Journal of Soil Science and Plant Nutrition, 2016, 16 (2), 477-489

RESEARCH ARTICLE

Impact of different tree species on soil phosphorus immediately following grassland afforestation

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Abstract

Previous studies have revealed that significant changes in soil phosphorus (P) occurred as a consequence of grassland afforestation, although when these changes occurred and the influence of different tree species remains largely unknown. This study involved assessing changes in soil phosphorus (P) over a 10 year period following the afforestation of grazed pasture with 3 contrasting tree species (*Pinus radiata*, *Cupressus macrocarpa*, *Eucalyptus nitens*) in a replicated field trial at Orton Bradley Park, New Zealand. A combination of techniques (sequential fractionation, alkaline phosphatase hydrolysable P, solution ^{31}P nuclear magnetic resonance spectroscopy) was used to quantify changes in the nature and bioavailability of soil P. Results revealed that the establishment and growth of trees caused a significant decrease in soil organic P within 10 years, indicating net organic P mineralisation. Surprisingly this trend was similar under all three tree species, which suggested similar soil P acquisition despite differences in the type of mycorrhizae associated with each species: *P. radiata* is ectomycorrhizal, *C. macrocarpa* is arbuscular mycorrhizal, and *E. nitens* can beectomycorrhizal or arbuscular mycorrhizal. The observed changes in soil P dynamics were attributed a combination of tree growth and P uptake irrespective of species and changes in P inputs and organic P turnover associated with the cessation of grazing following tree planting. Changes in the nature of organic P determined 10 years after establishment indicated that organic matter inputs associated with tree growth were having an increasing influence on soil P dynamics with time.

Keywords: Soil phosphorus bioavailability, organic phosphorus mineralisation, soil phosphorus fractionation, *Pinus radiate, Cupressus macrocarpa, Eucalyptus nitens*

1. Introduction

Native and managed plantation forests account for one third of the land area in New Zealand and play a vital role in the country's ecological, environmental and socio-economic prosperity and sustainability. These forest ecosystems provide an ideal template to investigate and quantify the key properties and processes that drive soil nutrient dynamics and bioavailability, including phosphorus (P).

Between 1985 and 2000 almost 1 million hectares of improved grassland (i.e. grazed fertilized pasture established following clearance of native forest) was converted to short-rotation plantation forestry which was predominantly radiata pine (*Pinus radiata*). This dramatic land-use change was mainly driven by declines in the economic viability of pastoral farming in many hill and high country areas of New Zealand (Davis, 1998; Glass, 1997). In the absence of replicated long-term field experiments under contrasting land-uses, investigation of the impacts of grassland afforestation on soil properties and processes relied on paired-site comparisons at a single point in time after forest establishment (Chen *et al*., 2000; Condron *et al*., 1996b; Davis and Lang, 1991). This approach involved using transects to sample soil under adjacent grassland and recently established forest, which was effectively a form of pseudo-replication. Nonetheless, a large number of such paired-site comparison studies were carried out in New Zealand, and consistently revealed that significant changes occurred in the amounts and forms of soil P as a consequence of afforestation, resulting in enhanced mineralization of organic P and concomitant significant increases in plant-available inorganic P (Chen *et al*., 2008).

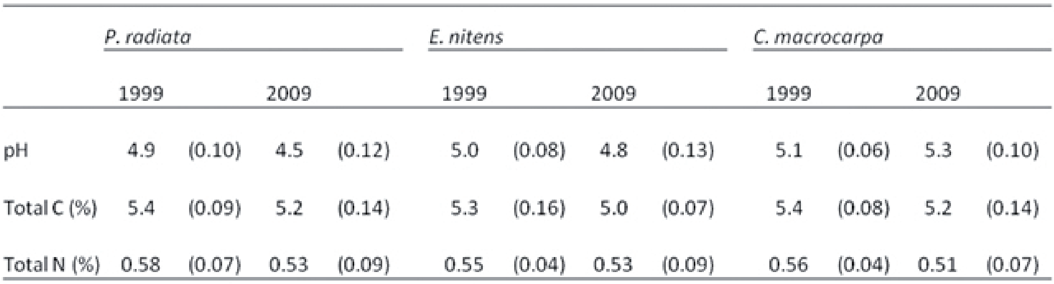
The pair-site comparison studies cited above could not show how soil P changed with time following land-use change, and assessment of changes in soil P with time following forest establishment would provide more information on the mechanisms responsible for enhanced mineralization of soil organic P. Furthermore, there is very little known about the effects of different plantation forest tree species other than radiata pine, which in turn may also provide some insight into the mechanisms responsible for the dramatic changes in soil P associated with afforestation of grassland (Chen *et al*., 2008). The main objective of this study was to determine changes in the chemical nature and availability of topsoil P over a period of 10 years following afforestation of long-established grazed hill country pasture in a replicated field experiment which included three contrasting plantation forest tree species.

