Aust. J. Agric. Res., 1975, **26**, 423–36

Physiological Responses of Semiarid Grasses. I The Influence of Phosphorus Supply on Growth and Phosphorus Absorption

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Abstract

Experiments were carried out under controlled conditions to investigate the physiological bases for species differences in yield and nutrient responses to variations in phosphorus supply. Buffel grass (*Cenchrus ciliaris*), and to a less extent Mitchell grass (*Astrebla elymoides*), showed a much larger yield response to increasing phosphorus supply than mulga grass (*Thyridolepis mitchelliana*). Mitchell and mulga grasses had much lower relative growth rates than buffel grass. Mulga grass required a lower external phosphorus concentration for optimal growth than Mitchell and buffel grasses; this was attributed to its superior system for absorbing and transporting phosphate from low concentrations, but was not associated with any yield advantage, yield being related more to the photosynthetic than to the nutritional characteristics of the plants.

Differences between species in their external phosphorus requirements for growth and their distribution in semiarid Queensland are discussed.

Introduction

Although it has been established that semiarid native plant communities have a lower production than sown buffel pastures (Ebersohn 1970), the physiological bases underlying these differences have not been explored, and little is known of the response of native species to environmental factors. In this work the physiological responses to temperature, soil phosphorus and water supply of two valuable native grasses were compared with those of buffel grass (*Cenchrus ciliaris* L.), an introduced species of wide edaphic tolerance. The development of the root systems was also investigated because of its influence on the uptake of nutrients and water. *Thyridolepis mitchelliana* (Nees) S. T. Blake, a ground-storey component of the mulga shrublands of south-west Queensland, has long been regarded as one of the more valuable mulga grasses (Turner 1895), but in most situations has been seriously depleted by overgrazing (Whittet 1964). *Astrebla elymoides* F. Muell. ex F. M. Bailey, the other native species investigated in this work, together with *Astrebla lappaceae* (Lindl.) Domin forms the characteristic community of the rolling Mitchell grass downs of central-western Queensland (Blake 1938).

The soil phosphorus concentration of the mulga communities of south-west Queensland is much less than that of the Mitchell grasslands of central-western Queensland (Skerman 1958), but little is known of the physiological responses of these grasses to phosphorus supply. This paper describes the effect of phosphorus supply on the growth of, phosphate absorption by, and transport in *Thyridolepis mitchelliana* (mulga Mitchell, hereafter called mulga grass), *Astrebla elymoides*

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(Mitchell grass) and Biloela buffel grass. In the first experiment the effect of phosphorus supply on the growth of and phosphate absorption by these three grasses was examined. The second was a study of the relationship between rate of absorption and rate of transport of [^{32}P]phosphate by mulga and buffel grasses.

Experiment 1

Materials and methods

Plant Culture

The test plants were grown in standard solution culture over a range of phosphorus concentrations, with the other nutrients at or near optimal levels. Intact caryopses of each species were sterilized in a dilute solution of calcium hypochlorite, rinsed thoroughly with demineralized water, and then raised in coarse sand for 4 days at 28°C in a growth cabinet. By this time the first leaf on all seedlings had fully expanded. Each seedling was transferred to a polyethylene vessel containing 4·5 l. of nutrient solution (Arnon 1938), the vessels being arranged in randomized blocks. The base of the stem of the seedlings was in contact with the solution. Air, filtered through activated charcoal and cotton wool, was supplied to all pots for 40 min in every hour. The pH (5·5–6·0) was checked daily and adjusted when necessary. The temperature of the glasshouse varied from 22 to 32°C, and the mean total solar radiation was 24·4 MJ m^{-2} day^{-1}.

In the main experiment there were five 10-fold increments in concentration from 0·003 ppm (10^{-7}M) to 30·0 ppm (10^{-3}M) phosphorus. These levels were chosen after an initial trial. Ammonium dihydrogen phosphate was the source of both phosphorus and ammonium nitrogen, and the level of the latter was kept constant by adding ammonium sulphate as required. Solutions were renewed weekly for the first 3 weeks and thereafter twice weekly. Subsequent analyses showed that not more than 15% of the solution phosphorus was absorbed in any treatment, except between weeks 5 and 6, when up to 30% was absorbed in some of the high phosphate treatments.

Harvesting and Chemical Analysis

Dry weights of emerged leaves, stems (including leaf sheath) and roots were obtained at six harvests taken at weekly intervals after transplanting. Leaf areas were measured by means of an integrating photometer. Two replicates of the root system of each treatment were selected at each of the first three harvests and photographed, so that total length and diameter of the root system could be estimated.

