem in Hawaii (Hedin et al., 2003). Higher soil pH and EC in Transect 3 could also be the result of receiving more sea spray with high basic cations (Whipkey et al., 2000), as it is located closer to the current shoreline. The foliage acts like a collector for the sea spray, rain will wash the deposition down into the soil (this is discussed more in Chapter 6). Inputs of significantly larger amount of Na, Mg, and K were evident in early study (Smith et al., 2016) (Table 5.3); and substantial Na enrichment was also found by Eger et al. (2011). Higher soil pH and MBC probably promoted soil nitrogen mineralization, resulting in higher ammonium-N. Lower nitrate-N in M1 might be due to lower pH which is unfavourable to the nitrification processes (Clough et al., 2004).

In terms of soil microbial biomass P, Turner et al. (2013) indicated its increasing importance to either the soil organic P or biomass P (plant and microbial) alongside the long-term ecosystem development in Franz Josef chronosequence. This partly explains the low soil MBP in the younger M3 in the present study. However, the reasons that MBP concentration was higher in R3 and U3 compared to M3 remained unclear. This could be because of the different vegetation hence different microbial communities between the three plots (Yin et al., 2016; Zak et al., 2003), as R3 and U3 have mixed grass cover with abundant fine grass roots. Unlike in Turner et al. (2013), there was not a further correction of potential contributions of fine leaf fragments and roots to the microbial P measured by the fumigation method in the present study. This could lead to potential overestimation of microbial P in the surface soils. Additionally, it is worth noting that surface soil biological properties, in particular microbial properties are highly sensitive to changing environmental conditions such as temperature and moisture. Thus, results from a one-time sampling event in the present study might not reveal long-term changes in soil biological properties. Long-term study of effects of vegetation restoration and composition on soil microbial P dynamic would be a valuable property to study.

Surface soil P fractions in the present study mainly agreed with the conceptual model proposed by Walker and Syers (1976), as the younger (less weathered) soils at Transect 3 had overall larger soil P pools than the older (more weathered) soils at Transect 1. Similar results of soil P factions on long-term soil chronosequences and ecosystem development had been reported in many studies (e.g. Crews et al., 1995; Parfitt et al., 2005; Eger et al., 2011; Izquierdo et al., 2013; Chen et al., 2015). On the other hand, the concentration of P (org) and proportional importance of P (org) to P (tot) had been significantly improved by the restoration of native plants, compared to unplanted mixed grassland (Table 5.4 and Figure 5.3). There was not comparable studies regarding forest restoration in this super-humid climate of the West Coast, New Zealand. Similar pattern of soil inorganic and organic P transformations was observed in a 40-year *Pinus sylvestris* natural revegetation site in North-western Russia (Celi et al., 2013).

However, different results were reported relating grassland afforestation in dry high country areas of Canterbury, New Zealand, indicating that lower organic P concentration in the topsoil of pine stands compared with adjacent grassland (Davis and Lang, 1991; Condron et al., 1996; and Chen et al., 2000). They accounted this for the enhanced mineralization of soil organic P under pine. Differences observations between studies could possibly due to: (i) different degrees of organic material decomposition because of the different ages of restoration or afforestation (De Schrijver et al., 2011; Zhang et al., 2016); (ii) multi-species restoration versus single species afforestation resulting in different strategies of P mining and P dynamics (Oelmann et al., 2011; Rosling et al., 2016); and (iii) different environmental conditions (dry versus wet climate) (Chen, Condron, & Xu, 2008). In the present study, it could be extrapolated that organic P pool in restoration soils would approach the level in the mature forest soil and got stabilised in the future.

Low inorganic P fractions, including primary apatite P (Ca) and secondary mineral P (Fe/Al), in the mature forest soils could be due to more intense weathering, which is promoted by diverse mature vegetation. Released P might have been subsequently transformed into soil organic P, immobilized in the biomass, or lost via leaching and runoff (Hedin et al., 2003). Losses of soil nutrients in more weathered soils were also reflected in lower total Al and Fe at the mature forest plots (Table 5.5). In this scenario, the restoration of native plant species at the oldest restoration site (R1) had substantially promoted the weathering of soil minerals, but these weathered minerals were not lost yet. Thereby, significant high concentrations of both oxalate and citrate-dithionite extractable Al and Fe were found in the R1 surface soils. In the present study, Al and Fe contents in the rocks or gravels were not included in the analyses, but more than half (50%-75%) of surface materials were gravels at the younger Transect 3 (see profile description in the Appendix D.1). This could possibly explain that lower concentrations of total Al and Fe found at the younger Transect 3, compared to the older Transect 1.

Although soil occluded P fractions were not significantly different between plots, they still become slightly more important as soils age (from Transect 3 to Transect 1). This is probably because of the relatively small soil age gap between transects at the present study. However, occluded P fractions were proportionally less important in restoration plots, compared to mature and unplanted plots at both transects (Figure 5.3). This is partially attributed to promoted P transformation by restored vegetation, as reflected in increased importance of organic P. Similar results were also observed in a 300-yr post-landslide tropical forest development at Puerto Rico (Frizano et al., 2002). They attributed this to the potential release of P from occluded pool by soil biota. However, Zhang et al. (2016) found an increase in occluded P fraction in the middle (90-yr old) forest successional stage, but decreased to the late (ca. 400-yr old) successional stage at South China. They indicated, although increased soil microbial activity in the middle successional stage had promoted the release of inorganic P into soil solution, but might quickly be precipitated by Al and Fe mineral in the favourable pH environment of tropical soils and become occluded.

5.4.2 Profile soil chemistry

Differences in profile soil chemical properties between ages of transects were evident in profile soils in this super-humid temperate coastal ecosystem. In the soil profiles, differences of soil chemical properties between mature (M), restoration (R) and unplanted (U) plots were shown, in particular in the top two soil horizons. In the present short-term soil chronosequence study, several observed changes of soil properties, for instance soil pH, C and N, were supported by previous soil chronosequence studies (e.g. Crews et al., 1995; Eger et al., 2011; Chen et al., 2015).

Soil pH decreased as soils age, as the older Transect 1 (ranging 4.7-5.5) was overall more acid than younger Transect 3 (ranging 5.3-6.2). It has been suggested that soil will be acidified by the release of organic acids from litter decomposition, and by the decreases of acid buffering capacity due to continuous losses of soil basic cations along with ageing soil and ecosystem (Hedin et al., 2003). Soil EC in the Ah horizon soils at the younger Transect 3 could have been highly influenced by marine spray, as it is located close to the current shoreline (ca. 150 m from the present high water mark). Incoming sea spray deposits (e.g. Na^+, K^+, Mg^{2+}, Cl^- and SO_4^{2-}) on the plant foliage got wash down via trunks and stems into the soil (Warneck, 2000; Whipkey et al., 2000). In addition, higher soil pH in the lower soil horizons at the Transect 3 might also be affected by shallow saline water tables (McLaren & Cameron, 1996), because its position may mean there may be some saline water flushing through gravel from the beach. However, the slightly elevated beach ridge (ca. 1-4 m) is unlikely to be low enough to reach the water table, since soil EC did not show a sharp increase in the bottom horizon (Figure 5.5, h). Unplanted U1 and U3 Ah horizons were prone to have higher nitrogen mineralization rate (as reflected in NH_4-N concentrations), as they rely more on rapid acquisition of nutrient from soil compared to forest system with more conservative nutrient strategy (Dickinson, 1984; Solly et al., 2014). At M3 Ah horizon, high soil organic carbon content encouraged vigorous microbial activities (as reflected in high

MBC), and this coincided with surface soil results previously. However, it is also possible that these high values could just be outliers observed under heterogeneous field conditions. At last, relatively higher concentration of nitrate-N species along the deeper horizons of unplanted plots also indicated higher potential of N leaching losses.

5.4.3 Soil phosphorus and Fe/Al minerals

Soil Phosphorus dynamics

In the present short-term coastal sand dune chronosequence, the initial concentrations of total soil P (ca. 518 – 865 mg kg^{-1} on a 75-yr terrace) in the A horizon at the younger Transect 3 were similar to the youngest site on Franz Josef schist outwash glacial chronosequence (ca. 554 mg kg^{-1} on a 130-yr terrace) (Parfitt et al., 2005); but higher than that on the Haast sand dune chronosequence (ca. 220 mg kg^{-1} on a 370-yr terrace) (Eger et al., 2011). These differences could be first attributed to soils developing from different parent materials and also different degrees of weathering. In comparison with Eger et al. (2011), apart from potentially more soil P lost due to soil age differences, the presence of ilmenite sand in the present study site could contribute to larger soil P pool. The inclusion of primary apatite P in the ilmenite sand was investigated in Syers et al. (1967) and Cescas et al. (1970). This contribution 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 5.6, c and e). This change of parent material (from Bw to 2Bw, see profile description in the Appendix D.1) also led to a low stock of primary mineral P in the upper horizons at U1 profile (Table 5.7). 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 super-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).

Different depth trends of soil P (tot) and P (Fe/Al) presented between Transect 1 and 3 could partly be attributed to different degrees of parent material weathering (Figure 5.6, 5.7). Soil P factions in the profile soils were more modified in the Transect 1 compared to Transect 3. This is coupled with the different patterns of soil pH. At the Transect 1 profile and the top horizons at Transect 3, stronger soil acidity has promoted the weathering of parent material, liberated formerly occluded bedrock P and released into soil solution. However, these solution P could either have been assimilated into biomass and incorporated into soil organic matter, or had gradually reacted with various weathered cations forming secondary phosphates, mainly Fe and Al phosphates (Tiessen et al., 1984). It is 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 5.6). Zhou et al. (2013) suggested that soil P fractionation was more governed by changes of soil pH, microbial activity and vegetation cover in short-term young soil chronosequence. In addition, a greater degree of pedogenesis in the soils at Transect 1 compared to Transect 3 was also supported by lower primary apatite phosphate concentrations, but higher soil occluded P in the upper horizons at Transect 1 compared to Transect 3 (Figure 5.6); and by the Fe_o/Fe_d ratio, which indicates the degree of soil aging (Table 5.9).

Nevertheless, the presence of primary 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. In terms of soil occluded P fractions, the present findings support the model proposed by Walker and Syers (1976), as more weathered P had been transformed into occluded forms (organic or inorganic) at the older Transect 1 compared to Transect 3. However, such occlusion might not be permanent as occluded P could be re-released via symbiosis of plant and mycorrhizal (Tiessen et al., 1994; Courty et al., 2010; Shen et al., 2011). This beneficial mechanism could potentially remediate ecosystem retrogression in future or delay the reaching of terminal steady stage of ecosystem development, as P is the critical nutrient for ecosystem succession (Wardle et al., 2004b). Other potential beneficial mechanisms could be external aeolian inputs (e.g. dust deposition in Crews et al., 1995 and Eger et al., 2013) or seabird guano deposition (will discuss in the next chapter).

Fe/Al mineral dynamics

With regard to soil extractable Fe and Al concentrations by oxalate, citrate/dithionite and pyrophosphate extractions, restoration soil samples were not analysed (Figure 5.8). Although the effects of vegetation cover differences on the weathering of soil parent material and clay minerals are known, a longer time scale is often required in order to observe notable distinct differences (Egli, Mirabella, & Sartori, 2008; Lucas, 2001). In the present study, since the oldest restoration plot (R1) was initiated in 2009 from unplanted grassland to restored stand, the effects of vegetation restoration on mineral weathering would likely be small or negligible. However, the effects of different vegetation covers on soil mineral weathering would expect to be noticeable between mature forest soils and unplanted grassland soils. Observed differences in extractable Fe and Al minerals between mature forest and unplanted grassland were mostly confined to the Ah and Bw horizons (Figure 5.8). Although only a short time, this is a dynamic environment with high rainfall, producing high weathering rates, so it is expected to see changes in Fe/Al minerals.

Depth trend of Al_p concentrations were related to soil organic carbon contents in the profile, since pyrophosphate can effectively extract organic-matter Al and organic-matter Fe, but is poor in extracting allophane- or imogolite-related Al and ferrihydrite- or goethite-related Fe (Parfitt and Childs, 1988). It was suggested that peptization of soil clays might result in the overestimations of pyrophosphate extractable Al and Fe (Skjemstad et al., 1992). These could help to explain the absence of inorganic Al, and high Al_p/Al_o and Fe_p/Fe_o ratios in the present study (Table 5.9). The increases of Al_p/Al_o and Fe_p/Fe_o ratios from Ah to Bw in most of the horizons could potentially indicate the eluviation of Al and Fe minerals from Ah and upper Bw via organic acids, and subsequent illuviation in the lower Bw horizon. These patterns coupled with the accumulation of soil organic carbon, indicate a pre-podsolization or early stage of podsolization conditions (Eger et al., 2011). Since all three extractants (oxalate, dithionite-citrate, and pyrophosphate) were capable of effectively extracting Fe and Al from organic-matter related minerals, substantial high content of organic carbon at M3 Ah has resulted in overall significantly higher Fe and Al concentrations in all extractions.

Higher amounts of crystalline Fe minerals in the unplanted grassland soils than mature forest soils, indicated more primary mineral weathering promoted by organic acid originated from diverse vegetation in the mature forest. In the Ah horizons, abundant organic matter that has impeded the better crystallization of Fe oxides (goethite and hematite), which led to high Fe_o/Fe_d ratios (Cornell and Schwertmann, 2003). Except for U1 plot, slightly higher Fe_o/Fe_d ratios were shown in 2Bw and 2BC horizons without containing enough organic carbon contents. This may be resulted from the presence of ilmenite sand. Furthermore, overall lower Fe_o/Fe_d ratio in Transect 1 soils than transect 3 soils might indicate the increasing maturity of soils within the present soil chronosequence (Simón et al., 2000). The good fitted linear correlation between Fe_o and Al_o indicates the relationship of amorphous Fe and Al minerals, between ferrihydrite-Fe and allophane-/imogolite-Al (Figure 5.9). This relationship indicated the presence of ferrihydrite and allophane in soils are often associated under similar conditions (Childs et al., 1991).

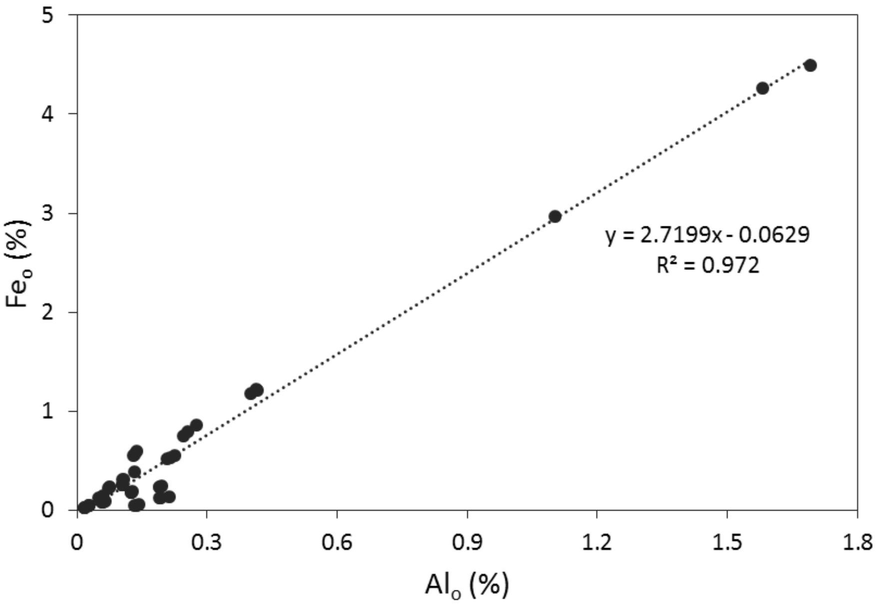


Figure 5.9 Relationships between Fe_o and Al_o in Transect 1 and 3.

Overall, the present study does not attribute the differences in soil profile data (presented on different stages of ecosystem development (M, R and U plots)) were all due to the short-term vegetation restoration, rather they were due to the original site differences. These observed differences were more likely to be a combination effect of ecological restoration and site heterogeneity.

5.4.4 The importance of soil pedogenesis in the ecological restoration

Soils with two different development stages have responded differently to ecological restoration practices in the present study. This is evident for example in changes of soil pH, mineral nitrogen, and microbial biomass C and P dynamics. Valuable comparisons are provided in the present study: (i) restoration site and reference mature forest indicate the differences between existing and past soil forming pathways; and (ii) differences between restoration site and unplanted grassland reveal the effects of ecological restoration on soil forming pathways. Ecological restoration is thought to re-supply ecosystem services by accelerating or reconstructing ecosystem succession (Prach and Walker, 2011). It has been argued that integration of soil pedogenesis into ecological restoration studies does help to predict future soil development of restored ecosystems (Moorhead, 2015). In addition, it was found that there were diverse responses to ecological restoration on soils developed from 3 different types of parent materials in a 9,000 ha degraded landscape (Abella et al., 2015). Therefore, knowledge of soil pedogenesis definitely needs to be considered when undertaking rehabilitation or restoration of ecosystem across landscape consisting contrasting soils.

In terms of nutrient dynamics along a long-term soil chronosequence, it is known that soil nutrient dynamics transformed from N limiting at early stage to P limiting at later stages of ecosystem development, will eventually lead to ecosystem retrogression if no major disturbance occurs (Peltzer et al., 2010). An accompanying increase in substrate N:P ratio occurs during this long-term process. The end-point is a reduction of standing plant biomass and ecosystem productivity in old regressive forest ecosystems (Wardle et al., 2004b). This soil nutrient transformation obviously has critical implications when ecological restoration practices are undertaken on large-scale landscapes consisting of distinct stages of soil development (e.g. newly developed versus highly weathered soils). Selecting appropriate native plant species that fit the corresponding soil nutrient status could be crucial for future native vegetation establishment and ecological restoration success. Vegetation composition changes along a long-term chronosequence: from angiosperm dominated to conifer dominated temperate rain forest in Franz Josef post glacial chronosequence (Richardson et al., 2004); and from conifer dominated to mixture of conifer-angiosperm temperate rain forest in Haast chronosequence (Turner et al., 2012); and in *Metrosideros polymorpha* (Myrtaceae) dominated tropical rain forest but with changes of other genera of trees and shrubs in Hawaii island chronosequence (Crews et al., 1995). These studies all suggested that plant community changes were mainly driven by soil nutrient dynamics alongside long-term soil development. Pioneer N-fixing species are critical in the early stages, while plants adjusted to P-poor soils (e.g. mycorrhizal symbiosis) perform well in the late stages.

Nevertheless, the extrapolation of the established knowledge is that soil P stocks in the present study site will face continuous losses as soil and ecosystem age under this super-humid climate, including in the restoration plots. However, unlike the initial proposed model by Walker and Syers (1976), a later study in Yang and Post (2011) indicated that soil labile organic P and secondary mineral P (Fe/Al) (non-occluded P in Walker and Syers' model) continue to show their dynamics and proportional importance throughout different weathering stages. In addition, the accumulation of organic P during soil and ecosystem development consist of a variety of compounds which are subject to different availability to biochemical mineralization (Turner et al., 2007). These two soil P factions provide an investment for future ecosystem development and maintenance, and they will be re-available for uptake by plant via special P-acquisition strategies when the ecosystem enters P-limiting stage (Lang et al., 2016; Rosling et al., 2016). This is also applicable for the restored ecosystem. Furthermore, considering the bio-availability of soil P during ecological restoration, better soil nutrient management could potentially enhance ecosystem productivity and soil C sequestration, as well as minimize impacts on nearby water environment via reduction of N and P lost (Parfitt et al., 2005).

5.5 Conclusions

(1) Soil biogeochemistry, including soil P dynamics, responded differently to the trajectory of ecological restoration on old and young soils.

(2) Dynamics of soil organic matter (accumulation and decomposition) and increasing demand of N from fast-growing plants early in the restoration result in a rapid nutrient mineralization.

(3) The results support Walker and Syer's conceptual model of a loss of soil total P, increase of occluded P and increasing importance of soil organic P as soils age.

(4) The present study is based on a relatively short-term soil chronosequence limiting the capacity to interpret soil nutrients dynamics in a longer-term ecosystem and period soil development.

(5) The importance of incorporating knowledge of soil pedogenesis into ecological restoration was evident in the project for PCRP. This could be more critical when extrapolated from the PCRP site into larger-scale landscape restoration consisting of different soil types and highly weathered soils.

(6) The importance of organic P, progressive changes P fractions and loss of total soil P, help us to understand how to sustainably manage the restoration process and predict the fate of soil development of restored ecosystems. There is a diverse response to ecological restoration along the gradient.

(7) Based on the findings from the short-term soil chronosequence and ecological restoration in this study, not only soil pH, extent of soil organic matter accumulation, and N and P availability should be routinely monitored, but also soil parameters that inform the stage of soil development either soil P status (total P, organic P, secondary mineral P and primary mineral P) or soil Fe/Al minerals. A background study of a proposed restoration site should at least include a proper survey of soil types and soil descriptions, which is important for replanting species selection and ongoing vegetation development.

Chapter 6

Soil P and Mineral Dynamics under Different Vegetation Stands

6.1 Introduction

Vegetation cover is an influential soil-forming factor, in addition to the effects of climate, time, topography, parent material and soil biology (McLaren & Cameron, 1996). It has long been suggested that plant species can alter soils in different ways, such as through the modification of physical properties by root morphologies, the quantity and quality of carbon compounds added to soil and relating to associated soil biota (Binkley & Giardina, 1998). Plants also play a critical role in mineral weathering, including Al and Fe, in the course of soil pedogenesis (Lambers et al., 2009). It was known that plant species affect soil weathering processes via primarily soil organic matter accumulation and different strategies of weathering agent productions (e.g. CO_2, organic acids, and ligands); particularly in the rhizosphere (Kelly et al., 1998; Augusto et al., 2000; Eviner & Chapin; 2003; Marie-Pierre et al., 2009). Therefore, plant species are able to influence soil pedogenesis to some extent through multiple and interactive processes.

Numerous previous studies had been focused on investigating the effects of different plant species on soil N and P mineralization via plant litter inputs and decomposition (e.g. Scott & Binkley, 1997; Manzoni et al., 2010; Hobbie, 2015) or via root turnover (e.g. Aerts et al., 1992; Hobbie, 1995). In contrast, there significant differences have been found in N and P mineralization between different species composition of spruce and birch stands in Norway (Saetre et al., 1999). Studies have also compared soil P dynamics under N-fixing and non-N-fixing plant species (e.g. Zou et al., 1993; Compton and Cole, 1998); and soil P dynamics modified by forest plantations, for example pine afforestation in New Zealand grassland (Chen et al., 2000).It has been recommended that studies of plant species effects on soil biogeochemistry or even ecosystem processes should investigate multiple factors and plant traits beyond plant litter quality and decomposition (Eviner, Chapin, & Vaughn, 2006).

Phosphorus (P) is known to have a particularly critical ecological significance (Walker & Syers, 1976). From a pedogenesis point of view, most soil P has its origins in parent material (McLaren & Cameron, 1996). Phosphorus may become a major limiting nutrient for plant growth and ecosystem development, since P can be lost via soil erosion or become locked up in biomass (Vitousek et al., 2010). As a consequence, mature and old ecosystems may enter retrogression if no major disturbance occurs (Peltzer et al., 2010). It has been suggested that external inputs of P from dust deposition, when parent mineral P depleted, could continue to support the productivity of old forest to some extent

(Chadwick et al., 1999); so that seasonal inputs of P from nectar-feeding birds during flowering could work the same way.

In the present study, I question whether the forms of soil P and Fe/Al minerals are affected by the effects of different vegetation types, including stands of flax, palm and grassland, in natural coastal ecosystem under super-humid climate on the West Coast. The work presented in this chapter aims to investigate:

(1) whether there are differences of phosphorus dynamics under three types of vegetation;

(2) differences of soil minerals under these types of vegetation; and

(3) the importance of bird guano deposition to phosphorus status in these components of a restoration ecosystem.

6.2 Materials and methods

Three vegetation stands were selected, dominated by Nikau palm (*Rhopalostylis sapida*, H.Wendl. et Drude, Arecaceae), New Zealand flax (*Phormium tenax*, J. R. Forst. et G. Forst, Xanthorrhoeaceae), and abandoned grassland (unplanted reference) respectively (Figure 6.1, 6.2).

Nikau palm (*R. sapida*) is the only palm endemic to New Zealand, and is the most southerly distributed species of the family Palmae. This monocotyledonous tree (up to 15 m in height) is widespread as a sub-canopy to canopy tree in coastal to lowland forest, distributed from the extreme north of North Island to Okarito in the Westland, South Island (Wardle, 2002). Nikau palm has large fronds (up to 3 m long, 2 m wide), forming a large round leaf base. Shed leaves are slow decomposing due to high fibre contents. These fronds act like a funnel, capturing rainwater and aerosol spray, transporting stem flow to the base of the plant. It was suggested that a Nikau palm could be maintained by the captured nutrients from stem flow (Enright, 1987). Nikau Palm is flowering (red/pink) in spring and followed by berries (February to November), which hang from just below the leaf base; native birds feed on the nectar and berries. The root system of Nikau palm is characterized by a primary tap root with few secondary fine roots outgrowths (Wardle, 2002).

New Zealand flax (*P. tenax*) is one of two monocotyledonous herbs in the *Phormium* genus, and is endemic to New Zealand (Wardle, 2002). This tussock species (up to 3 m in height) is widely distributed from coastal and lowland areas to montane forest, and is usually seen around wetlands and river banks throughout New Zealand. Flax has sword-shaped leaves (1 – 3 m long, 50 – 120 mm wide) grow in fan-like, robust tufts. This feature also provides a funnel-like collector, receiving rainwater and aerosol spray and transporting them to the base of the plant. Flax flowers in summer from around November to February, forming tall and distinctive flower stalks (up to 5 m height). Native birds, such as tui (*Prosthemadera novaeseelandiae*, Meliphagidae) and bellbird (*Anthornis melanura*, Meliphagidae), heavily feed on flax nectar (Wehi & Clarkson, 2007), but this may not be a reliable food source due to high annual variability of nectar production (Craig & Stewart, 1988). Flax leaves contain a high proportion of fibre, and this species has high Māori cultural value for use in weaving; later it had high economic value as European settlers developed a fibre export industry which was productive until the 1920s (Wardle, 2002). Flax is characterized by an extensive fibrous root system with some roots penetrating more deeply to exploit water (Wehi & Clarkson, 2007).

The grassland reference sites is an agricultural grassland abandoned in approximately 2011 (Hahner et al., 2013). The grassland consists of 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.

The three vegetation stands are located on soils developed on alluvial fans over sand plain (Kamaka soil series). They belong to Orthic brown (Hewitt, 2010), and Dystrudept (Soil Survey Staff, 2014). Field moist surface soil samples were collected (5 replicates) using a stepping auger (diameter=3.5 cm, depth=10 cm). The grassland had an existing excavated soil pit (U4 from which soil samples down the soil profile were collected). Auger soil profiles were drilled in the approximate centre of palm and flax stands. Soil profile descriptions are given in the Appendix D.2 (Table D.2). Profile soil samples were collected from each described soil horizon down the profile (collecting at least 200-g of moist soil from each horizon). It was assumed that surface soil measurements could better show the overall effects of vegetation on soil properties compared to single soil profile, whilst profile soil sample measurements provide the soil history. The three vegetation stands are located on the parallel line that was fairly close to Transect 3. Based on the soil age estimation in Chapter 5, these stands' ages were about 75-yr.

