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John T. Scott · Leo M. Condron

Dynamics and availability of phosphorus in the rhizosphere of a temperate silvopastoral system

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Abstract A field rhizosphere study was carried out over a period of 12 months on a 6-year-old silvopastoral trial in New Zealand. The trial comprised radiata pine (*Pinus radiata*) with lucerne (*Medicago sativa*) and perennial ryegrass (*Lolium perenne*) understoreys. The study was initiated because of the unique interrelationships between roots in silvopastoral systems and a paucity of understanding about the processes involved in phosphorus (P) dynamics in temperate silvopastoral systems. Improving our understanding in this area has important implications for nutrient management in silvopastoral systems. Rhizosphere soils were analysed to determine inorganic (Pi) and organic (Po) P fractions, macroporous resin Pi and Po, phosphatase enzyme activity, microbial biomass carbon and pH. Concentrations of labile Pi were consistently greater and Po lower in tree rhizosphere soil compared to the companion understorey, indicating that radiata pine when grown with a productive understorey mineralised Po to a greater extent than either understorey species. Tree rhizosphere soil from under lucerne and lucerne rhizosphere soil contained the lowest concentrations of total Pi and Po compared with tree under ryegrass and ryegrass rhizosphere soils. This was partly attributed to higher levels of phosphatase enzyme activity in the lucerne rhizosphere soils. The results suggest the combination of lucerne with radiata pine may enhance greater utilisation of soil P, although this requires further investigation. Lower levels of labile Po, and higher levels of labile Pi and phosphatase enzyme activity, were determined in tree and understorey lucerne and ryegrass rhizosphere soils in spring compared with autumn. This data confirmed that overall rates of soil organic P mineralisation are greatest in spring.

Keywords Phosphorus fractions · Resin P · *Pinus radiata* · *Medicago sativa* · *Lolium perenne*

J. T. Scott · L. M. Condron (✉)
Soil, Plant and Ecological Sciences Division,
Lincoln University,
PO Box 84, Canterbury 8150, New Zealand
e-mail: CONDRONL@lincoln.ac.nz

Introduction

The use of trees in an agricultural context has occurred for at least 1,000 years (Brookfield and Padoch 1994) with many systems resulting from a variety of tree and agricultural activities. In New Zealand, as net economic returns from some forms of pastoral agriculture have declined, 440,000 ha of grassland and scrub were planted between 1990 and 2000 with exotic forest species, primarily radiata pine (*Pinus radiata* (D. Don)) (Davis and Condron 2002). The combination of conifer species and grazed pasture, referred to as silvopasture or pastoral agroforestry, comprise part of this area and have been considered, under certain conditions, as viable productive systems (Knowles 1991). In New Zealand, the main tree species grown has been radiata pine, with perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) the predominant understorey pasture species (Mead 1995). The economic importance of temperate silvopastoral systems necessitates investigation of nutrient dynamics that are peculiar to such systems.

Many workers have found species and even varietal differences in the utilisation of inorganic (Pi) and organic (Po) soil phosphorus (P) (Helal 1990; Tadano et al. 1993; Davis 1995; Tyler and Ström 1995; Condron et al. 1996; Trolove et al. 1996). For example Davis (1995) and Condron et al. (1996) demonstrated that radiata pine actively mineralised Po and increased plant available Pi compared with cocksfoot (*Dactylus glomerata*). Conversely, under newly established grass-clover pasture, soil Po has been found to increase (Magid et al. 1996). In silvopastoral systems in which over and understorey species are combined, P availability for one species can be affected by the other. Gillespie and Pope (1989) found that P uptake by black walnut (*Juglans nigra*) was greater when grown with lucerne (*Medicago sativa*) than with cocksfoot. Consequently the understorey species grown in a silvopastoral system may affect the forms and availability of soil P with important implications for nutrient management.

Although roots of the same species generally avoid contact, intertwining of different species has been observed, especially legumes and non-legumes (Gardner and Boundy 1983). Mycorrhizal hyphae links between species have also been reported (Newman 1988), which can result in nutrient transfer (Francis et al. 1986; Haystead et al. 1988; Hamel et al. 1991). Agroforestry systems alter the microclimate through changes in light and water infiltration. This affects the respective activity of understorey species (Hawke and Wedderburn 1994; Yunusa et al. 1995; Hawke and Knowles 1997), which in turn may affect root activity of the overstorey and the degree of root interaction between species. Silvopastoral systems represent important economic farm enterprises with possibly unique interactions between the roots of the companion species. Because the most chemically, biochemically and biologically active microsite in soil is found in the rhizosphere, no more than a few millimetres from plant roots (Tarafdar and Jungk 1987; Bowen and Rovira 1991; Jungk et al. 1993; Chen et al. 2002), to further our understanding of soil P dynamics in silvopastoral systems requires investigation of rhizosphere processes in the field. The main objective of this study was to investigate the influence of a *Pinus radiata* overstorey and legume- (lucerne) and grass- (ryegrass) based pasture understoreys on the forms and availability of P in the rhizosphere over a 12-month period.

