Growth and Phosphorus Uptake of Lupins (*Lupinus angustifolius* L. and Great Brome (*Bromus diandrus* Roth.) Grown in Different Phosphorus Concentrations in Solution Culture

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Abstract

Investigation of the competitive abilities of lupin *(Lupinus angustifolius)* and great brome *(Bromus diandrus)* at different P supply under controlled conditions was aimed at understanding the mechanism of nutrient competition between these two species. Under suboptimal P supply, great brome, with higher root area per unit root weight and relative growth rate, took up limited amounts of P faster than lupins. By so doing, great brome partly overcame its disadvantage of lower initial seed size within 35 days after transplanting, and had higher P productivity than lupins. However, under high P supply, lupins tended to have higher potential to respond to P than great brome.

This experiment was aimed at further understanding of the mechanism of competition for P between lupins and great brome. Great brome *(Bromus diandrus* L), one of the common weeds infesting lupin growing areas, was expected to compete for phosphorus mainly due to its high plant density and high root length density, particularly within 10 cm from the soil surface. The high root density of great brome implies that it can exploit a greater soil volume and absorb more nutrients and water than lupins. However, results from previous experiments suggested that differences in root architecture between these two species are not the determinant factor for nutrient competition between these species (Rugkhla, 1987).

Throughout southwest Western Australia large areas of sandy and gravelly surfaced soil, mostly suitable for lupin cultivation, are acutely deficient in P. To ensure an economic return in lupin production, a considerable quantity of superphosphate is applied. However, when phosphorus in the soil solution is higher than 1 ppm it tends to leach down the soil profile and in some cases may be lost altogether (Fitzpatrick, Burvill and Toms 1962; Donald 1964). Phosphate also has a low diffusion coefficient ($0.3-3.3 \times 10^{-9}-cm^{-2}s^{-1}$, Rowell *et al.*, 1967). Under such conditions, if two or more species are competing for the same limited resource, species which have a vigorous growth habit and an ability to rapidly extract the nutrients coupled with rigorous internal economics for the use of P will be of competitive advantage (Crowley, 1975; Dunlop *et al.*, 1979).

This paper reports on an investigation of mechanisms of growth and nutrient uptake under different levels of P supply. Although competition between these two species is only a problem when soil P status is low, we extended our attention to a range of concentrations normally found after superphosphate application.

The physiological factors of growth and nutrient uptake considered to affect competitive ability under different environments were:

a) a high relative growth rate per unit P supplied.

b) a high rate of P uptake per unit root surface area at the same level of P supply.

c) an increase in the P utilisation quotient (dry

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matter production per unit P content, g mg^{-1}).

d) an increase in the P productivity index (gDM d^{-1} mg^{-1}P) which is the rate of growth per unit P content.

Materials and Methods

Plant Culture

The experiment was conducted in a sunlit phytotron at day/night temperature of 20/15°C at the University of Western Australia Perth. Narrow leafed lupins (*Lupinus angustifolius* var. Yandee) and great brome (*Bromus diandrus* L.) were grown in solutions with P concentrations of 0.003, 0.03, 0.3, 3.0 and 30 ppm. The five P treatments chosen were based on the P concentration in soil solution in nature before and after superphosphate application. The treatments were arranged in a complete factorial randomised complete block design with two replicates.

Twelve uniform seedlings of lupins and 15 of great brome were placed in polyethylene vessels containing 3.5 L of modified Hoaglands nutrient solution minus P (Table 1). The supply of these elements were sufficient except for P.

The solution was stirred and aerated by vigorous streams of air. The pH was checked daily and adjusted when necessary to 5.7±0.2. Solutions were renewed every 5 days for the first 15 days and every 3 days thereafter.

Table 1. Composition of modified Hoagland solution.

Macronutrient	gL^{-1}	Micronutrient	gL^{-1}
$NaNO_3$	63.99	H_3BO_3	0.28
KNO_3	60.67	$MnCl_2$ $4H_2O$	0.10
KCL	14.91	$CuSO_4$ $5H_2O$	0.05
$MgSO_4$ $7H_2O$	98.59	$ZnSO_4$ $7H_2O$	0.06
NH_4NO_3	32.02	$(NH_4)_6Mo_7$ O_{24} $4H_2O$	0.12
$Ca(NO_3)_2$ $4H_2O$	141.60	FeEdTA	6.60
KH_2PO_4	5.44		

Sampling and Analysis

At transplanting, 4 replications of 4 lupins and 25 great brome seedlings were taken for determination of initial dry matter, root length, leaf area and P content.