The shoot (leaves, stems and inflorescence where applicable) and root components were ground, and duplicate subsamples dry-ashed for 24 hr and then digested in 6N hydrochloric acid. After dilution, phosphorus concentration in the digest was determined by the molybdenum blue method with ascorbic acid as reductant (Williams and Twine 1967). The optical density of the phosphomolybdate complex was determined at 820 nm on a Unicam SP1800 spectrophotometer.

Growth Analysis

The least squares method was used to fit polynomials to the regressions of the natural logarithms of the weights and leaf areas on time. Cubic equations were found to be adequate.

The derived equations were of the form

$$\log_e W = a + bt + ct^2 + dt^3, \tag{1}$$

and

$$\log A = e + ft + gt^2 + ht^3, \tag{2}$$

where W was total plant dry weight (mg), A leaf area (cm^2) and t time in days.

Differentiation of equation (1) gave tnstantaneous values of the relative growth rate (R_W)

$$\frac{d(\log_e W)}{dt} = \frac{1}{W}\frac{dW}{dt} = b + 2ct + 3dt^2. \tag{3}$$

Instantaneous values of the net assimilation rate (E_A) were derived from the expression

$$E_A = \frac{1}{A}\frac{dW}{dt} \tag{4}$$

from the fitted curves of leaf area and total plant dry weight on time. Estimates of the leaf area ratio (F_A) were obtained from the relationship

$$F_A = 7(R_W/E_A). \tag{5}$$

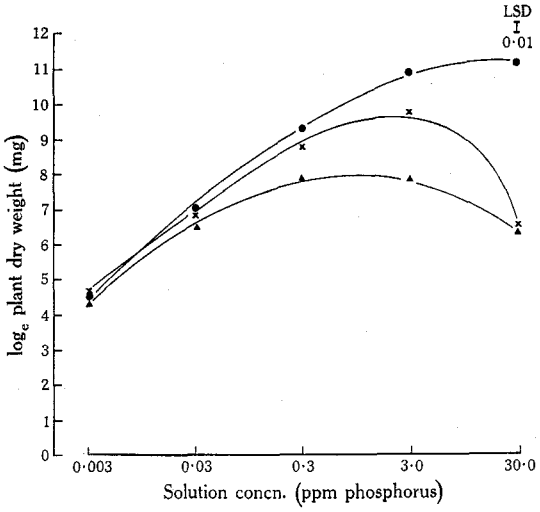

Fig. 1. Dry weight achieved in 6 weeks by mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses over the solution concentration range 0·003–30·0 ppm phosphorus.

Results

Buffel grass responded to phosphorus concentration over the whole range, the growth at the end of the experiment being greatest at 30·0 ppm but varying little between 3·0 and 30·0 ppm phosphorus (Fig. 1). The optimal solution concentrations for growth of mulga and Mitchell grasses were about 0·3 ppm and 3·0 ppm phosphorus respectively. The growth of both native grasses was greatly reduced at 30·0 ppm phosphorus, mulga grass to 20% and Mitchell grass to 3% of their yield at the optimum concentration. The final dry weight of buffel grass was greater than both native grasses over the entire range except at 0·003 ppm phosphorus. A summary of growth characteristics at the end of the experimental period is shown in Table 1.

Mulga grass had greater shoot/root ratios at low concentrations than Mitchell and buffel grasses, but the ratio for mulga grass did not vary greatly with concentration. In contrast, the shoot/root ratios of Mitchell and buffel grasses increased greatly with concentration. At the lowest concentration plants did not tiller, and species differences in leaf area were small. At phosphorus concentrations of 0·03 ppm and 0·3 ppm, mulga grass had more tillers and leaves than either Mitchell or buffel grasses, but this did not result in any advantage in leaf area because mean leaf size was smaller. Up to 30·0 ppm phosphorus, buffel grass had greater tiller and leaf numbers, as well as a larger area of individual leaves, than the native grasses. At the highest concentration, the leaf and tiller numbers of both native grasses were considerably reduced.