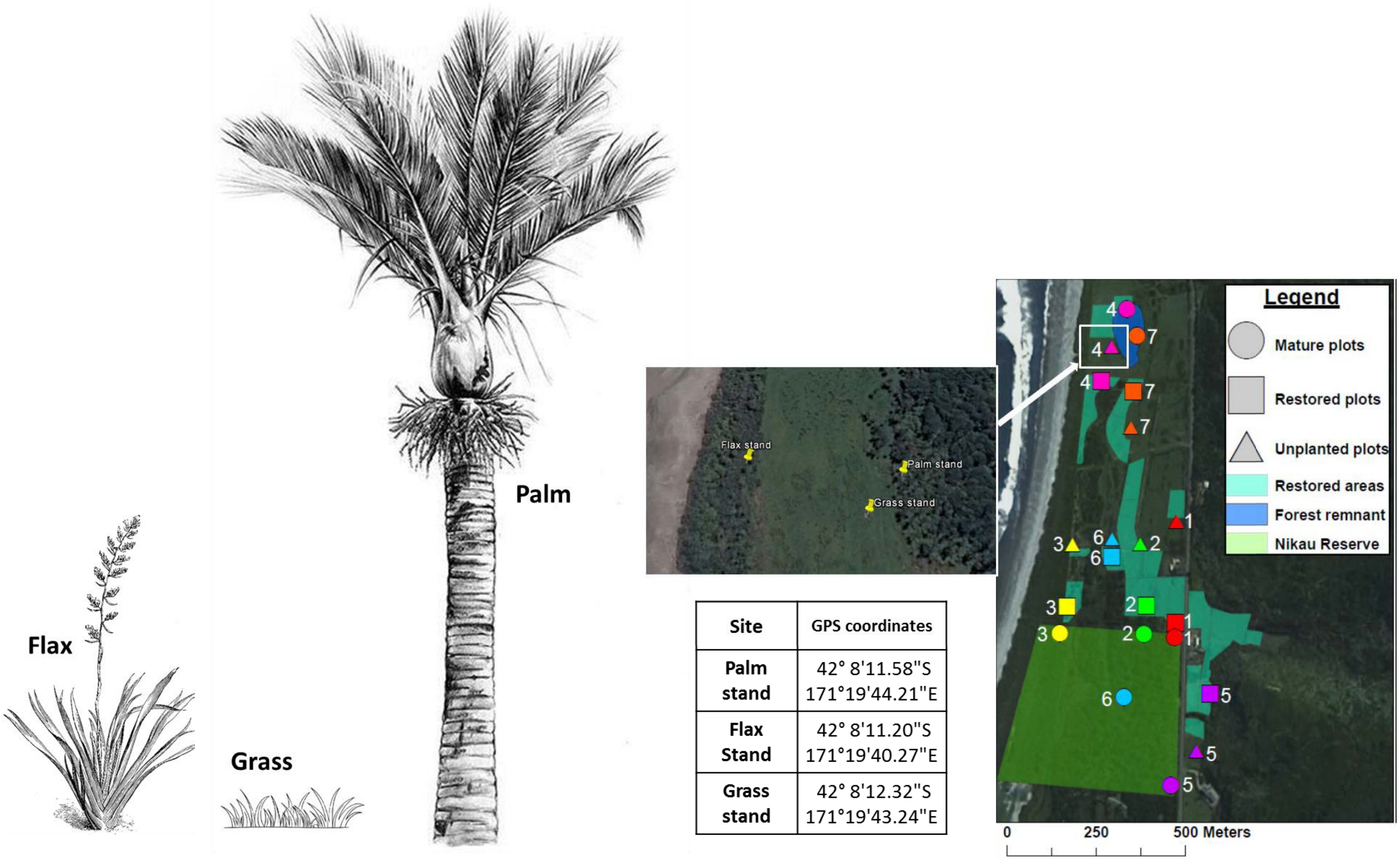
Soil samples were sieved (< 2 mm) and stored in zip-lock polyethylene bags at 4 °C for less than 1 week prior to analysis, with additional sub-samples for air drying (25°C for up to 1 week). Treatment of soil samples and analyses of soil properties follow the same protocols previously described in Chapter 2 (General Materials and Methods). Soil moisture content, 2M KCl-extractable nitrogen, microbial biomass carbon and microbial biomass phosphorus were determined on fresh soil within one week. Soil pH, electrical conductivity (EC), the first soil phosphorus (P) fractionation scheme, and soil extractable Fe and Al were determined on air-dried soils.

The first soil P fractionation scheme (non-sequential) followed Eger et al. (2011), which includes (1) total soil P: P (tot); (2) organic P: P (org) was the result of subtracting P (acid) from the 0.5M H_2SO_4-extractable P after ignition, (3) acid-extractable P: P (acid) was the 0.5M H_2SO_4-extracted phosphorus; (4) Fe/Al-bound P: P (Fe/Al) and Ca-bound P: P (Ca); (5) inorganic P: P (in) was the difference between P (tot) and P (org); and (6) occluded P: P (occ) was calculated as P (tot) - P (org) – P (Fe/Al) - P (Ca).

Extractable Fe and Al were extracted separately using acid oxalate (Fe_o and Al_o), citrate-dithionite (Fe_d and Al_d) and pyrophosphate (Fe_p and Al_p) for different forms.

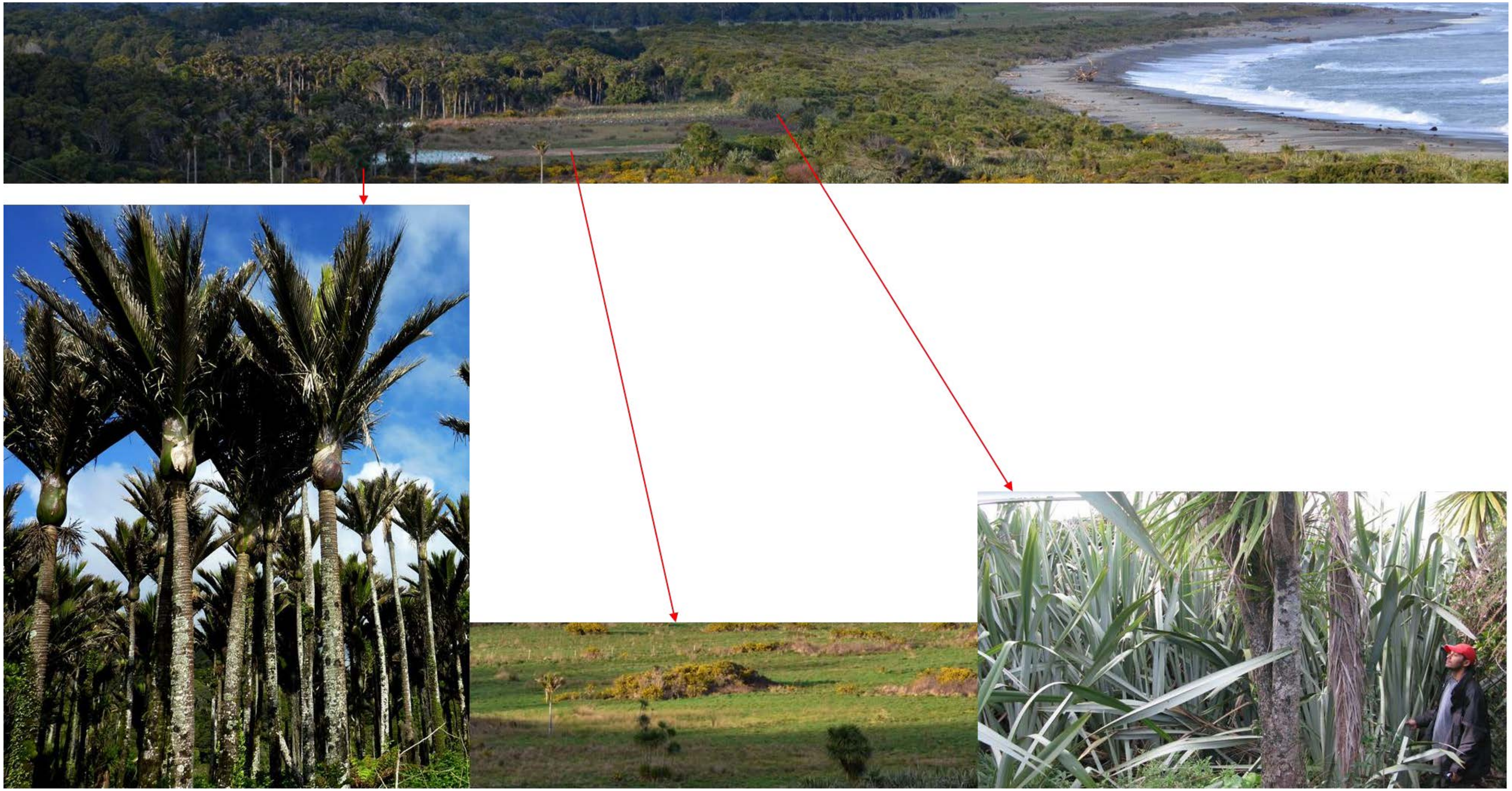
The area-based soil properties (g m^{-2}) were calculated using the concentrations and soil volume density data (Blakemore et al. 1987). To allow a fair comparison between three vegetation stands, area-based total amounts of P fractions were calculated down to 40 cm depth (Ah and Bw horizons).

Data analyses used Minitab (Minitab Inc., State College, Pennsylvania, USA), performing one-way ANOVA with the Fisher’s least-significance-difference post-host test, Pearson correlation analyses for key soil parameters with P fractions, and non-parametric Kruskal-Wallis tests for profile soil properties comparisons between palm, flax and grass stands.



Site	GPS coordinates
Palm stand	42° 8'11.58"S 171°19'44.21"E
Flax Stand	42° 8'11.20"S 171°19'40.27"E
Grass stand	42° 8'12.32"S 171°19'43.24"E

Figure 6.1 Location of palm, flax and grass stands; and illustration of three plants (Illustrations are sourced from etc.usf.edu/ and imgrum.net/).



Nikau palm **Grassland** **Flax**

Figure 6.2 Layouts of three vegetation stands (Photographs by Mike Bowie and Nicholas Dickinson). The silver-like patch in the grassland indicates plastic combi guard.

6.3 Results

6.3.1 Properties of surface soil

Surface soil chemical properties differed under palm, flax and grass stands (Table 6.1); pH was higher in the palm stand compared with flax and grass stands. Soil EC was significantly lower in the grass stand. Soil NO_3-N concentration was significantly higher in the flax and palm stands. There were also significantly large variations in other measured parameters, but there was no significant differences in MBP between three vegetation stands.

Table 6.1 Selected surface soil chemical properties. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (*p*<0.05). EC: electrical conductivity; MBC: microbial biomass carbon; and MBP: microbial biomass phosphorus.

Sites	pH (1:5 H_20)	EC (dS m^{-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
Palm stand	5.61 $(0.09)^a$	0.10 $(0.01)^b$	2.0 $(0.7)^{ab}$	7.1 $(0.9)^a$	227 $(39)^b$	1.8 $(0.3)^a$	24 $(5)^b$
Flax stand	5.11 $(0.07)^b$	0.12 $(0.01)^a$	3.7 $(0.9)^a$	9.0 $(1.2)^a$	547 $(45)^a$	1.7 $(0.2)^a$	54 $(8)^a$
Grass stand	5.22 $(0.09)^b$	0.04 $(<0.01)^c$	0.8 $(0.2)^b$	2.2 $(0.9)^b$	458 $(155)^b$	1.4 $(0.2)^a$	34 $(4)^b$

The flax stand provided routinely different values for P fractionations compared to the other stands of vegetation (Table 6.2). The flax stand consistently had the highest P (tot), P (org), and P (in) concentrations; but there were no significant differences in P (acid) between the three vegetation stands. Soil P (Ca) was highest in the flax and palm stand, however P (Fe/Al) was highest at grass stand. The non-sequential method provided the sum of proportions of P (tot) values higher than 100% (as discussed earlier in Chapter 5) (Figure 6.3). Soil P (org) was the most important P fraction at the palm and flax stands (47% and 57% respectively), and the proportional importance of P (Ca) was larger than P (Fe/Al) in the palm and flax stands. In the grass stand, P (org), P (occ), P (acid) and P (Fe/Al) were almost equally important (ca. 30%), whilst the P (Ca) was the least important fraction.

Surface soil clay mineral analyses results showed that oxalate and citrate-dithionite extractable Al, Fe and Si concentrations, as well as the percentage of crystalline Fe were consistently higher in the flax stand (Table 6.3). The Activity Ratio (Fe_o/Fe_d) was lower in the flax stand.

Principal Component Analysis of surface soil properties between palm, flax and grass stands is shown in Figure (6.4). The first component accounted for the majority of data variation loadings (62.6%) which is mainly explained by P (tot), P (org) and extractable-Fe/Al contents. The second component (11.94%) is mainly explained in terms of pH, P (acid) and P (Fe/Al).

Table 6.2 Surface soil phosphorus fractions. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (p<0.05). Total phosphorus: P (tot); organic phosphorus: P (org); inorganic phosphorus: P (in); acid-soluble phosphorus: P (acid); primary apatite P: P (Ca); secondary mineral P: P (Fe/Al); and occluded phosphorus: P (occ).

Sites	P (tot)	P (org)	P (in)	P (acid)	P (Ca)	P (Fe/Al)	P (occ)
Palm stand	490 (68)^{b}	239 (51)^{b}	252 (21)^{b}	96 (24)^{a}	70 (23)^{ab}	39 (3)^{b}	142 (12)^{ab}
Flax stand	902 (87)^{a}	504 (40)^{a}	398 (65)^{a}	128 (9)^{a}	87 (8)^{a}	40 (3)^{b}	271 (67)^{a}
Grass stand	342 (24)^{b}	114 (12)^{c}	228 (23)^{b}	111 (17)^{a}	31 (5)^{b}	94 (22)^{a}	103 (25)^{b}

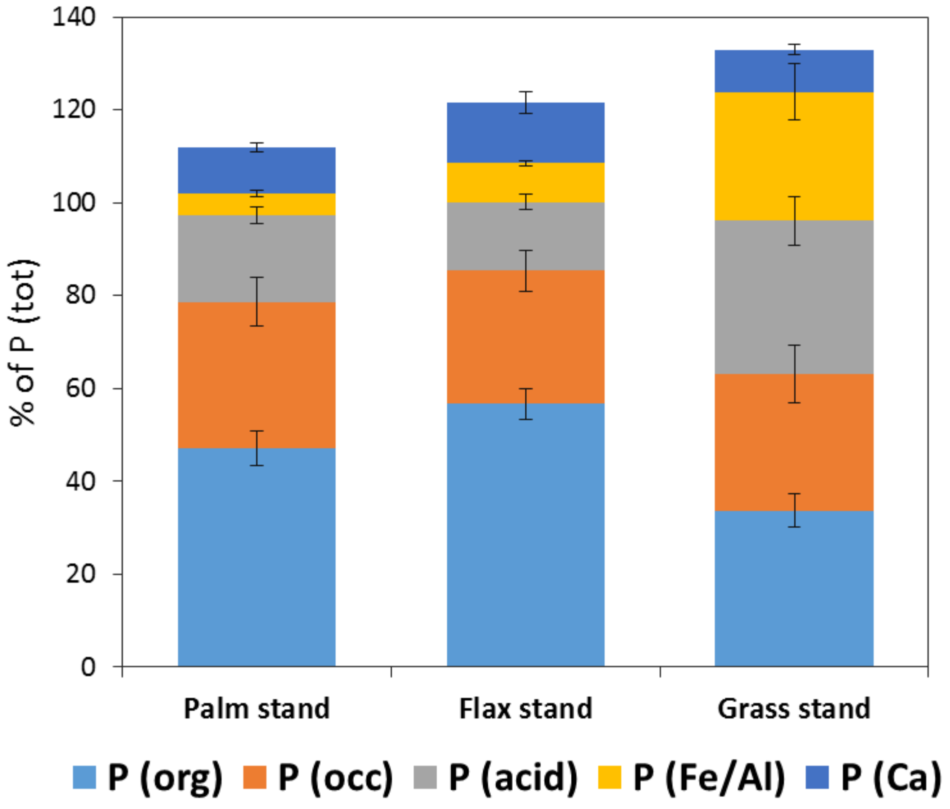


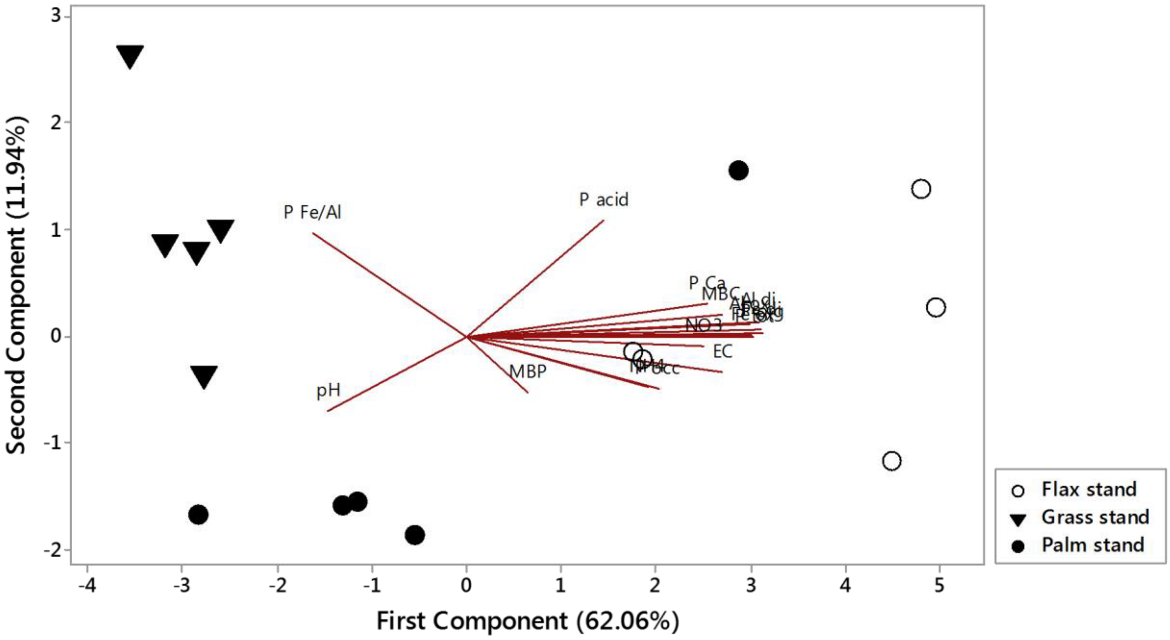
Figure 6.3 Proportion of organic P, occluded P, acid-extractable P, Fe/Al-bound P and Ca-bound P of Total P in surface soils at palm, flax and grass stands. Data are mean values ± standard error (n=5).

Table 6.3 Surface soil clay mineral analyses results. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (p<0.05). Where: (i) Al_o, Fe_o and Si_o are oxalate-extractable aluminium, iron and silicon; and Al_d, Fe_d and Si_d are citrate/dithionite-extractable aluminium, iron and silicon.

Sites	Al_o %	Fe_o %	Si_o %	Al_d %	Fe_d %	Si_d %	Crystalline Fe % [(1)]	Fe_o/Fe_d [(2)]
Palm stand	0.19 (0.03)^b	0.73 (0.1)^b	0.01 (<0.01)^b	0.13 (0.03)^b	0.68 (0.13)^b	0.04 (0.01)^b	0.04 (0.11)^b	1.09 (0.14)^b
Flax stand	0.57 (0.06)^a	1.56 (0.13)^a	0.05 (0.01)^a	0.64 (0.09)^a	2.37 (0.32)^a	0.11 (0.02)^a	0.58 (0.19)^a	0.77 (0.07)^c
Grass stand	0.11 (0.01)^b	0.38 (0.03)^c	0.01 (<0.01)^b	0.06 (0.01)^b	0.27 (0.04)^b	0.03 (<0.01)^b	-0.06 (0.04)^b	1.22 (0.16)^a

(1) crystalline bound Fe is estimated by $Fe_d - Fe_o$ representing free iron oxides in crystalline bonds (Harrison et al., 1990);

(2) Fe_o/Fe_d is the activity ratio indicating the degree of ageing or crystalline of free iron oxides (Cornell and Schwertmann, 2003);



Variable	pH	EC	NH_4-N	NO_3-N	MBC	MBP	P (tot)	P (org)	P (acid)	P (Fe/Al)	P (Ca)	P (occ)	Fe ox	Al ox	Fe di	Al di
PC1	-0.146	0.273	0.193	0.252	0.271	0.066	0.305	0.315	0.147	-0.163	0.257	0.205	0.304	0.301	0.313	0.311
PC2	-0.368	-0.180	-0.247	-0.049	0.103	-0.279	-0.003	0.019	0.569	0.503	0.162	-0.259	0.003	0.057	0.033	0.074

Figure 6.4 Principal component analysis of selected soil properties in surface soils at palm, flax and grass stands.

6.3.2 Properties of profile soil

In the profile soils, pH appeared to increase with depth in all three stands, but was lower in the Ah horizon in the grass stand (Figure 6.5). Soil pH was significantly different between the three vegetation stands (p<0.0001) (Table 6.4). Soil EC generally decreased with depth in all three stands (p<0.0001). Soil organic carbon contents decreased with depth in all three stands, but flax had the highest SOC contents in each corresponding horizon (p<0.0001). This was reflected to some extent in soil MBC (p<0.0001). Soil MBC concentrations were significant higher in the top two horizons (Ah and Bw) of the palm stand. Both NH_4-N and NO_3-N concentrations were highest in the Ah horizon of the grass stand (p<0.0001).

Soil P fractionation showed that the concentration of P (tot) and P (org) were markedly different in the flax stand (Figure 6.6). The flax profile had the highest organic P concentration in each corresponding horizon. In terms of the other P fractions, the flax stand data separated from the other sites, and significantly from the grassland. All measured P fractions were significantly different between the three vegetation stands (p<0.0001) (Table 6.4). The proportional importance of soil P (org) was evident in the Ah and Bw horizons of the palm and flax stands (ca. 50% - 80% of total P), but it contributed little to the total soil P pool in the grassland (Figure 6.7). Soil P (acid) was the most important fraction throughout the profile (ca. >80% of total P) in the grassland. Soil P (occ) fraction was more substantial in the palm stand than the other stands, but P (Fe/Al) contributed less beneath palms. Soil P (Ca) became proportionally more important with depth at palm and flax stands. The area-based stocks of P fractions in the top 40 cm were consistently higher in the grassland, apart from P (org) (Table 6.5).

The results of Pearson Correlation analyses showed that soil organic carbon content was positively correlated with P (org) (Table 6.6). Soil pH was negatively correlated with EC. Soil P (acid) was positively correlated with P (Fe/Al) and P (Ca). Soil P (tot) had no correlation with any of tested parameters.

Results of soil extractable Fe and Al concentrations by three different extractions showed significant differences in the flax stand (Figure 6.8). The flax stand had significantly higher extractable - Al and Fe in three extractions, particularly in the Ah, Bw and upper BC horizons. Data from palm stand consistently lie in-between. All measured extractable- Al and Fe concentrations were significantly different between three vegetation stands (Table 6.4).

Analyses of Al/Fe minerals showed significant differences in the flax stand compared to the other stands (Table 6.7). Al fractions showed that inorganic-related and allophane Al forms were overall higher in the top three horizons of the flax stand, particularly allophane Al in the Bw of the flax. Amorphous and crystalline Fe forms were consistently higher in the Ah and Bw horizons of the flax stand. The ratios of Fe_o/Fe_d, Fe_p/Fe_o and Al_p/Al_o was all below 1 among three stands, except for C horizon of the palm stand.

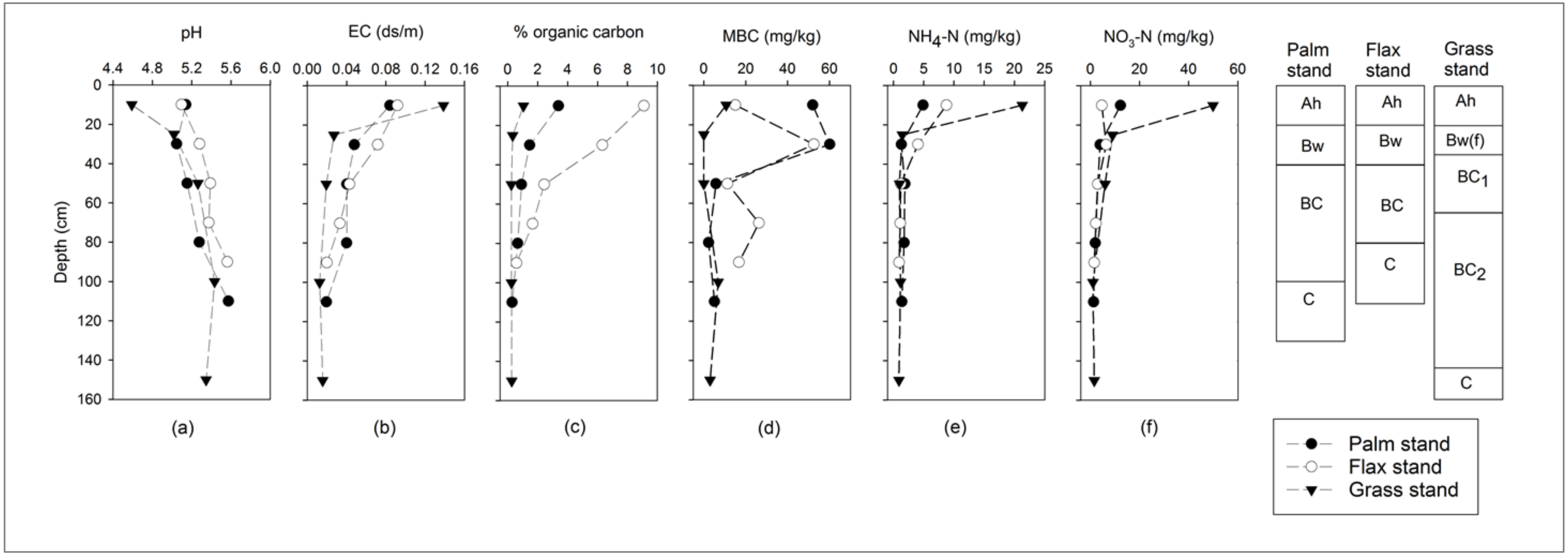


Figure 6.5 Selected profile soil chemical properties at palm, flax and grass stands. EC and MBC stand for electrical conductivity and microbial biomass carbon respectively.

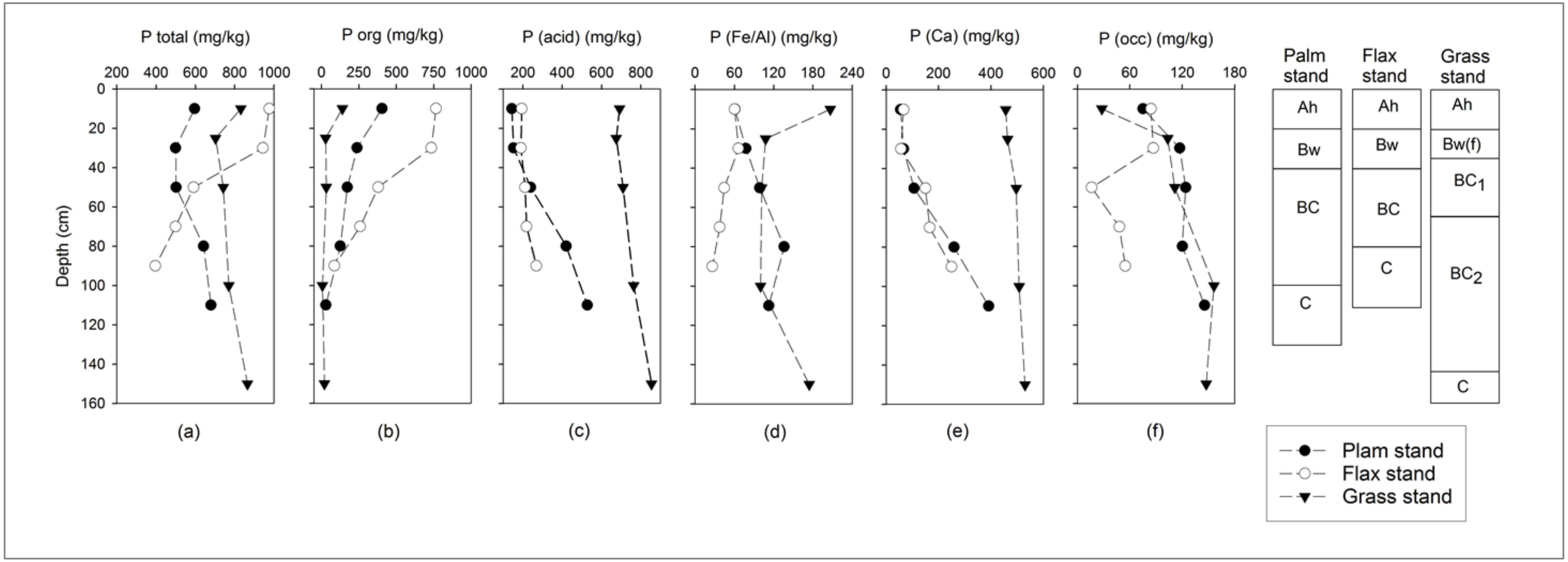


Figure 6.6 Profile soil phosphorus fractionations at palm, flax and grass stands. Total phosphorus: P (tot); organic phosphorus: P (org); inorganic phosphorus: P (in); acid-soluble phosphorus: P (acid); primary apatite P: P (Ca); secondary mineral P: P (Fe/Al); and occluded phosphorus: P (occ).

Table 6.4 Kruskal-Wallis test results of significant difference between palm, flax and grass stands on selected profile soil chemical properties.

	pH	EC	NH_4-N	NO_3-N	MBC	% SOC	P (tot)
P value	0.103	0.026	0.212	0.751	0.005	0.026	0.002
	P (org)	P (acid)	P (Fe/Al)	P (Ca)	P (occ)	Al_o	Fe_o
P value	<0.0001	<0.0001	<0.0001	<0.0001	0.001	<0.0001	<0.0001
	Si_o	Al_d	Fe_d	Si_d	Al_p	Fe_p	Si_p
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

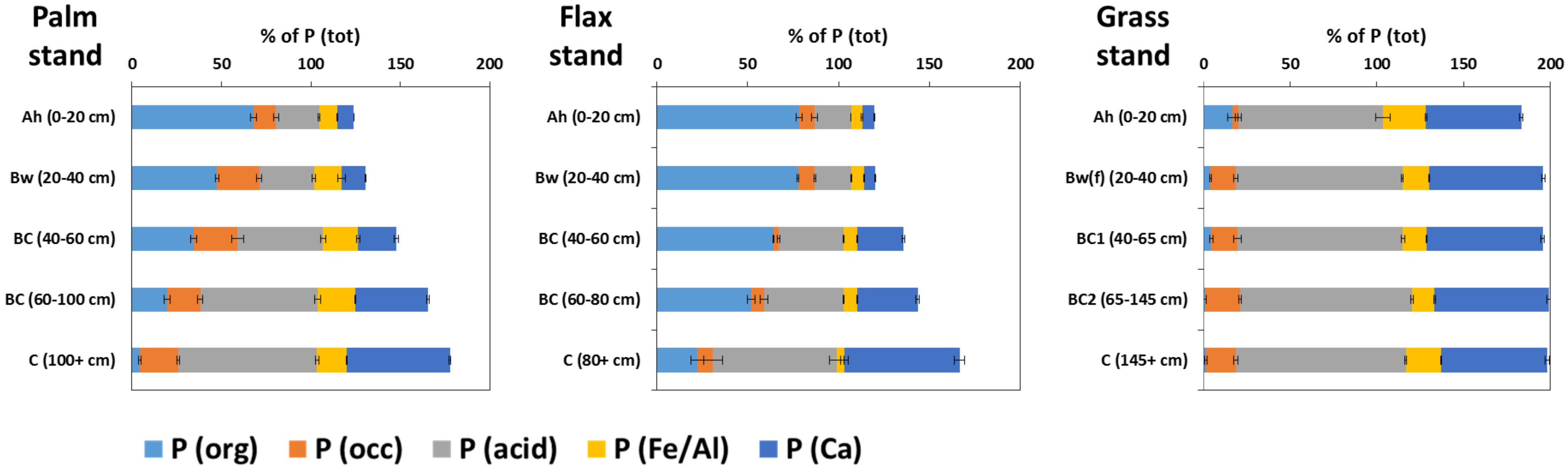


Figure 6.7 Proportion of organic P, occluded P, Fe/Al bound P and Ca bound P of total P in soil profiles at palm (left), flax (middle) and grass (right) stands.