2. Materials and Methods

2.1. Study site and soil sampling

Orton Bradley Park is located near Charteris Bay on Banks Peninsula, Canterbury, New Zealand (43o 39´ S, 172o 42´ E). The soil is a Takahe silt loam (Mottled FragicPallic soil, NZ classification; TypicFragiustept, USDA classification) formed in greywacke loess. The altitude is 100-150 m, mean annual rainfall is approximately 1000 mm and mean annual temperature is 12.1oC. A replicated afforestation trial was established in 1999 at Orton Bradley Park in an area that had been developed under grazed pasture with limited fertilizer inputs on a north-east facing slope at 70-150 m elevation. The trial comprised 4 replicates of three contrasting commercial plantation forest trees (radiata pine, *Cupressus macrocarpa* [macrocarpa], *Eucalyptus nitens* [eucalyptus]) arranged in a randomized block design of twelve plots each measuring 30 m x 30 m. The plots were developed under grazed pasture [macrocarpa], *Eucalyptus nitens* [eucalyptus]) arranged in a randomized block design of twelve plots each measuring 30 m x 30 m. The plots were developed under grazed pasture (*Lolium perenne and Trifoilum repens*) with low rates of superphosphate fertilizer inputs (<100 kg ha^{-1}). The plots were fenced off at trial establishment and trees were planted at 1250 stems/ha (Huang *et al.*, 2011).The plots were not grazed or fertilized since tree planting and trees were pruned and thinned in accordance with commercial silvicultural practice. Data presented in Table 1 shows values of pH, Total C and Total N in the topsoil (0-5 cm). After ten years of afforestation, the plots under *P. radiata* showed a thick litter layer with 2 to 11 cm in thickness. The amount of litter found under *E. nitens* and *C. macrocarpa* was negligible (Huang *et al*., 2011). A detailed soil sampling protocol was developed for the trial at its inception in 1999. Samples of mineral topsoil (0-5 cm) were taken using a 6 cm diameter corer from five sites randomly located near the middle of each replicate plot in spring (September-October) in 1999 and 2009. For each sampling event, soil samples were collected from each of the 4 replicate plots of each species (12 plots), and were air-dried, sieved <2 mm and stored prior to analysis.

Table 1. Soil properties in the 0-5 cm layer at the time of planting, and 10 years after afforestation. Means (± standard deviation) are based on four replicates



	P. radiata				*E. nitens*				*C. macrocarpa*			
	1999		2009		1999		2009		1999		2009	
pH	4.9	(0.10)	4.5	(0.12)	5.0	(0.08)	4.8	(0.13)	5.1	(0.06)	5.3	(0.10)
Total C (%)	5.4	(0.09)	5.2	(0.14)	5.3	(0.16)	5.0	(0.07)	5.4	(0.08)	5.2	(0.14)
Total N (%)	0.58	(0.07)	0.53	(0.09)	0.55	(0.04)	0.53	(0.09)	0.56	(0.04)	0.51	(0.07)