Samples were then taken at 7 day intervals until 28 days after transplanting for both species and at 35 days for lupins only. At each harvest three lupins and four great brome seedlings were taken. For all harvests, shoot and root samples were dried in an oven at 70°C for 36 hours after measuring leaf area, root length (Comair root length scanner) and mean root radius (determined by randomly measuring each root category under a binocular microscope).

The shoot and root components were ground and sub-sampled for digestion in HNO_3:$HClO_4$(1:1 v/v). After dilution, phosphorus concentration in the digest was determined by the Molybdovanado phosphoric acid method (Boltz and Luech, 1954).

Growth analysis

Polynomial regressions were fitted to the natural logarithms of plant dry matter and leaf area as they changed with time. Linear equations were found to be adequate. The derived equations were of the form:

$$\ln W = a + bt \quad (1)$$

$$\ln A = a' + b't \quad (2)$$

Where W is the total plant dry matter (g), A is leaf area and t is time in weeks. Differentiation of equation (1) gave the instantaneous value of the relative growth rate (RGR) (Huges and Freeman, 1967).

$$\frac{d\ln W}{dt} = b \quad (3)$$

Net assimilation rate (NAR) was derived from equations (1) and (3) as

$$\frac{1}{A}\frac{dW}{dt} = b\,\frac{\exp(a+bt)}{\exp(a'+b't)} \quad (4)$$

$$= b \exp\{(a-a') + (b-b')t\} \quad (5)$$

Leaf area tatio (LA) was estimated as

$$LA = \frac{RGR}{NAR} \quad (6)$$

Plant uptake analysis

Although some authors have suggested that root volume would be the most suitable root unit for P uptake in nutrient solution, particularly at high concentrations (Nye, 1973), the aim of this experiment was to compare the uptake between the two species which differed in their root morphology i.e. root area/volume ratio. Therefore, root area is the most desirable. The derivation of the equation in the uptake model was analogous to those of plant growth analysis.

$$\ln U = c + dt \quad (7)$$

$$\ln RA = c' + d't \quad (8)$$

Where U is total P content (mg), RA is root area.

From equations (7) and (8) uptake per unit root surface (F) was determined:

$$F = \frac{dU}{dt}\frac{1}{RA}$$

$$= d \exp \{ (c - c') + (d - d')t \} \quad (9)$$

According to the Nye and Tinker (1969, 1977) model dU/dt may be written as

$$\frac{dU}{dt} = 2\pi a \alpha LC \quad (10)$$

Where α is the root absorbing power, a is root radius, L is root length and C is nutrient concentration at the root surface. The uptake rate can also be written as:

$$\frac{dU}{dt} = N\frac{dW}{dt} + W\frac{dN}{dt} \quad (11)$$

Where N is the concentration of phosphorus in the plant (mgg^{-1}). Combining equations (10) and (11) gives

$$\alpha = \frac{W}{2\pi aL}\frac{N}{C}(RGR + RNR) \quad (12)$$

Where RNR is the relative concentration rate.

The Phosphorus productivity index, which is the rate of growth per unit of P content, is expressed as:

$$P_r = \frac{\ln P_2 - \ln P_1}{t_2 - t_1}\frac{W_2 - W_1}{P_2 - P_1} \quad (13)$$

Where W_1 and W_2 are total plant dry matter and P_1 and P_2 are total P contents at times t_1 and t_2 respectively. P and W are assumed to be linearly related.

Statistical Analysis

The significance of treatments was tested by analysis of variance of all plant parameters. When harvest 5 was taken into account, unbalanced regressions were tested for significance of the differences between treatments using the GENSTAT statistical program.

Results

Growth Response to External Phosphorus

At the start of the experiment lupins had 45 times the shoot dry matter and 17 times the P content of great brome. However, lupins had half the shoot P concentration and root weight ratio (root dry matter as a percentage of total plant dry matter) of great brome. There were no significant differences (P = 0.05) between species in root P concentration and root P ratio (Table 2).

