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The acquisition of phosphorus by *Lupinus albus* L.

I. Some characteristics of the soil/root interface

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Key words Iron Lupins *Lupinus albus* L. Manganese Phosphorus Proteoid root Soil/Root interface

Summary It has been demonstrated by an agar film technique that *L. albus* can cause the breakdown of colloids of iron/silicate, iron/phosphate, aluminium/silicate and aluminium phosphate and destabilise suspensions of manganese dioxide, calcium mono-hydrogen phosphate and ferric hydroxide. Dissolution of these compounds was most marked in areas adjacent to proteoid roots (dense clusters of secondary laterals of limited growth which develop on lateral roots) and parts of the tap root. Soil associated with these regions of the root system contained more reductants and chelating agents than the bulk soil. Soil from around the roots of *L. albus* exhibited much greater reducing and chelating activity than that associated with the roots of rape and buckwheat.

Introduction

Three ways are recognised by which phosphorus reaches plant roots and is absorbed: mass flow in water moving to the roots as a result of transpiration; interception by the growing root system; and diffusion as a result of absorption at the root surface[1,32]. Because of the low phosphorus concentration in the soil solution[2,5,31] mass flow is relatively unimportant. Interception by the root system is also of only minor importance particularly as roots mainly penetrate existing voids in the soil[36]. Most of the phosphorus absorbed, therefore, moves to the roots by diffusion, and it is this process which is the limiting step in the acquisition of phosphorus from soil by plants.

The rate of phosphorus absorption by a plant may be enhanced by increasing either the surface area of roots towards which diffusion may occur or, the rate at which phosphorus reaches the root surface. The former situation is typified by fine roots with a moderate growth of root hairs and/or extensive mycorrhizal associations[4,8]. The latter situation is thought to occur in the case of rape plants[9], but the mechanism is not understood.

The morphology of the root system of *L. albus* and its ability to grow in soils low in available phosphorus suggest that the rate of phosphorus movement to its

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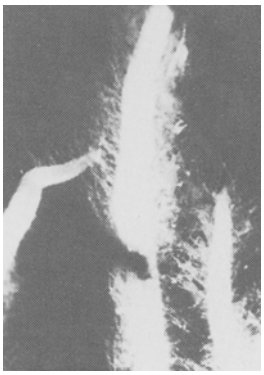

Fig. 1. Rootlets of *L. albus* covered in a dense growth of root hairs.

roots may be enhanced by some mechanism. Soil in the vicinity of its roots contains more hydrogen ions, reductants and chelating agents than the bulk soil[11]. This paper presents a more detailed examination of some characteristics of the soil/root interface of *L albus*.

Description of the root system of L. albus

The root system of *L. albus* consists of a prominent tap root, from which numerous lateral roots approximately 1 to 2 mm in diameter arise in two opposite rows. At irregular intervals along the lateral roots there are dense clusters of rootlets of limited growth. These appear to be similar to those found in some genera of the Proteaceae and in *Viminaria juncea* (Schrad. and J. Wendl) which have been previously described and referred to as proteoid roots[20,21,35]. The rootlets in *L. albus* are 0.5 to 1.5 cm long, are covered in a dense mat of root hairs up to 2 mm in length (Fig. 1) and emerge sequentially from the lateral root, the youngest being furthest from the tap root. Proteoid parts of lateral roots (Fig. 6) may be 8 cm in length, but are most commonly 3 to 4 cm and are not usually branched. These parts commonly account for as much as 40% of the dry weight of the lateral root system of field and glasshouse grown *L. albus* plants.

Random samples of roots were taken from field plots at the Rutherglen Research Institute, Victoria and were stained and examined for the presence of mycorrhizal associations. None were found on either *L. albus* or *L. angustifolius* L., although wheat roots from the same plots were generally mycorrhizal.