Materials and methods

Field site

This study was carried out on the Lincoln University experimental silvopastoral site (Mead et al. 1993; Chang et al. 2002). It was established in 1990 to investigate competition between radiata pine and a range of pasture species in a temperate sub-humid climate. The understorey treatments used in this study were bareground (vegetation was prevented by herbicide spraying), lucerne and ryegrass-clover pasture. Initial soil sample (0–15 cm) results taken at establishment (1990) showed pH 6·0, Olsen P of 17 μg ml^{-1}, 0.88 $cmol_c$ K kg^{-1} ; 7.2 $cmol_c$ Ca kg^{-1}, 0.83 $cmol_c$ Mg kg^{-1} and 0.17 $cmol_c$ Na kg^{-1} (Mead and Mansur 1993). No fertiliser was applied to the experimental site during or after establishment.

Soil sampling and sample preparation

Rhizosphere and bulk (non-rhizosphere) soil was collected following the method of Teng and Timmer (1995), from the north side of tree rows in combination with bareground, lucerne and ryegrass at 0- to 20-cm depth. After a gentle shake, soil adhering to roots was considered rhizosphere soil and peds devoid of roots, after having their surfaces shaved to remove any possible soil that had been in contact with roots, were deemed bulk soil. One tree from each plot was selected and rhizosphere and bulk soil was collected from a 30-cm wide band from 0.5–1.5 m north of the tree. The eight different soil classes collected were referred to as:

- bulk soil from under bareground—bareground bulk (Bb)
- tree rhizosphere soil from under bareground—bareground tree rhizosphere (BTr)
- bulk soil from under lucerne—lucerne bulk (Lb)
- tree rhizosphere soil from under lucerne—lucerne tree rhizosphere (LTr)
- lucerne rhizosphere soil (Lr)
- bulk soil from under ryegrass—ryegrass bulk (Rb)
- tree rhizosphere soil from under ryegrass—ryegrass tree rhizosphere (RTr)
- ryegrass rhizosphere soil (Rr).

Soil samples were taken in May 1996 (autumn), August 1996 (winter), November 1996 (spring), and January 1997 (summer). Roots with rhizosphere soil attached were placed in a plastic bag. When sampling was complete the bag was placed on chipped ice. On returning to the laboratory, field-moist soil was carefully removed from the roots by hand, then 2-mm sieved and returned to the refrigerator until further analysis. Soil used for P fractionation was air-dried and finely ground (<150 mm).

Soil analyses

Field-moist soil from all four seasons was analysed for acid (PMEac) and alkaline (PMEal) phosphomonoesterase enzyme activity, phosphodiesterase activity (PDE), and microbial biomass carbon (C) (Cmic) while pH was determined from 2-mm air-dried soil (soil:water ratio 1:2.5). Microbial biomass C was determined by the fumigation-extraction method described by Vance et al. (1987) using a conversion factor (K*c*) of 0.45. PMEac and PMEal activities were measured according to the method of Tabatabai and Bremner (1969) at near ambient soil pH. PDE activity was measured by the method of Browman and Tabatabai (1978). The substrate used in this analysis was *bis*(p-nitrophenyl) phosphate (Sigma, N1256).

Soils collected in May and November were analysed for macroporous anion exchange resin (Lewatit MP500A in HCO_3^- form) Pi and Po and detailed P fractionation was carried out. Resin soil P (total, inorganic and organic) was determined by the method of Rubæk and Sibbesen (1993). Resin Pi in eluents was determined by the method of Murphy and Riley (1962) while total P was by perchloric ($HClO_4$) and sulfuric acid (H_2SO_4) digestion. The difference between total resin P and resin Pi was considered resin Po.