Table 2 Seedling characteristics at the commencement of the experiment (9 days after imbibition).

Characteristics	Lupins	Great brome
Shoot dry matter ($mgplant^{-1}$)	91.4	2.0
Root dry matter ($mgplant^{-1}$)	16.9	1.2
Shoot P concentration (%)	0.12	0.30
Root P concentration (%)	0.21	0.22
Total P concentration (%)	0.137	0.276
Total P content ($mgplant^{-1}$)	0.148	0.0088
Root P ratio (% of total P)	24.3	29.9
Root weight ratio (% of total DM)	15.4	36.0

At the two lowest phosphorus levels (0.003 – 0.03 ppm), P deficiency stunted the growth of both species. Symptoms were more severe in great brome. The absolute yield of lupins was greater than that of great brome over the entire range. These differences were partly due to the difference in the seedling weight at the start of the experiment and the subsequence growth rate. Total dry

matter of both species was depressed at 0.003 and 0.03 ppm P solution concentration. At the final harvest, the maximum dry matter of great brome was achieved at 3 ppm with no further increase at 30 ppm while that of lupins responded up to 30 ppm P supply (Figure 1).

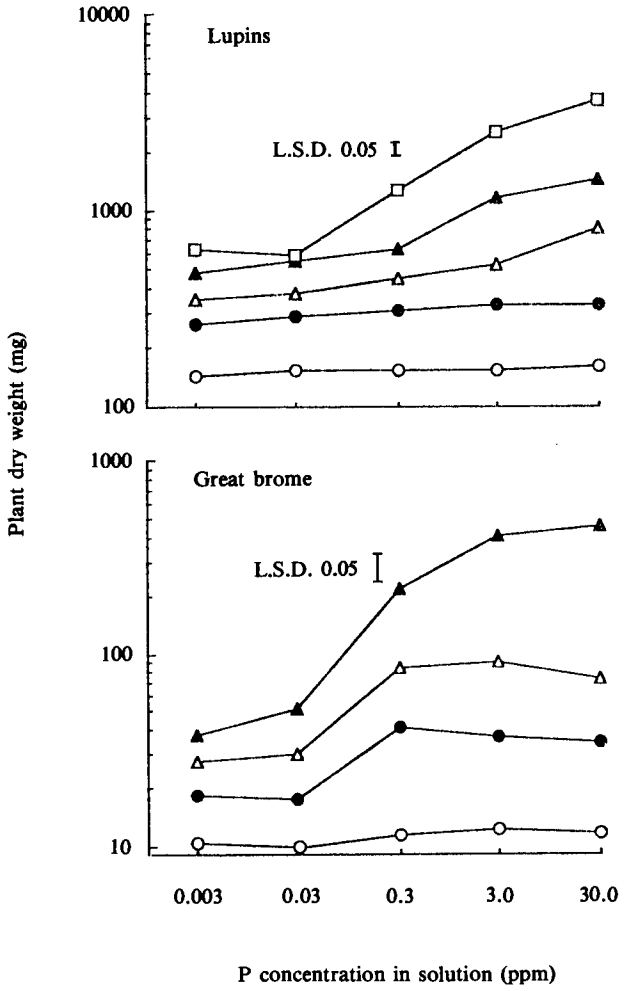

Figure 1. Dry weight of lupins and great brome at 7 (○), 14 (●), 21 (△), 28 (▲) and 35 (□) days after emergence in relation to solution concentration of P. Vertical bars are lsd (p = .05) of log transformed data.

The linear relationship (equation 2) between the log of plant dry matter and time suggested that, over the experimental period, growth was exponential. In lupins, the stability of RGR over time resulted from a decrease in NAR and an increase in LA ratio with time (Figures 2a, b). By contrast, RGR was stable in great brome because NAR increased and leaf area ratio decreased with time (Fig.2c,d).