Table 1. Growth characteristics at the end of the experimental period

Parameter	Species	Phosphorus concentration (ppm): 0·003	0·03	0·3	3·0	30·0
Total dry weight (g)	mulga	0·073	0·64	2·41	2·50	0·52
	Mitchell	0·103	0·90	5·85	17·86	0·57
	buffel	0·088	0·94	12·43	52·83	83·32
Dry weight of shoots (g)	mulga	0·046	0·45	1·84	2·03	0·42
	Mitchell	0·062	0·64	4·71	16·60	0·51
	buffel	0·045	0·49	9·45	49·08	79·19
Dry weight of roots (g)	mulga	0·027	0·19	0·57	0·47	0·10
	Mitchell	0·041	0·36	1·14	1·26	0·06
	buffel	0·043	0·45	2·98	3·75	4·13
Shoot/root ratio	mulga	1·7	2·4	3·2	4·3	4·2
	Mitchell	1·5	1·8	4·1	13·2	8·5
	buffel	1·0	1·1	3·2	13·1	19·2
Tiller number	mulga		5	29	31	9
	Mitchell		4	17	32	4
	buffel		1	8	39	48
Total number of emerged leaves	mulga	8	35	124	119	49
	Mitchell	7	23	116	206	30
	buffel	7	11	59	253	288
Leaf area (cm^2)	mulga	5·1	38	252	263	73
	Mitchell	5·7	55	312	1398	63
	buffel	6·7	44	545	2720	4396
Mean area of leaf (cm^2)	mulga	0·6	1·1	2·0	2·2	1·5
	Mitchell	0·8	2·4	2·7	6·8	2·0
	buffel	0·9	4·0	9·2	10·8	15·2

Three phases of growth were evident: (i) an initial phase of slow seedling growth for the 7-day period following transplanting; (ii) a period of almost constant growth up to day 32; (iii) a later decline in most treatments, except for all species at the lowest concentration and both native grasses at the highest concentration. From the fitted curves for dry weight (whole plant) on time, the average relative growth rates for the seedling (days 4–11) and the vegetative (days 12–32) growth phases were calculated (Fig. 2). Relative growth rates (RGR) of all species were greatly reduced at 0·003 ppm phosphorus. Buffel grass had higher seedling RGR values than both native grasses for the concentration range 0·03 ppm to 30·0 ppm phosphorus, and

this superiority was maintained during the vegetative growth stage. Both native grasses, and particularly mulga grass, showed smaller variations in RGR as phosphorus

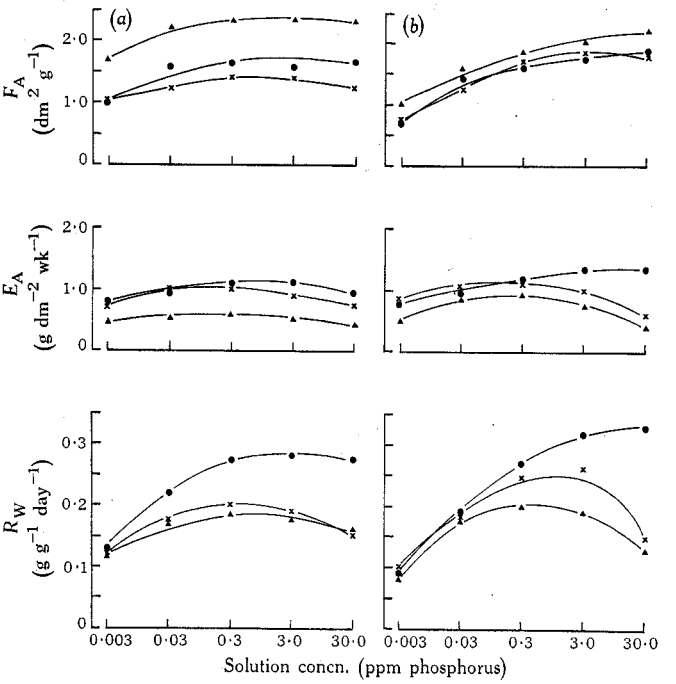

Fig. 2. Influence of phosphorus supply on relative growth rate (R_W), net assimilation rate (E_A), and leaf area ratio (F_A) of mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses during (*a*) seedling growth (days 4–11) and (*b*) vegetative growth (days 12–32).

concentration increased than buffel grass. At solution concentrations of optimal or near optimal phosphorus supply, values of RGR during vegetative growth were