The soil P fractionation procedure was adapted from Condron et al. (1996). Forms of soil Pi and Po were determined by sequential extraction of 1 g soil with 1 M NH_4Cl (discarded), 0.5 M $NaHCO_3$ (pH 8.5; BPi, BPo), 0.1 M NaOH (N1Pi, N1Po), 1 M HCl (HPi) and 0.1 M NaOH (N2Pi, N2Po). The Pi concentration was determined in extracts after acid precipitation of organic matter, while total P in each extract was determined by persulfate oxidation. The concentration of Po in each extract was calculated by the difference between total P and Pi (Tiessen and Moir 1993). Total P (TP) was determined by nitric perchloric acid digestion (Olsen and Sommers 1982). The difference between total extracted P (TEP) and total P by digestion (TP) was considered residual P (Res-P).

Statistical analysis

In each of the four seasons pH, PMEac, PMEal, PDE and Cmic ANOVA was performed using Genstat (VSN International, Oxford, United Kingdom) and a least significant difference (*LSD*) was determined to compare treatment means (Saville 1990). Since repeated measures analysis can be criticised because of the within-plot correlations, it was decided to use summary statistics, defined on a per-plot basis, to examine differences between seasons. For example, to examine the difference in PMEac activity between the months May and August (Aug), the plot level summary statistic was defined as May–Aug; this summary statistic was then subjected to analysis of variance with eight treatments (Bb, BTr, Lb, LTr, Lr, Rb, RTr, Rr) and three replicates; a least significant difference ($LSD_{0.05}$) at the 5% level was then calculated to compare the difference in the summary statistic (May–Aug) between rhizosphere and bulk soils. In addition, to determine if the difference between one month and another (e.g. May and August) was significant, i.e. different from zero, a statistic referred to as the least

significant effect (*LSE*) was calculated (Hurrel et al. 2001). The *LSE* is the half-length of the 95% confidence interval. Therefore, if the difference in PMEac activity between two months was greater than its *LSE*, the difference was significant. This *LSE* was calculated as an average over all eight rhizosphere soils and for each individual rhizosphere soil. Rhizosphere and bulk soil main effects were determined, and resin-extracted P and P fractionation in the two months, May (autumn) and November (spring), were also analysed by ANOVA and a *LSD* was determined to compare treatment means.

Results and discussion

The important contribution to nutrient availability of the rhizosphere to the plants was clearly evident with generally all parameters being greater in rhizosphere than bulk soil (Figs. 1, 2). This is consistent with the findings of many workers (McLaughlin et al. 1987; Bowen and Rovira 1991; Chen et al. 2002). Microbial biomass C (Fig. 1) was consistently lower in bulk soil compared with rhizosphere soil and was up to 4 times greater in the rhizosphere. Because this is consistent with many findings that root-derived organic material enhances microbial growth and activity (Bowen and Rovira 1991), the categorisation and collection of bulk and rhizosphere soil collected in this study appears credible. In addition the activity of all three phosphatase enzymes (Fig. 2) was much lower in the bulk soil than in the rhizosphere soil, and this was consistent with previous findings (Tarafdar and Jungk 1987; Häussling and Marschner 1989; Chen et al. 2002). Only micro-organisms produce PMEal (Tabatabai 1994) and its activity in the different soils reflected Cmic levels. Furthermore, acid and alkaline phosphatase enzyme activities were determined at near ambient soil

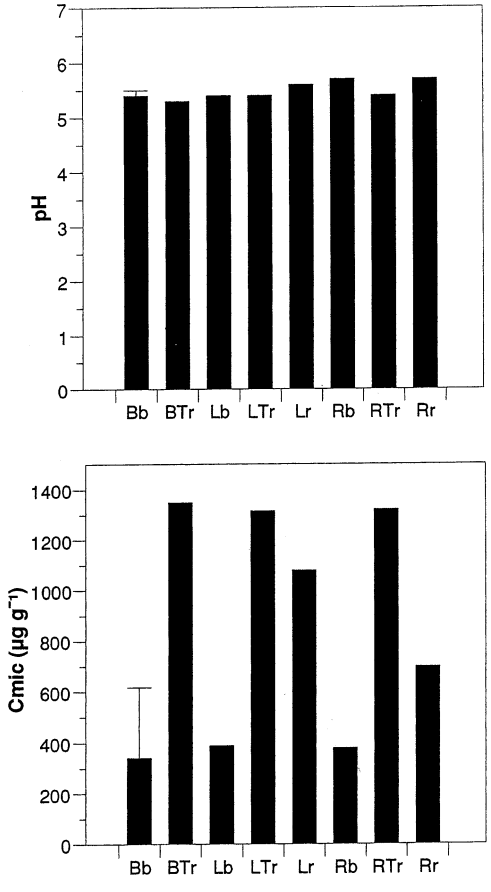

Fig. 1 Soil pH and microbial biomass C (Cmic) determined in rhizosphere and bulk soil over the four seasons from May 1996 to January 1997. The *error bars* represent the *LSD* at the 5% level

