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Phosphorus efficiency of plants

I. External and internal P requirement and P uptake efficiency of different plant species

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Abstract

Plant species differ in their P efficiency, *i.e.* the P content in soil needed to reach their maximum yield. The differences in external P requirements can be attributed to either a lower internal P requirement for optimum growth or higher uptake efficiency of the plant. The objective of this research was to investigate the reasons for different P efficiencies of seven plant species.

Onion, ryegrass, wheat, rape, spinach, tomato and bean were grown in a P-deficient subsoil fertilized with 0, 2, 5, 10, 20, 40 and 80 mg P 100 g^{-1}. All species showed a strong yield increase due to P fertilization. To reach 80% of maximum yield onion and tomato needed 17 and 11 mg P 100 g^{-1} respectively, corresponding to a soil solution concentrations of 6.9 and 5.7 μmol P l^{-1}, whereas ryegrass, wheat and rape needed about 5 mg P 100 g^{-1} corresponding to only 1.4 μmol P l^{-1} in soil solution. These differences in external P requirement cannot be explained by differences in their internal P requirement since onion, with the highest external P requirement, only contained 0.14% P in the shoot at 80% of maximum yield, while wheat, as the most P efficient species, contained 0.28%.

P efficiency was related to the uptake efficiency of the plant which is determined by both root-shoot ratio and absorption rate per unit of root (influx). Species of low efficiency such as onion, tomato and bean had low influx rates and low root-shoot ratios, whereas species of medium to high efficiency had either high influx rates (rape and spinach) or high root-shoot ratios (ryegrass and wheat). The combination of both high influx rate and high root-shoot ratio was not found in any of the species studied.

Introduction

Plant species and even varieties of the same species differ in their ability to grow on soils low in P. Alt and Ladebusch (1984) have shown that on plots which had not received P fertilizer for 20 years, the yield of lettuce was reduced by about 50% whereas that of spinach and cabbage remained unaffected. Also McLachlan (1976), van Ray and van Diest (1979) and Bekele *et al.* (1983) found that species differ in their P efficiency. Therefore, P uptake not only depends on the amount of available P in soil but also on plant properties.

Phosphorus efficiency may be defined as the ability of a plant to produce a certain percentage of its maximum yield at a certain level of soil P. Phosphorus efficiency is therefore often called external P requirement, *i.e.* the P content in soil required to produce 80% of maximum yield.

Basically, there are two ways in which different P efficiencies can arise: 1) the efficiency with which P is utilized to produce yield, *i.e.* the amount of P needed in the plant to produce one unit of dry matter (Loneragan and Asher, 1967). This is often called internal P requirement and is the P concentration in plants to produce 80% of maximum yield. 2) the uptake efficiency of the plant, which is the ability of the root system to acquire P from soil and accumulate it in the shoots. This depends on the capability of roots to absorb P, the active lifetime of roots, and on the amount of root per unit of shoot.

The components of uptake efficiency have been evaluated by Loneragan and Asher (1967) and Woodhouse *et al.* (1978). Claassen and Jungk (1984) showed that the components of uptake efficiency were related to the nutrient concentration of the shoots as follows:

$$\%\,P = I_n(L/W)\bar{t} \times 100 \qquad (1)$$

where I_n = uptake rate per unit of root length (influx), L/W = root-shoot ratio, L = root length and W = shoot dry weight and $\bar{t}$ the average period of time the roots absorb P. For a growing root system, there are young and old roots so that the period of uptake of a root segment depends on its age. For roots growing exponentially the average age of the root system is equal to the reciprocal of the relative growth rate (Claassen and Jungk, 1984).

When plants are grown under the same soil and aerial conditions and P is the growth limiting factor, the P concentration of their shoots can be used to quantify their uptake efficiency, and at the same time the components of uptake efficiency can be determined.

The aim of this study was to investigate to what extent plants differ in their P efficiency *i.e.* their external P requirements, and whether these differences are due to different internal P requirements or to different uptake efficiencies. Furthermore, the influence of P status of the plants on the components of uptake efficiency were investigated.