2.2. Soil analyses

Various forms of extractable soil inorganic P (P_i) and organic P (P_o) were determined using the sequential fractionation scheme outlined by Chen *et al.* (2000), which in turn was a modification of the method developed by Hedley *et al*. (1982). This scheme involved sequential extraction of 1g soil with 1M NaCl, 0.5M $NaHCO_3$ (pH 8.5), 0.1M NaOH (NaOH-I),1M HCl and 0.1M NaOH (NaOH-II). Labile P was represented by the sum of the most readily extracted forms of P (NaCl P_i and $NaHCO_3$ P_i). Total extractable P_i was the sum of labile P, NaOH-I Pi, HCl-P_i and NaOH-II P_i, while total extractable Po was the sum of $NaHCO_3$ P_o, NaOH-I P_o and NaOH-II P_o. Following the method proposed by O'Halloran and Cade-Menun (2008) alkaline phosphatase (from *Escherichia coli*, SIGMA, USA) enzyme hydrolysable P was determined in $NaHCO_3$ extracts of air dried <2 mm sieved 0-5cm soils collected in 1999 and 2009 under radiata pine. Detailed analyses of organic P forms using ^{31}P nuclear magnetic resonance spectroscopy (NMR) analysis of NaOH-EDTA extractable organic P from was carried out on the same soil samples collected under *Pinus radiata*, using a standard protocol described by Turner *et al.* (2003), although extracts from each of the 4 replicates from each year were combined for NMR analysis.

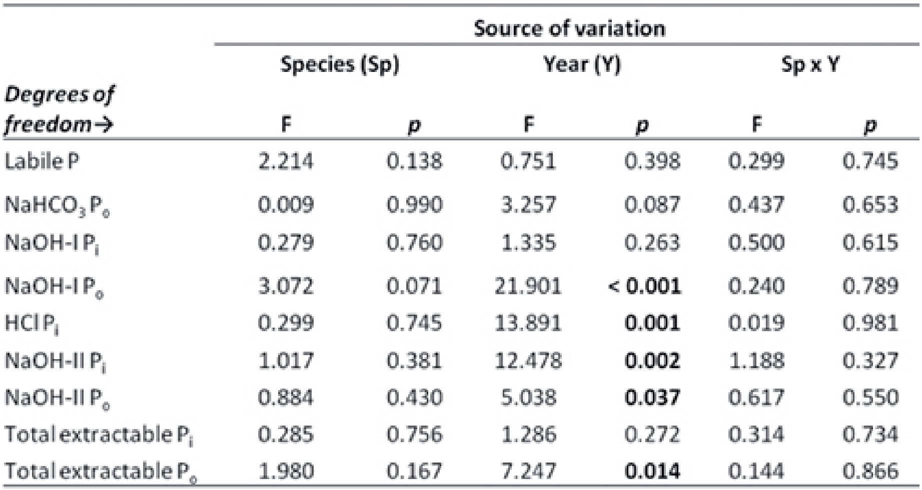
2.3. Statistical analysis

One and two way analysis of variance (ANOVA) were carried out on the data to test for the effects of sampling year (1999 and 2009) and tree species on soil P fractions. One way ANOVA was also carried out to test the temporal effects on the enzyme labile P. Where F ratios were significant treatment means were compared by least significant differences (*lsd*).

3. Results

Data presented in Table 2 shows the ANOVA F values and their levels of significance for all of the soil P fractions for the different tree species and years of sampling, together with the corresponding interaction. There were no significant differences observed between the three tree species for any of the soil P fractions, although significant differences ($p<0.05$) occurred between sampling years for NaHCO$_3$P$_o$, NaOH-IP$_o$, NaOH-II P$_o$ and total extractable P$_o$. Accordingly, data for labile P, NaOH-IP$_o$, HClP$_i$, NaOH- II P$_i$, NaOH-II P$_o$ and total extractable P$_o$ averaged across all tree species for samples taken in 1999 and 2009 for 0-5 cm soil are shown in Figure 1.

Table 2. F values with levels of significance from analyses of variance for all the soil P fractions for species and year and the interaction between species and year (Sp x Y) for 0-5cm soil. Numbers in bold show significant differences (p <0.05).