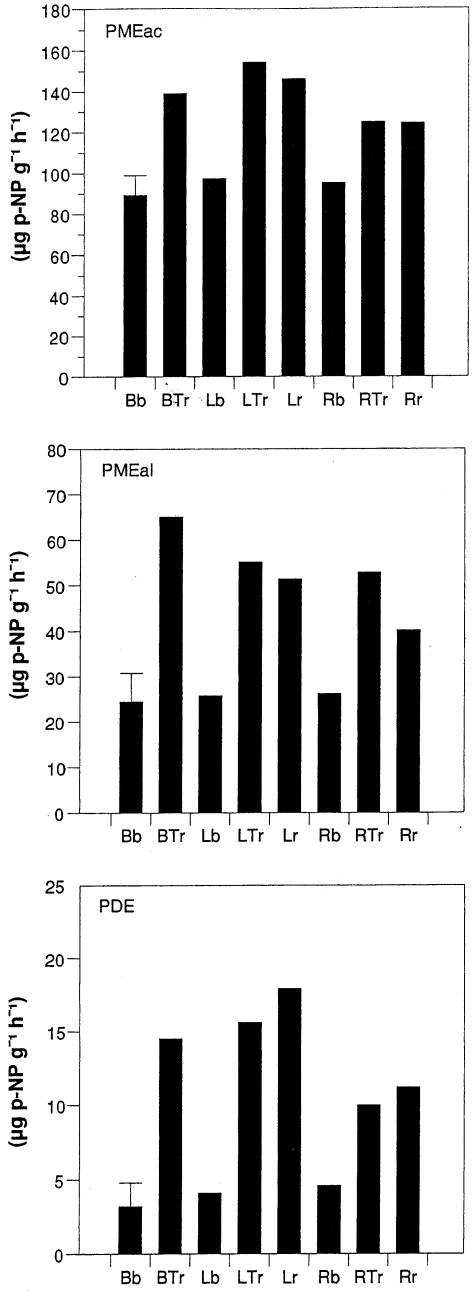

Fig. 2 Acid (*PMEac*) and alkaline (*PMEal*) phosphomonoesterase activity and phosphodiesterase (*PDE*) activity (µg p-nitrophenyl phosphate released per hour) determined in rhizosphere and bulk soils over the four seasons from May 1996 to January1997. The *error bars* represent the *LSD* at the 5% level

Table 1 Soil P fractions (μg P g^{-1}) determined in rhizosphere and bulk soils over two sampling dates, May 1996 (autumn) and November 1996 (spring)

	BPi[b]	BPo	N1Pi	N1Po	HPi	N2Pi	N2Po	TEPi	TEPo	Res-P	TP
Bb[a]	39.0	36.8	125.3	305.3	95.0	20.0	27.0	279	369	58	706
BTr	51.0	36.3	127.7	305.4	95.8	19.6	32.1	294	374	23	691
Lb	19.4	41.7	97.5	292.8	94.3	20.6	28.1	232	363	58	652
LTr	35.4	39.1	107.2	280.7	89.0	19.5	32.9	251	353	86	690
Lr	29.6	43.2	107.6	298.0	92.3	20.0	31.7	250	373	77	700
Rb	33.5	36.8	134.2	295.5	112.1	21.4	28.0	301	360	60	722
RTr	62.0	28.2	144.8	340.3	108.8	20.9	30.2	337	399	35	770
Rr	48.3	35.8	144.1	320.3	110.7	21.3	30.5	324	387	74	785
$LSD_{0.05}$	8.1	5.9	15.0	38.7	17.6	2.0	3.7	37	43	61	79

[a] Soil samples: *Bb* bareground bulk, *BTr* bareground tree rhizoshere, *Lb* lucerne bulk, *LTr* lucerne tree rhizosphere, *Lr* lucerne rhizosphere, *Rb* ryegrass bulk, *RTr* ryegrass tree rhizosphere, *Rr* ryegrass rhizosphere
[b] P fractions: *Pi* inorganic P, *Po* organic P; sequentially extracted with: *B* NaHCO3, *N1* NaOH, *H* HCl, *N2* NaOH; *TEP* total extracted P, *TP* total P by acid digestion, *Res-P* residual P (difference between TP and TEP)