Table 6.5 Area-based stocks of soil phosphorus fractions in the top 40 cm at palm, flax and grass stands.

Site	Depth (cm)	P (tot)	P (org)	P (occ)	P (acid)	P (Fe/Al)	P (Ca)
		(g m^{-2})					
Palm stand	0 - 20	154.4	104.9	19.5	37.2	15.7	14.3
	20 - 40	141.7	67.5	33.3	43.3	22.0	18.9
Profile mass to 40 cm		**296.2**	**172.4**	**52.7**	**80.5**	**37.8**	**33.2**
Flax stand	0 - 20	167.7	131.3	14.5	33.3	10.4	11.5
	20 - 40	176.7	137.5	16.3	35.5	12.4	10.6
Profile mass to 40 cm		**344.4**	**268.8**	**30.8**	**68.8**	**22.7**	**22.1**
Grass stand	0 - 20	237.8	40.1	8.0	197.9	59.1	130.6
	20 - 40	214.3	8.5	31.5	205.8	32.8	141.5
Profile mass to 40 cm		**452.1**	**48.6**	**39.5**	**403.8**	**91.9**	**272.0**

Table 6.6 Pearson correlation coefficients among key chemical properties and phosphorus factions in profile soils at palm, flax and grass stands. * indicates p < 0.05 and ** p < 0.01 (n=69); ns means not significant.

Correlation coefficient (r)	pH	EC	SOC %	P (tot)	P (org)	P (acid)	P (Fe/Al)	P (Ca)
EC	-0.778*							
SOC %	ns	0.543*						
P (tot)	ns	ns	ns					
P (org)	ns	0.557*	0.964**	ns				
P (acid)	ns	ns	-0.559*	ns	-0.691*			
P (Fe/Al)	ns	ns	ns	ns	ns	0.741*		
P (Ca)	ns	ns	-0.644*	ns	-0.768*	0.978**	0.650*	
P (occ)	ns	-0.540*	ns	ns	ns	ns	ns	ns

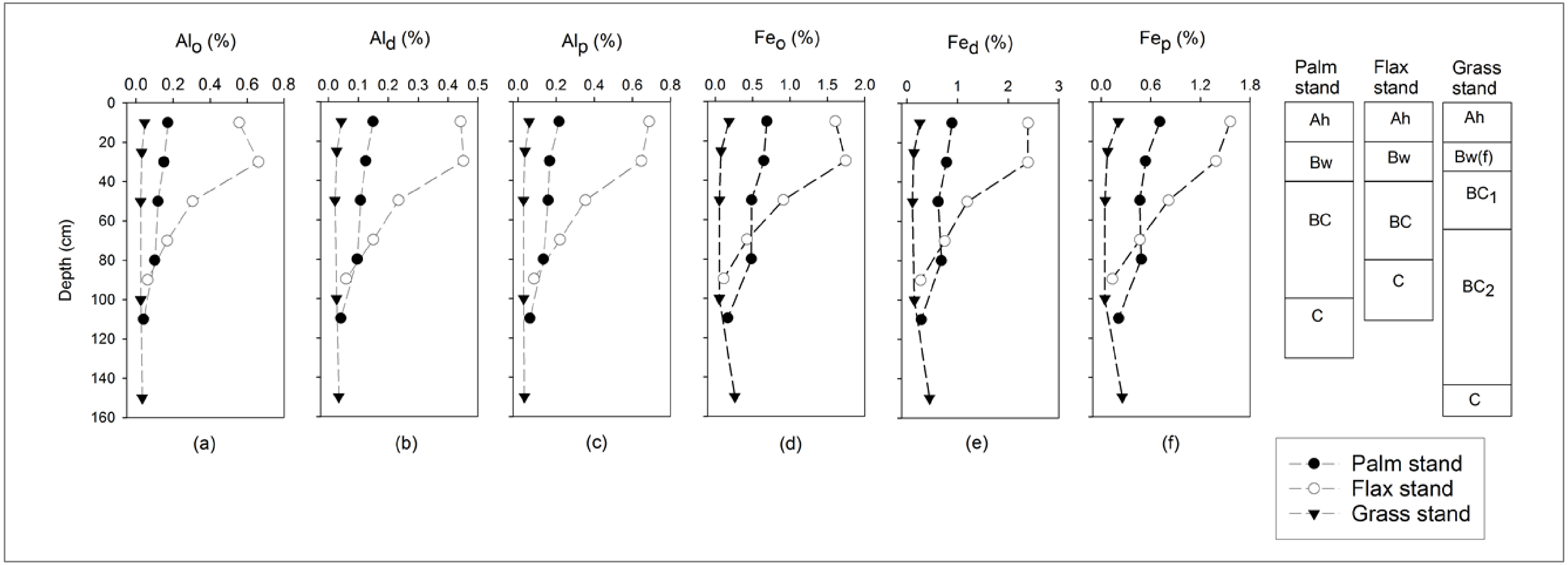


Figure 6.8 Profile soil mineral analyses at palm, flax and grass stands. Where Fe$_o$ and Al$_o$, are oxalate-extractable aluminium and iron; and Fe$_d$ and Al$_d$ are citrate/dithionite-extractable aluminium and iron; and Al$_p$ and Fe$_p$ are pyrophosphate-extractable aluminium and iron.

Table 6.7 Analyses of clay Al and Fe factions in soils under palm, flax and grass stands.

Site	Horizon	Depth (cm)	Non-organic Al (%) (1)	Allophane % (2)	Amorphous Fe (%) (3)	Crystalline Fe % (4)	Fe_o/Fe_d (5)	Fe_p/Fe_o (6)	Al_p/Al_o(6)
Palm stand	Ah	0-20	0.021	0.099	0.689	0.206	0.770	0.726	0.884
	Bw	20-40	0.035	0.086	0.647	0.143	0.834	0.588	0.778
	BC	40-60	0.008	0.043	0.486	0.136	0.782	0.675	0.933
		60-80	0.007	0.041	0.482	0.202	0.706	0.707	0.928
	C	80+	-0.003	0.012	0.168	0.119	0.586	0.880	1.083
Flax stand	Ah	0-20	0.076	0.290	1.606	0.787	0.672	0.680	0.864
	Bw	20-40	0.209	6.378	1.746	0.643	0.729	0.566	0.697
	BC	40-60	0.057	0.448	0.912	0.281	0.765	0.627	0.813
		60-100	0.014	0.066	0.425	0.324	0.571	0.774	0.915
	C	100+	0.004	0.033	0.114	0.160	0.421	0.841	0.948
Grass stand	Ah	0-20	0.005	0.026	0.184	0.075	0.711	0.793	0.898
	Bw(f)	20-40	0.005	0.019	0.076	0.065	0.544	0.709	0.841
	BC_1	40-65	0.005	0.018	0.055	0.059	0.489	0.618	0.812
	BC_2	65-145	0.005	0.024	0.053	0.090	0.374	0.594	0.817
	C	145+	0.010	0.050	0.261	0.189	0.585	0.686	0.707

(1) non-organic bound Al is calculated by $Al_o - Al_p$ (Parfitt and Henmi, 1982);

(2) percentage of allophane is calculated by $100*Si_o/\{23.4-(5.1[(Al_o-Al_p)/Si_o]\}$ (Laffan et al., 1989);

(3) amorphous bound Fe is the Fe_o (Parfitt and Childs, 1982);

(4) crystalline bound Fe is estimated by $Fe_d - Fe_o$ representing free iron oxides in crystalline bonds (Harrison et al., 1990);

(5) Fe_o/Fe_d is the activity ratio indicating the degree of ageing or crystalline of free iron oxides (Cornell and Schwertmann, 2003);

(6) Eger et al. (2011).

6.4 Discussion

6.4.1 Soil chemistry

There is no similar study in the literature of the effects of the types of vegetation targeted in the present study on the soil chemistry under field conditions. All measured soil properties tended to be consistently higher under flax, although this differed for mineral N in the profile soil. In the surface soils of the site of the present study, chemistry is likely to be influenced by marine spray. Flax and palm might be expected to capture larger amounts of Na and K from this source due to their morphological features. This might have been reflected in higher soil EC in flax and palm stand soils. However, soil pH in the flax stand was not significantly elevated in response to enrichment of base cations, probably due to: (i) base cations might be lost from the system as flax did not assimilate them into biomass (refer to plant foliage chemical composition in Chapter 3) alongside good drainage of these soils; and (ii) a counterbalance from the acidifying effect of organic acids from litter decomposition or CO_2 produced from microbial respiration (as reflected in high soil MBC).

Soil N mineralization from organic matter and subsequent nitrification processes might have been associated with soil microbial activity in the flax stand. In the palm stand, soil MBC was lower, but nitrification processes (reflected in NO_3-N concentration) might have been facilitated by more favourable soil pH environment (Clough et al., 2004). Similar soil MBP concentrations in the present three vegetation stands indicated an abundant soil P pool without intense competition for P resources from soil microbes. This is typical of this relatively early stage of soil and vegetation development (Turner et al., 2013). Although soil microbial biomass or communities were found to be different under different tree species in common garden experiments, determination of how transferable they are in the natural ecosystem still requires further tests (Prescott & Grayston, 2013). In the profile soils, soil pH, EC, MBC and mineral N concentrations in the Ah horizons differed conform to the surface soil results. For example, EC and mineral N concentrations were highest in the grass stand, rather than in the flax stand. This may reflect site variability of differences in sampling protocols.

6.4.2 Multi-drivers of soil development

Soil P fractionation

Differences in soil P pools between three vegetation stands could be a combined effect of landscape hydrological gradients and external nutrient input by bird guano. Differences in total P concentration of about 400 mg kg^{-1} in the surface soil and about 200 mg kg^{-1} in the top two horizons between three stands (Table 6.2, Figure 6.6), were much larger than could be accounted for by differences in leaching rates, based on losses of approximate 0.01% of total P yr^{-1} in the West Coast, New Zealand (Eger et al., 2011). It is possible there are differences in the total soil P pool that are independent of vegetation types. The present vegetation stands became established on the most suitable sections of this alluvial fan overlying sand plain, with the flax stand locates on the ending edge of the fan, while grassland and palm stand locate further inland (away shoreline) toward the alluvial source (Figure 1.3 in Chapter 1). Flax and palm vegetation are likely to be more capable than grassland of intercepting sediment flow. Associated with the alluvial fan formation, landscape pattern and hydrological gradients (Schaetzl and Thompson, 2015), the flax stand may have accumulated most sediment, followed by the palm stand, and then the grassland. The flax stand, being located at the lower end of the gradient receiving most sediments, may have had higher total soil P (Smeck, 1985).

Another factor to consider is that, both flax and palm stands would be expected to receive substantial amounts of bird guano during the flowering period. Bird guano usually contains high concentrations of N and P (Marion et al., 1994); the guano nutrient contents would be expected to be similar between flax- and palm-feeding frugivorous birds (Emerson & Roark, 2007). Although both plants can act like funnels, flax stands are denser and would tend to accumulate and concentrate more nutrients. This may explain why the flax stand had higher total soil P. Additionally, inputs of N from bird guano could also have contributed to higher mineral N status in the flax and palm stands.

However, differences in the proportional importance of individual P fractions of total P could also be attributed to a vegetation effect. It has been suggested that the dynamics of soil organic P is mainly driven by biological processes and changes related to vegetation development (Brandtberg et al., 2010; De Schrijver et al., 2012; Zhou et al., 2013). Vegetation development promotes soil weathering via organic acid production from plant litter decomposition and root exudation (Binkley & Giardina, 1998; Lambers et al., 2009). For example, the proportional importance of the organic-P fraction of total-P was evident in the flax and palm stands in the present study (Figure 6.3, 6.7). Since, palm and flax litters contain a high proportion of fibre (low quality), which is recalcitrant for decomposition (see Chapter 3); their root systems would be expected to play a more important role in promoting soil P dynamics and related weathering processes. Part of the mobile P that is released via guano sources and soil weathering might be fixed by the organic compounds released from root exudates or related to root turnover. Positive correlations between soil organic P and soil organic carbon content has also been found in earlier studies, for example by Brandtberg et al. (2010) and Hou et al. (2014). This is particularly evident in the profile soils of the present study, reflecting the deeper root systems of palm and flax. Differences in the proportional importance of soil organic P between palm and flax profiles could be explained by their different root morphologies (primary tap root system of palm versus extensive fibrous root system of flax) (Hinsinger, 2001; Lambers et al., 2006). However, a contrast view was given in Talkner et al. (2009), who they indicated that tree species only significantly impact the P turnover in the organic layer, while dynamics of P in mineral soil were mainly controlled by original soil properties, in particular clay content. Detailed study of the different effects of palm and flax systems on soil properties is needed.

Less soil weathering effects would have been promoted under grassland, with a lower proportion of organic-P, but a higher proportion of primary apatite P and acid-soluble P in the top two soil horizons. Soil secondary mineral P and occluded P fractions also related to the degree of soil weathering, were proportionally less important in the flax stand soil (Figure 6.7). Two possible causes might explain this. Firstly, flax rhizospheres could be more efficient in transformation of released-P into organic forms, rather than allowing it to be bound with Fe/Al minerals or else being occluded; even though transported sediments also bring about Fe and Al mineral accumulation. Slightly higher soil pH in the flax profile might also facilitate this transformation (Figure 6.5); it has been suggested that soil mobile P tends to bind or precipitate with Fe/Al minerals when soil pH is lower than 5.5 (Brady & Weil, 2008). A second possible explanation for less secondary mineral P and occluded P beneath flax is that accumulated alluvium sediments might have also contained soil organic matter that contributed to the transformation of soil released-P into organic P. This fits with the proposed sediment accumulation pattern between different stands, as discussed above. This type of competition of mobile P into different P fractions is known to be intensive within the P cycle (Tiessen et al., 1984). In addition, an argument against inherent differences between stands prior to vegetation establishment is provided by evidence from deeper soil horizons. Concentrations of primary apatite P and its proportional importance in the lower C horizons were getting close between three profiles, indicating a similar age (or starting point) for the flax, palm and grassland soils (Figure 6.6, 6.7).

Soil Al and Fe minerals

In addition to containing a larger soil P pool, the flax stand soil had significantly higher extractable Al and Fe concentrations in the Ah Bw and upper BC horizons. Accumulation of sediments due to a landscape hydrological gradient and external nutrient inputs by bird guano could also contributed to the enrichments of Al and Fe. However, this contribution from bird guano would be relatively small compared to N and P, since guano elemental composition results indicate that around 0.2% of Al and 0.5% of Fe comparing with 3.5% of N and 1.4-12% of P in seabird guanos (data measured in the next Chapter). Unfortunately, elemental data for guano from frugivorous birds feeding on palm and flax were not obtained in the present study.

Depth trends of Al_p and Fe_p were related with soil organic carbon contents in the profile (Figure 6.5, 6.8). Pyrophosphate extraction mostly extracts (> 80%) organic-matter Al and organic-matter Fe, but is poor (< 10%) in the extraction of allophane- or imogolite-related Al and ferrihydrite- or goethite-related Fe (Parfitt and Childs, 1988), and this could explain relatively higher Fe_p/Fe_o and Al_p/Al_o ratios in the three stands.

Significantly higher Al_p and Fe_p concentrations in Ah and Bw horizon in the flax stand could potentially be due to higher rate of translocation of organic-acid chelated minerals. It is thought that continuous production of organic acids (in the flax stand) leads to podsolization processes (Schaetzl and Thompson, 2015). Alternatively, the significantly higher allophane content presented in Bw horizon at flax stand is coupled with sharp increase of Al_o concentration (Figure 6.8; Table 6.7). Oxalate extraction can effectively extracts allophane-/imogolite-Al contents, comparing to pyrophosphate extraction (Parfitt and Childs, 1988).

Higher ferrihydite-Fe mineral in the flax stand soil indicated more primary mineral weathering, which would be promoted by more organic acid production from root exudation. Higher organic matters may have impeded the crystallization of Fe oxides (goethite and hematite), which led to higher amorphous-Fe mineral at the flax stand than the palm stand (Cornell and Schwertmann, 2003). However, the activity ratio, Feo/Fed, did not well reflect the different degrees of crystallinity of free iron oxides between three vegetation stands in the present study. Because, this activity ratio may only reliable for certain types of soil and soil horizons (Blume and Schwertmann, 1969). The linear correlation (R^2=96%) between Fe_o and Al_o indicates the relationship between amorphous ferrihydrite-Fe and allophane-/imogolite-Al minerals (Figure 6.9). It has been suggested that the presence of ferrihydrite and allophane in soils are often associated under similar conditions (Childs et al., 1991).

Different effects of palm, flax and grass vegetation on soil mineral weathering cannot be ignored in the present study. Palm and flax stand profile soils showed more obviously more mineral weathering as overall higher non-organic-/allophane-Al, and amorphous-/crystalline-Fe, compared to grassland.

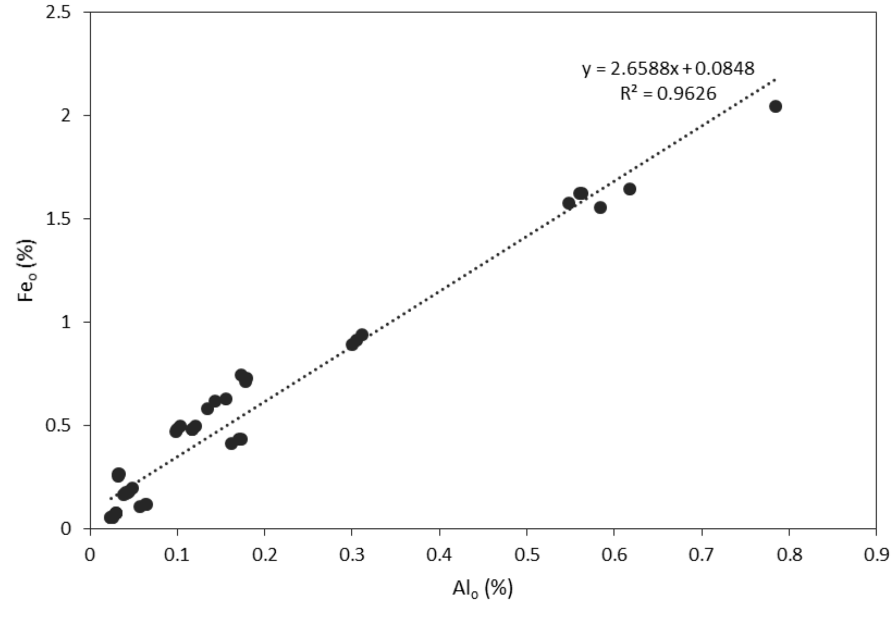


Figure 6.9 Relationships between Fe_o and Al_o in the soil beneath palm, flax and grassland.

6.5 Conclusion

(1) Substantial differences were recorded in soil pH, organic matter, P fractionation, and extractable-Al/Fe mineral contents between stands of flax, Nikau palm and grassland on the same gravel ridge at the PCRP site.

(2) Pre-existing differences in soil, prior to vegetation establishment were considered possible due to landscape hydrological gradients of alluvial fans.

(3) The findings indicate contributing effects from vegetation on soil chemistry; flax and palm vegetation stands have significantly promoted the soil development via mediating soil P transformations and Al/Fe mineral weathering.

(4) External nutrient inputs from guano deposition of nectar-feeding birds substantially contribute to the dynamics of soil N, P and Al/Fe minerals in the present study site;

(5) Differences in above- and belowground plant morphology between flax, palm and grassland also accounted for the observed soil pedogenic differences.

Chapter 7

Interactions between Earthworm, Flax and Guano on the P Dynamics: a glasshouse pot trial

7.1 Introduction

Phosphorus (P) is the second most important nutrient, after nitrogen (N), for plant growth (Raghothama, 1999); it plays a critical role in storage and transfer of energy in photosynthesis and respiration of plants (McLaren & Cameron, 1996); it is taken up by plants from soil solution in the form if orthophosphate (mainly $H_2PO_4^-$ in acid soil and HPO_4^{2-} in alkaline soil) (Shen et al., 2011). Phosphorus is by far one of the least available plant essential nutrients in soil, especially comparing with N (Vance, 2001). The bioavailability of inorganic P is of a particular concern in highly weathered soils of old ecosystems (Peltzer et al., 2010).

Soil P exists in various chemical forms, but primarily inorganic P (approx. 35-70% of total P) and organic P (approx. 20-80% of total P), and this proportional importance varies between soil types and management regimes (McLaren & Cameron, 1996). The transformation and dynamics of these P forms determine the bioavailability of P in soils, which is driven by several factors (Brady & Weil, 2008), for example: (i) the speciation and concentration of soil P; (ii) soil pH between 6-7 gives the best concentration of plant available P; (iii) desorption or dissolution of mineral-bound P and mineralization of organic P; (iv) competition of fixation sites from other soil anions; and (v) soil invertebrates e.g. earthworms, and microorganisms e.g. mycorrhizal symbiosis.

Bird guano contains variable concentrations of P, ranging from 0.12% up to 16% of P (Otero et al., 2015). Large coastal populations of seabirds in New Zealand are likely to have provided a significant source of this element which is known to be a key factor in forest development (Mulder & Keall, 2001; Roberts et al., 2007). However, excessive inputs of nutrients into aquatic and terrestrial ecosystems from bird guano, for example cormorant (*Phalacrocorax Spp*.), could lead to water eutrophication and degradation, as well as decline of vegetation (Boutin et al., 2011; Klimaszyk et al., 2015).

Earthworms are a key soil invertebrate, providing beneficial effects on soil processes and plant production, as 'ecosystem engineers'. Earthworm activities, such as feeding, digestion, excretion, burrowing and casting, substantially modify soil physical, chemical and biological properties of soil, in turn enhancing soil quality (Bertrand et al., 2015). These earthworms effects on soil properties could be different between earthworm species, and their ecological groups as epegeic, endogeic and anecic

(Sheehan et al., 2006); although some species may belong to multiple groupings e.g. epi-endogeic *Lumbricus rubellus* and epi-anecic *Lumbricus terrestris* (Vos et al., 2014).

Previous studies have focused on the mechanisms of earthworm effects on the promotion of plant production (summarized in van Groenigen et al., 2014). Many of these studies have focused on the effects of earthworms on soil N mineralization (e.g. Blair et al., 1997; Postma-Blaauw et al., 2006). Little is known about how earthworm activities affect the guano-P transformation in the plant-soil systems. It was reviewed that most studies on the effects of earthworms on soil P have focused on P availability to plants (e.g. Le Bayon & Milleret, 2009; Chapuis-Lardy et al., 2011), rather than on the effects on soil P fractionation.

Chapter 6 showed that soils beneath flax (*Phormium tenax*) at Punakaiki had different soil P dynamics, which may be related to root morphology and external nutrient inputs from bird guano. The work presented in the present Chapter, a glasshouse pot trial was carried out to simulate a scenario in which soil beneath flax plants receives bird guano and interacts with earthworms. The aim of this chapter is to investigate the effects of flax-earthworm-guano interactions on soil P dynamics.

7.2 Materials and methods

7.2.1 Soil

Soil from the Mature Forest plot (M1) at Punakaiki (42°8'38.39"S, 171°19'50.36"E) was chosen for this pot trial. This soil is described as Mahinapua soil developed on the sand plain [Sandy brown (Hewitt, 2000); Dystrudept (Soil Survey Staff, 2014)]. The reasons of choosing M1 soils for this pot trial, rather than using flax stand soils are twofold. Firstly, according to my results in the last two chapters, M1 surface soil has relative low total P (approx. 400 mg kg^{-1}), compared to the flax stand (approx. 900 mg kg^{-1}), making the simulation of external guano nutrient fertilization onto a relative 'P-poor' soil possible. Secondly, the M1 plot (Mature Forest) was the only place at the Punakaiki site where the endogeic species *Megascolecidae Sp.1* could be collected for enough adult numbers (see Kim et al., 2015). This mature forest plot contains three earthworm functional groups based on site observation. After removing the surface litter, soil (0-20 cm) was collected using a spade, then sieved through a 6 mm steel sieve and stored for 3 weeks prior to use in the pot trial.

7.2.2 Earthworm

Three earthworm species, (*Eisenia fetida*, Lumbricidae), (*Megascolecidae Sp.1*, Megascolecidae), and (*Maoridrilus transalpinus*, Megascolecidae) were selected for this pot trial study, representing epigeic, endogeic, anecic functional groups respectively (Buckley et al., 2015; Kim et al., 2015). Two of the species are native earthworms, but the exotic *E. fetida* earthworms were obtained from local compost heaps in the absence of good source of native epigeics. Although a native epigeic species *Deinodrilus gorgon* (Boyer et al., 2011) was found in the litter layer at M1 plot, its scarcity in the field and low survivorship under laboratory conditions make it unfeasible for the glasshouse pot trial. The two native species were selected mainly because of the abundance of adults during field sampling at Punakaiki and their good survivorship under laboratory conditions. These three earthworm species were kept in a laboratory incubator separately for up to three weeks and checked routinely to pick out dead or injured individuals, so that healthy earthworms were available for this glasshouse pot trial.

7.2.3 Guano

Less than 5-g of Westland Petrel (*Procellaria westlandica*, Procellariidae) dry guano was collected from a viewing platform and on plant debris at a small petrel colony (42°9'56"S, 171°20'16"E). To replace this, Spotted Shag (*Stictocarbo punctatus*, Phalacrocoracidae) guano was collected from King Billy Island (43°38'5.39"S, 172°41'8.14"E), Lyttelton Harbour in South Island, New Zealand, was used in the pot trial. Guano was air-dried, ground using a metal-rod, then sieved through 0.5 mm brass sieve, and stored in clean screw-top polyethylene containers. The elemental composition of guano was determined using ICP-OES (Varian 720 ES, Australia) following microwave digestion (Microwave digester, CEM MARS Xpress, USA) of the sample in 5M HNO_3. Total C and N contents were determined using Dumas combustion method on a CNS Elemental Analyser (LECO Elemental Analyser, NSW Australia) (Blakemore 1987). Organic phosphorus concentration was estimated by subtracting the 0.5M H_2SO_4-extracted phosphorus after and before ignition (Saunders & Williams, 1955). Results are expressed on an oven-dry (105°C) basis.

Only shag guano was used in this pot experiment. The reasons for choosing shag guano to use in this study were threefold. Firstly, it was impracticable to collect enough guano from birds (tui, *Prosthemadera novaeseelandiae*, Meliphagidae and bellbird, Anthornis melanura, Meliphagidae) feeding on flax and palm during one flowering season for the pot trial. Secondly, the Westland Petrel feeds at sea which would provide an obvious external input of P around the nesting colony. Petrel guano was readily mixed with nesting materials and soils due to colony maintenance by petrel, and aided by frequent and abundant rainfall in this region. Thirdly, the existing biggest petrel colony site is protected in the Special Protected Area inside the Paparoa National Park, Department of Conservation. It was too difficult to collect sufficient petrel guano for this experiment.

7.2.4 Flax-guano-earthworm pot trial

The pot trial was conducted in a glasshouse (glass roofing with side venting) in the nursery at Lincoln University (Figure 7.1). One-year old flax (*Phormium tenax*) seedlings were obtained from the

Motukarara nursery, Department of Conservation. The plant plugs contained potting mix, which was a barked-based medium amended with lime and nutrients. This was gently washed off the roots when transplanting each flax plant into a plastic pot (5 L) filled with Punakaiki soil (approx. 5 kg fresh weight each pot). 45 pots were planted, with 5 more pots unplanted as a control (in total 50 pots). The bottom of each plant pot was sealed with mesh curtain and tape. Newly transplanted flax plants were acclimated to glasshouse conditions for one week before inoculating earthworms on 20th of November, 2015. There were 5 replicates of each treatment that consisted of: 3 species of earthworms (*3) with (+) and without (-) guano additions (*2), another 5 pots with double-amount (++) guano addition without earthworm, and plus 5 pots remain unplanted as control (+).