Materials and methods

The basis of this research was a pot experiment with seven plant species and seven P fertilizer rates. The soil used was a P-deficient loess subsoil from Holtensen near Göttingen with a pH of 7.7. Pots were filled with 5 kg of air dry soil at a bulk density of 1.3 g cm^{-3} and watered to 20% by weight.

Table 1. P application and P content of the soil

Fertilizer rate mg P per 100 g soil	P_{CAL} mg P per 100 g soil	Soil sol. conc. μmol P l^{-1}
0	0.36	0.17
2	0.48	0.53
5	1.28	1.40
10	4.54	5.50
20	11.30	7.50
40	30.40	10.90
80	64.20	10.40

Phosphorus was added as $Ca(H_2PO_4)_2 \cdot H_2O$. Fertilizer rates and the resulting P content of the soil was determined by the CAL method (Schüller, 1969) and the soil solution concentration by the displacement procedure of Adams (1974) are shown in Table 1. The remaining nutrients were added as follows (quantities are per pot): 400 mg N (NH_4NO_3), 430 mg K (K_2SO_4), 200 mg Mg ($MgSO_4$), 0.05 mg Mo ($(NH_4)_6Mo_7O_{24}$), 0.5 mg Cu ($Cu(NO_3)_2$), 1 mg Zn ($ZnSO_4$), 25 mg Fe (EDTA, Fetrilon).

Plant species and planting densities are listed in Table 2. Pots were kept outdoors except during rainfall when they were moved into a glasshouse. At harvest, shoot dry weight and P content (after wet digestion) were determined. Shoot dry weight of ryegrass, rape and spinach for the P rate of 10 mg · 100 g^{-1} were lost, and the values for these treatments were estimated from their P contents. These values are indicated by ( ) in Fig. 1. Roots were washed out of the soil and their length determined after Newman (1966).

For calculating influx two harvests are necessary, as described by Claassen and Jungk (1984). At the first harvest two pots per treatment were used and three pots at the second harvest. Pots for the first harvest had a higher plant density in order to provide enough plant material for analysis. Mean root age, $\bar{t}$, was calculated by eq. (2), assuming exponential root growth.

$$\bar{t} = (t_2 - t_1)/(\ln L_2 - \ln L_1) \qquad (2)$$

where t is time, L is root length and the subscripts refer to the first and second harvest.

Results

Plant growth and P content of shoots

Figure 1 shows the relative yields as a function of P fertilizer rate. Yields are expressed as % of maximum yield in order to compare all 7 species. Yields on the unfertilized soil are very low and depend on P content of the seed. Plants with small seeds have yields of about 5%, and larger seeded plants such as wheat and bean have yields around 20% of

Table 2. Plant species, time between sowing and the first and second harvests and the number of plants per pot

Plant species	Time until harvest (days)		Number plants per pot	
	t_1	t_2	1 harvest	2 harvest
Bean *Phaseolus vulgaris* var. nanus, cv. Loma	30	40	6	3
Rape *Brassica napus*, cv. Quinta	28	43	8	4
Wheat *Triticum aestivum*, cv. Kolibri	23	41	20	10
Spinach *Spinacea oleracea*, cv. Medania	34	44	8	4
Tomato *Lycopersicum esculentum*, cv. Eurocross B	49	57	12	6
Ryegrass *Lolium perenne*, cv. Printo	34	50	40	20
Onion *Allium cepa*, cv. Stuttgarter Riesen	55	69	40	20

maximum. These low yields indicate that plants are not able to absorb P when soil solution concentration, C_{li}, is 0.17 μmol P l^{-1}. This concentration corresponds to C_{min}, *i.e.* the concentration at which no uptake takes place. For bean, C_{min} seems to be even higher, since an increase of C_{li} to 0.53 μmol P l^{-1} had no effect on growth. In contrast, for the same increase in C_{li}, wheat, rape, rye grass and spinach showed a strong increase in yield, while tomato and onion showed only a small increase. At