Table 2 Macroporous anion exchange resin-extracted Pi and Po (μg P g^{-1}) determined in rhizosphere and bulk soils at two sampling dates, May 1996 (autumn) and November 1996 (spring). The LSD at the 5% level is represented by $LSD_{0.05}$ and *LSD same month* is the LSD to compare soils in the same month

Season	Soil[a]	Resin Pi	Resin Po
May (autumn)	Bb	19.9	16.6
	BTr	25.3	20.9
	Lb	10.0	10.8
	LTr	18.4	15.8
	Lr	13.4	13.4
	Rb	22.1	13.3
	RTr	29.4	23.4
	Rr	21.7	27.4
November (spring)	Bb	20.7	4.8
	BTr	39.0	14.0
	Lb	10.4	5.2
	LTr	24.8	7.3
	Lr	20.5	9.0
	Rb	14.0	4.4
	RTr	43.0	15.0
	Rr	31.6	8.1
$LSD_{0.05}$		9.8	16.2
LSD same month		7.6	8.5

[a] For explanation of soil abbreviations see Table 1

pH that may have more clearly indicated field activity than at an optimum pH.

A detailed investigation of soil P by sequential extraction and macroporous anion exchange resin was performed using the May (autumn) and November (spring) soil to determine if the forms and availability of rhizosphere soil P were affected by season and species. All Pi fractions (BPi, N1Pi, HPi, TEPi and resin Pi), except N2Pi, were consistently lower in lucerne rhizosphere soil and tree rhizosphere soil under lucerne than ryegrass (Tables 1, 2). Tree rhizosphere BPi, N1Pi and TEPi under lucerne were also lower than the tree rhizosphere soil in bareground. Consequently Pi fractions were generally highest in ryegrass rhizosphere soils. Lower concentrations of all Pi fractions and resin Pi in all lucerne soils may be related to greater P uptake. Root sequestration of P and low mobility of P in response to concentration gradients may be applicable (Teng and Timmer 1995). In the first 3 years of the trial, until February 1993, there was no difference in the dry matter production of understorey species (Pollock et al. 1994). However, between 1994 and 1996, lucerne dry matter was about 50% greater than ryegrass (Chang et al. 1999). Although tree heights and diameters in lucerne were less than in ryegrass the differences were only about 5%. Consequently, the difference in tree biomass between the trees in lucerne and ryegrass was not significant.

Although HPi values in all lucerne soils were lower than in the corresponding ryegrass soils they were not different from bareground soils, suggesting tree and lucerne rhizosphere processes may have some similarities in solubising Ca-P. Both pines and lucerne have been shown to acidify the rhizosphere by anion/cation imbalances and exudation of organic anions (Smith 1976; Malajczuk and Cromack 1982; Lipton et al. 1987; Gillespie and Pope 1989; Alfredsson et al. 1998; Monaghan et al. 1998). Chen et al. (2002) did not find a decline in acid soluble P in the rhizosphere of *Pinus radiata* or ryegrass. Ryegrass usually increases soil pH, as shown in this study, although this does not necessarily prevent depletion of acid-soluble P by grasses (Armstrong and Helyar 1992). Ryegrass may not have been able to reduce the Pi concentration enough in the soil solution below the solubility product of the Ca-P compounds in this soil to make these compounds available. This could be because available P levels in this soil were relatively high (Bieleski 1976). If the soil was very low in available P, ryegrass may have reduced Ca-P.

The similarity between Pi concentrations in tree and understorey rhizosphere soils under the corresponding understoreys indicates that there was interaction between the trees and the respective understoreys. In addition, under ryegrass, tree rhizosphere BPi, N1Pi, HPi and consequently TEPi were greater than tree rhizosphere soil in lucerne and bareground. Lucerne roots were observed to entangle and wrap around tree roots and therefore lucerne rhizosphere processes possibly influenced tree rhizosphere soil. Gardner and Boundy (1983) noted that the roots of legume and non-legume plants tend to