Four earthworms of each species were added to each earthworm-treatment pot. All earthworms were weighed prior to inoculation. The upper part of each pot (in total 50 pots) was then covered with mesh curtain, attaching tape. Covering and sealing of the pots were to keep earthworms from escaping and also keep pot conditions uniform. Earthworm survival was checked daily in the following 5 days. In 2 of two of the endemic earthworm treated pots, all the earthworms died, and they were replaced with the same species of earthworm (biomass reweighed). In another 3 pots, one of the four earthworms had died, and dead earthworm bodies on the soil surface were removed carefully; but without adding new earthworms. After the first 5 days of stabilization, bird guano was added to guano-treatment pots fortnightly on 25th of November, 9th of December, and 23rd of December in 2015 respectively, receiving 1.5 g of guano three times (equivalent to about 2.6 g P m^{-2} each time), while double-amount guano treatment received 3 g of guano three times (equivalent to about 5.2 g P m^{-2} each time). Guano was added by open the curtain, top dressed to each guano-treated pot and the curtain was re-sealed and watered as scheduled.

Plant pots were maintained in a glasshouse with average day and night temperatures of 30 and 25 °C respectively throughout the trial. Soil water content of each pot was maintained by watering same amount of water daily as required and subjectively judged to be optimal. Plant pots were arranged in a complete randomized block design. Due to a limited number of native earthworm adults, a planned treatment to combine three functional groups of earthworms was unfeasible.

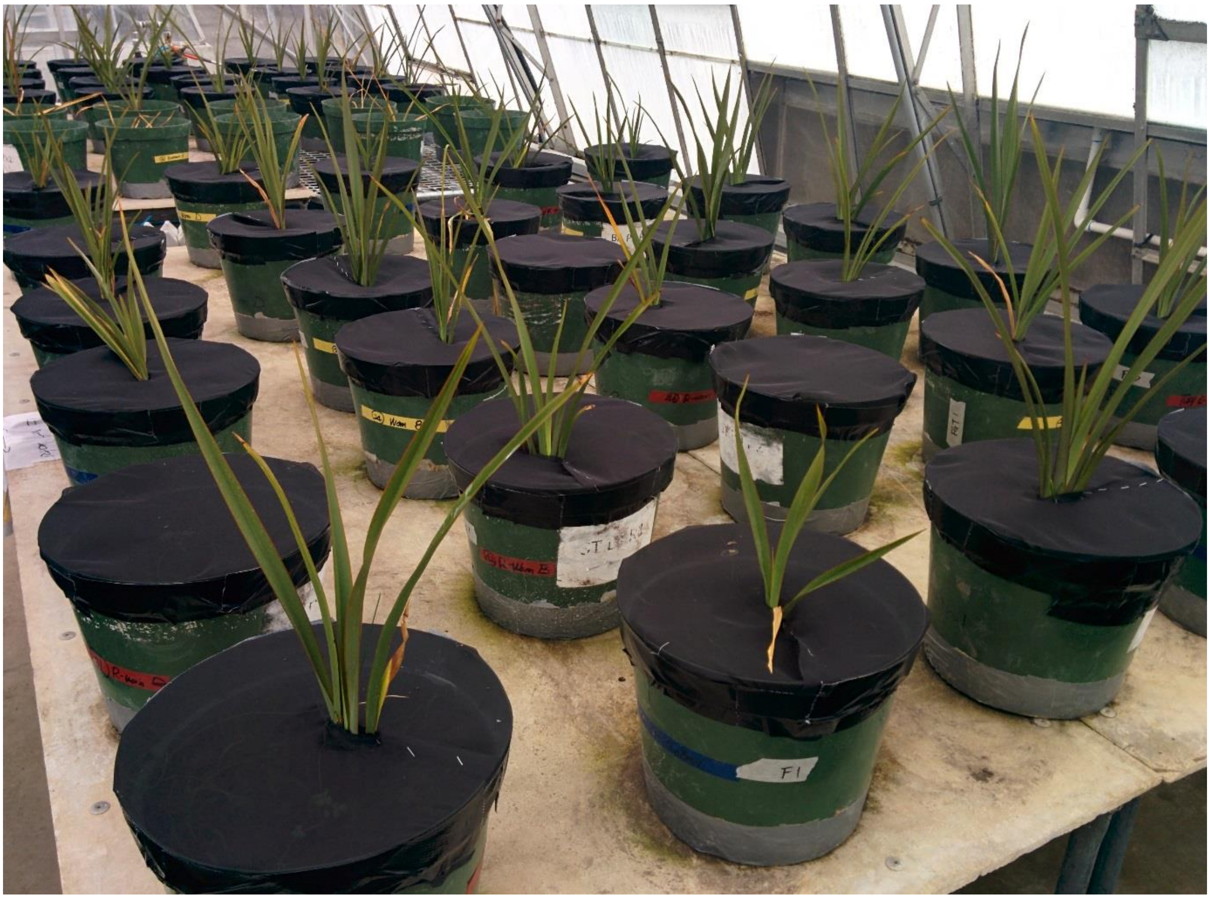


Figure 7.1 Experimental layout of flax-guano-earthworm glasshouse pot trial. Pots are randomly arranged.

7.2.5 Analytical: plant and soil

This pot trial was harvested on 21st – 22nd of January 2016 after 9 weeks of earthworm inoculation. Following the harvest of plants, roots were gently washed and patted dry by absorbent paper. They were then weighed and recorded for plant fresh biomass. Plant shoots and roots were separated and weighed. Plant samples were stored in paper bags, and dried for 48 hrs at 60 °C, then re-weighed for dry biomass. Earthworms were carefully collected from each treated pot, assessed for survivorship and re-weighed the fresh biomass.

After removing any surface moss cover (up to 2 cm depth), soil was carefully collected from the rhizosphere, then crumbled and sieved (< 2 mm) to remove roots. Moist soils were stored in clean zip-lock polyethylene bags at 4 °C for less than 1 week, and sub-samples were air-dried. Treatment of soil samples and analyses of soil properties follow the same protocols previously described in the Chapter 2 (General Materials and Methods). Soil were analysed for: moisture content, 2M KCl extractable soil mineral nitrogen, microbial biomass carbon, microbial biomass phosphorus and dehydrogenase activity (performed on moist soils within one week), and pH, EC, and the second soil phosphorus fractionation scheme (performed on air-dried soils).

The second soil P fractionation scheme extracts soil biologically based phosphorus fractions, which simulates mechanisms of plant and microbial phosphorus acquisition (DeLuca et al., 2015). In brief, each P fraction was measured in parallel by shaking a 1 g of soil with 20 ml of each extractant for 3 h. Extracts were then centrifuged at 2280*g* for 30 min, and filtered through Whatman 42 filter papers. Filtrates were stored in fridge prior to analysis.

The first extraction, 0.01M $CaCl_2$ extractable P ($CaCl_2$-P) represents soluble and weakly adsorbed inorganic P, simulating P acquired by direct root interception. The second extraction, 0.01M citrate extractable P (citrate-P) represents active inorganic P pool adsorbed to clay particles or weakly bound in inorganic precipitates, simulating the P pool that could potentially be released by organic acids produced from plant root and microorganisms. The third extraction, 1M HCl extractable P (HCl-P) represents inorganic P pool that moderately bound to clay minerals or precipitate Fe, Al, or Ca minerals, simulating more recalcitrant P pool that could potentially be solubilized via proton excretion (inorganic acids) promoted by plant root and microbial processes. Sequentially, the $CaCl_2$-P fraction has high bioavailability, followed by medium bioavailability of citrate-P fraction, and then the low bioavailability of the HCl-P fraction.

In addition, soil organic phosphorus (organic-P) was estimated by subtracting the 0.5M H_2SO_4-extracted phosphorus after and before ignition (Saunders & Williams, 1955). Soil total phosphorus concentration was estimated by NaOH fusion in a nickel crucible (Smith & Bain, 1982). Soil inorganic phosphorus was calculated as the difference between total P and organic P.

7.2.6 Statistical analysis

Data were analysed using Minitab (Minitab Inc., State College, Pennsylvania, USA), performing one-way ANOVA with the Fisher's least-significance-difference post-host test, and two-way ANOVA (guano and earthworm interaction) of selected soil chemical properties and P factions, and the main effect analysis of an independent variable (guano or earthworm) at each level of the other independent variable (guano or earthworm) on selected soil chemical properties and P factions.

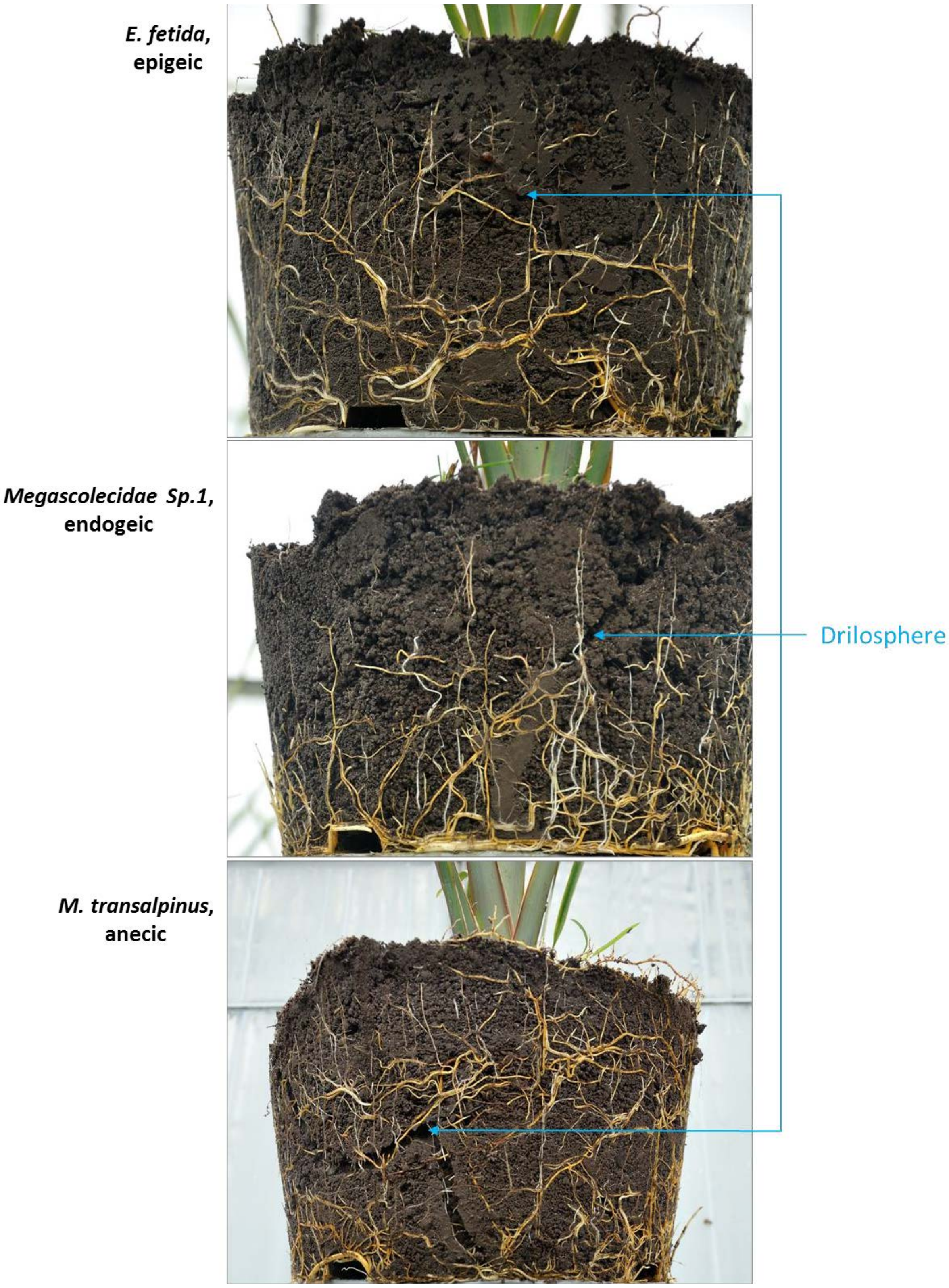


Figure 7.2 Evidence of earthworm casting and burrowing activities during pot trial experiment (randomly selected).

7.3 Results

7.3.1 Bird guano chemistry

In comparison with petrel guano, shag guano had almost a 10 times higher P content, but contained about 20 times lower concentration of cadmium (Cd) (Table 7.1). This difference would result in to a significantly lower Cd loading with 1.7 mg and 305 mg Cd per kilogram of applied P from shag guano and petrel guano respectively. Shag guano contains mostly inorganic P, and an almost 10 times higher concentration of Ca than petrel guano. For other nutrients, differences between shag and petrel guano were less distinct. On the other hand, shag guano has similar concentration of C compared with P, but lower N content. This results in a C:N ratio of about 3.5 for shag guano. Due to the availability of petrel guano, concentrations of C, N and organic P were not available.

Table 7.1 Comparison of guano chemistry between Spotted Shag (*Stictocarbo punctatus*) and Westland Petrel (*Procellaria westlandica*). Data in Shag guano column are means (n=3) with standard errors in parenthesis, while no standard errors for Petrel guano column due to the availability of guano.

	Shag guano	Petrel guano
Total C %	11.4 (0.3)	-
Total N %	3.5 (0.5)	-
Total P %	12.1 (0.2)	1.4
Organic P %	0.08 (0.01)	-
Ca %	23.0 (0.4)	2.4
K %	0.7 (<0.01)	0.5
S %	0.7 (0.03)	0.2
Mg %	0.6 (0.1)	0.3
Na %	0.4 (0.03)	0.1
Al %	0.3 (0.04)	0.2
Fe %	0.2 (0.03)	0.5
Zn %	0.05 (<0.01)	0.02
Mn %	0.02 (<0.01)	0.02
Cd (mg kg^{-1})	0.2 (<0.01)	4.2
mg Cd (kg P) $^{-1}$	1.7 (0.3)	305

7.3.2 Earthworm and plant growth

By the end of this glasshouse pot trial, all native earthworms had died, however all *E. fetida* individuals had survived. Growth of *E. fetida* showed a 23.5% increase in no-guano (-) pots, but their biomass doubled (106%) in guano (+) treated pots (Table 7.2).There was considerable evidence of burrowing activities in all inoculated pots, including the two native earthworm species, compared to exotics (Figure 7.2). This indicated substantial burrowing activities before they died. It is worth noting that there were no obviously visible dead earthworm bodies or decaying tissues from two native earthworm treated pots at the end of the experiment. This indicates that they probably died around mid-term of this experiment.

At the end of this pot trial, plant dry mass was highest in no-earthworm (+) pots (Table 7.2). In the earthworm treatments, *E. fetida* (+) promoted slightly higher flax growth then *E. fetida* (-) pots, but no significant difference between native earthworm pots. Flax in no-earthworm (++) pots had only similar biomass with no-earthworm (-) treatments. There was no significant differences in plant root/shoot ratio between treatments.

Table 7.2 Earthworm growth and selected plant properties of the flax-guano-earthworm incubation glasshouse pot trial. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (*p*<0.05). '-' and '+' indicate without and with guano addition, '+ +' indicates double amount of guano addition.

Treatments Earthworms	 Guano	Earthworm survivorship (%)	Earthworm growth (%)	Plant dry mass (g)	root/shoot ratio
No-earthworm	**-**	-	-	9.9 (1.3)^{c}	0.52 (0.05)^{a}
	+	-	-	17.2 (1.7)^{a}	0.48 (0.02)^{a}
	+ +	-	-	9.2 (1.0)^{c}	0.48 (0.05)^{a}
M. transalpinus	**-**	0%	no data	16.7 (3.5)^{ab}	0.44 (0.02)^{a}
	+	0%	no data	15.4 (3.3)^{abc}	0.51 (0.07)^{a}
Megascolesidae. Sp.1	**-**	0%	no data	14.5 (1.7)^{abc}	0.53 (0.05)^{a}
	+	0%	no data	11.7 (3.1) ^{abc}	0.60 (0.16)^{a}
E. fetida	**-**	100%	23.5	10.3 (0.9)^{bc}	0.40 (0.03)^{a}
	+	100%	106	13.5 (2.2) ^{abc}	0.45 (0.03)^{a}

7.3.3 Soil chemistry

Overall, soil pH was significantly increased (0.2 to 0.4 units) by the growth of flax, compared with control (+) pots (without flax) (Table 7.3). *E. fetida* (+) had the highest soil pH. Almost all other measured parameters decreased compared to control. Soil electrical conductivity (EC) was highest in the no-earthworm (++) and control (+) pots, compared with others. At the end of pot trial, control (+) pots contained the highest soil organic matter content. Ammonium-N (NH_4-N) concentration was highest in no-earthworm (++) pots and followed by controls (+). Nitrate-N (NO_3-N) concentration was significantly higher in controls (+) compared with others. There was no significant difference in soil nitrate-N concentration between earthworm treatments. There was no significant difference in soil microbial biomass carbon (MBC) between treatments. Soil microbial biomass phosphorus (MBP) concentration was significantly higher in plant pots with *E. fetida* (+) and no-earthworm (++) than other pots. Soil dehydrogenase activity (DHA) was highest in plant pots with *E. fetida* (+), and lowest in pots with no-earthworm (++) and controls (+).

With regard to soil biologically based P pools, soil $CaCl_2$-P, citrate-P and HCl-P pools have been modified differently by the flax-earthworm-guano treatments, compared to control (+) pots (Figure 7.3, A, B, C). The $CaCl_2$-P was high in *Megascolesidae. Sp.1* (-) pots, and followed by no-earthworm (++) pots. All treatment pots had lower $CaCl_2$-P than the control (+) (approx. 5 mg kg^{-1}). Only *E. fetida* (+) and no-earthworm (++) pots had higher citrate-P and HCl-P concentrations than the control. Similarly, soil inorganic P concentrations were significantly higher in no-earthworm (++) and *E. fetida* (+) pots than the control (Figure 7.3, D). There was no significant difference in soil organic P concentration among treatments, and they were all far lower that control (+) pots (approx. 450 mg kg^{-1}) (Figure 7.2, E). Soil total P concentrations followed a similar pattern with inorganic P between treatment pots, but they were all lower than control (+) pots (588 mg kg^{-1}) (Figure 7.3, F).

The proportional importance of P fractions was modified by the flax-earthworm-guano treatment (Table 7.4). The proportional importance of soil MBP to organic P was more evident in *E. fetida* (+) and no-earthworm (++) pots (approx. 4.6% and 4.3% respectively). The proportional importance of soil organic P to total P was highest in control (+) pots (76%), while *E. fetida* (+) and no-earthworm (++) pots had the lowest (approx. 65%). The proportional importance of soil $CaCl_2$-P to inorganic P was most evident in control (+) pots (0.037%), followed by *Megascolesidae. Sp.1* (-) pots (0.021%). The citrate-P fraction had showed significant importance over the inorganic P pool in *E. fetida* (+) and no-earthworm (++) pots (approx. 27.4% and 24.9% respectively), compared to others. Similarly, the proportional importance of soil HCl-P to inorganic P, and inorganic P to total P, were most evident in *E. fetida* (+) and no-earthworm (++) pots compared to others.

Results of two-way ANOVA and main effects analyses showed there was a significant interaction between the effects of guano and earthworm additions on the soil DHA (p=0.014), citrate-P (p=0.001), and HCl-P (p<0.001), while a relatively weak interaction on the soil $CaCl_2$-P (p=0.050) (Table 7.5). The main effects analysis showed that earthworm species had significantly more effects on soil DHA and $CaCl_2$-P, while guano additions had significantly more effects on citrate-P and HCl-P. However, the interaction between the effects of guano and earthworm additions on other soil properties were not significant. However, the overall mortality of two native earthworm species at the end of this pot trial has diminished the validity or solidness of this two-way ANOVA analysis of interaction between guano and earthworm treatments.

Added guano-P had been lost by different degrees at the end of this pot trial, particularly in no-earthworm (++) pots (Table 7.6). Apart from *E. fetida* (+) pots, the rest of guano treated pots had lost either more or similar amount of P by the presence of flax and earthworm, compared to control.

Table 7.3 Selected soil properties of the flax-guano-earthworm incubation glasshouse pot trial. Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference ($p<0.05$). SOM: soil organic matter; MBC: microbial biomass carbon; MBP: microbial biomass phosphorus; and DHA: dehydrogenase activity; '-' and '+' indicate without and with guano additions, '+ +' indicates a double amount of guano addition.

Treatments		pH (1:5 H_2O)	EC (ds m^{-1})	% SOM	NH_4-N (mg kg^{-1})	NO_3-N (mg kg^{-1})	MBC (mg kg^{-1})	MBP (mg kg^{-1})	DHA (mg kg^{-1} dry soil h^{-1})
Earthworms	Guano								
No-flax/No-earthworm	+	4.41 (0.04)^{e}	0.08 (<0.01)^{a}	2.9 (0.3)^{a}	13.3 (1.1)^{ab}	33.4 (3.5)^{a}	611 (56)^{a}	5.7 (2.8)^{b}	1.65 (0.05)^{c}
No-earthworm	-	4.77 (0.08)^{abc}	0.06 (0.02)^{cd}	2.2 (0.2)^{bcd}	3.5 (0.2)^{d}	3.8 (0.6)^{bc}	531 (30)^{a}	2.0 (0.7)^{b}	1.95 (0.08)^{b}
	+	4.66 (0.05)^{cd}	0.07 (<0.01)^{b}	2.3 (0.1)^{bcd}	5.5 (1.2)^{cd}	3.7 (0.9)^{bc}	556 (32)^{a}	3.8 (0.3)^{b}	1.91 (0.07)^{b}
	+ +	4.63 (0.01)^{d}	0.10 (0.03)^{a}	2.6 (0.1)^{abc}	19.4 (3.6)^{a}	7.6 (2.4)^{b}	490 (35)^{a}	15.2 (4.5)^{a}	1.54 (0.02)^{c}
M. transalpinus	-	4.67 (0.02)^{bcd}	0.07 (<0.01)^{b}	2.0 (0.1)^{d}	5.3 (1.2)^{cd}	3.1 (0.2)^{c}	529 (38)^{a}	3.1 (0.7)^{b}	2.01 (0.09)^{ab}
	+	4.73 (0.03)^{abcd}	0.07 (<0.01)^{bc}	2.1 (0.1)^{cd}	8.6 (2.7)^{bcd}	3.3 (0.3)^{c}	616 (46)^{a}	3.6 (0.5)^{b}	1.96 (0.09)^{b}
Megascolesidae. Sp.1	-	4.76 (0.01)^{abc}	0.05 (<0.01)^{d}	2.0 (0.2)^{cd}	4.0 (0.8)^{d}	2.3 (0.3)^{c}	599 (41)^{a}	4.2 (1.6)^{b}	2.00 (0.05)^{ab}
	+	4.70 (0.05)^{abcd}	0.07 (<0.01)^{b}	2.8 (0.4)^{ab}	10.8 (3.1)^{bc}	3.2 (0.5)^{c}	495 (54)^{a}	3.8 (1.4)^{b}	1.85 (0.02)^{b}
E. fetida	-	4.78 (0.02)^{ab}	0.05 (<0.01)^{d}	1.9 (0.1)^{d}	2.9 (0.1)^{d}	2.9 (0.2)^{c}	582 (49)^{a}	4.2 (1.0)^{b}	1.91 (0.04)^{b}
	+	4.80 (0.04)^{a}	0.07 (0.01)^{bc}	2.8 (0.2)^{ab}	8.3 (3.5)^{bcd}	2.6 (0.2)^{c}	550 (78)^{a}	16.6 (8.1)^{a}	2.16 (0.08)^{a}

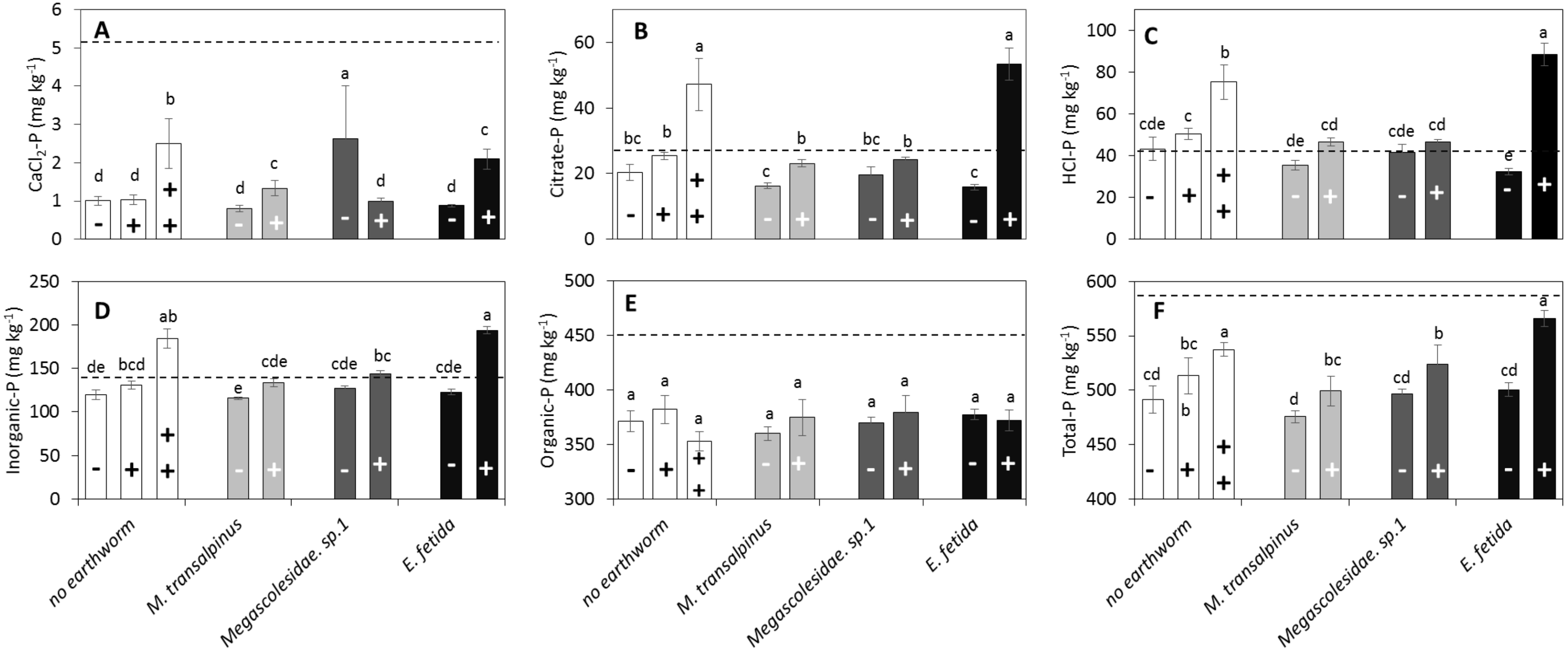


Figure 7.3 Concentrations of P fractions in the flax-guano-earthworm incubation pot trial. Data are mean values ± standard errors (n=5). The same letters indicate no significant difference (p<0.05). '-' and '+' indicate without and with guano additions, '+ +' indicates a double amount of guano addition. Dashed lines indicate mean values of pots without flax and earthworms.

Table 7.4 Analysis of proportional importance of P factions of the guano-earthworm-flax pot trail, and in comparison with original forest soil (M1 in the Chapter 5). Data in columns are means (n=5) with standard errors in parenthesis. The same letters indicate no significant difference (*p*<0.05). '-' and '+' indicate without and with guano addition, '+ +' indicates a double amount of guano additions. Where MBP: microbial biomass phosphorus; n.d. means no data available.

Treatment		MBP/organic-P (%)	Organic-P/total P (%)	CaCl$_2$-P/inorganic-P (%)	Citrate-P/inorganic P (%)	HCl-P/inorganic P (%)	Inorganic-P/total P (%)
Earthworms	Guano						
No-flax/No-earthworm	+	1.3 (0.6)^{b}	76.1 (1.2)^{a}	0.037 (0.003)^{a}	19.4 (2.2)^{b}	30.6 (2.5)^{cd}	23.9 (1.2)^{d}
No-earthworm	-	0.5 (0.2)^{b}	75.6 (0.8)^{ab}	0.008 (0.001)^{c}	16.7 (1.2)^{bcd}	35.5 (3.1)^{bc}	24.4 (0.8)^{cd}
	+	1.0 (0.1)^{b}	74.4 (0.3) ^{abc}	0.008 (0.001)^{c}	19.4 (0.4)^{b}	38.4 (1.1)^{b}	25.6 (0.3)^{bcd}
	+ +	4.3 (1.2)^{a}	65.7 (1.8)^{d}	0.013 (0.013)^{bc}	24.9 (2.9)^{a}	40.3 (2.1)^{ab}	34.3 (1.8)^{a}
M. transalpinus	-	0.9 (0.2)^{b}	75.6 (0.5)^{ab}	0.007 (0.001)^{c}	14.1 (0.6)^{cd}	30.6 (1.7)^{cd}	24.4 (0.5)^{cd}
	+	1.0 (0.1)^{b}	73.2 (0.4)^{bc}	0.010 (0.002)^{bc}	17.4 (0.9) ^{bc}	34.9 (1.0)^{bc}	26.8 (0.4)^{bc}
Megascolesidae . Sp.1	-	1.1 (0.5)^{b}	74.5 (0.6)^{abc}	0.021 (0.011)^{b}	15.4 (1.7)^{bcd}	32.6 (2.4)^{c}	25.5 (0.6)^{bcd}
	+	1.1 (0.4)^{b}	72.4 (0.4)^{c}	0.007 (0.001)^{c}	16.9 (0.6)^{bcd}	32.2 (1.0)^{c}	27.6 (0.4)^{b}
E. fetida	-	1.1 (0.3)^{b}	75.4 (0.5)^{ab}	0.007 (<0.001)^{c}	12.9 (0.5)^{d}	26.2 (0.9)^{d}	24.6 (0.5)^{cd}
	+	4.6 (2.3)^{a}	65.7 (0.9)^{d}	0.011 (0.01)^{bc}	27.4 (2.0)^{a}	45.4 (2.0)^{a}	34.3 (0.9)^{a}
Original forest soil	-	2.7	58.9	0.011(1)	n.d.	18.8	41.1

(1) this percentage was calculated based on NH$_4$Cl extractable P value representing soluble or loosely bound P fraction, which is reasonably equivalent to CaCl$_2$-P.