Materials and methods

Mobilization of phosphorus, manganese and iron in agar films

Clear plastic ellipses were made so that they formed sloping bases (at an angle of approximately 30° from vertical) in 11-cm diameter cylinders[13] (Fig. 2). Cuts were made into the edges of the ellipses at 3 to 4 cm intervals and string wound about them to serve as anchors for an agar film which was poured

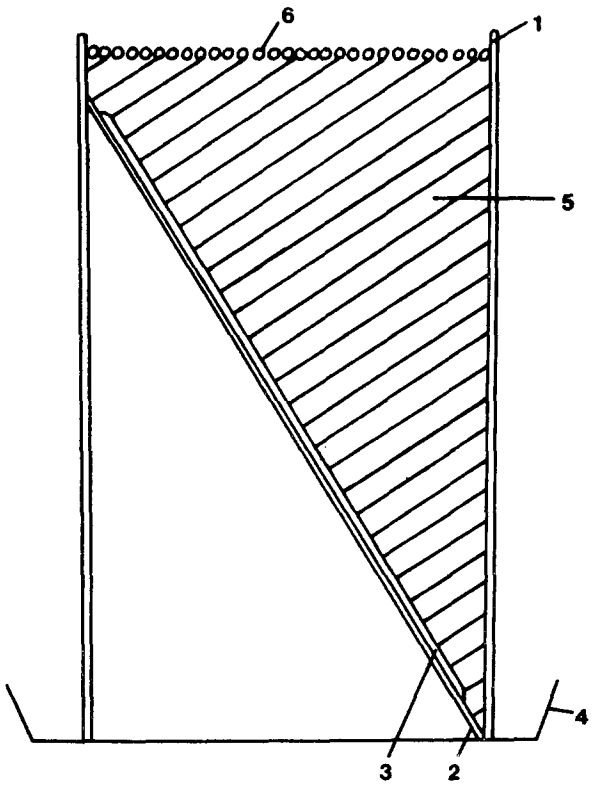

Fig. 2. Diagram of the apparatus used to grow roots in agar films (after Gerretsen[13]).
1. perspex cylinder; 2. perspex ellipse; 3. agar film; 4. saucer; 5. vermiculite; 6. plastic beads

onto the upper surface. The ellipses were placed in the cylinders, which were then filled with vermiculite and covered with a layer of plastic beads to reduce evaporation. The apparatus was kept in a saucer of water. A seed of *L. albus* cv. Hamburg was sown above the upper edge of each ellipse, and the subsequent root system developed both in the agar layer and the vermiculite. Plants were grown in a controlled environment cabinet under a 20/15°C, 18/6 h, day/night regime and harvested between four and eight weeks of age. The following suspensions, in two per cent agar, were used to make films on the ellipses:

(i) A solution of 2% KH_2PO_4 and 2% $CaCl_2$ was prepared at pH3 and the pH raised to 7 by adding NaOH with continuous stirring thus forming a finely divided precipitate of $CaHPO_4$.

(ii) A colloidal suspension of an insoluble manganese oxide of indefinite composition, referred to here as 'MnO_2', was prepared by adding ammonia solution to a boiling solution of 1% $KMnO_4$. It was adjusted to pH 7 and a concentration of 0.5% wt/vol. with respect to MnO_2.

(iii) A layer containing 2% $CaHPO_4$ and 0.5% MnO_2 was prepared using a combination of the above methods.

(iv) A suspension of $Fe(OH)_3$, (0.5% with respect to Fe) was prepared by neutralizing a solution of $FeCl_3$ with 10% NaOH.

(v) Colloids of aluminium/silicate, aluminium/phosphate, iron/silicate, and iron phosphate were prepared as detailed by Mattson[28] in Tables 33, 34, 37A and 37B. The colloids were prepared at their isoelectric points, allowed to settle, then centrifuged, washed in distilled water and resuspended to

make the agar films. Compositions of the colloids[28] were $Al_2O_3(SiO_2)_{2.26}$, $Al_2O_3(P_2O_5)_{0.857}$, $Fe_2O_3(SiO_2)_{2.26}$, and $Fe_2O_3(P_2O_5)_{0.914}$.

The plants were given 100 ml of a phosphorus free nutrient solution[15] three weeks after germination. At harvest, pH measurements were made on the agar surface next to the perspex ellipse using a flat-bottomed, combination pH electrode. Three 4 mm diameter cores were also taken from sections of the agar, extracted for at least 24 h in 5 ml 1 *N* HCl, and the dissolved iron or aluminium determined by atomic absorption spectroscopy. Plant tops were dried at 70°C, ground, ashed in a sulphuric acid/peroxide digest and the phosphorus content determined by the vanadomolybdate method[16].