intermingle. They found that wheat grown with lupins had access to more P and N than when grown in monoculture. It is likely that N availability was greater in both bareground and lucerne tree rhizosphere soils, enabling greater phosphatase activity (Fig. 2; Olander and Vitousek 2000), and greater plant production and P uptake. The trees growing in bareground showed the poor form that results from ample soil N (Will and Hodgkiss 1977). Ryegrass has a high fine-root density (Chen et al. 2002) and comparing rhizosphere soil per se may not give a true indication of what is happening on a volume basis, as ryegrass may have more rhizosphere soil per unit volume of soil. Tree rhizosphere soil may have been influenced to a significant degree by ryegrass rhizosphere processes. However, most ryegrass roots were confined to the surface 0–10 mm (Jackman 1964; Gautam 1998) and the tree roots were generally below this depth (Gautam 1998). Soil moisture content can have a significant effect on Cmic (Díaz-Raviña et al. 1995) and consequently enzyme activity and nutrient availability. However soil moisture content where the sampling occurred was not dissimilar between the forages, although under bareground it was greater (Yunusa et al. 1995). The similarity between tree and understorey Pi concentrations may also be partly attributed to mycorrhizal hyphae, from both tree (ectomycorrhizae) and understoreys (vesicular-arbuscular mycorrhizae), influencing the respective rhizospheres of each species. Ectomycorrhizal hyphae extend several metres from roots (Finlay and Read 1986) and mobilise various forms of soil P (Dighton 1983; Bolan et al. 1987; Marschner and Dell 1994; Joner et al. 1995). Therefore the spatial separation of tree and forage roots may not be an impediment. In addition, hyphal links between species, resulting in nutrient transfer, have been observed (Haystead et al. 1988; Newman 1988; Hamel et al. 1991).

Under ryegrass, BPo was the lowest in both rhizosphere soils (Fig. 3), even though enzyme levels (Fig. 2) were generally lowest. However N1Po in tree rhizosphere soil under ryegrass was the greatest (Table 1). Consequently TEPo in tree rhizosphere soil under lucerne, which was less than tree rhizosphere soil under ryegrass, was the only difference in TEPo between soils (Table 1). The relatively high Pi levels in the soil may have reduced the need for significant depletion of Po. The site had been used for intensive arable cropping prior to the establishment of the silvopastoral system and there had been a general build-up of TEPo and soil C since establishment, not only under pasture areas less affected by tree roots but also directly under the trees with minimal pasture influence. In a rhizosphere study, Chen et al. (2002) found BPo accumulation under ryegrass and *Pinus radiata* and, although no change occurred in N1Po under ryegrass, N1Po was depleted under the trees. Their study did not involve a combination of the two species. The results in the present study may be attributable to the mutual effect of each species on the other, as outlined above. In addition, the site in the present study reflected the characteristics observed in permanent pasture development over time, reported by Jackman (1964) and

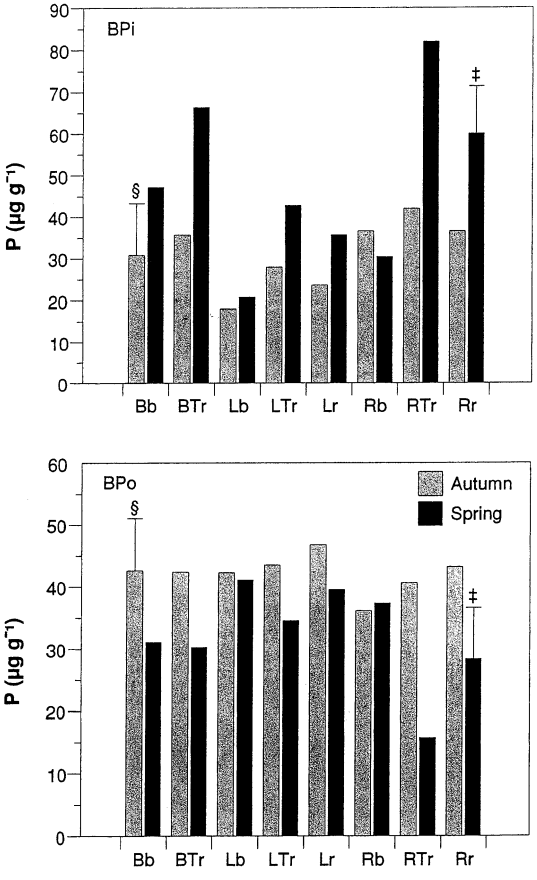

Fig. 3 Soil P fractions (µg P g^{-1}—BPi, BPo) determined in rhizosphere and bulk soils at two sampling dates: May 1996 (autumn) and November 1996 (spring). The *error bars* represent the *LSD* at the 5% level with *§* to compare between seasons and ‡ same season

Condron and Goh (1989). Higher levels of phosphatase enzymes in the two lucerne rhizosphere soils may have contributed to the lower TEPo found in those soils (Tarafdar and Junk 1987; Häussling and Marschner 1989).