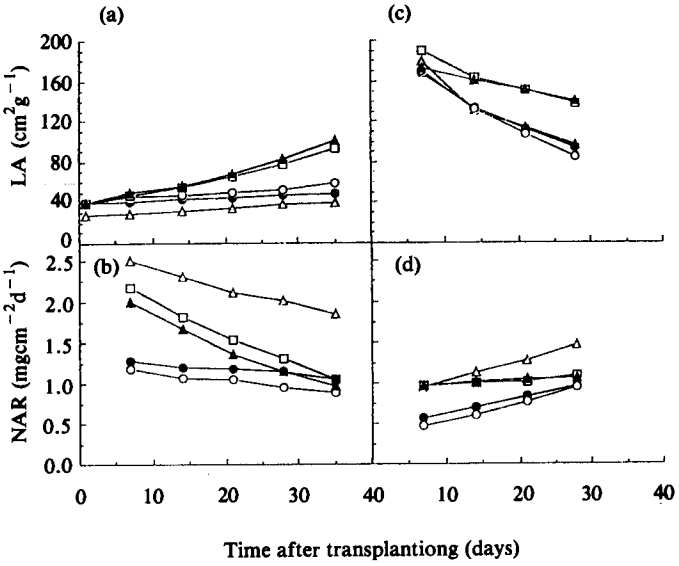

Figure 2. The changes of leaf area ratio (LA) and net assimilation rate (NAR) of lupins (a,b) and great brome (c,d) at P concentrations of 0.003 (○), 0.03 (●), 0.3 (△), 3 (▲) and 30 (□) ppm during vegetative growth.

Relative growth rate and relative uptake rate

Relative growth rate increased as phosphorus concentration in solution increased up to 3 ppm in great brome and 30 ppm in lupins (Figure 3a). The response was influenced mainly by the increase of NAR which was highest at 0.3 ppm in both species, the stable RGR at higher P supply (>3 ppm) resulted from the decrease of LA with P external concentration. Great brome RGR was about two times higher than lupins because although great brome NAR was about half that of lupins, LA was 4 times higher.

The relative uptake rate of great brome was about double that of lupins at 0.003 ppm. With further increments of P supply up to 0.3 ppm, relative uptake rate per unit of P supply in great brome increased to 3 times that of lupins (Figure 3b). Within the range of 0.3 – 3 ppm, relative uptake rate of lupins increased

sharply, but that of great brome was always higher (Figure 3). In both species the response to P supply declined above 3 ppm.

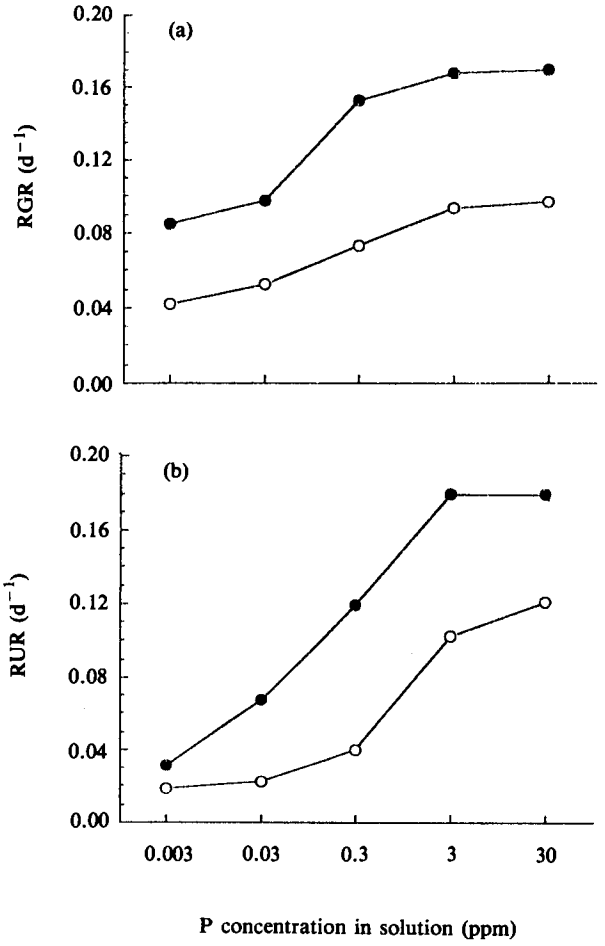

Figure 3. Effect of P concentration in solution on relative growth rate (a) and relative uptake rate (b) of lupins (○) and great brome (●) 28 days after emergence. P concentration is plotted on a log scale.