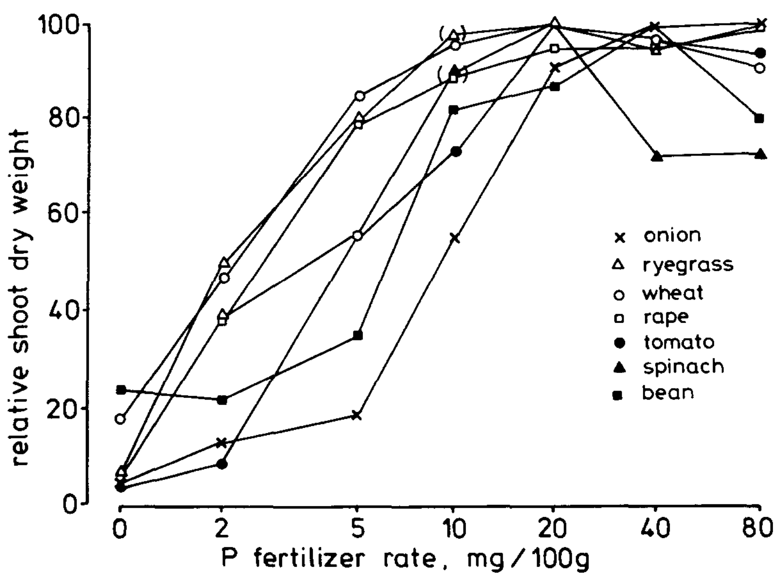

Fig. 1. Relative shoot dry weight of different plant species in relation to P fertilization (highest yield = 100).

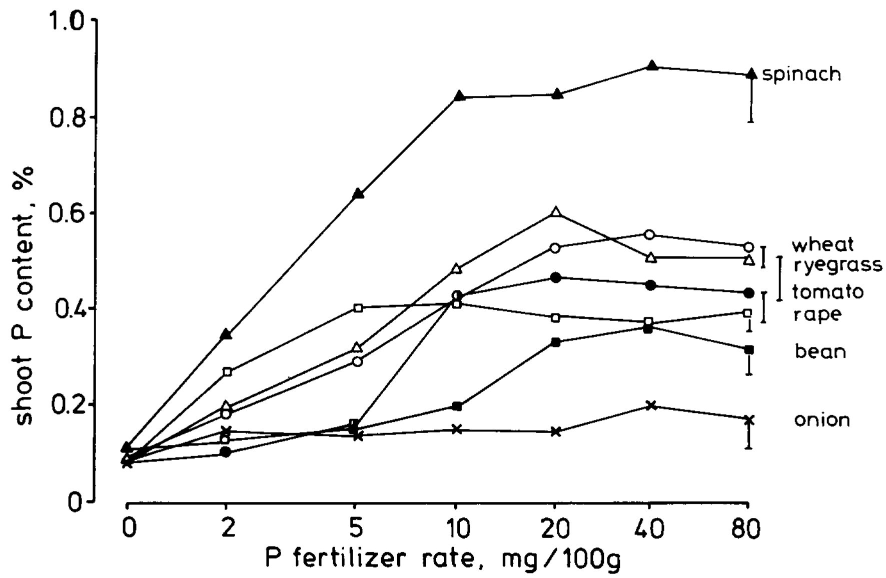

Fig. 2. P content of the shoot of different plant species in relation to P fertilization (*vertical bars* from Dunnet's test, $p = 0.05$).

a fertilizer rate of 10 mg P 100 g^{-1}, which corresponds to a C_{li} of 5.5 μmol P l^{-1}, most species reached almost maximum yield. Only onion and tomato needed 20 mg P 100 g^{-1} or more to reach maximum yield.

Phosphorus content of the shoots as a function of fertilizer P level is shown in Fig. 2. The increase in P content differed among species: it was largest for spinach, and smallest for onion. The highest P content in rape was obtained at 5 mg P.100 g^{-1}. In contrast rye grass, wheat and bean reached their maximum content with 20 mg P.100 g^{-1}. The P content of onion did not show any further increase beyond a fertilization of 2 mg P.100 g^{-1}, even though dry matter yield increased very strongly. However, root P content (not shown here), changed according to P fertilization. Apparently, onion shoot growth was influenced by the P status of the root.