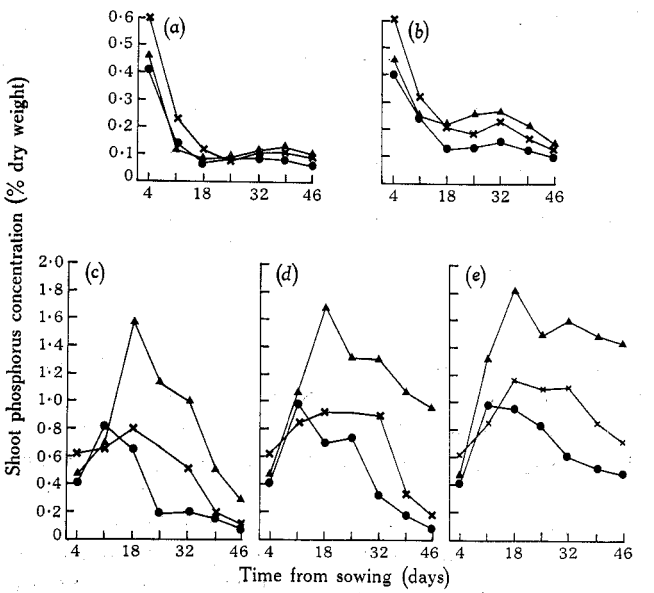

Fig. 3. Influence of phosphorus supply on shoot phosphorus concentration of mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses, at solution concentrations of (*a*) 0·003 ppm; (*b*) 0·03 ppm; (*c*) 0·3 ppm; (*d*) 3·0 ppm; (*e*) 30·0 ppm phosphorus. Note that *y*-axes of (*a*) and (*b*) differ from those of (*c*)–(*e*).

higher than at the seedling stage, and this was associated mainly with increases in the net assimilation rate of mulga and buffel grasses and the leaf area ratio of Mitchell

grass. The lower RGR values of mulga grass compared with Mitchell and buffel grasses over the whole phosphorus concentration range resulted from its lower net assimilation rates, and this was associated with greater leaf area ratios (Fig. 2). The reductions in RGR of both native grasses at 30·0 ppm phosphorus were associated primarily with decreases in net assimilation rate, whereas the low RGR values for all species at the lowest concentration resulted mainly from low leaf area ratios.

Uptake of Phosphorus

The phosphorus concentration in shoots and roots increased with the solution concentration; both native grasses, especially mulga grass, had high tissue concentrations (Figs. 3, 4). At solution concentrations of 0·003 and 0·03 ppm phosphorus,

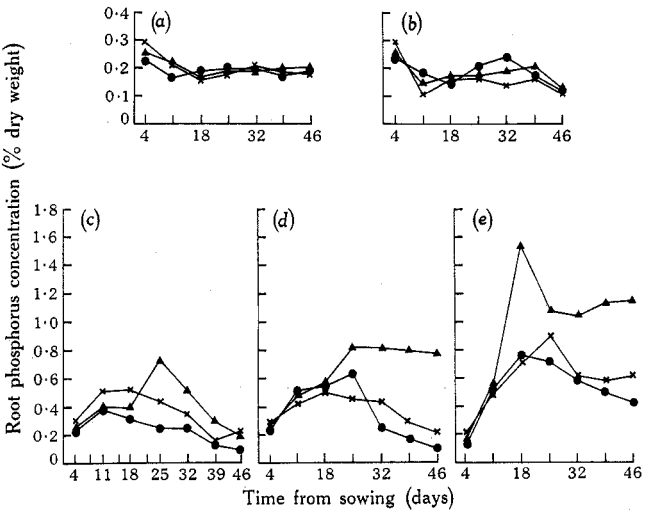

Fig. 4. Influence of phosphorus supply on root phosphorus concentration of mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses, at solution concentrations of (*a*) 0·003 ppm; (*b*) 0·03 ppm; (*c*) 0·3 ppm; (*d*) 3·0 ppm; (*e*) 30·0 ppm phosphorus. Note that *y*-axes of (*a*) and (*b*) differ from those of (*c*)–(*e*).

tissue concentrations decreased with time, but between 0·3 ppm and 30·0 ppm the tissue concentrations tended to increase with time up to about day 18 before declining. At a solution concentration of 0·003 ppm phosphorus, the phosphorus concentration was greater in roots than in shoots over most of the experimental period. At 0·03 ppm, the phosphorus concentration in both native grasses was greater in shoots than in roots: in buffel grass the reverse applied. An important factor in transport of phosphorus to the shoots is the relative sizes of shoots and roots. Values for the shoot/root ratio were fairly constant between days 12 and 32, except in Mitchell and buffel grasses at near-optimal phosphorus concentrations, where the ratio increased after day 25. The distribution index (ratio of phosphorus absorbed to

phosphorus transported to the shoots in a given time) was greater for mulga, and to a smaller extent for Mitchell grass, than for buffel grass when the relative proportions of shoots and roots were taken into account (Fig. 5). As the solution concentration increased, the shoot/root ratio and distribution index increased in all species, but both declined in mulga and Mitchell grass at the highest concentration.