	Source of variation					
	Species (Sp)		Year (Y)		Sp x Y	
Degrees of freedom→	F	*p*	F	*p*	F	*p*
Labile P	2.214	0.138	0.751	0.398	0.299	0.745
NaHCO$_3$ P$_o$	0.009	0.990	3.257	0.087	0.437	0.653
NaOH-I P$_i$	0.279	0.760	1.335	0.263	0.500	0.615
NaOH-I P$_o$	3.072	0.071	21.901	**< 0.001**	0.240	0.789
HCl P$_i$	0.299	0.745	13.891	**0.001**	0.019	0.981
NaOH-II P$_i$	1.017	0.381	12.478	**0.002**	1.188	0.327
NaOH-II P$_o$	0.884	0.430	5.038	**0.037**	0.617	0.550
Total extractable P$_i$	0.285	0.756	1.286	0.272	0.314	0.734
Total extractable P$_o$	1.980	0.167	7.247	**0.014**	0.144	0.866

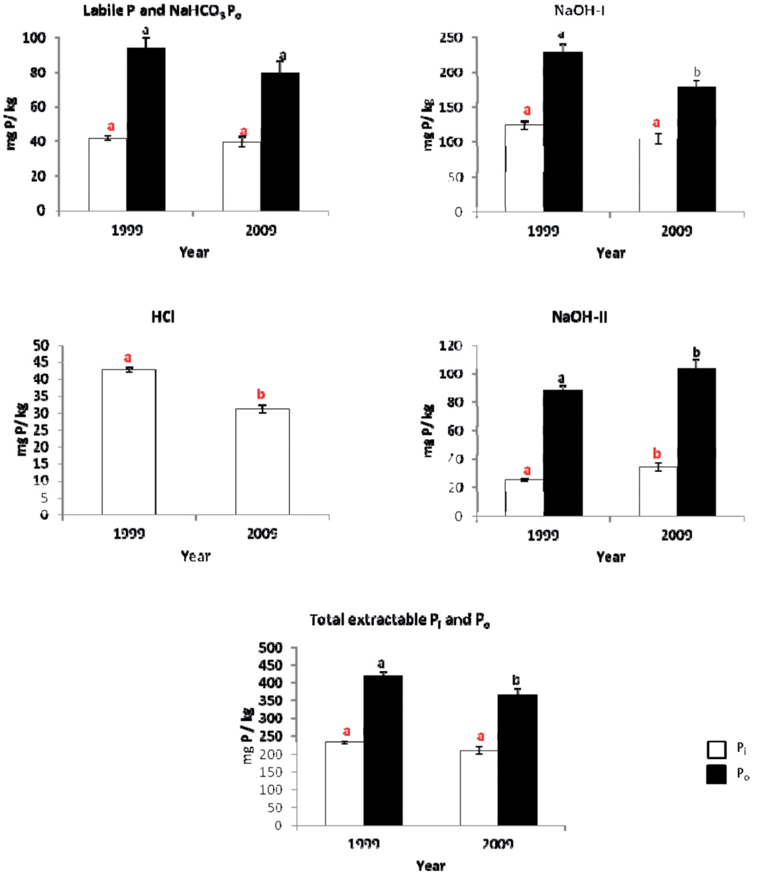


Figure 1. Mean concentrations (mgP /kg) in different P fractions determined for 0-5 cm soil sampled in 1999 and 2009 averaged over the three tree species (radiata pine, macrocarpa, eucalyptus). The error bars represent standard errors of means. Different letters indicate that means differ significantly between sampling years ($p < 0.05$).

Labile P,NaHCO$_3$ P$_o$, NaOH I-P$_i$ and total extractable P$_i$ did not show significant changes among years, and while concentrations of NaOH-I P$_o$ and HClP$_i$ decreased significantly between 1999 and 2009, NaOH-II P$_i$ and NaOH-II P$_o$ increased significantly between 1999 and 2009. Total extractable P$_o$ decreased significantly between 1999 and 2009. Alkaline phosphatase hydrolysable P decreased significantly between 1999 and 2009 from 70 to 50 mgP/kg (Figure 2).