Table 3. External and internal P requirement of seven plant species for 80% of maximum yield

Plant species	Fertilizer rate (mg P per 100 g)	Soil sol. conc. (μmol P l^{-1})	P conc. in D.M. %
Onion	17	6.9	0.14
Ryegrass	5	1.4	0.33
Wheat	4	1.2	0.28
Rape	5	1.4	0.39
Tomato	11	5.7	0.45
Spinach	9	4.6	0.83
Bean	9	4.6	0.20

External P requirement (or phosphorus efficiency)

To compare differences in external P requirement, 80% of maximum yield was chosen, since this was easily read from the graphs. The results in Table 3 show that the amount of fertilizer or the P concentration of soil solution needed to reach that value, varies among species. A soil solution concentration of about 1.5 μmol P l^{-1} is adequate for rye grass, wheat and rape, whereas 5 μmol P l^{-1} are needed for tomato, spinach and bean. Onion has the highest external P requirement of about 7 μmol P l^{-1}.

Internal P requirement

The P concentration in the shoots needed for 80% of maximum yield is shown in Table 3. It can be seen that spinach needed 0.83% P, while 0.14% was sufficient for onion. The other species were in between, ranging from 0.2% to 0.4% P. This shows that plants differ greatly in their efficiency in utilizing P for dry matter production.

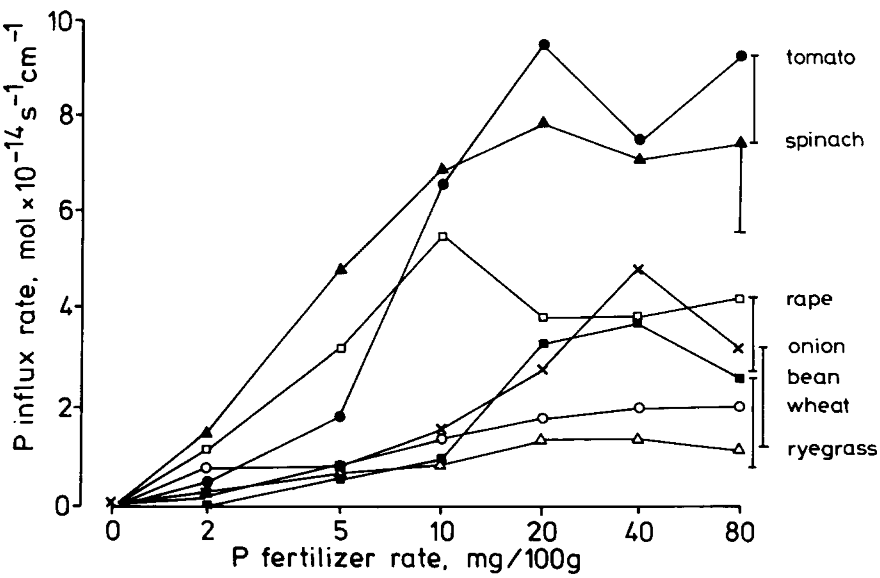

Fig. 3. P uptake rate of different plant species in relation to P fertilization (*vertical bars* from Dunnet's test, $p = 0.05$).

Phosphorus uptake efficiency of the plant

The fact that plants like rye grass, wheat and rape, with not very different internal P requirements have similar external requirements, or that onion with a low internal requirement but a high external P requirement, is a result of differences in uptake efficiency. As explained in the introduction, the components of the uptake efficiency are influx, root-shoot ratio and the period a root segment takes up P.

Phosphorus influx, as a function of fertilizer rate, is shown in Fig. 3. It was almost nil in the unfertilized soil. Increasing soil solution concentration