Reducing capacity of leachates from soil associated with proteoid and non-proteoid roots

Plants of *L. albus* were grown in 14 cm diameter plastic pots containing either a mixture of peat, perlite, sand and soil (a red-brown earth, Dr 2.33[38]) or acid washed sand. The pots were placed in a glasshouse and watered to field capacity twice a week. At harvest, the potting mixture was divided into that associated with proteoid roots ('proteoid soil') and that from other regions of the pot ('non-proteoid soil'). The two samples were placed in glass tubes 22 cm long and 2.5 cm diameter and the soil leached slowly with distilled water. Leachates from 'proteoid soil' are referred to as 'proteoid extracts' and those from 'non-proteoid soil' as 'non-proteoid extracts'.

The reducing activity of the two extracts compared by measuring the concentration of manganese brought into solution when 3 ml were incubated for 24 h at 35°C with 3 ml of 0.2 *M* sodium acetate buffer (pH 5.0), 0.5 ml of 0.5% 'MnO_2', and 2 drops of chloroform to suppress microbial activity[10].

Extractable iron in soil associated with proteoid and non-proteoid roots

Plants were grown for eight weeks and the soil divided as described in section 2. Five to ten g of each 'soil type', were placed in 100 ml aliquots of 0.1 M phosphate/citric acid buffer at pH's of 7.0, 6.5, 6.0, 5.5, 5.0, 4.5, 4.0. Approximately 4 g of activated, acid-washed charcoal and 2 g of $CaSO_4$ were added and the suspensions shaken for 30 minutes on a reciprocating shaker. They were then centrifuged at 2,500 *g* for 10 minutes, and the supernatant filtered. An aliquot of the filtrate was further centrifuged at 2,500 *g* for 10 minutes and the Fe present in this supernatant determined by colorimetric measurement at 600 mu after reaction with ferron[19]. There were four replicates at each pH level.

Comparison of white lupin, rape and buckweat

Plants of white lupin (*Lupinus albus*). rape (*Brassica napus* L.) and buckwheat (*Fagopyrum*

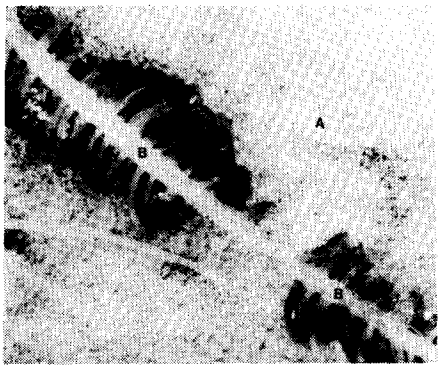

Fig. 3. Proteoid roots growing in an agar containing a precipitate of $CaHPO_4$ (× 5)
A – white ppte of $CaHPO_4$ in agar
B – proteoid roots showing the zone of $CaHPO_4$ dissolution

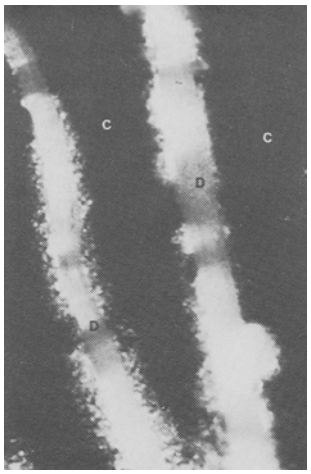

Fig. 4. Undifferentiated lateral roots growing in an agar film containing MnO_2 (× 10)
C – agar + black MnO_2
D – lateral roots showing narrow zone of MnO_2 dissolution

esculentum Moench.) were grown in 14 cm diameter pots containing potting mixture maintained between 60 and 80% field capacity by watering to weight as required. Unplanted pots were included in the experiment as controls.

After seven weeks two pots from each species and two controls were sampled. Six 8 mm cores were taken from each pot, mixed thoroughly and assayed for extractable Fe at pH 5.5 as described above except that the Fe was measured by atomic absorption spectroscopy using a nitrous oxide/acetylene flame. The soil in each pot was then leached with water and the leachate centrifuged at 22,000 g. The Fe in solution and the reducing activity of the supernatants were then determined.

A third pot of each treatment was harvested and the soil divided into 'rhizosphere' (adhering to the roots) and 'non-rhizosphere' soil. These fractions were assayed for extractable Fe at pH 5.5.