Table 3 shows the concentration of P compounds determined by ^{31}P NMR in extracts of 0-5 cm soils under radiata pine sampled in 1999 and 2009. The sum of all phosphate monoesters accounted for 92-96% of the P$_o$ compounds detected, and decreased with time from 408 mg P/kg in 1999 to 343 mg P/kg in 2009. This was mainly due to decreases in the "other monoester" fraction, while the only other change noted was a fourfold increase in phosphonate-P between 1999 and 2009.

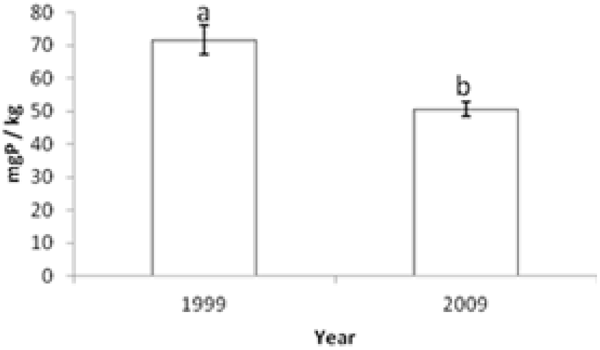


Figure 2. Mean concentrations of alkaline phosphatase hydrolysable P (mgP /kg) determined for $NaHCO_3$ extracts from 0-5cm soil sampled under radiata pine in 1999, 2004 and 2009. The error bars represent standard errors of means. Different letters indicate that means differ significantly between sampling years ($p < 0.05$).

Table 3. Concentrations (mgP /kg) of different organic P compounds determined by ^{31}P NMR analysis of NaOH-EDTA extracts of 0-5 cm soils sampled under radiata pine in 1999 and 2009. Values in parentheses are the proportion (%) of the total P extracted by NaOH-EDTA.

Year	Organic P (mgP /kg)					
	Phosphate monoesters			Phosphate diesters		Phosphonates
	myo-IP_6	*scyllo*-IP_6	Other	DNA	Phospholipids	
1999	56 (11)	20 (4)	332 (49)	6 (1)	5(1)	5 (1)
2009	57 (12)	29 (6)	257 (36)	8 (2)	5 (1)	20 (4)

4. Discussion

It was hypothesised that the quantities and nature of soil P would change during the 10 years following afforestation and that any changes in soil P would be affected by tree species. However, the three tree species had a very similar overall impact on the amounts and forms of P determined over the first 10 years following establishment. This was particularly surprising given the different growth rates of the three tree species (Table 5), which were clearly demonstrated in their different impact on the grassland understorey. After 10 years (2009), complete canopy closure was evident in the *P. radiata* plots and the grassland understory had been effectively buried under a combination of needle litter and course wood debris from thinning and pruning (Figure 3) (Figure 4). On the other hand, there was no grassland understory evident under *E. nitens*, which was probably attributable to competition for soil moisture by the trees. Over the same period, the grassland understory persisted under *C. macrocarpa*, which probably reflected slower growth rates compared with *P. radiata* and *E. nitens*. The fact that NaOH-I P_o and total extractable P_o decreased significantly between 1999 and 2009 indicated that forest establishment had resulted in net mineralization of soil organic P. This is consistent with previous paired site comparison studies which showed that significant mineralization of soil organic P occurred 10-20 years after the change in land-use (Chen *et al*., 2000; Condron *et al*., 1996a; Davis and Lang, 1991; Hawke and O'Connor, 1993)

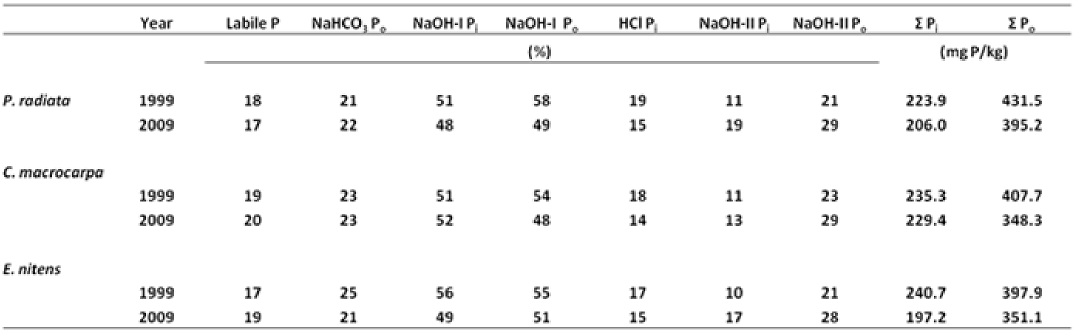
Figure 3. Status of the understory under a) *Pinus radiata*, b) *Cupressus macrocarpa* and c) *Eucalyptus nitens* in 1999.