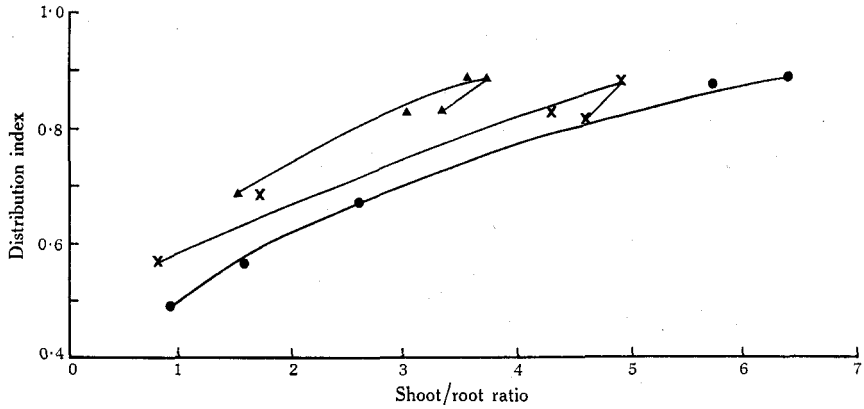

Fig. 5. Influence of shoot/root ratio on the distribution index of mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses during vegetative growth (days 12–32).

Over the vegetative growth period large responses in relative growth rate were recorded, as the tissue concentration increased up to about 0·3, 0·65 and 0·63% for mulga, Mitchell and buffel grasses respectively; above these levels smaller increases in growth rate occurred. At a solution concentration of 30·0 ppm phosphorus, the high shoot concentrations found in mulga and Mitchell grasses respectively were associated with a reduction in relative growth rate (Figs. 2, 3).

Table 2. Total phosphorus absorbed after 28 days' growth in culture solutions of different phosphorus concentrations

Solution concentration (ppm)	Phosphorus uptake (mg)		
	Mulga grass	Mitchell grass	Buffel grass
0·003	0·02	0·03	0·02
0·03	0·4	0·5	0·8
0·3	2·6	5·7	6·6
3·0	3·1	7·6	33·4
30·0	1·1	1·2	69·2

The total amounts of phosphorus absorbed over the first 28 days of growth are shown in Table 2. At 0·003 ppm phosphorus, uptake was negligible. Responses to increases in concentration were large at low levels but at high levels became insignificant or negative.

The rate of phosphorus absorption per unit weight of root was derived from the fitted curves or root dry weight and absolute phosphorus content (whole plant)

on time following Williams (1948), who pointed out that the instantaneous rate of intake I_P of phosphorus per unit weight of roots is given by

$$I_P = \frac{1}{W_R}\frac{dP}{dt}, \tag{6}$$

where W_R is the weight of the root system at any particular instant. As with relative growth rate, two fairly constant phases of absorption were evident over the seedling growth (days 4–11) and vegetative growth (days 12–32) stages. In plants at near-optimal phosphorus concentrations, I_P values were greater during vegetative growth than during seedling growth, whereas in phosphorus-deficient plants I_P declined following seedling growth, as external supply limited growth (Fig. 6). Average values for I_P at the seedling stage increased with solution concentration up to 0·3 ppm phosphorus for both native grasses and to 30·0 ppm for buffel grass; during vegetative growth, when plants were dependent on external phosphorus for their requirements, the absorption rate continued to increase up to 0·3, 3·0, and 30·0 ppm for mulga, Mitchell and buffel grasses respectively (Fig. 6). At solution concentrations

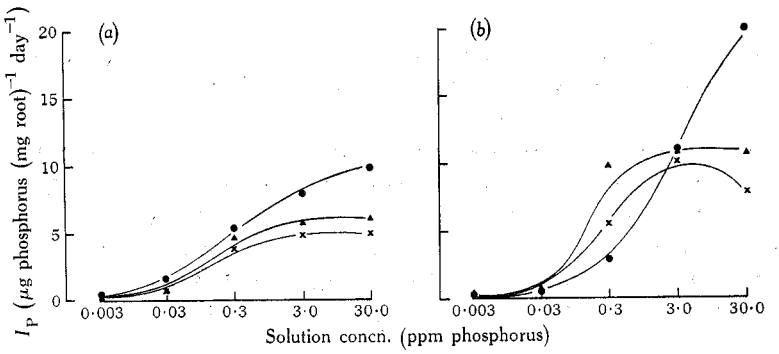

Fig. 6. Influence of phosphorus supply on the rate of phosphate absorption per unit weight of root (I_P) by mulga (▲—▲), Mitchell (×—×) and buffel (●—●) grasses, during (*a*) seedling growth (days 4–11) and (*b*) vegetative growth (days 12–32).