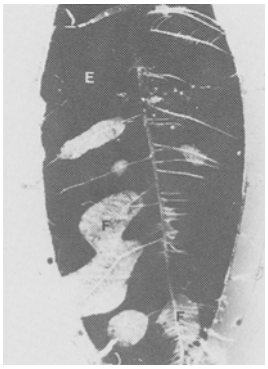

Fig. 5. The root system of *L. albus* growing in a film of agar containing MnO_2 (× 0.4)
E – agar + black MnO_2
F – zones of dissolution about areas of dense lateral formation on the tap root and proteoid roots

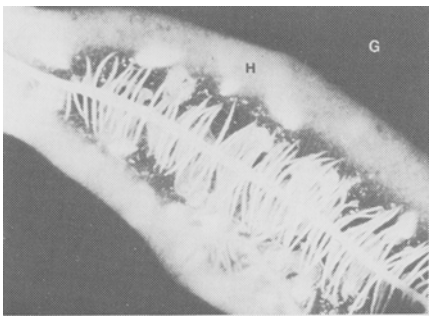

Fig. 6. A proteoid root growing in agar containing $CaHPO_4$ and MNO_2 (× 5)
G – agar + $CaHPO_4$ + MnO_2 (black)
H – agar + $CaHPO_4$ (white) – MnO_2 has been dissolved
I – clear agar (photographed with incident light)

Results

Mobilization of phosphorus, manganese, aluminium and iron in agar films

Dissolution of the $CaHPO_4$ and $Fe(OH)_3$ precipitates was observed only in the vicinity of proteoid roots and areas of high lateral root density on the tap root (Figs. 3 and 7). In the case of the agar layers containing MnO_2 a narrow zone (< 2 mm) of dissolution occurred around all the roots (Fig. 4), but was up to 3 cm wide near proteoid roots and areas of high lateral root density on the tap root (Fig. 5). Samples of the cleared areas of agar were taken with a corkborer, dissolved in hot water, filtered and analysed for Mn by atomic absorption

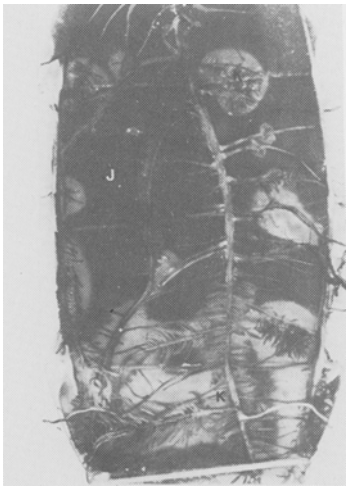

Fig. 7. The root system of *L. albus* growing in agar containing $Fe(OH)_3$ (× 0.5)
J – agar + dark $Fe(OH)_3$
K – zones f dissolution about areas of dense lateral formation on the tap root and proteoid roots.

Table 1. pH and concentration of Fe or Al* in agar films** measured in areas where dissolution had (clear) or had not occurred (non-clear)

Description	'Clear area'		'Non-Clear' area		%P in tops
	pH	Fe or Al ppm	pH	Fe or Al ppm	
FeSi colloid					
(i)	7.2	2.5	7.8	19	.13
(ii)	7.1	0.9	8.0	23	.15
$FePO_4$ colloid					
(i)	7.2	11	7.7	32	.31
(ii)	5.9	1.8	7.7	29	.31
AlSi colloid					
(i)	7.9	0	8.2	9.6	.11
$AlPO_4$ colloid					
(i)	7.4	0	8.0	5.4	.30
(ii)	6.6	.4	8.1	6	.27

* Concentration which resulted from placing three 4 mm diameter cores of agar in 5 ml of 1 *N* HCl.
** Plants were grown in association with a range of colloidal films and the percentage phosphorus in the tops was also measured.

spectroscopy. Appreciable concentrations of Mn were found in the clear agar, declining to zero near the roots, indicating that dissolution of MnO_2 preceded uptake by the root. In the mixed $CaHPO_4$ and MnO_2 agar layers, dissolution of MnO_2 preceded that of $CaHPO_4$ but both compounds were dissolved at the same sites (Fig. 6).