Rate of Phosphorus Uptake per unit root surface area (flux)

There was a significant increase in P flux with external P concentration in both species (Figure 4). At lower external P concentrations (0.003 – 0.3 ppm), both species had a similar rate of uptake per unit root surface area. However, most of the response of P flux to P supply in great brome was between 0.3 and 3 ppm while the lupin response was more gradual and continued up to 30 ppm. The change of flux with time for the two species was different at high P levels (3 – 30 ppm), i e. as lupins aged, flux declined but flux of great brome tended to be more stable.

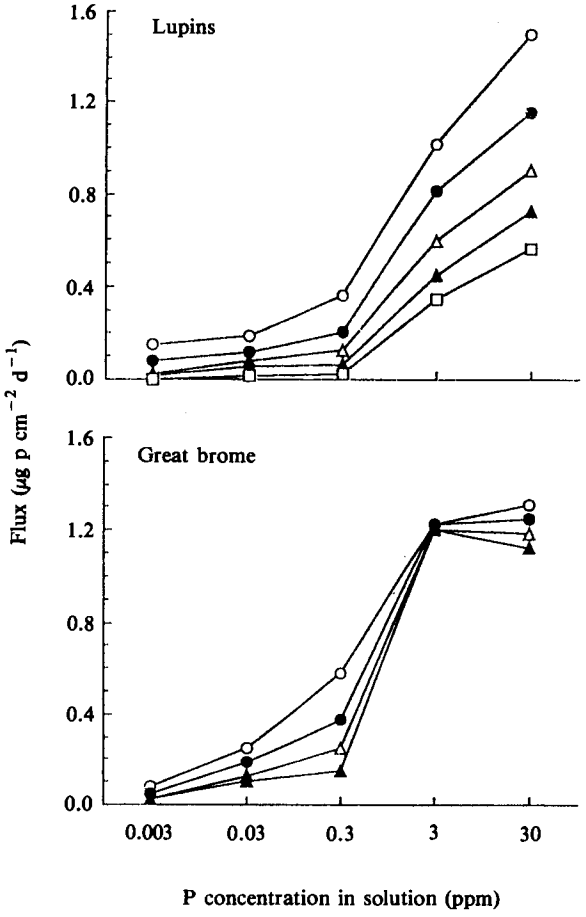

Figure 4. Effect of P concentration on the rate of P absorption per unit root area (Flux) by lupins and great brome 0-7 (○), 7-14 (●), 14-21 (△), 21-28 (▲) and 28-35 (□) days after transplauting (initial P concentrations were accounted for in the flux calculations. P concentration is plotted on a log scale.

Root absorbing Power (α)

At the lowest P concentration, lupins had high α in the first and second harvests, then decreased at

subsequent harvests (Table 3). Generally, α was higher for great brome than lupins especially at 0.03 – 30 ppm P supply and between 14 and 28 days. In both species α declined with time and with increasing external P concentration. However, the trend was not consistent in great brome.

Table 3. Effect of P concentration in solution on the root absorbing power (α) and root demand coefficient (αa).

Species	Time (days)	P in nutrient solution (ppm)				
		0.003	0.03	0.3	3.0	30
		Root absorbing power (α) ($cm^{-2}s^{-1}$ *10^6)				
Lupins	7	604	39.4	31.6	4.9	0.68
	14	293	19.4	5.0	2.3	0.43
	21	128	16.0	4.0	2.7	0.39
	28	106	8.8	3.8	2.0	0.29
	0	94	10.9	1.8	1.3	0.23
Great Brome	7	252	53.8	23.2	5.4	0.59
	14	158	129.0	35.9	14.1	1.62
	21	289	69.7	13.9	14.1	0.78
	28	171	85.8	9.7	9.4	1.13
	Root demand coefficient (αa) ($cm^{-1}s^{-1}$)					
Lupins	7	56.7	3.45	2.86	0.48	0.70
	14	29.1	2.10	0.50	0.23	0.14
	21	12.3	1.90	0.46	0.31	0.40
	28	12.9	1.09	0.47	0.29	0.04
Great Brome	7	6.65	1.18	0.52	0.10	0.01
	14	2.14	1.86	0.68	0.32	0.03

Relationships between growth and uptake

The internal P concentration in shoots increased with the external P concentration (Figure 5) with great brome having a higher tissue concentration than lupins. Shoot P concentration of lupins responded to external P concentration over the whole range, while great brome shoot P concentration responded up to 3 ppm. Shoot P concentration in great brome at the highest level of P declined from day 21 to 28 thereby demonstrating a deleterious effect. The level at which this effect became evident seemed to depend on the plant's age. However, this happened without significantly suppressing the total growth of great brome.