Table 7.5 *p* value report of two-way ANOVA analysis of guano-earthworm interaction of selected soil chemical properties and P factions, and the main effects analysis of independent variable (guano or earthworm) on the soil DHA, CaCl2-P, citrate-P and HCl-P. SOM: soil organic matter; MBC: microbial biomass carbon; MBP: microbial biomass phosphorus; and DHA: dehydrogenase activity; n.a. indicates no main effect analysis applicable since the earthworm-guano interaction is not significant.

Factor	pH	EC	% SOM	NH_4-N	NO_3-N	MBC	MBP	DHA	$CaCl_2$-P	Citrate-P	HCl-P	Organic-P
Guano	0.335	0.143	0.001	0.002	0.333	0.657	0.041	0.372	0.559	<0.001	<0.001	0.823
Earthworm	0.137	0.072	0.239	0.821	0.101	0.721	0.184	0.052	0.606	0.004	0.002	0.584
Interaction	0.088	0.708	0.140	0.725	0.671	0.248	0.229	0.014	0.050	0.001	<0.001	0.836
Main effect	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	**Earthworm**	**Earthworm**	**Guano**	**Guano**	n.a.

Table 7.6 Phosphorus mass balance calculation of this flax-guano-earthworm pot trial. Where: expected initial total P = P (M1) + P (guano) at the beginning of pot trial; final total P = measured total P at the end of pot trial; flax P = flax dry mass * flax P concentration; lost P = expected initial total P – final total P – flax P. '-' and '+' indicate without and with guano additions, '+ +' indicates a double amount of guano addition. Data in columns are means (n=5) with standard errors in parenthesis. Given values are dry mass basis.

	Control	No-earthworm			*M. transalpinus*		*Megascolesidae. Sp.1*		*E. fetida*	
	+	-	+	+ +	-	+	-	+	-	+
Soil initial total P (mg)	1323 (12)	1145 (24)	1748 (22)	2136 (14)	1160 (16)	1738 (23)	1173(26)	1717 (23)	1163 (12)	1702 (21)
Soil final total P (mg)	1145 (53)	1407 (50)	1549 (71)	1411 (10)	1380 (25)	1492 (46)	1456 (23)	1539 (74)	1454 (21)	1639 (35)
Flax P (mg)	0.0 (0.0)	4.4 (0.6)	7.7 (0.7)	4.1 (0.4)	7.4 (1.5)	6.9 (1.5)	6.5 (0.8)	5.2 (1.4)	4.6 (0.4)	6.0 (1.0)
Lost P (mg)	177.8 (53)	-267 (37)	192 (55)	721 (13)	-227 (17)	240 (41)	-290 (8)	172 (57)	-296 (18)	56 (21)

Note: (1) Flax P concentration was based on data from the Chapter 3.

(2) Earthworm biomass P was not included because all native earthworms died at the end of pot trial and only exotic *E. fetida* survived, and *E. fetida* biomass are relatively low and negligible.

(3) Negative values were due to the variable total P concentration of M1 soils (400 ± 78) based on result in chapter 5.

7.4 Discussion

7.4.1 Guano chemistry

The distinct differences in elemental composition between Spotted Shag and Westland Petrel guano could mainly be attributed to their diet and feeding differences. On the one hand, Spotted Shag mainly feed on Ahuru (*Auchenoceros punctatus*), red cod (*Pseudophycis bachus*), Graham's gudgeon (*Grahamichthys radiata*), and sprat (*Sprattus antipodurn*) about up to 16 km offshore deep water (Lalas, 1983). They are abundant found along Canterbury coast, in the South Island of New Zealand. However, around Lyttelton Harbour, the main fish species is *Rhombosolea plebeia* (Pleuronectidae) and shags probably feed close to the shore (N.Dickinson, pers.comm). In comparison, Westland Petrel feeding range stretches from the west coast to Kaikoura on the east coast, New Zealand. However, since the hoki fishery was developed in 1970s, Westland petrel have been found to opportunistically rely on scavenging fishery waste from fishing boats particularly during chick-rearing period. Species such as Hoki (*Macruronus novaezelandiae*), the rattails *Caelorinchus sp.* and *Lepidorhynchus denticulatus* and the morid cod (*Pseudophycis* Spp.) have been found in Westland petrel diet samples (Freeman, 1998; Freeman and Wilson 2002).

On the other hand, the difference may be partly due to different proportion of regurgitant in the guano, as shag guano had visible remnants of fish bones, which is evident in the analytical results. Excluding bones, animal tissues normally contain 0.3-4% P, and 0.03-0.3% of Ca, but 4-10% of N (Allen et al., 1989). Guano nitrogen content was low (3.5%) in the shag guano, compared to 5.3-12.4% of N in wading bird guano reported by Irick et al. (2015). This difference may be in part due to relatively old guano was collected in the present study, which some N might have already lost via NH_3. About 32% of N content excreted from seabird was volatilized as NH_3-N (Blackall et al., 2008). With regard to the Cd loading in the guano, 27-641 mg Cd per kilogram of applied P is normal content of typical sedimentary rock phosphate (McLaughlin & Hamon, 2001). In the present study, petrel guano is at the medium level, while Cd loading in shag guano is only minor (Table 7.1).

7.4.2 Earthworm and flax growth

It was unsurprising that all *E. fetida* individuals survived in the present glasshouse pot trial. Organic matter rich forest soil provided good food resource for *E. fetida*, contributing to their biomass increases. Whilst this is an epegeic species, they appear to move freely in all layers of the pots, which probably contain less compacted soil than in the field situation (Figure 7.2). Significantly higher biomass increase of *E. fetida* in guano treated pots compared to no-guano pots indicated that: (i) added guano might have provided extra food for them; and (ii) P-enriched (as well as other guano nutrients) organic matter transformed from guano might have benefited their growth. Also known as tiger worm, *E. fetida* has been long known as a resilient earthworm species that can survive even growing under some extreme or toxic environments (e.g. Edwards and Bater, 1992; Contreras-Ramos et al., 2005; Kinney et al., 2012). No studies have investigated tolerance in the endogeic *Megascolesidae. Sp.1* species. Recently, Kim (2016) found that native anecic *M. transalpinus* could not survive well in dairy farm soil, losing biomass in biosolid treatment, and dying in two days in pure biosolid. However, Butt (1993) investigated the growth of anecic Lumbricidae earthworms under laboratory conditions (15 to 20 °C) which survived over 3 months. Although there were no toxic conditions in the present study, possible extreme temperature (about 25 to 30 °C in the glasshouse) might have been critical for native species since this pot trial was conducted during summer (November to January, 2015). The importance of soil temperature and related soil moisture for earthworm was emphasized in Wever et al. (2001). The overall fatality of the two native earthworm species was most likely due to the unfavourable temperatures.

Added guano provide potentially quickly-available nutrients to the plants, which was reflected in highest flax biomass in no-earthworm (+) pots (Table 7.2). In contrast, flax in no-earthworm (-) and (++) pots had similar plant biomass, implying a possible over-fertilization in double-guano treatment pots which might have inhibited flax growth. P-rich soils are not typical in the west coast of New Zealand, probably due to heavy rainfall (McLaren & Cameron, 1996). In a recent glasshouse pot experiment, flax growth was mainly enhanced by N addition, but had no further increase when P and S were added (Franklin et al., 2015). Among earthworm treated pots, nutrients released from decaying earthworm tissues might have promoted flax growth in *M. transalpinus* and *Megascolesidae. Sp.1* pots. This has been reported in Whalen et al. (1999), where they found more than 70% of ^{15}N from labelled *Lumbricus terrestris* tissues had been incorporated into ryegrass shoot. In this circumstance, slightly higher flax biomass in *M. transalpinus* pots than *Megascolesidae. Sp.1* pots could be explained by higher initial body biomass of *M. transalpinusi* (approx. 11.06 g per pot) than *Megascolesidae. Sp.1* (approx. 6.05 g per pot). Unfortunately, the present study was unable to quantify the contribution of decaying earthworm tissues to flax growth. However, the contribution of decaying earthworm tissues to soil available nutrient pools and in turn promotion of plant growth could be minor compared to living earthworm effects; because van Groenigen et al. (2014) indicated that crop yield increases were no longer significant when earthworm survival rate was lower than 50%.

Higher flax biomass in *E. fetida* (+) than *E. fetida* (-) pots indicated the availability of guano-nutrients for flax may have been promoted by the presence of *E. fetida*. It is known that earthworms increase plant growth (Scheu, 2003). In a meta-analysis study, van Groenigen et al. (2014) showed that earthworms promote an overall 27.5% increase of aboveground plant biomass. Two possible causes are: (i) soil structure enhancement via earthworm casts and burrows and (ii) increasing soil nutrient bioavailability via excretion and increased microbial activities (Brown et al., 2004). However, van Groenigen et al. (2014) suggested that enhancement of plant growth by earthworms is mainly due to increased soil N mineralization and availability for uptake by plants. Other nutritional factors such as increased P availability could also benefit plant growth in the presence of earthworm (Vos et al., 2014). In the present study, however, earthworm and/or guano treatments did not have a significant effect on the carbon allocation towards root or shoot parts. Plant root/shoot ratio gives a proximate indication for carbon allocation in harvestable products (Mokany et al., 2006). In the present study, added guano contains multiple plant essential nutrients, which makes it difficult to determine the overwhelming factor contributing flax growth. It is more likely that both earthworm and guano nutrients, and their interactions had modified the soil biochemistry and subsequent affected flax growth.

7.4.3 Soil chemistry

Small changes of soil pH through the effects of earthworms were more evident than found in Kim (2016), with some of the same earthworm species. A possible reason could be because of the longer incubation period in the present study. Similar more pronounced changes of soil pH with longer earthworm incubation periods have been observed in previous studies, particularly in earthworm casts (e.g. Basker et al., 1994; Edwards and Bohlen, 1996; Lambkin et al., 2011; Vos et al., 2014). Although factors responsible for such increases are debated, production of $CaCO_3$-rich excretions by earthworm is likely to buffer soil pH (Lambkin et al., 2011). Added guano also contained high concentration of Ca and other base cations that could have contributed to the soil pH buffering. This also explains higher soil EC in guano-treated pots. Control (+) pots had similar soil organic matter (OM) contents to the original forest soil (approx. 3.0% of M1 soil in Chapter 5), the rest of the pots had lower OM contents. This indicates that added guano had contributed organic matter or losses were due to enhanced soil respiration in warm glasshouse conditions. The consumption of soil organic matter by *E. fetida* in guano (-) pots was evident, compared to no-earthworm (-) pots.

In terms of soil mineral nitrogen concentrations, added guano N content was substantially mineralized to ammonium-N and further nitrified to nitrate-N. This is consistent with the overall high soil MBC concentrations in all pots. Mineral N was taken up by the flax when compared with N status in control (+) (without flax) pots. However, since flax growth was lower in no-earthworm (++) pots, both high ammonium-N and nitrate-N concentrations could potentially have led to larger losses of N from this treatment. However, soil N mineralization was promoted by earthworms (between *E. fetida* (+) and (-) pots), although the effects of earthworms on soil nitrification processes were limited in the present study due to low pH (Ste-Marie and Paré, 1999; Clough et al., 2004). Comparing *E. fetida* treatment pots with no-earthworm pots, the effects of earthworms on promoting organic N mineralization was more evident. This beneficial effect has been reported in previous studies (e.g.; Araujo, Luizão, & Barros, 2004; Domínguez, Bohlen, & Parmelee, 2004; Postma-Blaauw et al., 2006; Sheehan et al., 2006;

Kim et al., 2015). This effect was further synthesised in van Groenigen et al. (2014); of course, this might be masked by guano additions of N in the present study.

Although the effects of earthworm and guano additions on the overall soil microbial community (MBC) were not significant between treatments in the present pot trial, soil MBP and DHA were influenced more. Conflicting results of the impacts of earthworm presence on soil MBC have been reported. For example, Zhang et al. (2000) found decreases of soil MBC (approx. -130 µg g^{-1}) and MBP (approx. -30 µg g^{-1}) after 24-hr incubation with a high-density of the anecic earthworm *Metaphire guillelmi* (synonyms: *Pheretima guillelmi*, Megascolecidae). Similarly, soil MBC decreased more with higher earthworm (*Diplocardia mississippiensis*, Megascolecidae) abundance in the top 3-cm soils after 110 days incubation (Callaham Jr & Hendrix, 1998). It was suggested that although selective feeding on soil microorganisms by anecic or edogeic earthworms had reduced the overall or standing soil microbial biomass, later increases of active components of soil microbial biomass were observed (Zhang et al., 2000; Scheu et al., 2002). This is different to epigeic earthworms which mainly feed on litter. In this context, it is extrapolated that the decomposition of earthworm tissues from two native microorganism-feeding species in the present study, might have refilled the soil microbial biomass loss gaps that were preferentially fed. Conversely, Kim et al. (2015) found overall increases (ranging from 20 to 100 µg g^{-1}) of soil MBC in a 3-week incubation study with different earthworm species. Similar increases of soil MBC through earthworm incubation have also been reported in Lavelle and Martin (1992). These differences could be driven by different factors, for example: (i) different time scales of earthworm incubation, (ii) different earthworm density used; (ii) the addition of guano in the present study, and (iii) initial high soil MBC in the mature forest soil. Guano P may also have provided a good source of quickly-available P to either soil microbes or earthworms or both. *E. fetida* in guano (+) pots significantly promoted the build-up of MBP to a similar level of MBP in no-earthworm (++) pots. Soil MBP will be discussed in the context of phosphorus dynamics as a fraction of soil P in the next section

Measured soil DHA values were higher overall (ranging from 1.6 to 2.2 in the mg kg^{-1} dry soil h^{-1}) in the present study, compared to < 1 mg kg^{-1} dry soil h^{-1} in Kim (2016) with similar earthworm species. This could be firstly because that different types of soils were used with different soil organic matter contents for earthworm incubation, and secondly the significant interaction between earthworm and guano in the present study. Soil dehydrogenase enzymes are mainly a oxidoreductase class that play a critical role in the initial stages of oxidizing soil organic matter via transferring hydrogen or electrons from substances to acceptors (Ross, 1971; Gu, Wang, & Kong, 2009). On the other hand, adding guano could potentially increase the soil DHA. For instance, Chu et al. (2007) found soil DHA was greatly increased during a long-term fertilization experiment. Lastly, the presence of *E. fetida* might have created some localized anaerobic conditions via gut passage and mucus secretion, which promote dehydrogenase activity via the activity of anaerobic microorganisms. It has been suggested soil DHA significantly increases under anaerobic conditions and most dehydrogenases are produced by anaerobic microorganisms (Brzezińska, Stępniewska, & Stępniewski, 1998; Włodarczyk, Stępniewski, & Brzezińska, (2002). However, decreases of soil DHA after inoculation which *E. fetida* have been observed in a mesocosm assay of sandy soil with organic residues (Caravaca & Roldán, 2003). These authors accounted for this as more intense predation of microorganisms by *E. fetida*. This predation effect is inconsistent with microorganism feeding behaviour of earthworms proposed by Zhang et al. (2000) and Scheu et al. (2002). Clearly, further research is required.

7.4.4 Phosphorus dynamics

In the present study, biologically-based P fractionations in soil were measured in the rhizosphere soil. The soil P pool that had been biotically modified by earthworms and plant rhizosphere processes and their interactions. This is different from some previous studies, which measured available P or P species in earthworm casts (soils after passage of intestinal tract) in comparison with bulk soils or un-ingested soils, for example using *Pontoscolex corethrurus* (Glossoscolecidae) by Chapuis-Lardy et al. (1998, 2009); Glossoscolecidae species by Kuczak et al. (2006); *L. terrestris* and *Aporrectodea caliginosa* by Le Bayon and Binet (2006); *L. rubellus*, *A. caliginosa*, and *L. terrestris*, Lumbricidae by Vos et al. (2014). They all reported higher soil available P concentrations, either in NaOH or $NaHCO_3$ or water extractable P, in earthworm casts compared to un-ingested soils. Therefore, it seems likely that soil P fractionation data in the present study reflected soil somewhere in-between earthworm casts and bulk soils, reflecting earthworm-incubated soil. Applying the same soil sampling protocol, Kim et al, (2015) found a marginal increase of soil available P, measured as $NaHCO_3$ extractable P, in a 3-week soil-earthworm incubation experiment.

Several factors contributing to the enhancement of P availability in casts were summarized in Le Bayon and Milleret (2009) and Chapuis-Lardy et al. (2011). They include: (i) the ingestion of a mixture of organic matter, microorganisms and sand grains which facilitate the mechanical breakdown of organic matter during the digestion processes, so that more accessible for microbes; (ii) raised soil pH (6.0-6.8) after transit through earthworm guts compared to pH of 5.0-5.4 in surrounding soil, leading to higher P solubilisation; (iii) greater competition of sorbing or binding sites by carboxyl groups from carbohydrate compounds released in earthworm mucus, in turn increasing soluble P; (iv) rearrangement and reconstruction of existing soil may occur during digestion, resulting in mobilization of clay particles and the formation of new binding bridges, therefore potentially promoting P solubility; and (v) increasing active microbial and enzymatic activities during gut transition, resulting in more mineralization of soil organic P.

Fatality of the two native earthworm species before the end of this pot trial might have diminished the effects of earthworms and their interactions with flax roots on the dynamics of soil P and guano P. It appears that decaying earthworm tissues from two native species had notable contributions to soil MBP. Comparing the two native earthworm (-) pots with no-earthworm (-) pots, however the contribution of decaying earthworm tissues to soil soluble or weakly absorbed P pool would be slight, because of the relatively low P phosphorus content in earthworm biomass and the competition for this from soil microbes and flax roots. It has been suggested that earthworm residues decompose rapidly and become available for microbial assimilation first, but later plants capture more released nutrients (Hodge et al., 2000). Under natural conditions living epigeic *E. fetida* earthworms might have relatively less contact with flax roots because they usually feed on litter. However, to some extent, earthworm activities of all three species and flax roots were limited in 5L pots in the present study, providing a rather homogenous environment without defined litter and soil horizons (see Figure 7.2). It seems feasible, therefore, to compare the effects of earthworm and flax root interaction on the soil and guano P dynamics.

Intense uptake of soil soluble P by flax plants, may have out-competed demand from soil microbes (comparing with control (+) without flax). On the other hand, lower soil pH (ranging from 4.4 to 4.8) in all pots would have limited the size of soluble or weakly absorbed P ($CaCl_2$-P) pool; a pH range of 6-7 gives the optimum P availability in soil (Brady & Weil, 2008). High soluble P levels but with big error bar in *Megascolecidae Sp.1* (-) pots are difficult to explain. It is possible that this species might have survived closer to end of experiment, since other P fractions stayed normal.

The role of earthworms in the mediation of P dynamics through interaction with guano was further confirmed in *E. fetida* treated pots, where *E. fetida* successfully maintained higher levels of different P fractions ($CaCl_2$-P, citrate-P, and HCl-P), particularly in comparison with no-earthworm (++) pots. No study has measured the effects of earthworms on citrate-extractable P fractions. Fortunately, Aira and Domínguez (2014) found a higher P concentration in *Postandrilus spp.* (Lumbricidae) casts by acetic acid extraction; and this is reasonably comparable to citrate-P in the present study. In addition, it was found that the acid extractable inorganic P (HCl-P) concentration was promoted in earthworm casts relative to un-ingested soil (Kuczak et al., 2006), suggesting earthworms indirectly enhance the binding of P to Fe/Al clay particles. Similar findings of Vos et al. (2014) compared the maintenance of soluble P supply by the effects of earthworms to plant P uptake with P fertilization. In a recent glasshouse study, Coulis et al. (2014) proposed that endogeic *Allolobophora chlorotica* (Lumbricidae) earthworms were ‘trouble shooters’ in mediating soil available P pool to meet the competing demand of two intercrops.

The interactions apparent in the flax-earthworm system stimulated the transformation of soil and guano P into different P fractions. This shows in changes of relatively proportional importance of P fractions in the present study, as compare to control (+) and original forest soil (M1 soil in Chapter 5)

(Table 7.4). Presumably, the exclusive contribution of soil microorganisms to the transformation of guano-P into different P fractions was reflected in control (+) pots, when compared to the original forest soil. It was evident that soil microbial activities had significantly promoted the build-up of organic P and moderately bound HCl-P fractions, while at the same time maintaining a reasonable level of soluble or weakly absorbed P fraction. Organic P was more important, but inorganic P was less important in the proportion of total P in the present pot trial, compared to original forest soil (approx. 60% of organic P to total P and 41% of inorganic P total P, respectively). The proportional importance of acid extractable P to inorganic P was higher than in original forest soil (approx. 19% of acid-P to inorganic P). Concerning the importance of soil MBP to organic P, apart from *E. fetida* (+) and no-earthworm (++) pots, the remaining pots had lower proportionally importance than original forest soil (approx. 3% of MBP to organic P). Since guano contains mostly inorganic P, it is reasonable to suppose that flax-earthworm interactions had substantial effects on the guano-P and soil P dynamics.

In terms of the effects on soil P dynamics, flax-earthworm interactions will of course interact with or mediate soil microbes to some extent. The critical role of soil microorganisms in P dynamics has long been emphasized, in particular the role of mycorrhizal symbiosis in natural ecosystem s, because they all interact with each other to some degree (Milleret, Le Bayon, & Gobat, 2009; Jansa et al., 2011; Jones & Oburger, 2011). Therefore, caution is needed when interpreting the findings of the present study due to the small scale of the experiment, case must be taken in transferring the findings to the natural ecosystem.

The overall losses of soil P from the current flax-earthworm-guano pot system could be due to: (i) increased losses of phosphorus via preferential flows in pores created by earthworm burrowing (Domínguez et al., 2004); (ii) potential leaching of phosphate because of the relatively low P retention capacity of sandy soils (M1 soil) (McLaren and Cameron, 1996); or (iii) possible minor losses of un-dissolved or un-transformed guano-P via surface material removal when pots were harvested (based on visual observation).

7.5 Conclusion

(1) The interaction of earthworms and flax had a substantial effect on the transformation of soil P and guano P into different P fractions.

(2) The interaction of earthworm and guano had significant effects on soil dehydrogenase activity, $CaCl_2$-P, citrate-P and HCl-P.

(3) Diet differences and the constituents of guano lead to substantial differences in guano chemistry between Spotted Shag and Westland Petrel, in particular of the content of phosphorus, calcium and cadmium; guano provides good source and quickly-available nutrients for uptake by flax.

(4) Flax growth was primarily differentiated by the supply of mineral N, but was also modified by the interaction between guano and earthworms. Nitrogen mineralization was promoted by the presence of earthworms, but an experimental error may have been introduced due to nutrient release from decaying earthworm tissues.

Chapter 8

The PCRP restoration trajectory: Analysis of findings, with incorporation of a wider dataset

8.1 Introduction

This chapter aims to investigate the relationships between soil chemistry, biodiversity and plants on the restoration trajectory at the Punakaiki Coastal Restoration Project (PCRP) site. A multivariable analysis of a wider dataset of the PCRP is presented, which includes vegetation, soil invertebrate and soil survey data in Hahner et al. (2013). The present author was involved in the soil survey work, but ecological data was collected by other members of the research team, as cited in the acknowledgement.

Soil development is a complex process that is controlled by factors of time, parent materials, climate, topography, and biota (McLaren & Cameron, 1996). Plants, soil animals and microorganisms contribute to soil development, modifying and mediating the soil environment and soil quality (Brady & Weil, 2008), but the interactive influence of these biota remains poorly understood (Bardgett & van der Putten, 2014; van der Putten et al., 2013). A soil-centric approach suggests that soil biogeochemistry supports and determines the biodiversity of vegetation, and belowground faunal and microbial communities (Tilman, 1982; C. Smith, pers. comm). In this thesis, I have attempted to also consider the opposite approach – investigating how biota modify the soil.

Restoration of degraded ecosystems aims to restore vegetation cover, and the ecosystem functions and services that soils support (Corlett, 2016; Frouz et al., 2008). It follows that the restored vegetation significantly contributes to the recovery of soil functionality (Perring et al., 2015). The development of vegetation not only provides physical protection of soils from surface runoff and erosion (Sayer, 2006), but also stimulates nutrient cycling, via plant litter accumulation and decomposition, as well as via plant rhizosphere processes, that initiates recovery of ecosystem functions (Bardgett & Wardle, 2010; Hobbie, 1992); at the same time increased size and diversity of soil faunal and microbes can accelerate this cycling process (on average by 27%) (García-Palacios et al., 2013).

It is proposed in the present study that some degrees of soil and ecosystem properties have been recovered on the restoration trajectory. Restoration of native plants was initiated in the middle of 2009 at the PCRP site (see Figure 2.1 for detailed planting timeline). Successful establishment of restored vegetation and canopy closure was evident in the most recent few years (see Figure 1.4 in Chapter 1), and accumulation of plant litter was evident (Figure 8.1). Alongside the progressive development of native vegetation cover, both soil chemistry and biodiversity have been modified to some extent from conditions in the unplanted grassland towards the reference mature forest.

Figure 8.1 Leaf litter accumulating within the oldest restoration plot, R1 (photography by James Washer, 2013).

8.2 Materials and methods

Datasets from monitoring work at the PCRP sites were collated using soil data (collected by J. Hahner, C. Smith and the author) supplemented by monitoring data from several other projects over the study period (M. Bowie, S. Boyer, A.Chassagneux, J. Segrestin and C. Mountier) (Hahner et al., 2013). Glossary of plant species abbreviations are available in the Appendix A (Table A.2). Soil Li, Ni, Cr, As, Cu and Pb concentrations from the dataset were not included in the analysis, because these elements have relatively low ecological relevance (Robinson et al., 2009). Soil data were then split into Ah and Bw horizons. Invertebrate data were more variable due to the difficulty of identification to species levels and in obtaining comparable quantitative data. This is slightly problematic as the dataset contained some species level data (e.g. *Dolomedes minor*) and some "group" data (e.g. snails, native earthworms). Soil mite data were grouped into Recognisable Taxonomic Units (RTUs).

The dataset was analysed by Hannah Franklin, in support of the author, using Principal Components Analysis (PCA) and Detrended Correspondence Analysis (DCA) separately. Both PCA and DCA are unconstrained ordination methods to extract gradients of maximum variation of data (McGarigal, Cushman, & Stafford, 2013). However, when analysing heterogeneous ecological data that contain many zeros, PCA may produce a so called "horse shoe" artefact, which does not differentiate dissimilar ends of the gradient in the matrix (Legendre & Gallagher, 2001). In comparison, DCA is based on a unimodal model of species distributions, which is well suited to community ecology; at the same time

DCA removes the autoregressive conditional heteroscedastic (ARCH) effect via detrending (Borcard, Gillet, & Legendre, 2011).

PCA was conducted on the Ah soil data for each site, using the Euclidian distance function on standardised data (scaled and centred). Ordination of soil data was conducted by Non-Metric Multidimensional Scaling (NMDS). The DCA was conducted on standardized data (standardized by the maximum to account for the presence of zeros in the data). The difference between each point in the resultant space was then compared to see how different or similar two ordinations were. Analyses were conducted using R, Version 3.0.1 (R Development Core Team, 2010, R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org/).

8.3 Synthesis of results

Correlations of soil chemistry between Ah and Bw soil horizons at PCRP showed that soil pH was positively correlated between the two horizons (Figure 8.2). It is evident in the groupings of these elements, soil base cations (K, Na, and Mg) were positively correlated, noticeably also with Zn. The PCRP site is highly influenced by marine spray, which probably brings significant amounts of base cations into this coastal sandplain forest ecosystem (as previous discussed in Chapter 4, 5 and 6). At the same time, under the super-humid climate, the well-drained sandy soils tend to face continuous losses of weathered cations downwards. However, this interpretation could be biased because PCRP soils are rather complex with three different stages of vegetation cover (Mature, Resorted and Unplanted plots), and three major soil types developed from sand dunes, alluvial fans over sand plain, and peatland. In addition, soil chronosequence was presented at PCRP (particularly in Transects 1 and 3). A more detailed correlation of soil physicochemical variables within each plot type for AH and Bw soils is given in in the Appendix E (Figure E.1).