Dissolution occurred in similar regions in the case of the iron and aluminium colloids. This could not be attributed to acidity since the pH of the agar was near neutral (Table 1), although it was slightly more acid in areas of dissolution than in areas not affected by the plant roots. The concentrations of both iron and aluminium declined markedly in areas of dissolution, and analysis of the shoots clearly demonstrated that phosphate was being obtained from the iron and aluminium phosphate colloids (Table 1). The levels of iron in the shoots were in the range 100 to 300 ppm.

Reducing capacity of leached extracts

The proteoid roots were the major zones of reducing activity in the root system (Table 2). The reducing activity of the extracts of soil from non-proteoid roots may have been due either to substances produced by those roots or contamination by soil from proteoid roots during harvest. The very high activity of the proteoid extract from the plant grown in sand is probably due to the more chemically and microbially inert nature of acid washed sand compared to soil.

Table 2. Ppm Mn in solution after incubating 3 ml extract with 3 ml 0.2 *M* acetate/borate buffer at pH 5 and 0.5% MnO_2 and 2 drops of chloroform for 24 h at 35°C.

	Reducing activity (ppm Mn^{2+})	
	Proteoid extract	Non-proteoid extract
Plant grown in sand	81	4
Plants grown in soil (mean of 4)	22 (0.7)	2.3 (1.6)
Water control	0.13 (0.05)	

Values in brackets are standard errors.

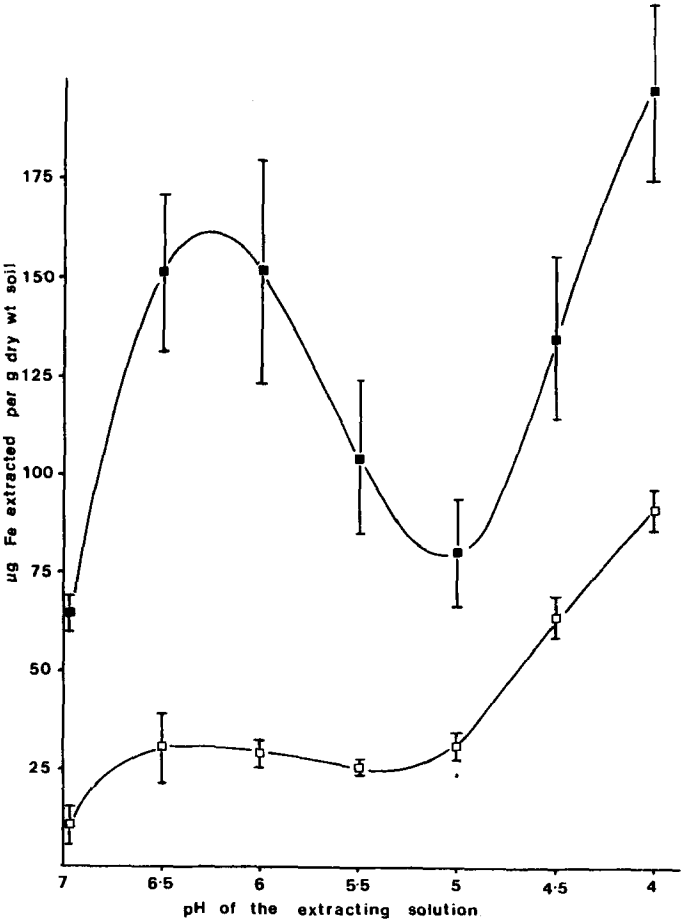

Fig. 8. µg extractable Fe/g dry soil measured by shaking between 5 and 10 g of soil with approximately 4 g of activated acid washed charcoal, 2 g of $CaSO_4$ and 100 ml of phosphate/citric acid buffer at a range of pH values. Bars represent 1 standard error either side of the point. Solid squares are values for proteoid soil, hollow squares are values for non-proteoid soil.

Effect on extractable iron

Soil associated with proteoid roots contained significantly more extractable iron than that from around non-proteoid roots at all but one pH level tested (Fig. 8).

Comparison of white lupin, rape and buckwheat

'Rhizosphere' soil from the vicinity of the root system of *L. albus* contained more extractable Fe than did soil in vicinity of the roots of rape or buckwheat. A similar pattern was observed in the case of the core samples.