less than 0·03 ppm phosphorus, values for I_P during vegetative growth were less than 2 μg phosphorus (mg root)$^{-1}$ day^{-1}, which was too low to support rapid vegetative growth. Tissue phosphorus concentrations were low, plants showed symptoms of phosphorus deficiency, and relative growth rates were reduced. As solution phosphorus increased to the optimal concentration for growth in each species, I_P values increased to about 10 μg phosphorus (mg root)$^{-1}$ day^{-1} during vegetative growth, the tissue phosphorus concentration increased, deficiency symptoms disappeared and the growth rate increased; there were, however, large species differences in relative growth rate at this absorption rate (Figs. 2, 6). Any further increases in absorption rate did not increase the growth rate, and phosphorus tended to accumulate in the tissues at concentrations greater than that necessary for optimum growth.

Over the 3-week period of growth when root lengths were recorded, large differences in the ratio of root length to root weight occurred: mean values varied from 138 to 366 m g^{-1}, with an overall mean of 240 m g^{-1}. This is slightly higher than the value of 210 m g^{-1} recorded in sand culture (Christie 1975), but plants grown in solution culture were much larger and root systems, particularly at near-optimal concentrations, were better developed; the maximum lengths of the whole root system at day 25 were 380, 1660 and 4980 cm for mulga, Mitchell and buffel grasses respectively. Lateral roots of the nodal system contributed most of the length of the root system after day 18, and this was associated with high values for the root length/weight ratio. At near-optimal phosphorus supply, the seminal system of mulga and Mitchell had died after about 35 days and that of buffel plants after 25 days. The average root diameter for the whole root system was also influenced by stage of growth and external concentration. Mean values for the 3-week growth period are shown in Table 3. These did not vary much from 0·003 to 3·0 ppm phosphorus, but there was a large increase for all species at 30·0 ppm. Both native grasses had 'finer' root systems than buffel grass.

Table 3. Influence of solution phosphorus concentration on the average diameter of the whole root system

Mean values for the 3-week period following transplanting

Solution concentration (ppm)	Average root diameter (μm)		
	Mulga grass	Mitchell grass	Buffel grass
0·003	349	344	371
0·03	356	372	408
0·3	353	332	415
3·0	341	338	428
30·0	409	420	524

Nutrient uptake has been related to the surface area of the root system and the external concentration. In the present study a curvilinear relationship was found between area and the flux of phosphorus across the root surface. The flux of phosphorus into the root can be represented by

$$F = \alpha C_r, \tag{7}$$

where F is the flux of phosphorus ions across the root surface (kg m^{-2} sec^{-1}), C_r the concentration of ions at the root surface (kg m^{-3}), and α the mean root uptake coefficient—a coefficient expressing the proportionality of flux to concentration (m sec^{-1}).

As might be expected, values of α decreased as external concentration increased (Table 4). Values of α tended to decline with time, but under some treatments showed increases after day 18. As the growth of the seminal system also declined after about day 18, these increases might be attributed to the nodal system. Both native grasses generally had superior absorbing power at low external concentrations but buffel grass had superior values at the highest concentrations.

As nutrient uptake (P) is proportional to the root surface area and the external concentration, then

$$\frac{dP}{dt} = 2\pi rL\alpha C_r, \tag{8}$$

where r is the root radius (cm) and L is the root length (cm). Also, as Nye and Tinker (1969) point out, over a period of weeks the continuation of uptake clearly depends on the growth of the plant, so that

$$\frac{dP}{dt} = \frac{d(XW)}{dt} = \frac{X\,dW}{dt} + \frac{W\,dX}{dt}, \tag{9}$$

where X is the mean phosphorus concentration in the plant (g g^{-1}) and W is the total plant dry weight (g). Equating (8) and (9),

$$\alpha = \frac{W}{2\pi rL}\frac{X}{C_r}\left(\frac{1}{W}\frac{dW}{dt} + \frac{1}{X}\frac{dX}{dt}\right). \tag{10}$$

Table 4. Effect of solution phosphorus concentration on the mean root uptake coefficients for phosphorus (α)

Species	Time (days)	Root uptake coefficient (10^{-8}M sec^{-1}) Solution concentration (ppm P): 0·003	0·03	0·3	3·0	30·0
Mulga grass	4	344	415	171	19	2·0
	11	297	128	95	12	1·2
	18	181	133	98	9	0·9
	25	215	235	127	13	0·7
Mitchell grass	4	1096	388	209	17	2·0
	11	333	214	79	7	0·7
	18	269	107	49	9	0·5
	25	147	131	53	7	0·7
Buffel grass	4	326	596	178	17	2·0
	11	146	205	100	16	2·0
	18	62	98	36	16	1·8
	25	69	51	20	9	1·3