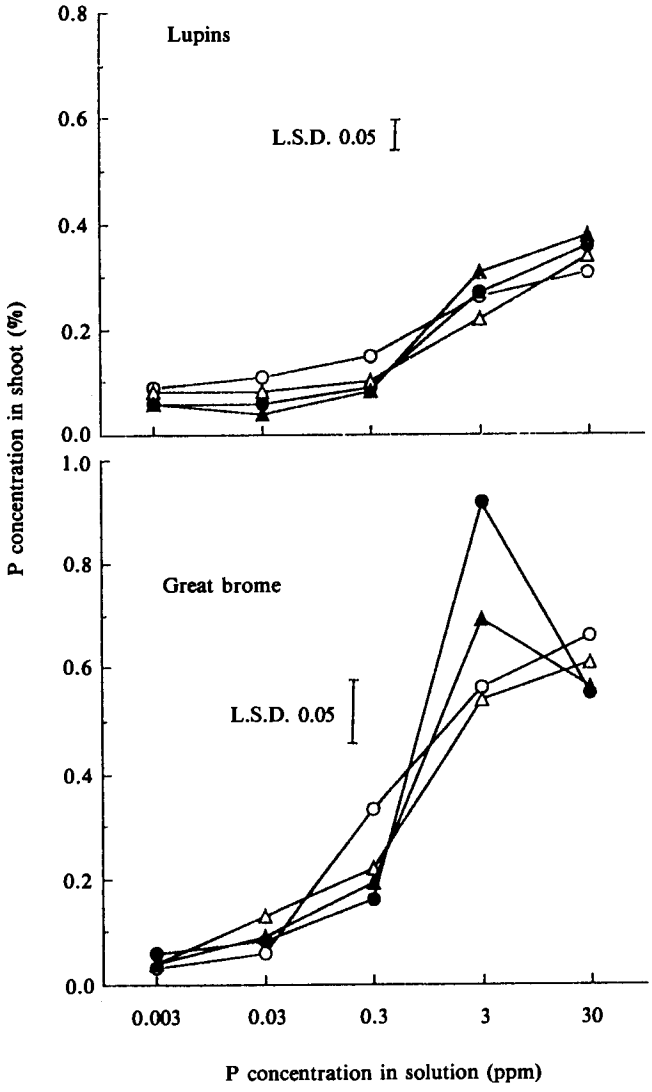

Figure 5. Effect of solution P concentration on shoot P concentration of lupins and great brome at 7 (○), 14 (●), 21 (△), and 28 (▲) days after transplanting. P concentration is plotted on a log scale.

The critical concentration, defined as the internal P concentration at 95% of the maximum RGR (average of the last two highest values), was approximately 0.4 mg P g^{-1} DM in great brome. It was not possible to estimate the critical P concentration in lupins from the data. Critical concentration also varied with the age of plant, a higher concentration being required in younger plants (Figure 6).

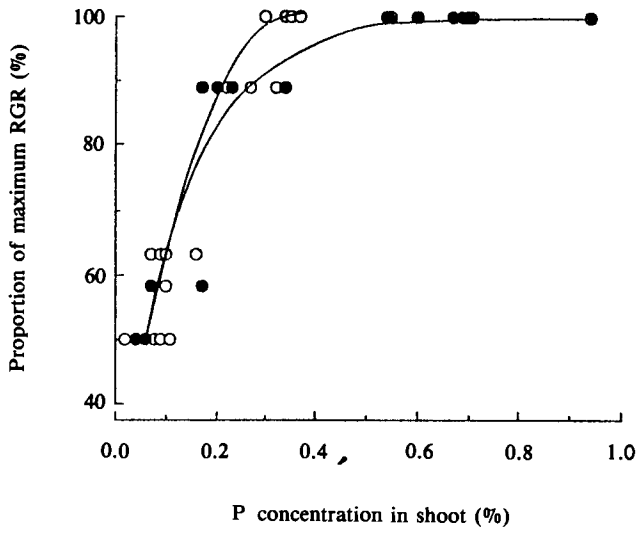

Figure 6. Association between shoot P concentration and proportion of maximum RGR of lupins (○) and great brome (●) 28 days after transplanting.