The soil solution from the *L. albus* pots differed from that of the other species in the high level of reducing activity it possessed and in the amount of soluble Fe present (Table 3). Preliminary investigations indicate that the Fe in solution carried a net negative charge and behaved on Sephadex gel columns as a compound with a molecular weight in excess of several thousand suggesting that it is associated with organic compounds.

Discussion

Published models of phosphorus uptake by plants are based on the assumption that plant roots act as sinks and by inducing a low phosphorus concentration in the adjacent soil[25,29,41] cause phosphate ions to diffuse to their

Table 3. Some characteristics of the soil solution, and levels of extractable iron (see text for methods) measured in soil cores, or 'rhizosphere' and 'non-rhizosphere' fractions of soil from pots in which either *L. albus*, rape, buckwheat or no plants had been grown.

Description		Core samples ppm Fe/g	Displaced soil solution		ppm Fe/g d.wt. Soil fractions	
			Reducing activity ppm Mn	ppm Fe in solution	Rhizosphere	Non-Rhizosphere
L. albus	1	176	49	48	603	163
	2	230	67	50		
Rape	1	108	2.0	.3	200	133
	2	138	3.1	1.3		
Buckwheat	1	140	4.3	.2	160	133
	2	126	3.8	0		
Control	1	146	1.1	.3	103	
	2	128	1.4	.7		
L.S.D. ($P < 0.01$)		46			315	

surface. From these theories it follows that because of the increased surface area they present, fine roots with moderate root hair development, or alternatively an extensive mycorrhizal mycelium in the soil, are the most efficient systems for the uptake of phosphorus[3,4,8,40]. It has been shown however that *L. albus* has relatively thick lateral roots (1 to 2 mm diameter), does not form extensive mycorrhizal associations and develops proteoid roots. Yet despite these apparent disadvantages, lupins are noted for their ability to grow in soils low in available phosphorus, suggesting that in some way they can enhance the movement of phosphorus to their root system.

The present results have shown also that the proteoid roots of *L. albus* produce an environment which, compared with that of the bulk soil, is acid, conducive to chemical reduction, and contains unusual amounts of organic compounds capable of complexing Fe. The first two of these factors are now considered alone and in combination from the viewpoint of their possible effect on phosphorus movement to the roots (the effect of chelating agents is considered in a subsequent paper).

Acidity

In most acid and neutral soils the concentration of phosphorus in the soil solution is determined by adsorption onto or into iron and aluminium hydroxide/oxide complexes and/or by the solubility of aluminium or iron phosphates. The solubility of phosphorus changes very little as pH is lowered in the former case[6], and decreases in the latter case[26]. Therefore, it is not likely that acidification will directly result in increased phosphorus availability in acid soils.

In those situations in which calcium phosphates control the concentration of phosphorus in solution (alkaline soils high in calcium), phosphorus does become more available as pH decreases. However, since lupins grow better on acid than on alkaline soils, the ability to extract phosphorus from hydrous oxides of aluminium and iron is more likely to have evolved than that of solubilizing calcium phosphates.

Reduction

It has been suggested[35,37] that reduction of manganese and iron can increase the availability of phosphorus. Some insight into the factors governing chemical reduction in the soil may be gained from a consideration of the general equilibrium situation:

$$x\,(\text{oxidized form}) + aH^+ + n\,\text{electrons} = y\,(\text{reduced form}) + a/2\,H_2O$$

$$Eh = E^\circ + \frac{RT}{nF}\,\text{In}\frac{(\text{oxidized form})^x}{(\text{Reduced form})^y}$$

Theoretically two or more redox systems of differing redox potentials will react together until all the systems attain a common Eh. In soil, the major

compounds which are readily reduced are O_2, NO_3^-, MnO_2 and $Fe(OH)_3$[33].

$$\tfrac{1}{4}O_{2(g)} + H_{(aqu)}^{+} + e = \tfrac{1}{2}H_2O \qquad E_o = 1.229\ V$$

$$1/5NO_3^- + 6/5H^+ + e = 1/10N_2 + 3/5H_2O \qquad E_o = 1.245\ V$$

$$\tfrac{1}{2}MnO_2 + 2H^+ + e = \tfrac{1}{2}Mn^{2+} + H_2O \qquad E_o = 1.229\ V$$

$$Fe(OH)_3 + 3H^+ + e = Fe^{2+} + 3H_2O \qquad E_o = 1.057\ V$$

These four reactions proceed more readily under acid conditions as can be seen from the above equations, but the extent of the reactions cannot be readily ascertained because this is determined by kinetic effects rather than considerations of Eh. This is demonstrated by the stability of aqueous Mn^{2+} solutions exposed to the atmosphere.