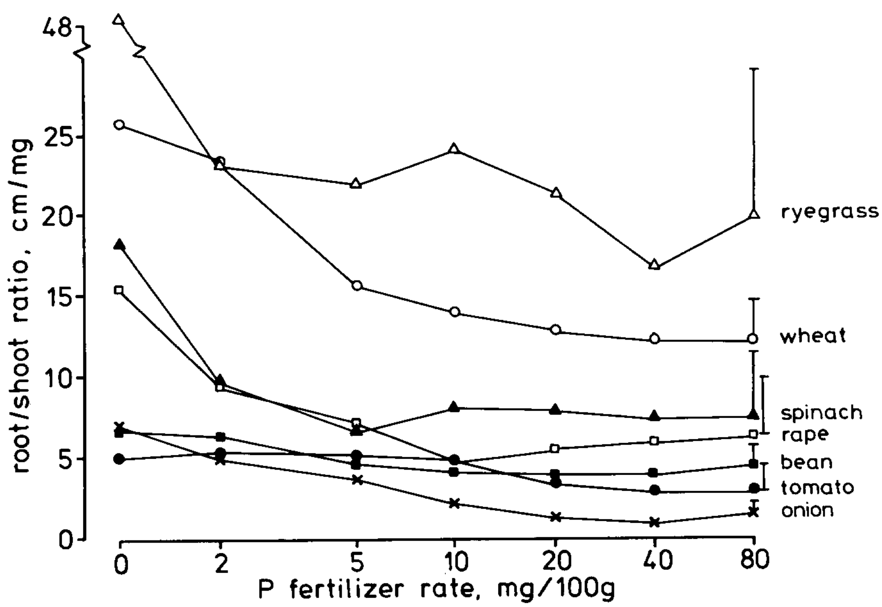

Fig. 4. Root-shoot ratio of different plant species in relation to P fertilization (*vertical bars* from Dunnett's test, $p = 0.05$).

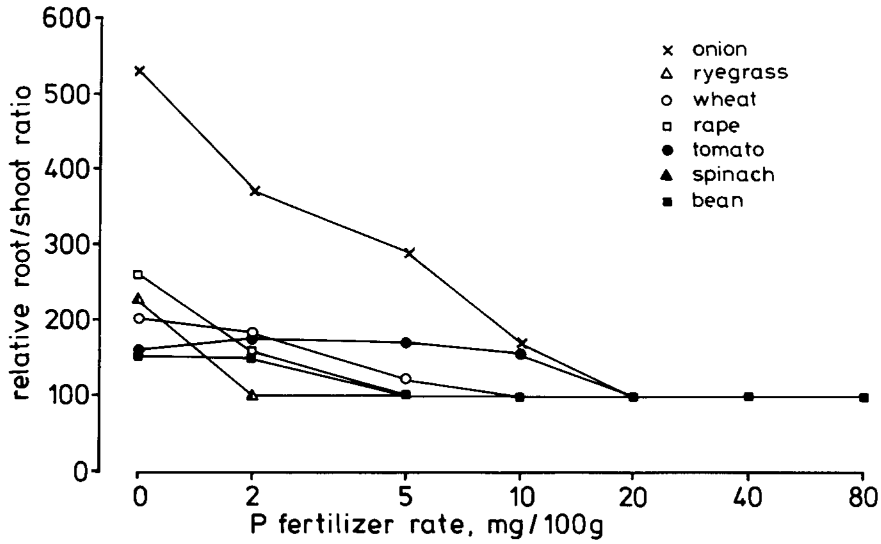

Fig. 5. Change of the root-shoot ratio of several plant species due to P fertilization. Values expressed relative to the lowest root-shoot ratio measured.

increased influx rate for all species except beans where influx was still zero at 2 mg P100 g^{-1} (0.53 μmol P l^{-1}). Influx increased for rape and spinach up to a fertilizer rate of 10 mg P.100 g^{-1} and up to 20 mg P.100 g^{-1} for the remaining species. This indicates that at about 20 mg P.100 g^{-1}, *i.e.*, a P soil solution concentration of 7.5 μmol l^{-1}, plants had reached their maximum uptake rate. The size of this rate differed greatly among species, being highest for tomato and spinach with 9 and 7.5 × 10^{-14} and smallest for ryegrass and wheat with 1 and 2 × 10^{-14} mol $cm^{-1} s^{-1}$.