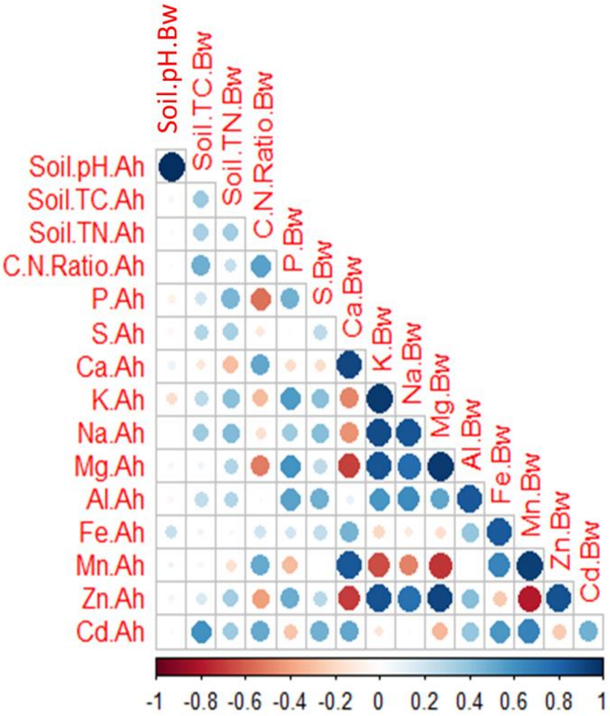


Figure 8.2 Correlation heat-plot comparison of Ah and Bw horizons. The increasing degree of blue colouration indicates stronger positive correlation and, vice versa, red colouration means negative correlation.

The PCA results showed that the first three principal component (PC) axes explained 80% of the ordination in soil data, with PC1 accounting for 46% and PC2 and PC3 explaining 18% and 15% respectively (Table 8.1). PC1 was weighted most strongly by Ca and Mn in the positive direction, and Zn, Na and P in the negative direction; PC2 was weighted most strongly by Al and Mg in the positive direction, and Total C (TC), Total N (TN) and C:N ratio in the negative direction (Figure 8.3, a). Overall, soils are relatively spreadout among the three stages of vegetation types. Mature sites are the most spreadout in ordination space, in particular M3 locates in the bottom-left corner with significantly higher soil organic C contents (evident in Chapter 5). Restored and Unplanted sites are rather variable, but they are clumped between the Mature sites.

The potential restoration trajectory was not well-reflected in the analysis of these data (Figure 8.3, b), apart from Transect 4 and 7 which were located at the northern end of PCRP site with soils developed on an alluvial fan over the sand plain. The restoration trajectory of these two transects does indicate soils have been restored away from the “unplanted” and towards the direction of mature soils. Ordination of these two transects are mainly driven by P, Zn, K, Mg and Mn contents. In the longer term, these soils may be more different, in terms of soil chemistry and further away from their unplanted counterparts. However, this was not shown in older restored Transect 1 and 2, and with Transect 3 and 6 moving toward opposite direction. This lack of pattern may not be surprising due to the high heterogeneity of soil across the PCRP site and short-term time frame since restoration planting.

Table 8.1 Proportion of the first three principal components (PCs) and loadings of tested variables.

Variables	PC1 (46.5%)	PC2 (18.5%)	PC3 (15.1%)
Soil pH	0.0275	0.0241	-0.0396
Soil TC	-0.2811	**-0.3751**	-0.0911
Soil TN	-0.3018	**-0.3274**	-0.0368
C:N Ratio	-0.0705	**-0.3507**	-0.3354
P	**-0.3240**	0.0930	-0.0362
S	-0.2945	-0.3184	-0.0368
Ca	**0.2812**	-0.0148	-0.2533
K	-0.2870	0.2865	-0.1985
Na	**-0.3344**	-0.0217	-0.2611
Mg	-0.2860	**0.3627**	-0.0512
Al	-0.0502	**0.3816**	**-0.4879**
Fe	0.1910	0.1711	**-0.4274**
Mn	**0.3193**	-0.1180	-0.2925
Zn	**-0.3507**	0.1442	-0.0882
Cd	0.1161	-0.3076	**-0.4302**

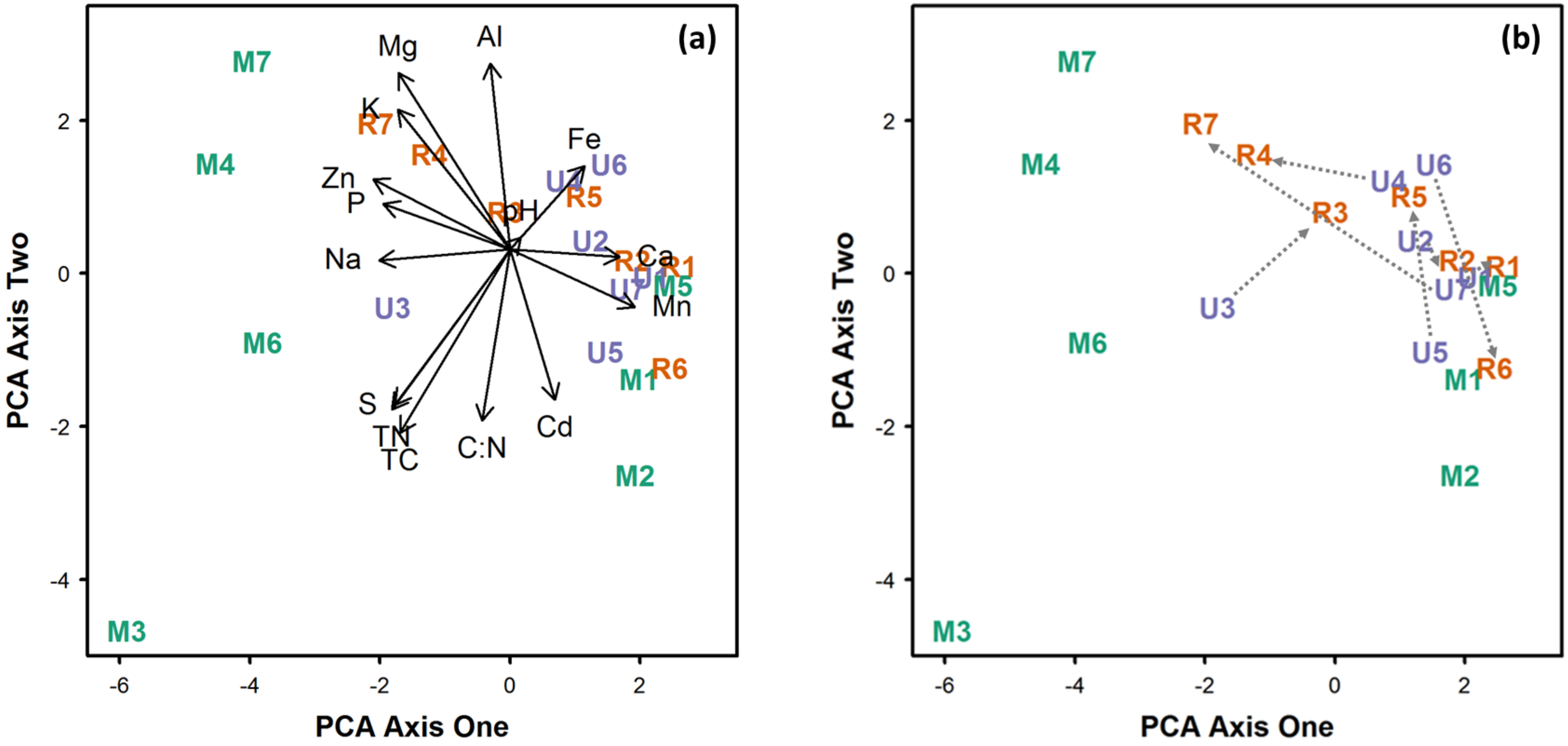


Figure 8.3 PCA ordination of Ah soil chemistry with bi-plot arrows showing the axes loadings (a), and (b) the relative spread of Mature, Restored and Unplanted sites. Dashed arrows indicate the potential trajectory of restored soil away from the ‘unplanted state’.

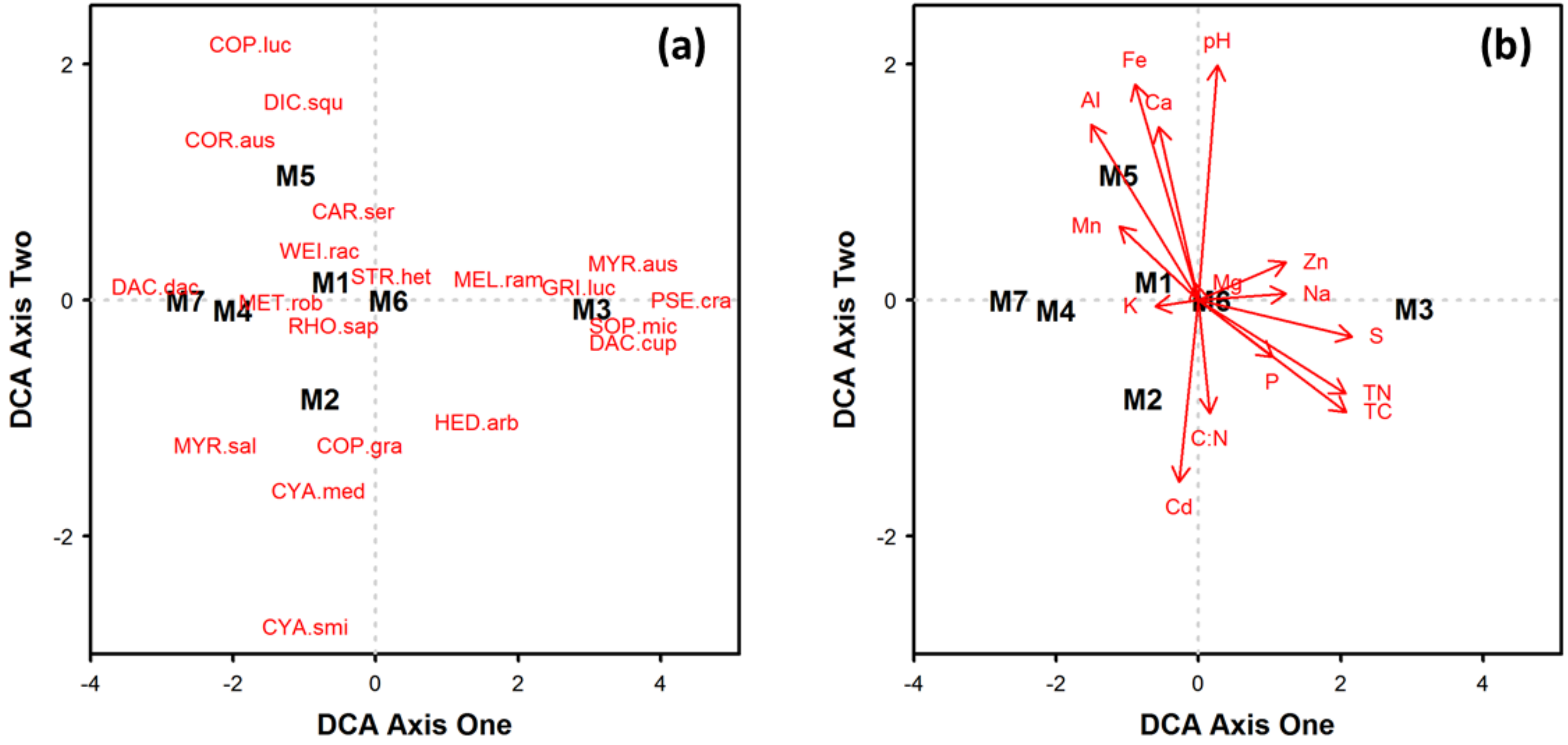


Figure 8.4 DCA of plant data at the Mature sites (a) showing the plant species scores, and (b) showing the results of vector fitting of the soil data to the plant DCA ordination.

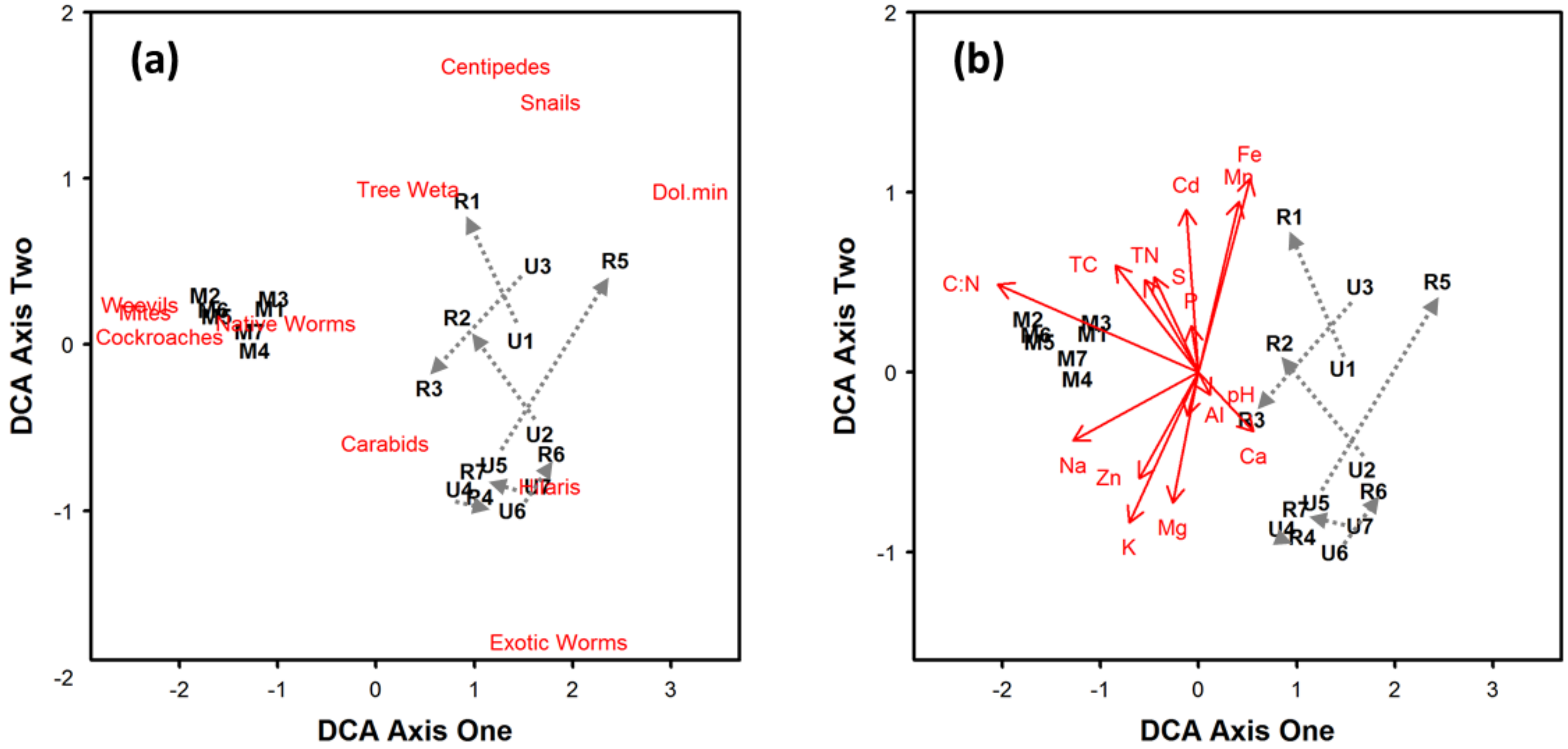


Figure 8.5 DCA of invertebrate data at the Mature, Restored and Unplanted sites (a) showing the invertebrate scores, and (b) showing the results of vector fitting of the soil data to the invertebrate DCA ordination. Dashed arrows indicate the potential trajectory of restored state away from the 'unplanted state'.

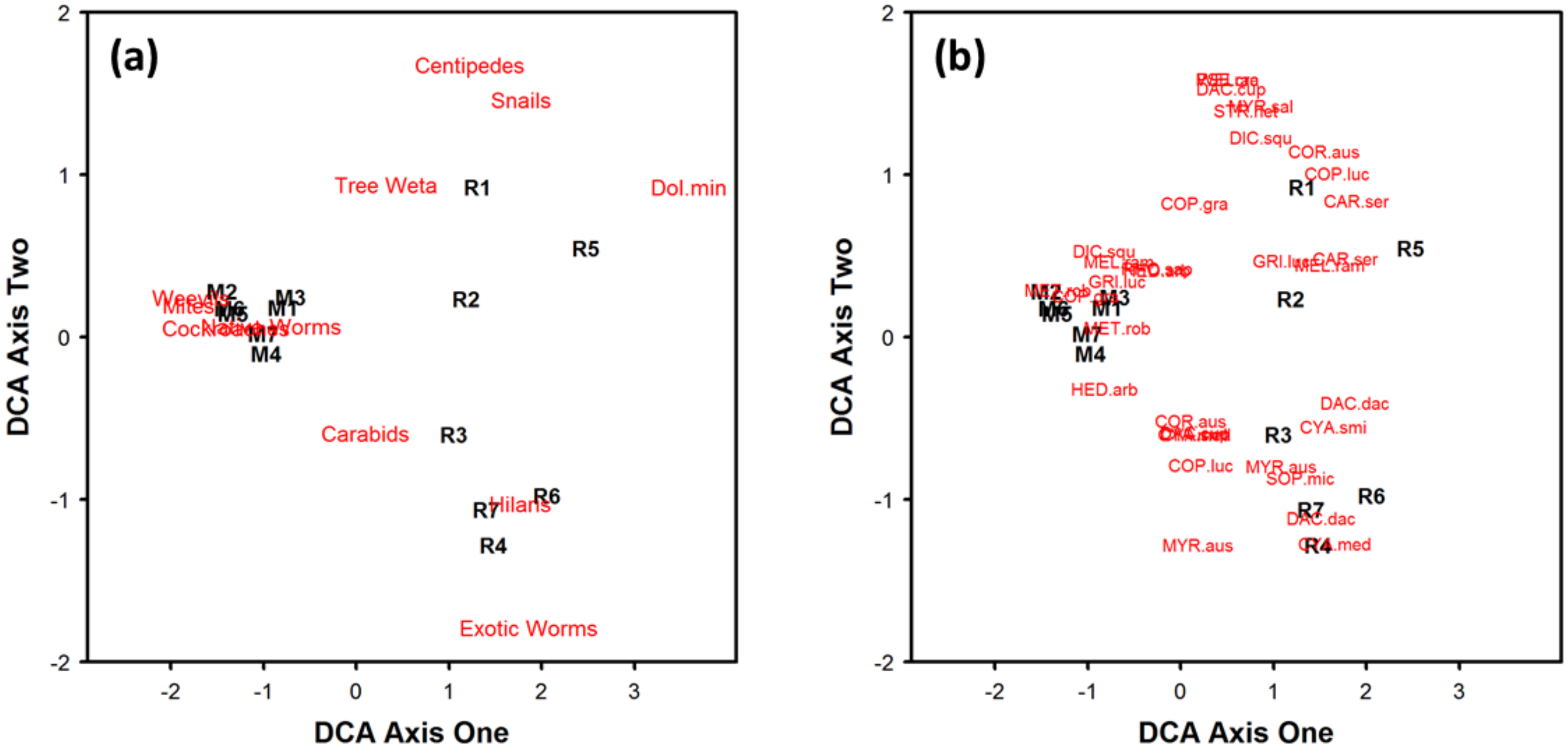


Figure 8.6 DCA of invertebrate data at the Mature, and Restored sites (a) showing the invertebrate scores, and (b) showing the results of vector fitting of the plant species to the invertebrate DCA ordination.

Incorporation of ecological data (plant species and invertebrate) into Detrended Correspondence Analysis (DCA), suggested potential relationships between plant composition and soil chemistry variables using vector fitting in Mature plots (Figure 8.4). Site M3 was more dissimilar than others in terms of plant composition and related soil chemistry. M3 has more *Pseudopanax crassifolius* (PSE.cra), *Myrsine australis* (MYR.aus), *Sophora microphylla* (SOP.mic), *Griselinia lucida* (GRI.luc) and *Dacrycarpus cupressinum* (DAC.cup); this appears to be related to higher soil TC, TN, S, Na and Zn contents. M4 and M7 are close together in terms of DAC.dac (*Dacrycarpus dacrydioides*), as well as soil K contents. This is a forest tree that tends to dominate wetter soils. The tree ferns *Cyathea* Spp. and *Dicksonia squarrosa* pulled in opposite directions on the DCA axis two; so that M2 has most *Cyathea Spp.* and M5 has most *D. squarrosa*. And, this might be related to soil pH and C:N ratio between M2 and M5. It is known that plant composition could be influenced by the distribution of soil resources. Of course, the plant species may also be responsible for modifying this soil chemistry. This potential relationship was not investigated in Restoration plots, given the fact that native species for re-planting were selected based on empirical experiences of the site manager (see planting scheme in Appendix A, Table A.1). Only 35 native species have been planted in the Restoration Plots, whilst more than 130 species present in the mature forest.

Assuming that any movement of invertebrates is random, vector fitting was also conducted with the soil variables, to investigate any relationships between the distribution of the invertebrates in Mature, Restoration and Unplanted plots (Figure 8.5). The invertebrate communities were much more similar among Mature plots dominated by native earthworms (e.g. *Megascolecidae Sp.1* and *Deinodrilus gorgon*), mites (e.g. Oribatida, Trombidiidae, and Uropodina), weevils (Curculionidae) and cockroaches (*Celatoblatta vulgaris*), and this could be related to soil C:N ratio. In contrast, Restoration and Unplanted plots have more exotic earthworms (e.g. *Lumbricus rubellus*), snails (*Oxychilus Spp.*) and spiders (*Dolomedes minor*), which might be related to higher soil pH and more clay minerals (Fe and Ca). The grey dashed arrows, which are the simulative movement trajectory of the invertebrate community, indicated that R1, R2, R3 and R7 had invertebrate communities shifting away from their corresponding "Unplanted state" to be more similar to the reference Mature sites. R4 has shifted relatively little, while R5 and R6 shifted in a similar direction but not towards the Mature sites. In comparison with PCA results, the restoration trajectory of soils seems more promising since the reference Mature soils were all clumped, meaning that most of restored soils could move towards to them (except for Transect 5). A relationship between soil chemistry and fauna communities has been previously suggested by Wardle et al. (2004).

To further investigate any potential relationships between the distribution of invertebrate with plant composition, vector fitting was conducted on Mature and Restoration plots (no plant data available for the unplanted grassland), although restored plantings were not random. Patterns in invertebrate distribution among sites were similar to those in the previous Figure 8.5, when unplanted sites were removed (Figure 8.6). Plant species of *Metrosideros robusta* (MET.rob), *Coprosma grandifolia* (COP.gra), *Griselinia lucida* (GRI.luc), *Dicksonia squarrosa* (DIC.squ) and *Melicytus ramiflorus* (MEL.ram) were more associated with native earthworms, mites, weevils and cockroaches in Mature sites. However, *Coprosma* Spp. might relate to the distribution of snails and exotic earthworms. Previous studies have investigated the influences of soil biota on the vegetation changes alongside ecological succession (Hättenschwiler & Gasser, 2005; Kardol, Martijn Bezemer, & van der Putten, 2006; Schnitzer et al., 2011). This raised another 'chicken and egg' situation of which comes first. Harris (2009) suggested that changes of soil microbial communities also have an important role in recovering ecosystem functions in ecological restoration, in terms of nutrient cycling, structural formation and plant interactions.

In summary, patterns within the heterogeneity of the PCRP site were revealed by the multivariate analysis, in terms of soil, plants and soil invertebrates. A potential soil restoration trajectory was shown in the PCA ordination, particularly in Transects 4 and 7. The DCA ordination showed that the relationships between soil chemistry and invertebrate communities were mainly driven by soil C:N ratio in the mature forest, which is related to the palatability of litter materials from trees. The interactions between soil, plants and soil invertebrate undoubtedly will have profound effects on the on-going development and succession of the restoration trajectory.

Chapter 9

Synopsis and Conclusions

9.1 Synopsis

In this chapter, results from both the present study and multivariate analysis of wider dataset are gathered and interpreted in the context of the restoration trajectory at PCRP. These findings are also tentatively extrapolated into the broader context of ecological restoration practices in an attempt to evaluate the practical value of this research.

A conceptual model is developed for the restoration trajectory at PCRP (Figure 9.1). This has been developed from analyses of data and is interpreted in the context of results presented in the earlier chapters. This model proposes that the following trends occur with the progression of the ecological restoration:

(i) Fast-growing species, particularly wine berry (*Aristotelia serrata*), reached canopy closure, shading out exotic grasses and herbs. Other woody species (e.g. *Coprosma robusta*) began to naturally establish beneath this canopy.

(ii) Leaf litter started to accumulate and decompose in the restored sites, which lowered soil pH and brought about a gradual increase of soil organic matter and decomposer communities of native soil invertebrate.

(iii) Native earthworms, as a key soil invertebrate, started to re-colonize the restoration soils as native plants become established, living alongside exotic earthworms that were in the former grassland; the number of native earthworms is likely to continue to increase and eventually colonize the developing restoration site. It is assumed that exotic species will gradually disappear with increased soil acidification.

(iv) Fast-growing plants in the restoration plots have promoted nutrient cycling mainly via increased soil microbial activity (as reflected in soil microbial biomass carbon and phosphorus) and demand for nutrients.

(v) Interactions between soil nutrients, plants (litter and rhizosphere) and soil biota (e.g. earthworms and microbes) make a significant contribution to the promotion of nutrient cycling and ecosystem development.

(vi) In terms of nitrogen mineralization and dissolved organic carbon, the increased rate of nutrient cycling is likely to slow down and plateau alongside ecosystem development in the longer term.

(vii) Soil Organic P, Microbial P and Occluded P increased as the restored ecosystem developed along with promotion of soil weathering and competition between soil organisms and weathered minerals.

(viii) Total soil P, Primary Mineral P and Secondary Mineral P decrease in the restoration stands and this is likely to continue in the longer term; these losses could be more intense in this super-humid climate and with the high leaching potential of sandy soils at Punakaiki.

(ix) Ecosystem nutrient status will develop from N-limiting to P-limiting if no major disturbances occur, but external nutrient inputs from seabird guano could potentially mitigate or delay reaching a ‘terminal steady state’ and an associated reduction of forest standing biomass and productivity.

(x) This project has compared 35 native species that have been introduced to the restoration area to the diverse reference mature forest that contained 157 native plant species. A number of the species planted in the restoration are early successional species that are absent or infrequent in the mature forest (e.g. wine berry and flax). Many of the plant species within the mature forest are native trees (the forest is dominantly Northern rata, *Metrosideros robusta* and kamahi, *Weinmannia racemosa*), but also include a large number of ferns (including tree ferns) and epiphytes. The longer-term successional trajectory of vegetation composition at PCRP is hard to predict based on the findings of current study.

The trajectory and longer-term course of ecological restoration requires on-going monitoring of vegetation re-establishment and faunal re-colonization, and also monitoring of how much has the soil being restored towards the reference ecosystem.

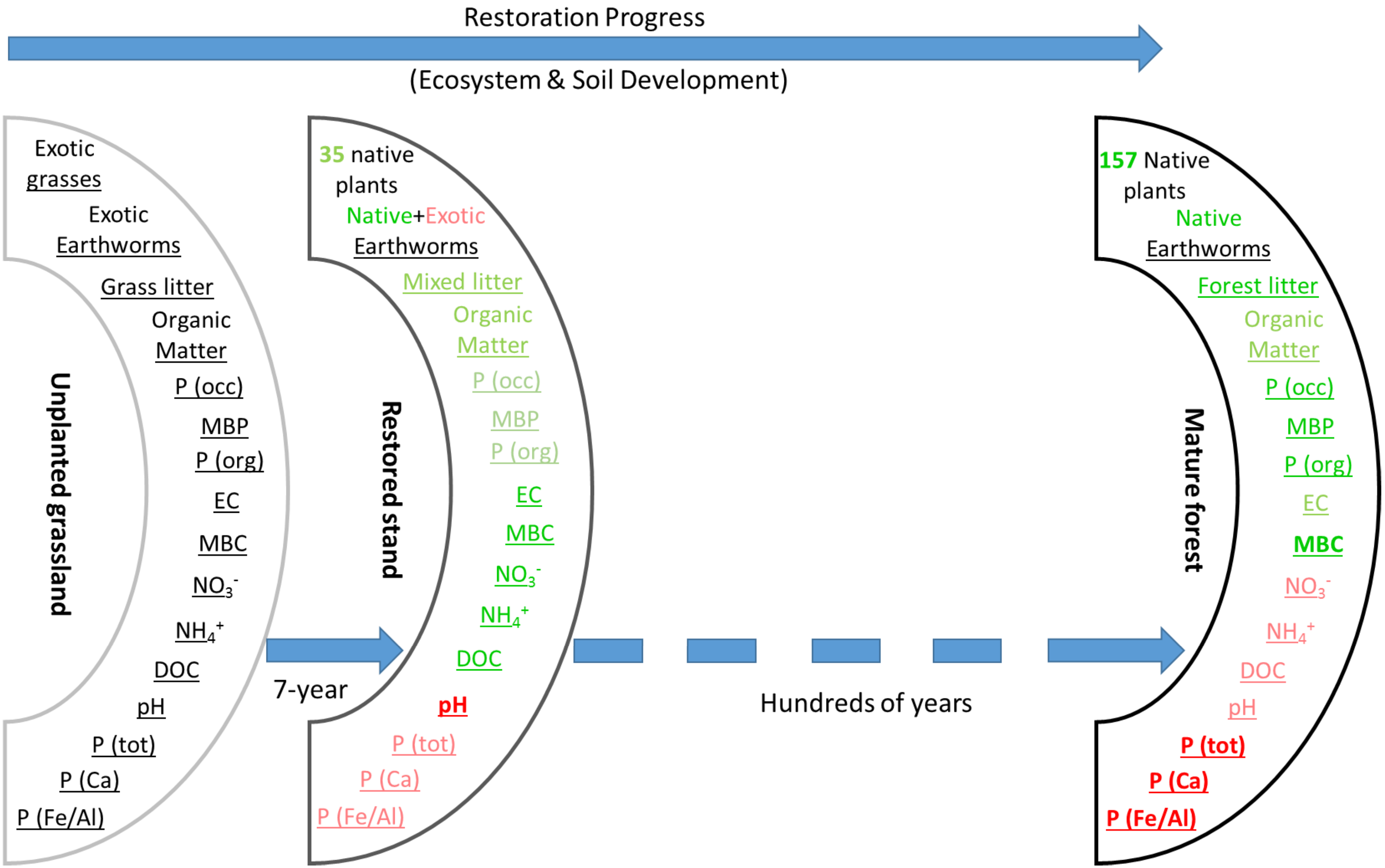


Figure 9.1 Conceptual model of changes of soil biogeochemistry on the restoration trajectory from the Unplanted grassland to Restoration stand to reference Mature forest at PCRP. The coloration scheme refers to increases and decreases in the stock market; green indicate increases while red indicate decreases; the brighter and bolded parameters mean more increases or decreases.