Macroporous anion exchange resin (Lewatit MP500A) has been used to determine labile P (Rubæk and Sibbesen 1993; Guggenberger et al. 1996). Rubæk et al. (1999) and Guggenberger et al. (2000) found, under different land use systems in Europe, that resin P was similar to NaOH extracted orthophosphate diester and teichoic acid Po. They concluded that resin Po represented P of microbial origin and was a biologically active pool involved in short-term turnover. In this study both resin Pi and Po were lower in both lucerne soils than in the tree rhizosphere soil under bareground, and in both rhizosphere soils under ryegrass (Fig. 4). Greater enzyme activity associated with the rhizosphere under lucerne may have contributed to the lower resin Po (Fig. 2). The greater enzyme activity under lucerne suggests a negative feedback mechanism exists whereby plant and/or microbes produce enzymes only in response to P deficiency (Häussling and Marschner 1989; Tadano et al. 1993). In

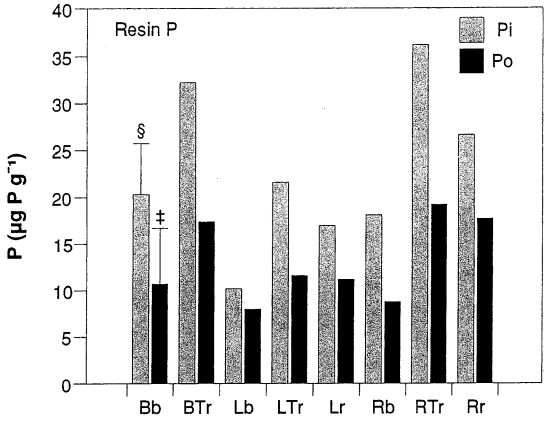

Fig. 4 Macroporous anion exchange resin-extracted Pi and Po (µg P g^{-1}) determined in rhizosphere and bulk soils over two sampling dates: May 1996 (autumn) and November 1996 (spring). *Error bars* represent the *LSD* at the 5% level with § to compare Pi and ‡ Po

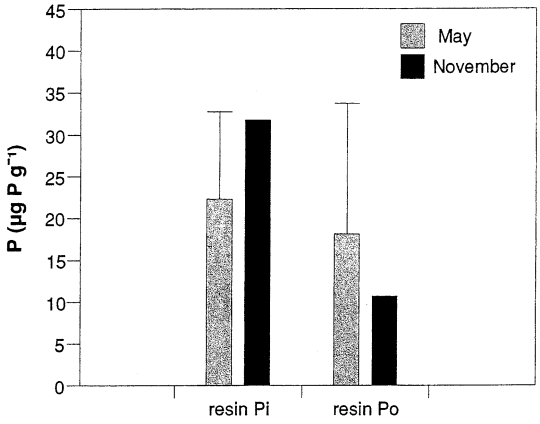

Fig. 5 Macroporous anion exchange resin Pi and Po (µg P g^{-1}) determined at two sampling dates: May 1996 (autumn) and November 1996 (spring) in rhizosphere (excluding bulk) soils. *Error bars* represent the *LSD* at the 5% level to compare between months

addition increased availability of N has been shown to enhance phosphatase activity and P availability (Zou et al. 1995; Olander and Vitousek 2000).

Seasonal changes

Although not significant, resin Po consistently decreased from autumn to spring (Table 2, Fig. 5). In addition BPo showed a significant decline from autumn to spring (Table 3). This was consistent with data presented by Tate et al. (1991) who found, under pasture in New Zealand, bicarbonate-extracted Po was highest in winter and lowest in summer. Perrott et al. (1990, 1992) found enhanced Po mineralisation in the growing season and calculated that 29 kg P ha^{-1} was released from labile Po fractions in late spring in fertilised pasture when fertiliser was discontinued. Chen et al. (2003a) found a variable change in BPo from winter to spring. In September (early spring), when soil temperatures were low, BPo declined but increased again in November (late spring). In the present study there was no seasonal change in TEPo, which was consistent with Chen et al's (2003a) findings under grassland and pine forest. However, Dormaar (1972) found Po decreased with crop growth and increased in winter. Although BPi and N2Pi showed an increase from autumn to spring and N1Pi a decrease, Tate et al. (1991) found Olsen P showed a winter maximum and spring minimum. Chen et al. (2003b) found no clear indication of BPi under grass or pine forest changing with seasons. Garbouchev (1966) found resin-extractable P greatest in summer and least in winter, which was consistent with the lower autumn and higher spring rhizosphere soil resin-extracted Pi and BPi in this study (Figs. 3, 5). There appears to be a developing consistency between resin-P studies to identify labile biologically active P, in contrast to some inconsistency found with the use of chemical extractants. The results from this study were consistent with these observations.