The oxygen and nitrate couples have very slow rates of reaction and are unlikely to react with reductants released from the root. Mn IV and Fe III are not kinetically limited in their reactions, but it can be deduced from rH values[24] that Fe III is more difficult to reduce than Mn IV, and therefore reductants released from roots into the soil will preferentially react with Mn IV. The levels of manganese which accumulate in *L. albus* indicate that considerable reaction does in fact take place; foliar levels in *L. albus* at Rutherglen (Vic.) are commonly more than 5,000 ppm and may reach 16,000 ppm whereas in wheat grown in the same soil they are less than 400 ppm.

The observed dissolution of the aluminium colloids in agar films must be attributed to a process other than reduction because aluminium could not possibly have been reduced in the agar films and the colloids were observed to dissolve. The chelating agent responsible for the dissolution of Fe III and aluminium colloids is identified and discussed in a subsequent paper[12].

It is unlikely under soil conditions that reduction of Mn IV would result in significant amounts of phosphorus becoming available to plants or that the supply would be enhanced through phosphate ion displacement by complexforming materials such as citrate, ketogluconate or malate. The primary reason for this is that the numbers of Mn IV, Fe III and aluminium atoms in the soil are much higher than those of phosphate ions, and therefore much of the reducing and chelating activity will not result in the release of phosphate ions into solution. Scondly, any ions which are released by these processes will enter the normal absorption equilibria of inorganic phosphate in the soil and suffer the same impedance in moving to the root surface as other phosphate ions[41]. Thirdly, not all of the phosphorus released by these processes and remaining in solution will move to the root, some may move away. A mechanism by which secretion of hydrogen ions, reducing and chelating agents may enhance the movement of phosphorus to the roots of *L. albus* is postulated in a subsequent paper[12].

Attempts have been made[18,22] to explain the function of proteoid roots in the Proteaceae in terms of increased surface area available for absorption of

phosphorus. However their clustered nature, and subsequent overlap of phosphorus depletion zones about the rootlets and root hairs would negate any advantage conferred by increased surface area[11,40]. Short term studies in solution culture[27] have shown that in *Banksia grandis* Willd proteoid roots take up phosphate at a faster rate than non-proteoid roots. However, the rate of phosphate uptake is enhanced by lowering the pH[14] and the differences reported may reflect a lowering of the pH in the undisturbed layers about the roots, rather than any difference in uptake mechanisms. It is considered therefore that the function of proteoid roots of *L. albus* is better explained in terms of 'phosphorus solubilization' by reduction, acidification, and complex formation than by considerations of proteoid roots as simple sinks for phosphorus.

The present results raise the question of whether the reducing, acidification, and complexing activities of proteoid roots of *L. albus* are unique. It may therefore be noteworthy that most plant species which form proteoid roots or analogous structures are not reported as forming mycorrhizal associations. Most members of the Proteaceae appear to be non-mycorrhizal[22], form proteoid roots and are noted for their ability to grow on soils low in available phosphorus. They also accumulate manganese when growing in soils which do not supply excessive amounts to other plant species, indicating that selective absorption occurs[17]. Rushes and sedges are non-mycorrhizal[34] and form dauciform roots[23] which in may respects are analogous to proteoid roots. Proteoid roots have also been reported on the legumes *Kennedia* sp.[42] two members of the Casuarinaceae, *Casuarina littoralis* Salisb. (Bowen, pers. comm.) and *Casuarina equisetifolia* L.[7], *Acacia mucronata* Willd.[39] and *Viminaria juncea*[21], but these species were also shown to be mycorrhizal. The possession in most cases of modified root structures rather than mycorrhizal associations suggests that they may perform similar functions. However, for the reasons mentioned earlier, these functions are unlikely to be explained in terms of their action as simple sinks for phosphorus as is the case in mycorrhizal associations, and it may be that their mode of action is similar to that suggested for the proteoid roots of *L. albus*.

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