Therefore, the root absorbing power may be regarded as a function of the plant dry weight per unit surface of root ($W/2\pi rL$), the ratio of internal concentration to external concentration at the root surface (X/C_r), the relative growth rate $(1/W)dW/dt$, and the relative concentration change $(1/X)dX/dt$. Changes in α would be reflected in any of these physiological factors, or more accurately in the relative changes between them. For all values recorded, the multiple regression on specific root surface, concentration ratio, and relative growth rate accounted for 91·7% of the variation in α. Furthermore, the partial correlation coefficients of these parameters indicated that α was influenced mainly by the concentration ratio ($r = 0{\cdot}86^{**}$) rather than the specific root surface ($r = -0{\cdot}06$) or relative growth rate ($r = -0{\cdot}12$); the latter two parameters increased as α declined.

** Significant at $P = 0{\cdot}01$.

Experiment 2

Materials and methods

Plant Culture

Plants were raised on coarse sand in a growth cabinet maintained at $27 \pm 1°C$. The seeds were sown at times such that seedlings of each species had two expanded leaves when they were transferred into the culture vessels. The vessels were 7 l. plastic drums, and each contained 15 seedlings. The plants were grown in complete nutrient solutions with a phosphorus concentration of either 0·03 or 3·0 ppm. The pH was maintained at 5·5–6·0 and the solutions were renewed daily. Each vessel was aerated continuously with a supply of filtered compressed air. The experiment was carried out in a 'Sherer' controlled environment cabinet (model CEL 37–13) at a constant temperature of $27 \pm 1°C$ and $50 \pm 10\%$ relative humidity. The photoperiod was 14 hr and the total irradiance was 6·93–7·35 MJ m^{-2} day^{-1}, depending on position. There were two replicates of each treatment arranged in blocks along the length of the cabinet.

Table 5. Influence of phosphorus concentration on the rate of absorption and rate of transport of [^{32}P]phosphate to the shoot

Species	Rate of absorption (μg P (mg dry root)$^{-1}$ day^{-1})		Rate of transport (μg P (mg dry root)$^{-1}$ day^{-1})	
	0·03 ppm P	3·0 ppm P	0·03 ppm P	3·0 ppm P
Mulga	1·1	8·7	0·48	2·9
Buffel grass	0·7	7·8	0·21	3·4

Harvesting and Chemical Analysis

Following 20 days' growth in the cabinet, the nutrient solution in each container was replaced by a nutrient solution of equivalent composition containing 50 μCi of carrier-free [^{32}P]phosphate. Sequential harvests were taken 1, 2, 4, 6 and 8 hr later. At each harvest, three seedlings per replicate were removed from each treatment and carefully separated into root and shoot components to follow the movement of radioactivity from the solution to and within the plant. To remove any [^{32}P]phosphate from the free space, the roots were washed for 9 min in non-radioactive nutrient solution at 1°C. They were then carefully blotted dry, placed in air-tight vials and fresh weights recorded. Shoot samples were also placed in air-tight vials at harvest and weighed. Roots from some samples of unlabelled material were oven-dried and weighed to determine root moisture content.

The fresh plant samples were digested in a mixture of nitric and perchloric acid. Radioactive phosphorus was counted with a liquid scintillation counter. All counts were adjusted for decay and specific activities calculated. On the assumption that no significant exchange of phosphate occurred in the roots, the amounts of phosphate absorbed by the roots and transported to the tops were calculated from the known specific activity of the phosphate solution.

Results

At both solution concentrations the phosphorus uptake was linear throughout the experiment. The transport of phosphorus was low initially but increased to an almost constant level after 4 hr, which indicated a lag of up to 4 hr between the absorption of a phosphate molecule and its subsequent export to the shoot. Estimated mean daily values for rate of uptake and rate of transport of phosphorus at the steady state, corrected for root dry weight, are shown in Table 5.