At a given influx the uptake per plant depends on the size of the root system. The root-shoot ratio for all seven species as a function of P fertilizer rate is shown in Fig. 4. This varies in the unfertilized soil from 48 cm mg^{-1} for rye grass to only 5 to 7 cm

Table 4. Average age, in days, of the root systems of seven plant species as a function of P fertilizer level

	mg P per 100 g soil						
	0	2	5	10	20	40	80
Onion	45.4	26.1	20.5	14.7	10.4	14.1	13.0
Ryegrass	20.7	10.2	7.6	7.7	7.5	7.5	7.3
Wheat	12.9	7.8	6.7	7.6	7.6	7.6	7.3
Rape	18.2	8.0	6.5	5.7	6.2	5.6	5.2
Tomato	72.7	14.0	5.2	4.5	6.1	7.3	6.1
Spinach	11.0	7.6	7.1	5.5	4.6	6.1	5.2
Bean	25.3	17.8	21.4	13.1	7.6	8.8	8.8

mg^{-1} for bean, tomato and onion. Increasing the soil P content decreased root-shoot ratio in all cases. At 20 mg P 100 g^{-1}, where maximum yield was achieved, ryegrass had a root-shoot ratio of about 20 and onion about 2.

This change in root growth due to P fertilization can better be seen when the root-shoot ratio is expressed relative to its value at the highest fertilizer rate. This is shown in Fig. 5. All species have their highest root-shoot ratio in the low P range. It decreases with increasing P supply until it reaches a minimum value which does not change any more with increasing P fertilization. Ryegrass reaches this minimum value at 2 mg P.100 g^{-1} while tomato and onion at 20 mg P.100 g^{-1}. The effect of P supply on the root-shoot ratio is only operating when P is limiting plant growth. Once maximum yield (Fig. 1) and for spinach and ryegrass even 50% of maximum yield is achieved an increase in P supply has no effect on the root-shoot ratio.

This shows that all species regulate the amount of roots produced according to P supply, however, the size of the change and the pattern varies greatly.

The actual period for which a root is able to absorb P is not well known, but in this experiment with young plants with exponential root growth, most roots are only a few days old and it can be assumed that most roots take up P for the time they remained in the soil. The average age of a root system can be calculated from the reciprocal of the

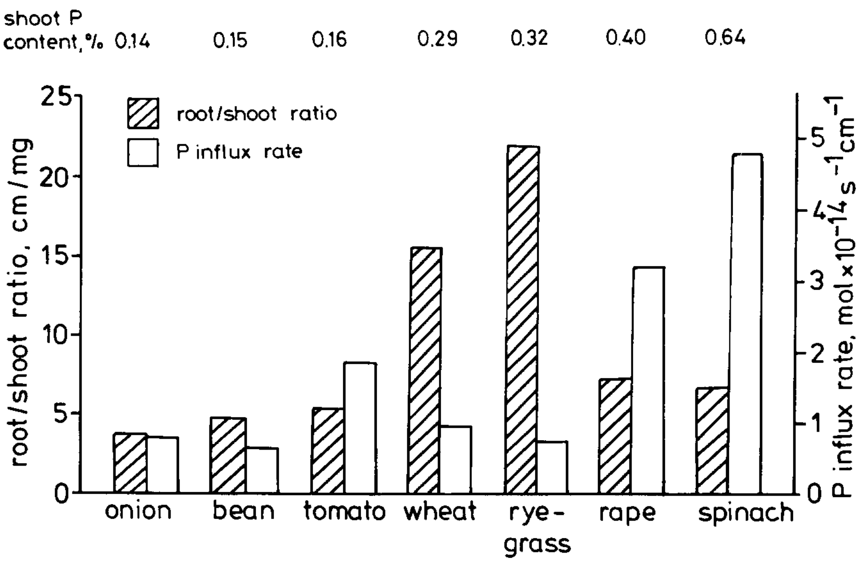

Fig. 6. Root-shoot ratio and P influx rate of seven plant species (fertilization: 5 mg P per 100 g soil).

relative growth constant of the roots if root growth is exponential (Claassen and Jungk, 1984).

Table 4 shows the average age of the root systems. When P is severely limiting growth, the average age is high. Once 50% of maximum yield is reached average age varies between 5 and 8 days for all species except onion where it is always above 10.

The phosphorus uptake efficiency of plants can be characterized by the P content of shoots (% P) when plants are growing under the same conditions and where P is limiting growth. Such conditions apply at the level of 5 mg P.100 g^{-1}. Figure 2 shows that the P content of shoots, at this fertilizer rate, varied from 0.14 to 0.64%, *i.e.* uptake efficiency among species varies by a factor 5. Onion, bean and tomato have a low efficiency, wheat, ryegrass and rape a medium efficiency and spinach a high uptake efficiency.