P utilisation and P productivity

The efficiency of P use for the rate of dry matter production (P productivity) was highest at the lower external P concentrations for both species (Table 4). Great brome P productivity was higher than lupins under a low P supply.

Table 4. The effect of P supply on rate of production of dry matter per unit P absorbed (P productivity) of lupins and great brome during vegetative growth (7 – 35 days after transplanting).

Species	Time after transplanting (days)					
		7 – 14	14 – 21	21 – 28	28 – 35	
	P concentration (ppm)	P productivity (gDM $mg^{-1}P\ d^{-1}$)				L.S.D. (p=0.05)
Lupins	0.003	0.057	0.059	0.131	0.097	0.047
	0.03	0.105	0.045	0.119	0.070	
	0.3	0.078	0.066	0.049	0.175	
	3.0	0.054	0.028	0.040	0.045	
	30.0	0.031	0.029	0.028	0.038	
Great Brome	0.003	0.074	0.078	0.089	–	0.034
	0.03	0.055	0.097	0.070	–	
	0.3	0.069	0.057	0.088	–	
	3.0	0.031	0.021	0.029	–	
	30.0	0.025	0.022	0.054	–	

The phosphorus utilisation quotient of lupins and great brome responded to external P supply differently (Figure 7). The quotient decreased rapidly for each increment of external P until the lowest values of 0.3 – 0.4 g DM in lupins or 0.1 – 0.2 g DM in great brome were reached at the highest P concentration. At the low P concentration range (0.003 – 0.3 ppm), P utilisation quotient increased with plant age but it was stable at high P concentrations (3 – 30 ppm). Lupins had a higher P utilisation quotient than great brome, particularly between 0.03 – 0.3 ppm.

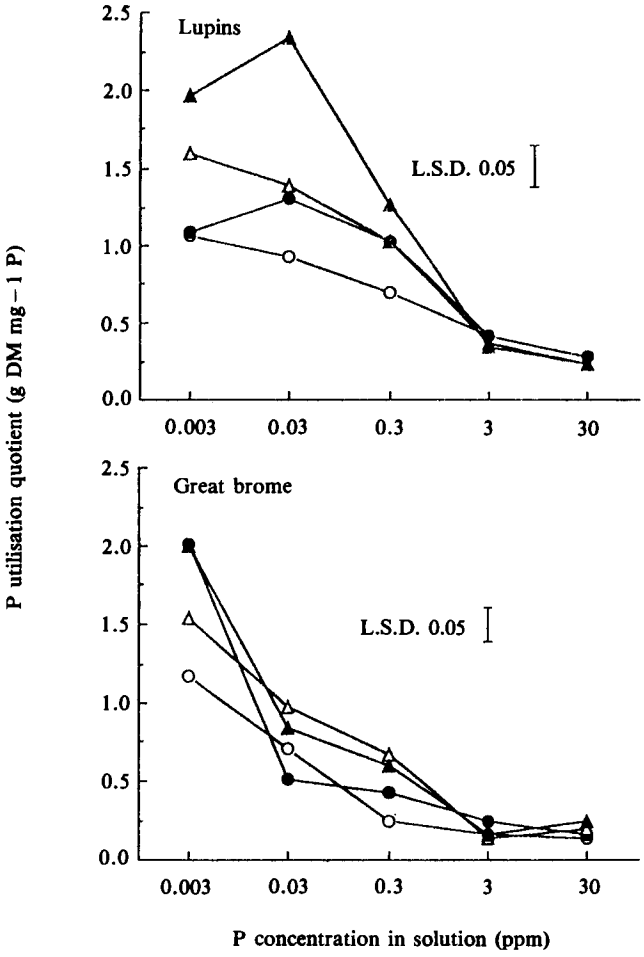

Figure 7. Effect of solution P concentration on the P utilisation quotient of lupins and great brome at 7 (○), 14 (●), 21 (△) and 28 (▲) days after transplanting. P concentration is plotted on a log scale.