Figure 4. Status of the understory under a) *Pinus radiata*, b)*Cupressus macrocarpa* and c) *Eucalyptus nitens* in 2009.

It is also possible that the significant decrease observed between 1999 and 2009 could be associated with bulk density changes promoted by the growth of tree roots, but unfortunately there is not data available to be compared between those years. Another explanation is that the organic forms of P were relocated in a non-extractable pool that was not observed through the fractionation method used here, however, the percentage of the organic fractions with respect to the total extractable Po showed a similar trend than that for concentrations (Table 4). Differences associated with soil sampling between years that altered the amount of total P would also have explained this behaviour. Phosphorus uptake by newly established trees may at least partly explain the enhanced mineralization of soil organic P, although it was surprising that this was similar under all three tree species despite differences in mycorrhizal associations, root physiology and growth rates. In particular, it was expected that differences in mycorrhizae between *P. radiata* (ectomycorrhizae [EM]), *C. macrocarpa* (vesicular-arbuscular mycorrhizae [VAM]) and *E. nitens* (EM/VAM) would result in different impacts on soil P. Previous studies have showed that short-term mineralization of rhizosphere soil organic P was significantly greater for radiata pine compared with perennial ryegrass (*Lolium perenne*) which has VAM (Chen *et al.*, 2002). The fact that soil organic P decreases were similar under all three tree species suggests that EM and VAM were equally effective at mobilising organic P by mineralisation, which is contrary to current understanding of the role of different mycorrhizal types in P acquisition (Chen *et al.*, 2002; Lambers *et al.*, 2008; Read and Perez-Moreno, 2003; Smith *et al.*, 2008; Smith and Read, 2008) although it is consistent with recent findings from tropical montane tree species (Steidinger *et al.*, 2015). Tree biomass measurements taken in 2009 showed that standing stem volumes (m^3/ha) were greater for *P. radiata* (211) and *E. nitens* (165) compared with *C. macrocarpa* (109) (Table 5). There was no corresponding data available for P content of the tree biomass, but the fact that changes in soil P were similar for all three tree species may indicate comparable quantities of biomass P uptake.

It is also possible that changes in P cycling associated with the cessation of grazing following tree planting could have contributed to the immediate significant decline in soil organic P. This in turn may be attributed to changes in the quantities of P being returned to soil and its consequent impacts on the balance between the respective rates of organic P inputs and turnover, especially since the $NaHCO_3$ and NaOH-I P fractions are generally considered to represent the more labile pools of soil organic P (Condron *et al*., 2005). This suggests that the quantity and turnover of organic P in soil may have been reduced following the cessation of grazing. Grazing animals play a very important role in the process of P cycling in pasture ecosystems since 95% of the P taken up by plants is returned to the soil in the form of feces and root residues (Haynes and Williams, 1993; Kemp *et al*., 2000), which in turn enhances biological cycling of P (Nash *et al*., 2014). Simpson *et al*. (2012) investigated the relative solubility of soil P under contrasting mowing regimes (no mowing, clippings removed, clippings left) which had been maintained in a field trial for 15 years. In approximate terms, the regime where clippings were left was equivalent to grazing while no mowing would be equivalent the situation at Orton Bradley Park following the cessation of grazing when trees were planted. They showed that biological and biochemical processes associated with enhanced mineralization of organic P were significantly greater in soils where were clipping left compared to no mowing, which reflected increased organic matter inputs under the clippings return regime.