The reasons for these differences in uptake efficiency are summarised in Fig. 6. The average time of uptake has been omitted, since with the exception of onion and bean, it did not vary very much, (Table 4). Low uptake efficiency (onion, bean, tomato) was associated with both a low root-shoot ratio and a low to medium influx rate. Medium uptake efficiency was associated with a high root-shoot ratio but a low uptake rate in the case of wheat and ryegrass. In contrast, rape achieved a similar uptake efficiency with a relatively low root-shoot ratio but a high influx rate. The high uptake efficiency of spinach was mainly due to its very high influx rate, since the root-shoot ratio was relatively low.

These results show that plants have developed different strategies for P uptake from soil: while some species increase the size of their root system others increase the uptake rate per unit of root.

Discussion

The results have shown that the seven plant species studied differed in their external P requirement, *i.e.*, in the P concentration in the soil needed for 80% of maximum yield. These differences in P efficiency were not related to the internal P requirement, on the contrary, onion and bean with the lowest internal P requirement were the least efficient species. It must therefore be concluded, that differences in external P requirement are caused by differences in the P uptake efficiency of the root system. This is mainly determined by the product of root-shoot ratio and influx. The time of uptake or average age of the root system did not vary very much among species, except when P was very deficient.

Plants of low uptake efficiency have a low influx rate and root-shoot ratio. The strategies that plants have developed for a high uptake efficiency differ among species. Some produce large root systems, like wheat and ryegrass, and others have a high uptake rate per unit of root length, like rape and spinach. None of the seven species studied had a combination of both high influx rate and high root-shoot ratio. If a species had the influx of spinach or rape and the root-shoot ratio of wheat or ryegrass, 2 mg P.100 g^{-1} would have been enough for maximum yield. However, this fertilizer rate only produced 50% or less of maximum yield in this experiment.

Furthermore, none of the species studied showed a combination of high uptake efficiency and low internal P requirement. This combination would further improve the P efficiency, *i.e.*, external P requirement would be reduced. Data from McLachlan (1976) show that buckwheat is a P efficient species due to its low internal P requirement. Whether its high P efficiency is also due to a high uptake efficiency cannot be seen from his data, since root length and influx rate were not determined.

In the search for P efficient plants, plant breeders should try to combine low internal P requirement with high uptake efficiency, *i.e.*, a high root-shoot ratio as well as a high influx rate.

Root-shoot ratio, as an important factor of uptake efficiency, not only varies among species but also depends on soil P content. At low P content the proportion of roots produced increases. This phenomenon has been observed by many authors for many species (Anghinoni and Barber, 1980; Atkinson, 1973; Böhm, 1974; Haynes and Ludecke, 1981 and Powell, 1974). This mechanism is an adaptation of plants to improve their uptake efficiency when P is limiting growth.

In the unfertilized soil, influx was almost nil for all species, and for bean even at a fertilizer rate of 2 mg P.100 g^{-1} (Fig. 3). This indicates that C_{min}, *i.e.*, the concentration at which no net influx occurs, is about 0.2 μmol P l^{-1} for most species, and about 0.5 μmol P l^{-1} for bean. This agrees with the solution culture results of Jungk (1974). At a soil P content of 5 mg P.100 g^{-1}, where P was still limiting growth, influx rate differed by a factor of 8 among species (Fig. 6). This indicates that plant species differ in their ability to improve P transport from soil to roots. These differences can be attributed to differences in root morphology such as root diameter and root hairs (Barber, 1984), or mycorrhizal associations (Yost and Fox, 1979) as well as chemical changes of the root environment (Gahoonia, 1987). More details on these aspects will be published later.

All species achieved maximum influx, I_{max}, at fertilizer doses between 10 and 40 mg P.100 g^{-1} soil. The maximum influx value depended on the root-shoot ratio, *i.e.* species with a high root-shoot ratio had a low I_{max} and vice versa. However, this relationship was poor.

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