Phosphorus productivity was more sensitive when comparing the efficiency of P use between these two

species which were significantly different in dry matter and P content.

Discussion

The relative growth rate and internal P concentration of both species increased with increasing external P concentration. Great brome, however, not only had double the RGR of lupins but also achieved maximum RGR at a lower external P supply than lupins; a consequence of the higher production of leaf area per unit shoot weight at lower external P supply. This provides evidence that both species have very different growth characteristics since the rate of dry matter production per unit leaf area (NAR) of great brome increased with time while that of lupins declined. In lupins, the increase in leaf area production possibly caused shading and a change in the balance between respiration rate and photosynthetic rate (Evans, 1972). Having higher RGR, great brome overcame its disadvantage of initial plant size (lupins were 45 times larger than great brome) since at 28 days great brome was nearly the same size as lupins, particularly at high P supply.

Evidently, RGR of both species declined when P was supplied in the range 0.003 – 0.3 ppm, as the internal concentration in the plant ranged between 0.06 – 0.22% in great brome and 0.08 – 0.10% in lupins (data averaged from 7 – 28 days after transplanting). However, there were no visual symptoms of P deficiency apart from stunted growth. The small range of P concentration in lupins (0.08 – 0.1%) at these levels of P supply suggested that they were dependent mainly on P in seed reserves. From 14 days after transplanting, at 3 ppm of P supply, the relative uptake rate exceeded the relative growth rate of lupins which resulted in an increase of P concentration in the shoot. The critical concentration of P supply for 95% of maximum RGR of great brome was 0.4%. These results are consistent with those of Gill (1985). The data in this study were not suitable for discerning the critical internal concentration for growth of lupins.

The greater ability of great brome to achieve maximum flux at lower external P concentration (3 ppm) than lupin could be attributed to complex internal mechanisms. Nevertheless, this experiment demonstrated that this can be expressed in the higher root absorbing power (α) of great brome. Furthermore, α of great brome was mainly influence by its high RGR and high tissue P concentration. The high value of α in lupins at the first harvest and lowest external P concentration was possibly due to the high specific root surface area ($w/2\pi$ aL) at that stage.

The decrease in root absorbing power as the plant aged was not a simple change, since α is a consequence of interacting factors determined by plant growth and uptake (Nye and Tinker, 1977). The decline of α with higher external concentration and plant age may be simply explained by plant demand (Nye and Tinker, 1977; Wild and Breeze, 1981). Plant P demand generally decreased with age as the proportion of meristematic tissue declined and phosphate was retranslocated from mature tissue to the growing points. However, in this experiment the plant demand, expressed as the relative uptake rate, did not significantly decline because only the early stages of vegetative growth were studied. It was evident that, as plants aged, root growth rate increased while relative uptake rate was approximately stable so that at 28 days, a flux of only 20 – 25% of that which occurred at 7 days was sufficient to sustain maximum RGR. Similar results were demonstrated in corn by Mengel and Barber (1974).

When making comparisons at the same age and P supply, the root demand coefficient ($a\alpha$) of lupins was generally higher than that of great brome because of the higher lupin mean root radius. This evidence contradicted that of Nye (1977), who determined that $a\alpha$ of *Bromus rigidus* was higher than that of *Lupinus digitatus*. The calculation was derived from data of Loneragan and Asher (1967) who did not measure root radius. Nye had

assumed equal root radius (0.015 cm) of these two species, and this appears to be responsible for the contradiction with the present result.

When considering the P utilisation quotient, lupins were more efficient. However, the utilisation quotient was considered to be not subtle enough to compare species of different growth rates, development and plant size. Phosphorus productivity would be more sensitive for comparison of these two species. At early growth, 7 – 21 days, great brome had a higher efficiency of use of internal P by producing more rapid growth at the lowest P supply. However, the growth rate of lupins per unit internal P was higher at 0.03 ppm P supply. These two characteristics of P efficiency also changed with plant age which was also a feature of the experiment of Lastuvka and Minar (1970).

These results revealed some possible mechanisms of competition between these two species particularly the higher competitive ability of great brome when P is in limited supply.

Acknowledgments

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