Discussion

Gerloff (1963) suggests that native plants occurring on infertile soils not only may have the capacity to survive and grow in these areas, but may have adapted to them in having a slow growth rate and a low yield response as the nutrient supply increases. This is so in mulga grass, as is evident when the relative yields of the three species (as percentages of maximum) are compared. After 6 weeks' growth at a solution concentration of 0·03 ppm phosphorus, mulga grass produced 25% of its maximum yield, compared with 5% and 1% for Mitchell and buffel grasses respectively. Evidently the higher relative yield of mulga grass at low concentrations was due to superior ability to absorb and transport phosphorus rather than to function at a lower internal concentration, since the concentration of phosphorus in the shoots was higher at all solution concentrations. The critical phosphorus concentration, i.e. the minimal concentration of nutrient present in the plant at maximal growth, was estimated as 0·25% for buffel grass tops at the immediate preflowering stage of growth (Andrew and Robins 1971). In this study, corresponding values at an almost similar growth stage were *c.* 0·48, 0·34 and 0·30% for mulga, Mitchell and buffel tops respectively. Antonovics *et al.* (1967) suggested that low yield may have considerable adaptive significance for plants on soils of low fertility, as they would make less demands on the soil nutrient supply. In addition, as suggested by Nassery (1970), a slow growth rate may allow more time for retranslocation of phosphorus from old tissues to the meristems; this permits a more efficient utilization of phosphorus for growth. The retention of phosphorus in the roots of phosphorus-deficient plants, particularly buffel grass, was consistent with the usual finding that requirements of tissues nearest the source of supply of a scarce metabolite tend to be satisfied at the expense of those further away (Williams 1948); Loneragan and Asher (1967) regard the distribution of phosphorus between shoots and root as the cause rather than the result of changes in the shoot/root ratio.

Measurements of relative growth rate made during seedling growth provide a good general index of the intrinsic physiology of the plant. The highest relative growth rates of mulga, Mitchell and buffel grasses measured during this study were 0·20, 0·26, and 0·33 g g^{-1} day^{-1}. This compares with maximum rates of 0·14–0·16 for C_3 grasses (Biddiscombe *et al.* 1969), 0·41–0·55 for some C_4 grasses (Ludlow and Wilson 1970), and 0·36 g g^{-1} day^{-1} for buffel grass grown in a plant house in south-western Queensland (Christie 1970).

The values found for net assimilation rate indicate that mulga grass may have a less efficient photosynthetic system than Mitchell or buffel grasses, and consequently that photosynthetic factors, rather than absorption or transport of phosphorus, are responsible for its lower yield. The supply of phosphorus, however, may have had an effect on the rate of photosynthesis. At 30·0 ppm the net assimilation rate of both

native grasses declined. Phosphorus interactions are complex, and it is well known that iron and potassium deficiency, as well as accumulation and damage in the apical regions of the youngest leaves, can be induced by an excess of phosphorus (Mullinson 1941; Biddulph and Woodridge 1952; Miller *et al.* 1960; Green and Warder 1973). These aspects were not pursued in this study. Also, it has been found in wheat that increasing applications of superphosphate beyond the rate required for maximum yield reduced net photosynthesis, and this was associated with increases in stomatal and residual resistances (Cartwright, personal communication). This tends to support the view that the decline in net assimilation rate at a solution concentration of 30·0 ppm phosphorus was a causal factor in the reduced growth of the native grasses. A need for further investigation is indicated.

It is difficult to extrapolate the results of solution culture experiments to soil, because the pattern of distribution of roots is different in soil, and different factors contribute to the supply of ions to the root surface. A close correlation has often been found between nutrient culture responses and the observed distribution of various grass species in the field, in relation to soil phosphorus concentration (Bradshaw *et al.* 1960), and in the present experiments the optimum concentrations in solution compared well with those in the soil. For example, the available phosphorus concentration of the soil group on which mulga grass occurs has been reported as 5–15 ppm (mean 8 ppm) by Christie (1970), and that of the soil group on which Mitchell grass is found in central-western Queensland as 2–306 ppm (mean 121 ppm) by Hubble and Beckmann (1956). Buffel grass requires a minimum concentration of 25 ppm phosphorus to establish successfully on mulga soils, and its establishment and rapid spread has only occurred on soils with high phosphorus concentrations such as the gidyea (*Acadia cambagei*) soils of central-western Queensland where available concentrations vary from 15 to 164 ppm (mean 104 ppm) (Christie, unpublished data). The differences between species in external phosphorus requirements for growth suggest that response to phosphorus is one aspect of the physiological adaptation of populations to soil conditions. Photosynthetic ability, however, is also important, as are responses to other mineral nutrients and soil physical conditions.

Acknowledgments

This work was carried out while one of us (E.K.C.) held an Australian Wool Corporation scholarship at Macquarie University. We gratefully thank Mr P. G. Hughes for writing the computer programs, Professor F. L. Milthorpe for criticism of the manuscript and Mr P. Milham for advice on plant phosphorus analyses.

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Manuscript received 1 August 1975