It seems that although there was no significant change in Cmic between seasons (Tables 4, 5), but a general increase in enzyme activity from autumn to spring and a decline in labile Po (Tables 1, 3), increased mineralisation of labile Po in the spring contributed to the increase in labile Pi. The decrease in N1Pi may be attributed to increased uptake, suggesting that N1Pi is a pool that is readily available to the plant. Chen et al. (2002) found that N1Pi was a P fraction that was readily depleted from rhizosphere soil by both ryegrass and *Pinus radiata*. In addition, Chen et al. (2003b) determined, on a range of grassland soils from throughout New Zealand, that the N1Pi fraction could be considered potentially available for pasture species over a growing season.

Conclusions

This study investigated the effects of lucerne and ryegrass understoreys and *Pinus radiata* on selected properties of their respective rhizosphere soils sampled at different

Table 3 Soil P fractions (µg P g^{-1}) in rhizosphere and bulk soils determined in May 1996 (autumn) and November 1996 (spring)

	BPi	BPo	N1Pi	N1Po	HPi	N2Pi	N2Po	TEPi	TEPo	Res-P	TP
May (autumn)	31.4	42.2	142.6	301.1	97.9	18.7	29.5	291	373	56	720
November (spring)	48.1	32.3	104.5	308.5	101.6	22.1	30.6	276	371	62	709
$LSD_{0.05}$	12.6	7.0	1.6	38.7	26.2	0.8	1.2	36	21	76	58

Table 4 Differences in acid (*PMEac*) and alkaline (*PMEal*) phosphomonoesterase activity and phosphodiesterase (*PDE*) activity (μg p-NP g^{-1} h^{-1}) in bulk and rhizosphere soils[a] calculated between four sampling dates [May (autumn), August (winter), November (spring), January (summer)]

	PMEac	$LSE_{0.05}$	PMEal	$LSE_{0.05}$	PDE	$LSE_{0.05}$
May–Aug	1.5	9.1	0.1	5.3	−1.5	2.0
May–Nov	−4.5	10.7	−5.8*	5.8	−0.5	1.9
May–Jan	26.1**	14.3	−1.5	6.9	4.3**	1.7
Aug–Nov	−6.0	8.4	−5.9	6.7	1.0	2.1
Aug–Jan	24.6**	12.4	−1.6	4.9	5.8**	1.6
Nov–Jan	30.6**	11.4	4.2	5.1	4.8**	1.1

*, ** Significance between seasons at the 0·05 and 0·01 probability levels, respectively, determined by the least significant effect (*LSE*)
[a] The mean of all eight soils

Table 5 Soil pH, microbial biomass C (*Cmic*), acid (*PMEac*) and alkaline (*PMEal*) phosphomonoesterase and phosphodiesterase (*PDE*) activity determined at four sampling dates [May 1996 (autumn), August 1996 (winter), November 1996 (spring) and January 1997 (summer)]

Month	pH	Cmic	PMEac	PMEal	PDE
		μg g^{-1}	μg p-NP g^{-1} h^{-1}[a]		
May	5.51	821	127	41	10.7
95% CI[b]	0.61	1,342	78	44	15.4
August	5.64	904	126	41	12.2
95% CI	0.62	1,267	65	44	17.0
November	5.41	775	132	47	11.2
95% CI	0.51	1,160	63	42	15.5
January	5.50	931	101	42	6.4
95% CI	0.55	1,433	69	41	9.9

[a] Release of p-nitrophenyl phosphate per hour
[b] 95% confidence interval for each month

times over a year. Lower levels of labile organic P and higher inorganic P in both tree and forage rhizosphere soil in the spring than in the autumn was consistent with other findings comparing seasonal changes in the forms of P under conifers and pasture. Tree and understorey rhizosphere soil for each P fraction and resin-P generally showed similar P concentrations suggesting significant influences between roots and/or mycorrhizae in the rhizospheres. Nevertheless BPi and resin Pi were greater, and BPo and resin Po less, in the tree rhizosphere soil compared to the companion understorey. Lucerne tree rhizosphere soil and lucerne rhizosphere soil showed the lowest levels of Pi and Po compared with other rhizosphere soils. This lower P concentration was associated with higher levels of PMEac, PMEal and PDE, which suggest that the combination of lucerne and radiata pine may enhance greater utilisation of soil P, although this requires further investigation.

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