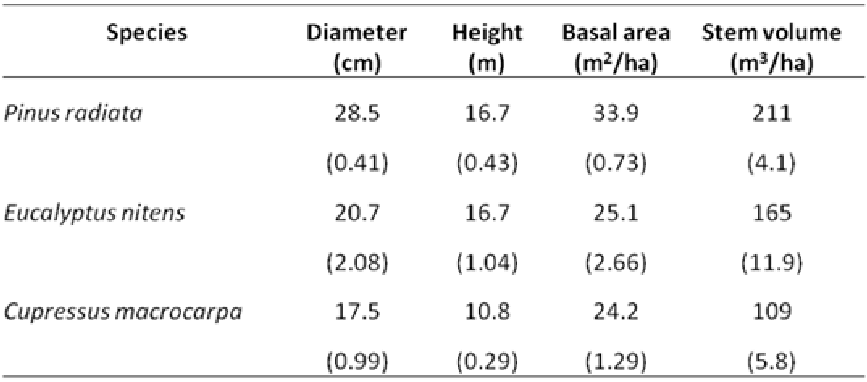
Table 4. Mean percentage (%) of labile P, $NaHCO_3$ P_o, NaOH-I P_i, NaOH-I P_o, HCl P_i, NaOH-II P_i, and NaOH-II P_o and mean concentration (mg P/kg) of total extractable P_i and P_o fractions under *P. radiata*, *C. macrocarpa* and *E. nitens* in 1999 and 2009.



	Year	Labile P	$NaHCO_3$ P_o	NaOH-I P_i	NaOH-I P_o	HCl P_i	NaOH-II P_i	NaOH-II P_o	Σ P_i	Σ P_o
		(%)							(mg P/kg)	
P. radiata	1999	18	21	51	58	19	11	21	223.9	431.5
	2009	17	22	48	49	15	19	29	206.0	395.2
C. macrocarpa										
	1999	19	23	51	54	18	11	23	235.3	407.7
	2009	20	23	52	48	14	13	29	229.4	348.3
E. nitens										
	1999	17	25	56	55	17	10	21	240.7	397.9
	2009	19	21	49	51	15	17	28	197.2	351.1

*Labile P is the sum of inorganic and organic P in NaCl; **ΣP_i is the sum of inorganic P in NaCl, $NaHCO_3$, NaOH-I, HCl, and NaOH-II; ***ΣP_o is the sum of organic P in NaCl, $NaHCO_3$, NaOH-I and NaOH-II, **** ΣP is the sum of ΣPi + ΣP_o.

Table 5. Comparative growth of the three tree species determined 10 years after planting (2009) (standard errors are shown in parenthesis).



Species	Diameter (cm)	Height (m)	Basal area (m^2/ha)	Stem volume (m^3/ha)
Pinus radiata	28.5	16.7	33.9	211
	(0.41)	(0.43)	(0.73)	(4.1)
Eucalyptus nitens	20.7	16.7	25.1	165
	(2.08)	(1.04)	(2.66)	(11.9)
Cupressus macrocarpa	17.5	10.8	24.2	109
	(0.99)	(0.29)	(1.29)	(5.8)

In addition, studies of long-term changes in soil P under grazed pasture in New Zealand and elsewhere have clearly and consistently demonstrated that concentrations of soil organic P increased significantly with time. This was attributed to elevated rates of organic matter and P inputs and turnover compared with soils under unimproved and native vegetation (Tiessen and Condron, 2005; Condron *et al.*, 2005; McDowell and Condron, 2012).