A question that should be addressed from the results of the present study is: how can this knowledge be of practical value to ecological restoration practice. Three generalized scenarios were proposed in a broader context of ecological restoration practices (Figure 9.2). Ecological restoration practitioners encounter variable landforms, which consist different soil types and different ages of soils, different stages of ecosystem development, as well as different histories of past land uses. All of these environmental and site-specific conditions will influence the restoration planning and target setting, and the success evaluation of a specific ecological restoration project.

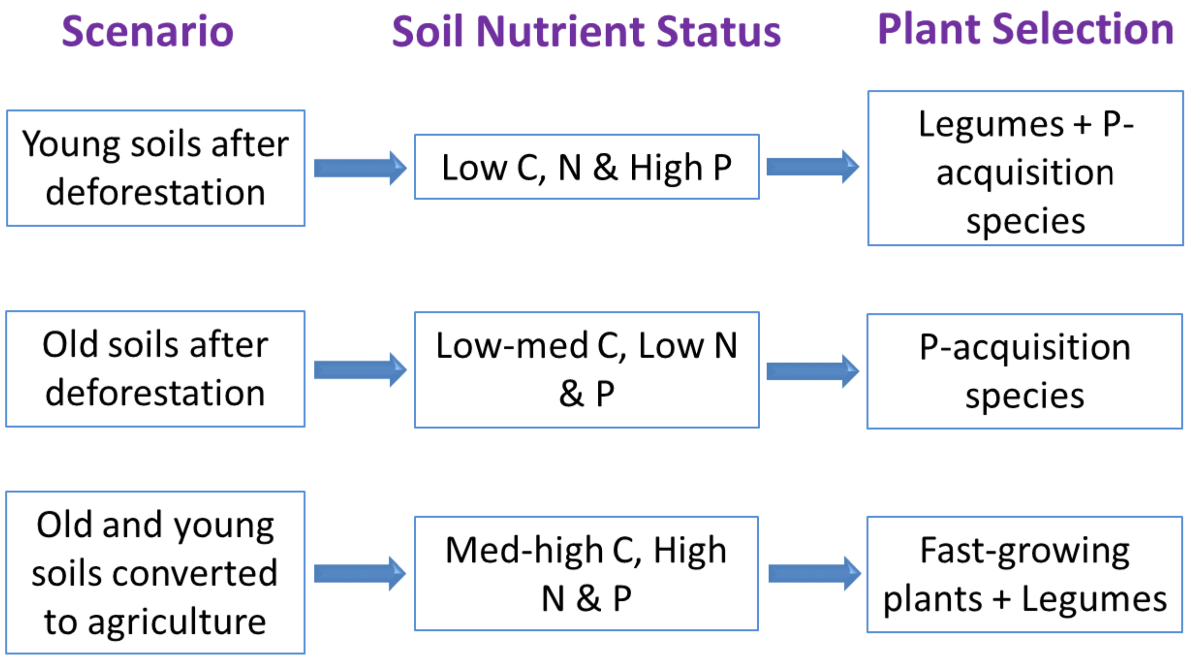


Figure 9.2 Generalized scenarios with corresponding soil nutrient status and plant selection recommendation.

Restoration of young soils after deforestation and habitat degradation requires N resources in the soils to be raised in order to allow plants to exploit the P reserves in the soils. Planting N-fixing and mycorrhizal species would be essential. Building up the soil C and N pools is essential, since N is the limiting nutrient in young ecosystems. It is important to assimilate or immobilize soil N and P into biomass, rather than being leached out to the wider environment (in particular high rainfall area). Lost N and P to wider water bodies could lead to water quality deterioration.

Restoration at old soils after deforestation and habitat degradation would require both N and P resources in the soils to be raised. Thus, planting specialized P-acquisition species, such as mycorrhizal symbiosis or cluster root-forming (carboxylate releasing) species may be critical for the initial establishment of vegetation. Phosphorus is the critical element for the processes of biological N-fixation. Application of N-rich organic soil amendments may be helpful where practicable.

In both old and young soils that have been converted to agriculture, restoration is relatively straightforward. At the PCRP site, there were high concentration of N, P and organic C from past agricultural activities. Planting pioneer fast-growing plants will preserve the N and P resources within the soil, in order to avoid the losses of them to wider environment. Following N-fixing plants introduction may help to maintain high N status of the soil, and sustain the further development of the restored ecosystem.

Of course, it is important to take site-specific conditions into consideration prior to restoration activities. This study illustrates that a preliminary and ongoing study of soils should be an essential part of restoration practice.

9.2 Concluding remarks

The conclusion of this study is that a combined knowledge of soil physicochemical and biological properties plays a fundamental role in the understanding of trajectory of the ecological restoration at the PCRP site. Ecological restoration of native vegetation has significantly modified soil nutrient cycling, particularly in terms of C, N and P dynamics, which are probably driven by litter fall, plant rhizospheres and related soil organisms. Laboratory studies showed that small additions of litter to soil can have a considerable impact on soil chemistry. Ammonium-N and NO_3-N concentrations in soil solution have been significantly increased by fast-growing restored vegetation.

Incorporation of knowledge of soil pedogenesis into this study has provided an important description of the soil template on which the ecological restoration is based. Clearly, this description is vital to the implementation of an ecological restoration on a large and diverse landscape; soil profiles were shown to be more valuable than could be predicted from a desk study. This study has identified significant changes of soil P and Fe/Al minerals on a short-term soil chronosequence at the site. Soil P fractionation agree with classical Walker and Syers' model of P transformations during pedogenesis; dynamics of Fe/Al minerals presented a pre-podsolization conditions under this super-humid environment.

Large inter-species differences were identified, in which bird guano deposition was found to be important. Interactions of flax, earthworm and guano had significant impact of soil P dynamics, which illustrated the likely complex relationships between soil fauna and plants on soil function in the restoration trajectory. A conceptual model is proposed to elucidate changes of soil biogeochemistry on the restoration trajectory.

This study has shown that soil biogeochemistry and progressive development of biodiversity on the restoration trajectory operate in synergy. The success of the restoration and establishment of flora and fauna are strongly influenced by soil variability, but the developing plant communities also substantially modify soil physio-chemistry.

9.3 Recommendations for further research

(1) Longer-term investigation of the dynamics of soil dissolved organic carbon and mobile nitrogen in soil solution alongside the progress of ecological restoration is needed. It would also be valuable to calculate the mass balance of soil carbon (including GHG emissions and carbon sequestration potential) along the restoration trajectory. Carbon and nitrogen management present major challenges in environmental science.

(2) Long-term study of change of soil microbial biomass phosphorus and its proportional contribution to organic P or biomass P (plant and microbial biomass) alongside the succession of ecological restoration would provide a picture of bacteria-fungi communities transformation (Turner et al., 2013).

(3) Incorporating soil pedogenesis to ecological restorations undertaken on larger-scale landscapes with distinct stages of soil development would further test the transferability of the knowledge of the proposed model.

(4) Long-term study to investigate the relationships and interactions between soil chemistry, biodiversity and plants on the restoration trajectory is needed. Recolonization and establishment of soil faunal and microbial communities alongside the progress of ecological restoration requires long-term monitoring to better understand the contribution of these organisms to nutrient cycling and ecosystem functioning.

(5) There is further test potential to investigate native species in amelioration of environmental concerns associated with nitrate leaching and greenhouse gases emissions, as well as nutrient losses to wider water bodies and consequent degradation.

(6) A more detailed study to investigate the significance of difference in guano chemistry between different New Zealand seabirds (e.g. penguins) and land birds related to their diets, and their potential contribution and impacts on local/habitat environment would provide interesting future study.

Appendix A

Selection of restoration species

This Appendix A includes: (i) Table A.1 outlines the selected restoration planting species and their planting scheme, which is kindly provided by PCRP site manager James Washer; and (ii) Table A.2 outlines the glossary of plant species abbreviations in the statistical analysis.

A.1 Selection of restoration species and planting scheme

Table A.1 Selection of restoration plant species and planting scheme according to site management practices.

PLANT SPECIES (FAMILY)	PREFFERED LOCATION SOILS ENVIRONMENTS	AVOIDED LOCATIONS	GENERAL COMMENTS
Aristotelia serrata (Elaeocarpaceae)	Prefers dry well drained soils	Avoided wet soils and exposed areas especially coastal areas subject to salt spray	Can be used as initial coloniser but can be vulnerable to frost and wind damage, fast growth and provides good initial canopy closure if planted with other colonisers
Astelia grandis (Asteliaceae)	Wet, dry and beach gravels	Avoided exposed open locations	Best planted under established canopy and prefers shaded, sheltered areas
Carex secta (Cyperaceae)	Wet, dry soils and beach gravels	Avoided shaded areas	Best planted in open wetland areas, hardy and fast growing
Carpodetus serratus (Rousseaceae)	Prefers dry and semi damp soils	Exposed locations	Grows well in shaded sheltered areas, not many planted on PCRP site
Coprosma grandifolia (Rubiaceae)	Wet, dry soils and beach gravels	Avoided exposed locations	Ideal in shaded, sheltered areas amongst previous plantings or under formed canopy
Coprosma lucida (Rubiaceae)	Prefers dry soils and beach gravels	Avoided wet soils and exposed locations	Slow growing and vulnerable to hare and frost damage

Coprosma propinqua (Rubiaceae)	Wet, dry soils and beach gravels	Planted in all locations	Hardy first stage coloniser, prefers open space
Coprosma robusta (Rubiaceae)	Wet, dry soils and beach gravels	Planted in all locations	Good first stage coloniser, produces lots of fruits, vulnerable to frost and hare damage, prefers open space
Cordyline australis (Asparagaceae)	Wet, dry soils and beach gravels	Avoided shaded areas as needs plenty of light	Vulnerable to hare damage, can handle grass competition
Cortaderia richardi (Poaceae)	Wet, dry soils and beach gravels	Can be planted anywhere in the open, avoided shaded areas	Great to plant anywhere but if planted amongst other species will eventually be shaded out, provides good initial shelter, vulnerable to hare damage
Cyperus ustulatus (Cyperaceae)	Wet, dry soils and beach gravels	Avoided shaded areas	Best planted in open wetland areas, hard and fast growing
Dacrycarpus dacrydioides (Podocarpaceae)	Wet, dry soils and beach gravels	Avoided open exposed areas	Prefers shaded sheltered areas amongst initial colonisers or under canopy of initial colonisers, can handle exposed locations but growth rate is considerably slower
Dodonaea viscosa (Sapindaceae)	Prefers dry soils and beach gravels	Avoided wet soils and fully exposed areas with salt spray	Only planted in coastal strip with shelter from coastal forest remnant as only naturally occurs in this area. Prone to frost damage but provides great canopy closure when established
Fuchsia excorticata (Onagraceae)	Prefers dry and semi damp soils	Exposed locations and coastal areas	Grows well in shaded sheltered areas, handles frost but survival rates not high in general

Fuchsia procumbens (Onagraceae)	Dry soils and beach gravels	Exposed locations and wet soils	Unsuitable for general restoration planting, ground cover that can only handle planting under canopy
Griselinia lucida (Griseliniaceae)	Prefers no soil initially but will eventually put roots into the ground (hemiepiphyte)	Avoided planting directly into the ground and exposed locations	Unsuitable planted directly in the ground, does well planted in branch forks of mature trees or fence posts, starts life as a epiphyte and can handle exposure once established terrestrially
Hebe salicifolia (Plantaginaceae)	Prefers dry soils but can tolerate wet soils	Beach gravels and salt exposure	Hard and fast growing, provides good mix with other first stage colonisers
Hedycarya arborea (Monimiaceae)	Prefers dry soils	Avoided exposed areas and beach gravels	Unsuitable in any exposed area, does well under established canopy
Hoheria sexstylosa (Malvaceae)	Prefers dry soils	Wet soils and beach gravels	Can handle open areas but provides a good mix amongst initial colonisers, prone to hare damage
Metrosideros robusta (Myrtaceae)	Prefers dry soils if planted terrestrially, can also be planted as an hemi-epiphyte as will eventually put roots down into the ground	Avoided exposed open locations, will handle exposure once established	Best planted under established canopy and prefers shaded, sheltered areas
Melicytus ramiflorus (Violaceae)	Prefers dry soils and beach gravels	Avoided wet soils and exposed locations	Ideal in shaded sheltered locations amongst previous established colonisers, vulnerable to frost and wind damage
Myrsine australis (Primulaceae)	Prefers dry well drained soils and beach gravels	Avoided wet soils	Does well on sheltered shady areas, slow growing

Myrsine salicina (Primulaceae)	Prefers dry and wet soils	Avoided beach gravels	Best planted amongst established colonisers with shelter, slow growing and prone frost damage
Olearia avicenniifolia (Asteraceae)	Prefers dry soils and beach gravels	Wet soils	Can handle open areas but provides a good mix with established colonisers, vulnerable to frosts
Phormium tenax (Xanthorrhoeaceae)	Wet, dry soils and beach gravels	Can be planted anywhere open, great in wet areas, avoided shaded areas, handles exposure and salt spray	Great to plant anywhere but if other species are planted in same area will be shaded out eventually but can provide initial shelter
Piper excelsum (Piperaceae)	Prefers dry soils and beach gravels	Avoided exposed locations and wet soils	Unsuitable in any exposed locations, ideal in full sheltered, shaded areas and under canopy of initial colonisers, prone to frost and hare damage
Pittosporum eugenioides (Pittosporaceae)	Prefers dry well drained soils and beach gravels	Avoided wet soils and exposure to salt and wind	Good second stage coloniser once a bit of shelter established, vulnerable to wind, frost and hare damage, fast growing and provides excellent initial canopy closure
Pittosporum tenuifolium (Pittosporaceae)	Prefers dry well drained soils and beach gravels	Avoided wet soils	Handles wind exposure, vulnerable to hare damage
Podocarpus totara var. totara (Podocarpaceae)	Prefers dry soils and beach gravels	Exposed locations, salt exposure and wet soils	Prefers shaded, sheltered locations amongst initial first stage colonisers or under established canopy of initial colonisers, can handle exposed locations but growth rate is considerably slower

Prumnopitys ferruginea (Podocarpaceae)	Prefers dry soils	Avoided wet soils and beach gravels	Best planted under established canopy and prefers shaded, sheltered areas
Pseudopanax crassifolius (Araliaceae)	Prefers dry soils and beach gravels	Wet soils and exposed areas	Slow growing, prone to hare damage and frost, more suited to planting under canopy or in sheltered shaded areas
Rhopalostylis sapida (Arecaceae)	Wet, dry and beach gravels	Avoided exposed open locations	Best planted under established canopy and prefers shaded sheltered areas
Schefflera digitate (Araliaceae)	Prefers dry and semi damp soils	Exposed locations	Grows well in shaded sheltered areas, dose not handle direct sunlight frost or exposed locations, suitable for under canopy plantings
Sophora microphylla (Fabaceae)	Wet, dry soils and beach gravels	Can be planted in most areas except full exposure to salt spray	Grows better amongst initial established colonisers, can be shaded out easily, very prone to hare damage and frosts
Weinmannia racemose (Cunoniaceae)	Prefers dry and semi damp soils	Exposed locations and salt exposure, wet soils	Can handle semi exposed locations but grows best in shaded, sheltered areas or under established canopy of initial colonisers

A.2 Glossary of plant species abbreviations

Table A. 2 Glossary of plant species abbreviations (modified from Hahner et al., 2013).

Abreviation	Scientific Name	Family
ACA.ans	*Acaena anserinifolia*	Rosaceae
ANA.lan	*Anarthropteris lanceolata*	Polypodiaceae
ARI.ser	*Aristotelia serrata*	Elaeocarpaceae
ASP.bul	*Asplenium bulbiferum*	Aspleniaceae
ASP.fla	*Asplenium flaccidum*	Aspleniaceae
ASP.pol	*Asplenium polyodon*	Aspleniaceae
BLE.nov	*Blechnum novae-zelandiae*	Blechnaceae
CAL.tug	*Calystegia tuguriorum*	Convolvulaceae
CAR.dis	*Carex dissita*	Cyperaceae
CAR.ser	*Carpodetus serratus*	Rousseaceae
CLE.pan	*Clematis paniculata*	Ranunculaceae
COP.gra	*Coprosma grandifolia*	Rubiaceae
COP.luc	*Coprosma lucida*	Rubiaceae
COP.pro	*Coprosma propinqua*	Rubiaceae
COP.rob	*Coprosma robusta*	Rubiaceae
COP.hyb	*Coprosma robusta x C. propinqua*	Rubiaceae
COP.rot	*Coprosma rotundifolia*	Rubiaceae
COP.spa	*Coprosma spathulata*	Rubiaceae
COR.aus	*Cordyline australis*	Asparagaceae
CYA.med	*Cyathea medullaris*	Cyatheaceae
CYA.smi	*Cyathea smithii*	Cyatheaceae
DAC.dac	*Dacrycarpus dacrydioides*	Podocarpaceae
DAC.cup	*Dacrydium cupressinum*	Podocarpaceae
DIC.squ	*Dicksonia squarrosa*	Dicksoniaceae
DOD.vis	*Dodonaea viscosa*	Sapindaceae
FRE.ban	*Freycinetia banksii*	Pandanaceae
FUC.exc	*Fuchsia excorticata*	Onagraceae
GRI.lit	*Griselinia littoralis*	Griseliniaceae
GRI.luc	*Griselinia lucida*	Griseliniaceae
HEB.sal	*Hebe salicifolia*	Plantaginaceae
HED.arb	*Hedycarya arborea*	Monimiaceae
HIS.inc	*Histiopteris incisa*	Dennstaedtiaceae
HOH.sex	*Hoheria sexstylosa*	Malvaceae
HYM.rev	*Hymenophyllum revolutum*	Hymenophyllaceae

HYM.sca	*Hymenophyllum scabrum*	Hymenophyllaceae
LIN.tri	*Lindsaea trichomanoides*	Lindsaeaceae
LYC.bil	*Lycopodium billardieri*	Lycopodiaceae
MEL.ram	*Melicytus ramiflorus*	Violaceae
MET.dif	*Metrosideros diffusa*	Myrtaceae
MET.per	*Metrosideros perforata*	Myrtaceae
MET.rob	*Metrosideros robusta*	Myrtaceae
MIC.pus	*Microsorum pustulatum*	Polypodiaceae
MIC.sca	*Microsorum scandens*	Polypodiaceae
MYR.aus	*Myrsine australis*	Primulaceae
MYR.sal	*Myrsine salicina*	Primulaceae
OLE.avi	*Olearia avicenniifolia*	Asteraceae
PAR.het	*Parsonsia heterophylla*	Apocynaceae
PHO.ten	*Phormium tenax*	Xanthorrhoeaceae
PIT.ten	*Pittosporum eugenioides*	Pittosporaceae
PIT.eug	*Pittosporum tenuifolium*	Pittosporaceae
POD.tot	*Podocarpus totara*	Podocarpaceae
PSE.cra	*Pseudopanax crassifolius*	Araliaceae
PSE.dis	*Pseudopanax discolor*	Araliaceae
PSE.axi	*Pseudowintera axillaris*	Winteraceae
PYR.ela	*Pyrrosia eleagnifolia*	Polypodiaceae
RHO.sap	*Rhopalostylis sapida*	Arecaceae
RIP.sca	*Ripogonum scandens*	Ripogonaceae
RUB.aus	*Rubus australis*	Rosaceae
RUB.fru	*Rubus fructicosa*	Rosaceae
RUB.sch	*Rubus schmidelioides*	Rosaceae
RUM.adi	*Rumohra adiantiformis*	Dryopteridaceae
SCH.dig	*Schefflera digitata*	Araliaceae
SOP.mic	*Sophora microphylla*	Fabaceae
STR.het	*Streblus heterophyllus*	Moraceae
TME.sp.	*Tmesipteris sp.*	Psilotaceae
TRI.ven	*Trichomanes venosum*	Hymenophyllaceae
WEI.rac	*Weinmannia racemosa*	Cunoniaceae

Appendix B

Supplementary data for Chapter 3

This appendix includes Supplementary data to accompany Chapter 3.

Table B. 1 Total carbon and nitrogen content of fresh leaf and leaf litter for some native species. (modified from Hahner et al. 2014).

	Green leaf			Leaf litter		
	N (%)	C (%)	C/N ratio	N (%)	C (%)	C/N ratio
P. tenax	1.07	44.63	43.65	0.36	46.24	128.94
C. richardii	1.43	44.27	32.32	0.72	44.88	62.22
K. ericoides	2.26	48.97	21.73	1.70	46.09	27.17
C. robusta	1.79	43.58	24.45	0.63	43.73	69.32
O. paniculata	1.42	47.71	33.53	0.98	46.78	47.53

Table B. 2 Selected soil chemical properties of *Olearia paniculata* litter-soil incubation using 1.5 g of leaf litter. Data are mean values ± standard error (n=3).

	Green leaf	Leaf litter	Control
pH	5.73 (0.01)	5.79 (0.01)	5.03 (0.04)
MBC	100.4 (10.4)	74.7 (12.6)	54.5 (17.7)
NH_4-N	14.4 (1.2)	8.4 (1.0)	28.5 (1.4)
NO_3-N	2.6 (0.4)	0.7 (0.2)	72.1 (10.6)

Appendix C

Soil DOC, NH_4-N and NO_3-N concentrations of each plot in each transect and sampling event

This appendix provides three figures to show soil DOC, NH_4-N and NO_3-N concentrations of each plot (Mature, Restoration and Unplanted plots) in each transect (Transects 1, 2 and 4) and sampling event (2014.08, 2014.11, 2015.01, and 2015.11).

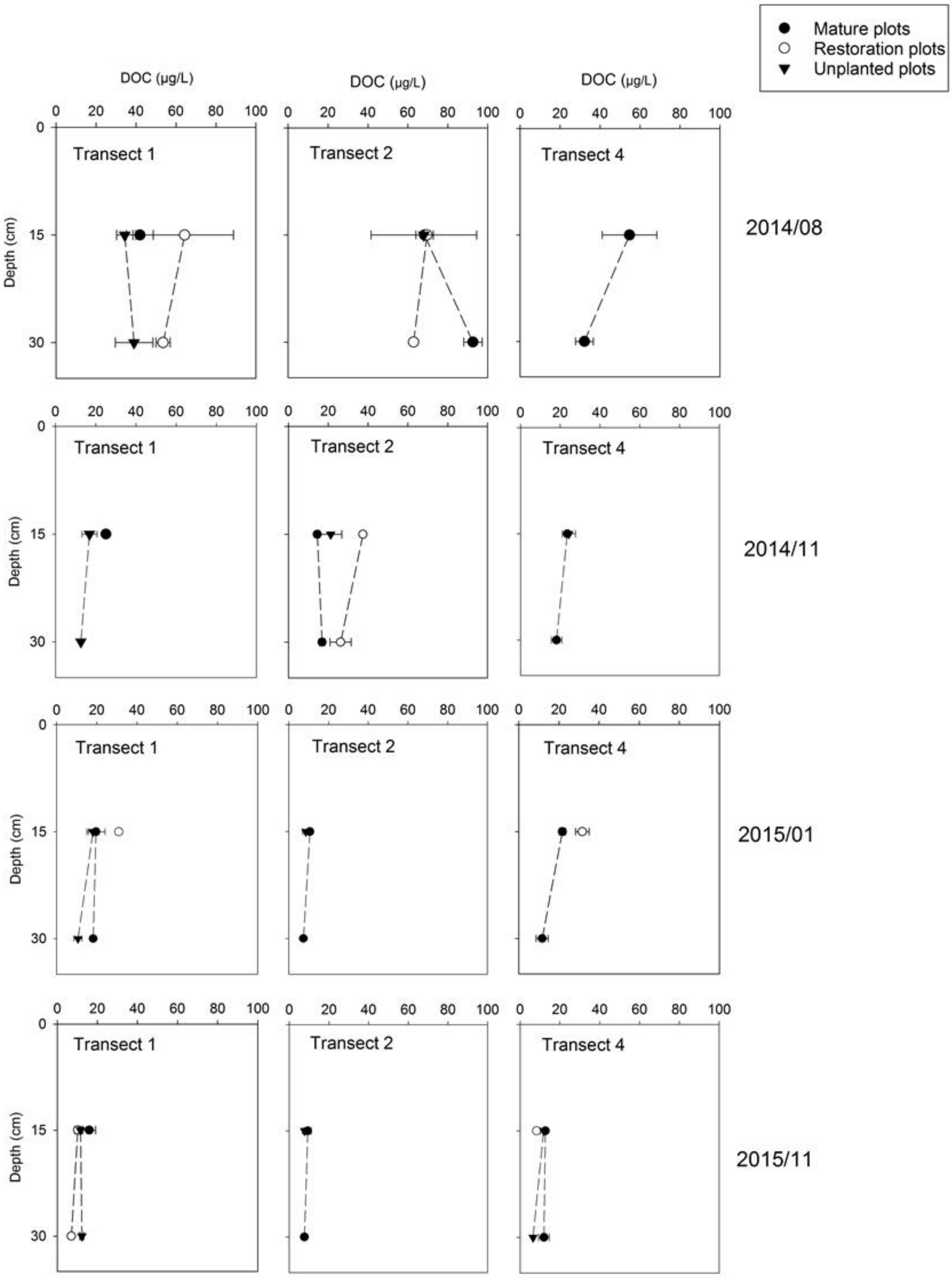


Figure C. 1 DOC concentrations in soil leachates in each plot and sampling event.

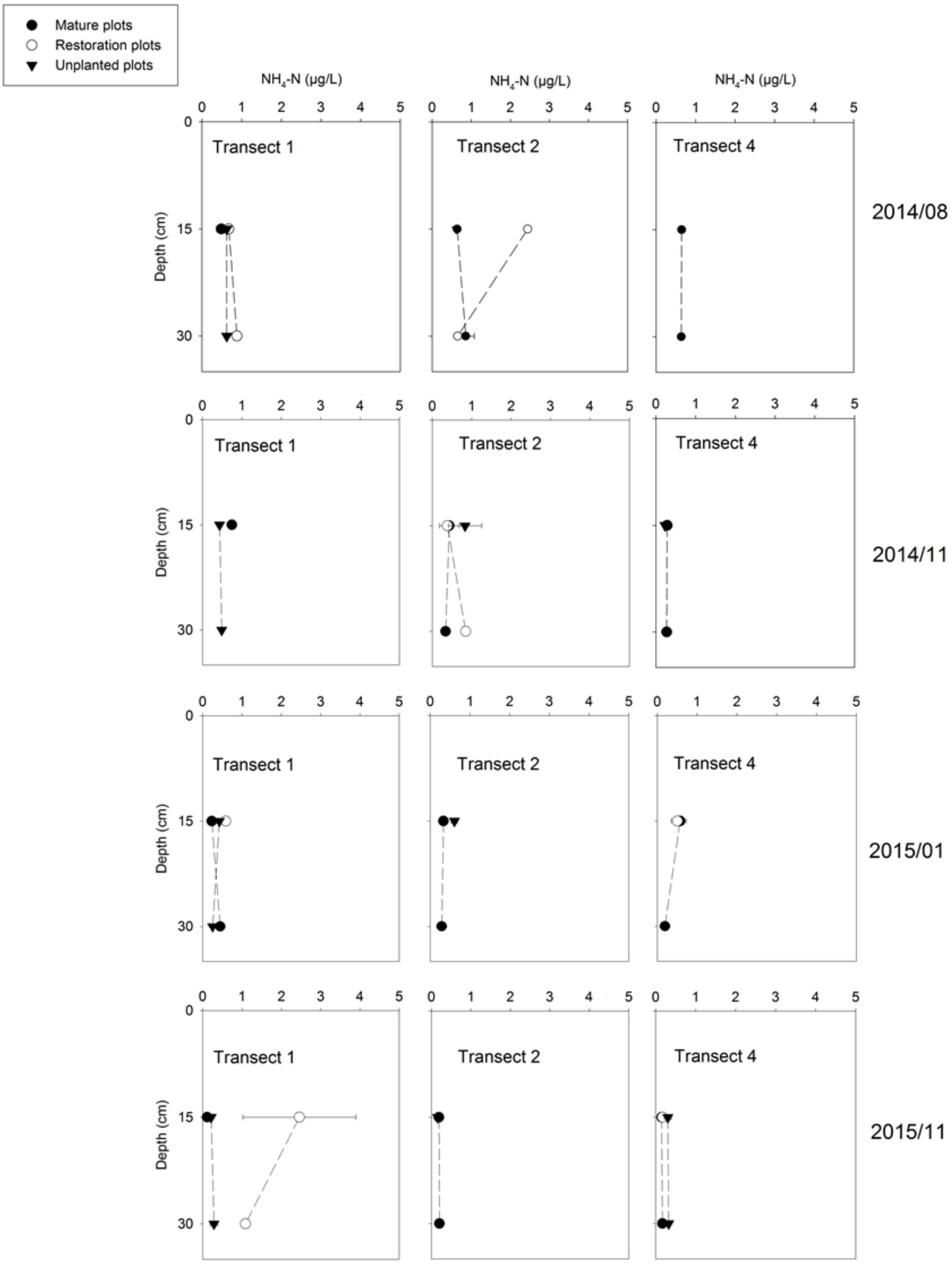


Figure C. 2 NH_4-N concentrations in soil leachates in each plot and sampling event.

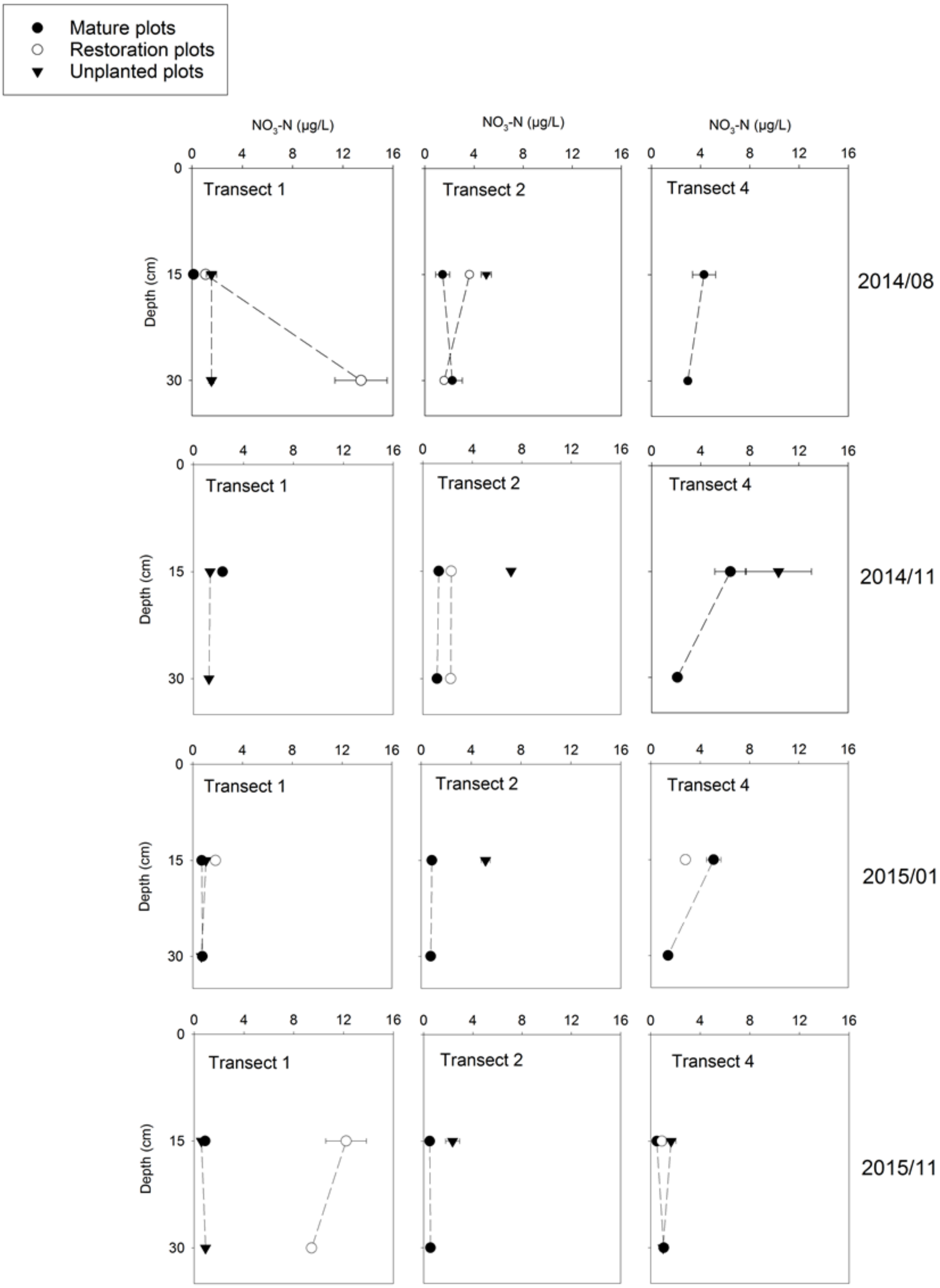


Figure C. 3 NO$_3$-N concentrations in soil leachates in each plot and sampling event.

Appendix D

Soil profile descriptions

This appendix includes pepological decsriptions of soil profiles.

Table D.1 outlines the profile descriptions for Transect 1 and 3 in Chapter 5. This soil profile descriptions were originally completed and outlined in Hahner et al. (2013).

Table D.2 outline the profile descriptions for palm, flax and grassland in Chapter 6.

D.1 Soil profile descriptions for Transect 1 and 3

Table D. 1 Soil profile descriptions for Transect 1 and 3.

Site: M1		
Ah	0-20 cm	10YR 3/1 Silt loam Volume density: 1.33 g/cm^3 Moderately developed crumb structure Peds 1-2cm breaking to 5mm (3.25% of gravel content) Strength- very weak deformable. Non-indurated Slightly sticky Plastic 10% roots common extremely fine. Few fine. Few medium Indistinct boundary
Bw1	20-40 cm	10YR3/1 Sandy loam Volume density: 1.39 g/cm^3 Structure weak/blocky peds 3cm breaking to 0.5cm very weak very friable non-indurated slightly sticky plastic slightly fluid rounded rod / rounded rod clasts 9cm Fresh to slightly weathered granite (sample) rounded rod 2cm sandstone / Positive Liquefaction test < Bw2 Indistinct boundary
Bw2	40-55 cm	10YR 3/2 loamy sand Volume density: 1.43 g/cm^3 Single grain structure rounded rod 7cm slightly weathered (sample) Very weak Brittle Friable Very weak induration Slightly sticky non-plastic, slightly fluid Roots 1% coarse 1% microfine roots indistinct boundary
C	55 cm +	10Yr 3/2 sand Volume density: 1.55 g/cm^3 Single grain structure Very weak Brittle Very weak induration Non-sticky Non-plastic Non-sensitive 1% extremely fine roots

Table D.1 continued:

Site: R1		
Ah	0-18 cm	10YR3/3 Fine sandy loam Volume density: 1.35 g/cm^3 Moderately to strongly developed crumb structure 2cm diameter Weak strength friable Very weak induration Moderately plastic Slightly sticky Peds blocky 1-0.5cm (4.20% of gravel content) Rare rounded 0.5-1cm clasts Quartz- slightly discoloured No mottling Roots 2-5% in root mat at top Roots-microfine 5% Diffuse boundary. Smooth.
Bw	18-38 cm	10yr3/3 sandy loam Volume density: 1.50 g/cm^3 Moderate sub-angular blocky structure 2cm peds Breaking to <5mm weak strength Brittle/(friable) slightly plastic Rare skeletal- rounded strongly discoloured 5cm-1cm pitted sandstone Roots-2% Very fine Boundary to BC diffuse to occluded smooth & occasional
BC(f)	38-53 cm	10yr3/6 sand Volume density: 1.76 g/cm^3 A pedal single grain no skeletal inclusions Very weak structure Very friable Non-indurated Non-sticky Worm burrows (10YR 3/3 Mottling fine faint med – coarse distinct Roots-2% Very fine Boundary to C diffuse to occluded 10%
C	53 cm+	5Y 4/2 Volume density: 1.84 g/cm^3 Single grained very weak very friable Non-indurated Non-plastic Mottling very few fine faint (10YR 4/4) Roots between 50-60cm – 1-2% very fine 10YR 4/4 Fe staining layers Fe stains between 80-100cm 1.2m+ darker ilmenite (3352)

Table D.1 continued:

Site: U1		
Ah	0-10 cm	10YR 3/2(fine sand)silt loam (ZL) Volume density: 1.36 g/cm^3 Medium to strongly developed crumb structure 2cm blocks break to 0.5cm (3.67% of gravel content) Weak friable strength Non-indurated, slightly sticky 5% extremely fine & 1%microfine roots Boundary- smooth and abrupt
Bw(g)$_1$	10-Varies 22/33 cm	10YR 3/2 Sandy loam (SL) Volume density: 1.41 g/cm^3 blocky 4cm break to 0.5cm Brittle fracture Weak strength Very weak induration Slightly sticky Non-plastic Mottle-2.5YR 2.5/4 Few(5%) very fine and distinct Roots – 1% microfine
Bfm$_1$	33 cm	2.5YR 3/6 to 2.5/4 Boundary – wavy sharp
Bw(g)$_2$	34-45 cm	10 YR 3/2 Sandy loam Volume density: 1.44 g/cm^3 Blocky structure weak brittle Very weak induration Slightly sticky Non-plastic Limestone and Granite gravels Mainly in top half of horizon Rounded to well-rounded disk 6cm to <1cm some iron concretion coating rare ghosts Mottles 2.5YR2.5/4 very few extremely fine in top half of horizon Roots 1% microfine
Bfm$_2$	45 cm	2.5YR 3/6 Boundary – wavy sharp
2Bw	46-60 cm	10YR3/3 Loamy sand Volume density: 1.65 g/cm^3 Single grain structure Strength weak to slightly firm Brittle to very weak induration Non sticky Non plastic Granite to Sandstone rock is well rounded 2cm-1cm rare 5cm very slightly gravely Fresh to slightly weathered very rare ghosts 1cm sandstone No mottles Roots 1%-<1%
2BC	60-110 cm	2.5Y3/3 Sand (S) Volume density: 1.69 g/cm^3 Strength weak to very weak Brittle Non-indurated Non-sticky Non-plastic Mottles 5YR3/4 Very few Extremely fine Faint No roots
fm	105-108 cm	2.5YR 3/6 Boundary wavy distinct

2C	110-160 cm	2.5Y4/1 Sand Volume density: 1.95 g/cm^3 Single grain structure Weak strength Friable Non-indurated Non-Plastic Non-sticky No clasts Many fine horizontal laminations Wavy <1cm Distinct to prominent contrasts Ilmenite 2.5Y3/1 Iron staining 7.5YR ¾ Distinct laminate ilmenite at base Boundary Wavy sharp
2B3fm	160 cm+	2.5YR 3/6

Table D.1 continued:

Site: M3		
SURFACE	0 cm	Well-rounded disk and blade Very large to small pebbles
Ah	0-30 cm	10YR2/1 Silt loam Volume density: 0.55 g/cm^3 Very weak Friable Non-indurated Slightly sticky Plastic Extremely gravely Small to large well rounded disk and blade pebbles 60.36% of gravel content Roots 5%microfine 5%extremely fine 10%very fine 10%medium 2%coarse Boundary wavy abrupt
Bw	30-80 cm	10YR2/2 Gravely Volume density: 1.22 g/cm^3 No consistence measured as too gravely – Extremely gravely Small to large well rounded disk and blade pebbles to 60cm Moderately gravely small to large well rounded disks and blades pebbles slightly discoloured (iron staining)60-80cm Roots 10%extremely fine 5%very fine 2%coarse Boundary wavy sharp
C	80-100 cm+	2.5Y3/2 Sand Volume density: 1.43 g/cm^3 Strength very weak Very friable Non-indurated Non-sticky Non-plastic 80-95 coarse sand with very slightly gravely small to medium pebbles 95-100 very coarse sand 100+ alternating layers of medium large pebbles and very coarse sand

Table D.1 continued:

Site: R3		
Ah	0-30 cm	10YR2/2 Silty sand Volume density: 1.25 g/cm^3 Well-developed crumb structure 3mm peds Very weak Very friable Non-indurated Non-sticky Non-plastic 10% Quartz grains amongst peds Slightly gravely fresh to slightly discoloured Granite Quartz Green (Chlorite?)rounded disks and blades Very large pebbles grading, and small to medium pebbles 0-10cm Very large pebbles and small to medium pebbles 10-35cm Medium to large-Medium to small pebbles 53.85% of gravel content Roots 10% microfine 5%extremely fine 2%very fine 1%medium Boundary abrupt smooth
Bw	30-50 cm	10YR3/4 Loamy sand Volume density: 1.54 g/cm^3 Very weak development granular/crumbs to single grains adhering with roots and organic matter Very weak Very friable Non-indurated Non-sticky Non-plastic Imbrication varies 10-15% Fe staining /colour in matrix where compressed around clast faces Lithology as before Extremely gravely Iron staining on clasts Medium pebbles 35-50cm Roots 1%microfine 2%extremely fine 1%veryfine Boundary abrupt smooth
BC	50-105 cm	7.5YR3/4 Coarse sand Volume density: 1.66 g/cm^3 Single grain Very weak Very friable Non-indurated Non-sticky Non-plastic 50-60cm Small pebbles 60-70cm Medium to large pebbles in medium to fine sand matrix Fe staining of medium fine sand matrix where compressed against pebble clasts Colour taken from here No roots 70-80cm Coarse sand 80-90cm Small to medium pebbles 90-100cm Large pebbles and Coarse sand No roots Boundary distinct smooth
C	105 cm+	2.5Y4/2 Sand Volume density: no data Single grain Very weak Very friable Non-indurated Non-sticky Non-plastic 100cm + Gravel to Very coarse sand Lithology as before fresh to slightly discoloured No roots

Table D.1 continued:

Site: U3		
Ah	0-10 cm	10YR2/2 Coarse sand Volume density: 1.14 g/cm^3 Moderately developed crumb structure 1cm breaking to 2mm strength very weak Friable Non-indurated Slightly sticky Plastic Slightly gravely well rounded medium pebble disks and blades of fresh 74.11% of gravel content Greywacke and slightly weathered Granite Fresh Quartz Boundary abrupt smooth
Bw$_1$	10-30 cm	10YR3/2 Coarse sand Volume density: 1.44 g/cm^3 Structure weakly developed sub-angular blocky 5mm Strength very weak Very friable Non-indurated Non-sticky Non-plastic Moderately gravely well rounded medium pebble disks and blades of fresh Greywacke and Slightly weathered Granite Roots 10%microfine 1%extremely fine Boundary distinct smooth
Bw$_2$	30-42 cm	7.5YR3/2 Coarse sand Volume density: 1.53 g/cm^3 Structure weakly developed sub-angular blocky 5mm Strength very weak Very friable Non-indurated Non-sticky Non-plastic Moderately gravely well rounded medium to large pebble disks and blades of fresh Greywacke and slightly weathered Granite Roots 10% microfine Boundary distinct wavy
BC	42-78 cm	10YR4/3 Coarse sand (42-55) to medium to large pebbles (55-70 cm) then medium sand (70-78cm) Volume density: 1.66 g/cm^3 Single grain very weak Very friable Non-indurated Non-sticky Non-plastic Moderately gravely well rounded medium to large pebble disks and blades of Fresh Greywacke and Slightly weathered Granite Very rare iron staining localised on clasts No roots Boundary distinct wavy

C	78-120 cm	2.5Y4/1 Large to Very large pebbles 78-98cm then medium sand 98-102cm then Coarse sand 102cm + Volume density: 1.80 g/cm^3 Single grain Very weak Very friable Non-indurated Non-sticky Non-plastic Moderately gravely to slightly gravely Well rounded disks and blades of Fresh Greywacke and Slightly weathered Granite Very rare iron staining localised on clasts 80cm -100cm large to very large pebbles No roots Laminations of ilmenite Shell fragment at 90cm

D.2 Soil profile descriptions for palm, flax and grassland.

Table D. 2 Soil profile descriptions for palm, flax and grassland.

Site: Palm stand		
Ah	0-20 cm	10YR 2/2 sandy loam Volume density: 1.30 g/cm^3 Medium-developed crumb structure, slightly sticky, 5% medium root, 1% fine roots
Bw	20-40 cm	10YR 3/2 sandy loam Volume density: 1.42 g/cm^3 Weakly-developed crumb structure, 1% medium roots
Upper BC	40-60 cm	2.5Y 4/2 sand Volume density: 1.50 g/cm^3 Few mottle (7.5YR 4/4), 5-10 cm pebbles, few medium roots, fine roots
Lower BC	60-100 cm	2.5Y 3/3 sand Volume density: 1.78 g/cm^3 >5 cm pebbles, few medium-fine roots, many mottles (7.5YR 4/4)
C	100 cm +	2.5Y 3/2 sand Volume density: 1.68 g/cm^3 Single grain sand, few fine roots

Table D.2 continued:

Site: Flax stand		
Ah	0-20 cm	10YR 3/4 silt loam Volume density: 0.86 g/cm^3 Medium developed crumb structure, sticky, 5% fine root, 1% microfine roots
Bw	20-40 cm	10YR 4/3 sandy loam Volume density: 0.94 g/cm^3 Slightly sticky, 1 % microfine roots
Upper BC	40-60 cm	2.5Y 4/3 loamy sand Volume density: 1.13 g/cm^3 Single grain sand (medium size), 1-5 cm pebbles, Fe staining, 0.5% very fine roots
Lower BC	60-80 cm	2.5Y 3/3 loamy sand Volume density: 1.23 g/cm^3 Few very fine roots, non-sticky, non-plastic, 5-10 cm pebbles
C	80 cm +	5Y 4/2 coarse sand Volume density: 1.45 g/cm^3 No roots, >5 cm pebbles

Table D.2 continued:

Site: Grassland		
Ah	0-20 cm	10YR 4/2 Sandy loam Volume density: 1.43 g/cm^3 Weakly developed crumb 5mm Strength Very weak Friable Non-indurated Non-sticky Non-plastic 7cm depth Slightly discoloured 4cm, Well-rounded Greywacke disk 4cm diameter 10cm discrete Sandy lense upper boundary a thin Fe pan2cm thick Roots 5% microfine Boundary Sharp irregular
Bw(f)	Varies 20-30/20-40 cm	20-25cm 2.5Y 6/2 Medium Sand Volume density: 1.53 g/cm^3 Single grain Very weak Very friable Non-sticky Non-indurated Non-plastic Mottles (7.5YR 4/4) 20-30cm (see photo) Roots 1%microfine between 20-30cm circular and lamina
BC$_1$	Varies 30-65/40-65 cm	From 45cm 2.5Y 3/1 Coarse sand Volume density: 1.73 g/cm^3 BC1 more indurated than BC2 + more brown mottles /Common mottling Turbation burrows at 40-70cm Boundary sharp irregular (see photo)
BC$_2$	65-145 cm	2.5Y 3/1 Coarse Sand Volume density: 1.64 g/cm^3 Single grain Medium sand size 90cm –Slightly discoloured Well rounded 5cm Greywacke Mottles Few (one class less than BC2) Boundary sharp irregular Bfm (2.5YR 2.5/4)
C	145 cm+	2.5Y 2.5/1 Sand Volume density: 1.79 g/cm^3 Single grain Very weak Very friable Non-indurated Non-sticky Non-plastic No mottles No roots

Appendix E

Correlation of soil physicochemical variable within each plot type

This appendix includes the correlation heat-plots of correlation of soil physicochemical variable within each plot type, for Ah and Bw soil.

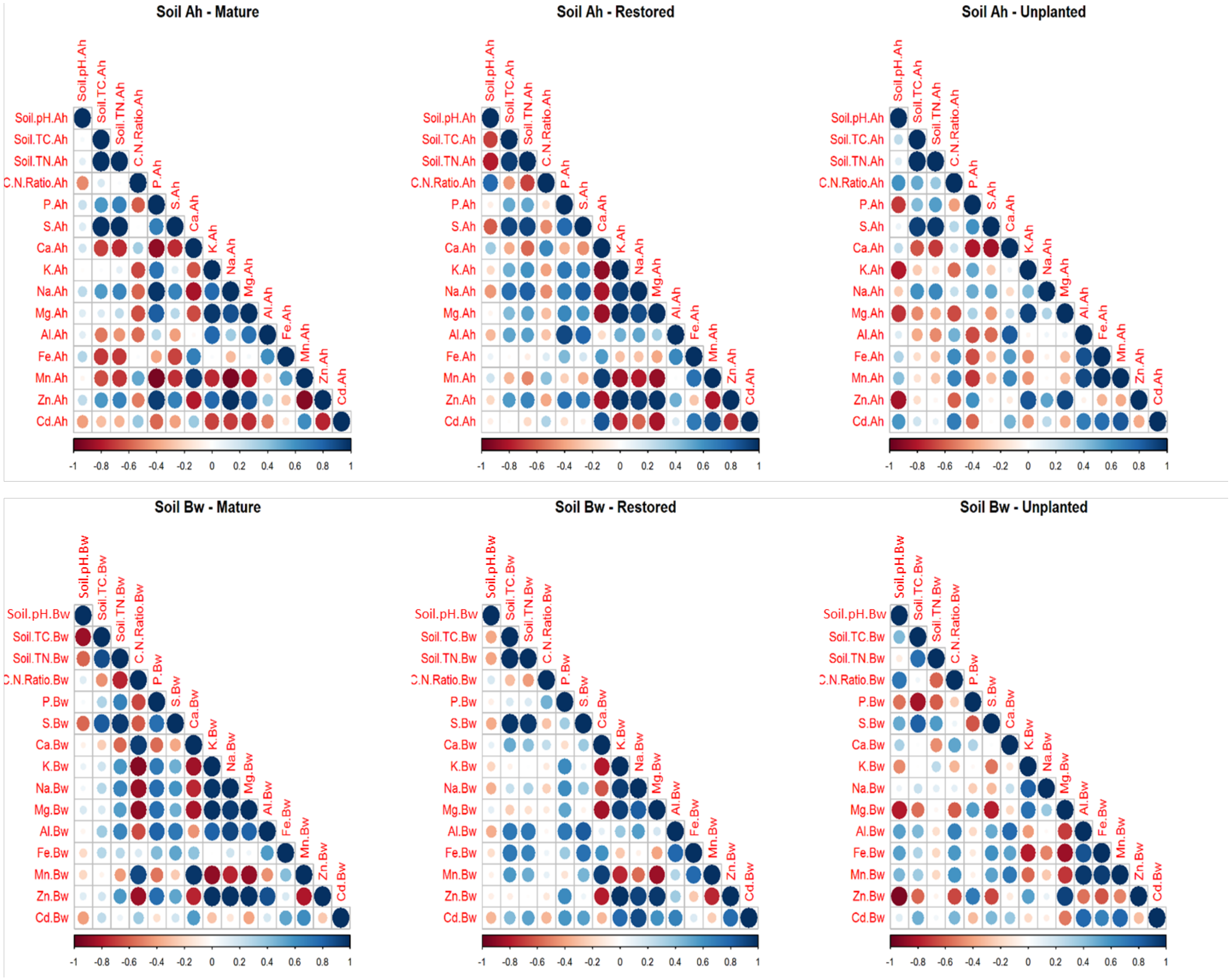


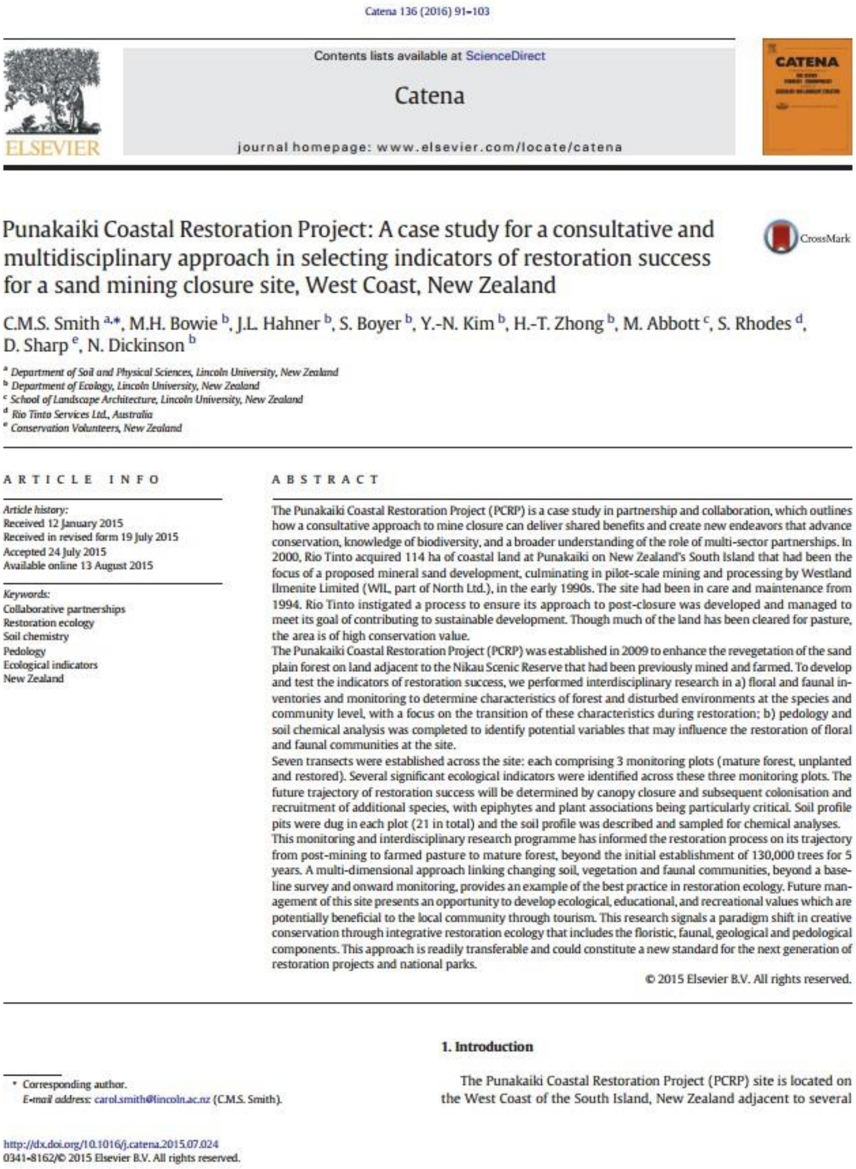
Figure E. 1 Correlation heat-plots of correlation of soil physicochemical variable within each plot type, for Ah and Bw soil.

Appendix F

Published Paper to accompany this study

This appendix introduces a published paper studied in the PCRP and a hyperlink is given:

Smith, C. M. S. Bowie, M. H. Hahner, J. L. Boyer, S. Kim, Y. N. **Zhong, H. T**. Abbott, M. Rhodes, S. Sharp, D. Dickinson, N. (2016). Punakaiki Coastal Restoration Project: A case study for a consultative and multidisciplinary approach in selecting indicators of restoration success for a sand mining closure site, West Coast, New Zealand. *CATENA*, *136*, 91-103. http://dx.doi.org/10.1016/j.catena.2015.07.024



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Punakaiki Coastal Restoration Project: A case study for a consultative and multidisciplinary approach in selecting indicators of restoration success for a sand mining closure site, West Coast, New Zealand

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ABSTRACT

The Punakaiki Coastal Restoration Project (PCRP) is a case study in partnership and collaboration, which outlines how a consultative approach to mine closure can deliver shared benefits and create new endeavors that advance conservation, knowledge of biodiversity, and a broader understanding of the role of multi-sector partnerships. In 2000, Rio Tinto acquired 114 ha of coastal land at Punakaiki on New Zealand's South Island that had been the focus of a proposed mineral sand development, culminating in pilot-scale mining and processing by Westland Ilmenite Limited (WIL, part of North Ltd.), in the early 1990s. The site had been in care and maintenance from 1994. Rio Tinto instigated a process to ensure its approach to post-closure was developed and managed to meet its goal of contributing to sustainable development. Though much of the land has been cleared for pasture, the area is of high conservation value.

The Punakaiki Coastal Restoration Project (PCRP) was established in 2009 to enhance the revegetation of the sand plain forest on land adjacent to the Nikau Scenic Reserve that had been previously mined and farmed. To develop and test the indicators of restoration success, we performed interdisciplinary research in a) floral and faunal inventories and monitoring to determine characteristics of forest and disturbed environments at the species and community level, with a focus on the transition of these characteristics during restoration; b) pedology and soil chemical analysis was completed to identify potential variables that may influence the restoration of floral and faunal communities at the site.

Seven transects were established across the site: each comprising 3 monitoring plots (mature forest, unplanted and restored). Several significant ecological indicators were identified across these three monitoring plots. The future trajectory of restoration success will be determined by canopy closure and subsequent colonisation and recruitment of additional species, with epiphytes and plant associations being particularly critical. Soil profile pits were dug in each plot (21 in total) and the soil profile was described and sampled for chemical analyses.

This monitoring and interdisciplinary research programme has informed the restoration process on its trajectory from post-mining to farmed pasture to mature forest, beyond the initial establishment of 130,000 trees for 5 years. A multi-dimensional approach linking changing soil, vegetation and faunal communities, beyond a baseline survey and onward monitoring, provides an example of the best practice in restoration ecology. Future management of this site presents an opportunity to develop ecological, educational, and recreational values which are potentially beneficial to the local community through tourism. This research signals a paradigm shift in creative conservation through integrative restoration ecology that includes the floristic, faunal, geological and pedological components. This approach is readily transferable and could constitute a new standard for the next generation of restoration projects and national parks.

1. Introduction

The Punakaiki Coastal Restoration Project (PCRP) site is located on the West Coast of the South Island, New Zealand adjacent to several

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