Previous paired-site studies clearly showed that both the size and activity of the soil microbial biomass, together with phosphatase enzyme activities, were consistently and significantly lower under forest compared with adjacent grassland (Chen *et al*., 2003; Chen *et al.*, 2008). He *et al*. (1997) concluded that fluctuations in the size and turnover of soil microbial biomass were very important to control the turnover of C, N and P, which in turn regulate plant availability of P. Chen *et al.* (2003) reported that concentrations of microbial biomass P were higher in grasslands compared to adjacent forest and concluded that it was mainly affected by returns of grass root litter in the first and by litterfall accumulation in the second. Increases in non-labile NaOH-II P_o that occurred between 1999 and 2009 may indicate a shift towards more recalcitrant organic matter in soil reflecting increased inputs of organic matter and P from tree residues and roots. Huang *et al*. (2011) analysed soils taken from the Orton Bradley Park trial over the same period (1999-2009) to quantify changes in soil C mass in light and heavy fractions. Although they found that C mass did not show significant differences in the soil heavy fraction, C mass in the light fraction displayed a similar pattern to that found in this study for NaOH-II P_o (most recalcitrant) by increasing its concentration between 1999 and 2009. They attributed the increased of C mass between year 1999 and 2009 to C inputs from tree residues. Condron and Newman (1998) used ^{13}C-NMR spectroscopy to investigate the chemical nature of the soil organic C under grassland and adjacent recently established coniferous forests (10-17 years). They found that under grassland the soil organic C was closely related to plant fragments and partially degraded residues derived from grass roots, while soil organic C was more recalcitrant under forest These changes in soil organic C are consistent with the increases in the recalcitrant NaOH-II Po fraction that was observed between 1999 and 2009. As the turnover of C in a system increases through plant addition, the biological processes of mineralization determine the availability of P (Bünemann and Condron, 2007; Richardson *et al.*, 2004). Furthermore, labile organic P could be mineralised by greater microbial activity to meet increasing plant demand in the early stages of tree establishment.

Specific results determined for changes in enzyme hydrolysable P and organic P under *P. radiata* over 10 years provided some important additional perspective on the nature of changes that occurred following tree planting. The fact that alkaline phosphatase hydrolysable P decreased significantly between 1999 and 2009, indicates that while the solubility of organic P in $NaHCO_3$ increased between 1999 and 2009, its susceptibility to enzyme mineralisation (i.e. its lability) actually decreased. The latter may indicate a shift towards more recalcitrant soil organic matter between 1999 and 2009 as discussed above. However, differences in soil organic P solubility and enzyme lability also highlights limitations in assigning relative lability/stability based on ease of extraction from soil (Condron and Newman, 2011). The NMR data showed that monoester forms of organic P decreased as a consequence of afforestation of grassland , which is consistent with studies which compared changes in soil organic P under radiata pine-and perennial ryegrass (Turner *et al.*, 2005). However, the decreases in organic P determined in the present study were confined to “other monoesters”, while the other studies noted significant depletion of *scyllo* and myo inositol hexakisphosphates. This may be at least partly related to the fact that the comparative studies cited above were carried out on soils from a 10 month glasshouse pot trial, as opposed to changes determined over 10 years under field conditions in the present study. The occurrence of phosphonates P in soil is linked to acidity (Condron *et al*., 2005), and the increase observed between 1999 and 2009 may be at least partly be attributed to a decline in soil pH on the trial from 4.9 in 1999 to 4.4-4.5 in 2009. This pH decline under trees may also account for the significant decrease in HCl P_i that occurred between 1999 and 2009 (Figure 1).

5. Conclusions

The findings of this study confirmed that significant net mineralisation of soil organic P occurred during the 10years following tree planting, but that this was similar under the three contrasting tree species despite differences in growth and mycorrhizal association. The latter suggested that EM and AM were equally effective at mineralizing soil organic P, and the observed changes in soil P could be attributed to tree growth and P uptake irrespective of species. However, reductions in P inputs and organic P turnover associated with the cessation of grazing may have also contributed to enhanced soil organic P mineralisation following forest establishment. In addition, changes in the nature of organic P determined between 0-10 years after establishment indicated that organic matter inputs and turnover associated with tree growth were having an increasing influence on soil P dynamics with time.

Acknowledgements

Funding for establishment and maintenance of the field trial at Orton Bradley Park was provided by the C Alma Baker Trust, the Brian Mason Scientific and Technical Trust and Lincoln University. The continued support provided by the Trustees of Orton Bradley Park is greatly appreciated. ICV was supported by a Lincoln University Doctoral scholarship.

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