Phosphorus uptake from insoluble soil sources by five forage legumes, winter wheat, and buckwheat
by Robert Mark Jacques

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Crop and Soil Science
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Abstract:

The absorption and utilization of phosphorus from insoluble tricalcium phosphate compounds commonly found in Montana soils by alfalfa (Medicago sativa L.), sainfoin (Onobrychis viciifolia Scop.) , yellow sweetclover (Melilotus officinalis L.), red clover (Trifolium pratense L.), subterranean clover (Trifolium subterranean L.), winter wheat (Triticum aestivum L.), and buckwheat (Fagopyrum esculentum Moench) were studied.

Legume seedlings in general had higher root surface area indexes (RSAI = wt of H2O removed from root surface/unit of root dry wt) then winter wheat and buckwheat seedlings. Ranking of species for root cation exchange capacity (CEC) depended on whether it was expressed on a dry wt basis or on a RSAI basis. Root CEC per unit of dry wt was significantly correlated with RSAI for all species. Since the density of cation exchange sites along a root surface normally varies little within a species, these correlations indicate that increases in root CEC per unit of dry wt within a species were likely a function of increased RSAI.

Sainfoin, yellow sweetclover, alfalfa, and buckwheat all responded well to insoluble calcium-phosphate P sources. Yellow sweetclover absorbed more P and had a higher % P in its tissue than the other forage legumes. Sainfoin absorbed less P from fluorapatite than both yellow sweetclover and alfalfa, but more efficiently translocated P absorbed from fluorapatite from roots to tops. Winter wheat roots absorbed considerable P from fluorapatite, but were very inefficient in translocating this P to tops. Yellow sweetclover, alfalfa, and sainfoin produced maximum dry matter while feeding on either pure fluorapatite or rock phosphate in small, restrictive containers, but only sainfoin responded to rock phosphate when the root density was much less.

RSAI generally increased as available P became more limiting for the forage legumes, but not for winter wheat and buckwheat. When no P was present, the density of cation exchange sites along the root surface decreased dramatically for yellow sweetclover, alfalfa, red clover, and subterranean clover, but not for sainfoin. An inverse relationship between root exocellular acid phosphatase activity and dry matter production occurred for most species. Forty-five sainfoin seedlings exhibited a wide range of rhizosphere pH values when subjected to P stress. Rhizosphere pH changes in response to P stress and Ca accumulation by plants from insoluble calcium-phosphate compounds appeared to be the most promising indicators of a plant's P feeding power from rock phosphate.

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Approved:

Raymond L Ditterline
Chairperson, Graduate Committee

Hayden Ferguson
Head, Major Department

Henry L Parsons
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

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ABSTRACT

The absorption and utilization of phosphorus from insoluble tricalcium phosphate compounds commonly found in Montana soils by alfalfa (Medicago sativa L.), sainfoin (Onobrychis viciifolia Scop.), yellow sweetclover (Melilotus officinalis L.), red clover (Trifolium pratense L.), subterranean clover (Trifolium subterranean L.), winter wheat (Triticum aestivum L.), and buckwheat (Fagopyrum esculentum Moench) were studied.

Legume seedlings in general had higher root surface area indexes (RSAI = wt of H_2O removed from root surface/unit of root dry wt) than winter wheat and buckwheat seedlings. Ranking of species for root cation exchange capacity (CEC) depended on whether it was expressed on a dry wt basis or on a RSAI basis. Root CEC per unit of dry wt was significantly correlated with RSAI for all species. Since the density of cation exchange sites along a root surface normally varies little within a species, these correlations indicate that increases in root CEC per unit of dry wt within a species were likely a function of increased RSAI.

Sainfoin, yellow sweetclover, alfalfa, and buckwheat all responded well to insoluble calcium-phosphate P sources. Yellow sweetclover absorbed more P and had a higher % P in its tissue than the other forage legumes. Sainfoin absorbed less P from fluorapatite than both yellow sweetclover and alfalfa, but more efficiently translocated P absorbed from fluorapatite from roots to tops. Winter wheat roots absorbed considerable P from fluorapatite, but were very inefficient in translocating this P to tops. Yellow sweetclover, alfalfa, and sainfoin produced maximum dry matter while feeding on either pure fluorapatite or rock phosphate in small, restrictive containers, but only sainfoin responded to rock phosphate when the root density was much less.

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INTRODUCTION

Although the total phosphorus content of many soils is relatively high, much of this P is commonly found in the form of insoluble phosphate minerals. Minerals containing insoluble P can be mined from the soil and degraded to available P fertilizer, but this process is expensive and requires a considerable use of fossil energy. Therefore, the development of plants capable of utilizing unavailable soil P is desirable.

Renewed interest in the ability of cultivated forage legumes to absorb P from insoluble soil sources resulted from observations that sainfoin (*Onobrychis viciifolia* Scop.), a forage legume grown in the Rocky Mountain region, seldom responded to P fertilization. Quite often, on the same soil, alfalfa (*Medicago sativa* L.) responds to P applications, but sainfoin does not. This lack of response to P applications by sainfoin indicated that it was absorbing P from existing soil sources.

This study investigates the absorption and utilization of P from insoluble tricalcium-phosphate compounds commonly found in Montana soils by alfalfa, sainfoin, yellow sweetclover (*Melilotus officinalis* L.), red clover (*Trifolium pratense* L.), subterranean clover (*Trifolium subterranean* L.), winter wheat (*Triticum aestivum* L.), and buckwheat (*Fagopyrum esculentum* Moench). My objectives were to rank these species according to their P feeding power from insoluble sources, determine what factors make some plants better feeders of insoluble P sources than others, and possibly develop a simple screening technique to distinguish good P feeders.

My results are reported in the following three chapters. The first chapter describes a relatively unknown method of estimating the surface area of an intact root system. The relationship between root surface area and root cation exchange capacity is also discussed. Chapter II deals with growth responses, P uptake rates, and root to top translocation efficiencies of P using fluorapatite as the sole source of P. The third chapter describes several plant characteristics which may enhance P uptake from rock phosphate. Possible screening techniques which might be used to distinguish good P feeders are also considered.

I. ROOT SURFACE AREA AND ITS RELATIONSHIP TO ROOT CATION EXCHANGE CAPACITY

INTRODUCTION

Root development is usually evaluated as a change in dry wt, moist wt, or volume. These measurements are often inadequate for plant nutrition studies. Root surface area is often a more important measurement, but is seldom used because it is difficult to measure accurately. Raper and Barber (10) stressed the importance of root surface area in determining the efficiency of seedling roots as nutrient absorptive surfaces. With relatively immobile nutrients such as P, increased root surface area could greatly enhance the efficiency of utilization (3). Root cation exchange capacity (CEC) measurements expressed per unit of dry wt are often inaccurate unless adjusted for differences in surface area per unit of dry wt (11).

Four methods used which estimate root surface area are: i) the titration method (12) in which root cation exchange sites are saturated with H^+ ions and subsequently titrated with a weak base, which is similar to the acid-washing technique (1) used to measure root CEC; ii) the gravimetric method (4) in which a beaker of $Ca(NO_3)_2$ solution is weighed, roots then dipped into it and lifted above the beaker to drain, and the remaining solution weighed to determine the amount of $Ca(NO_3)_2$ which was absorbed by the root surface; iii) calculations of root surface area from length and diameter measurements at representative segments of a root (1, 2, 5, 11); and iv) the differential centrifugation method (8) in which partial H_2O shells are removed from root surfaces and weighed.

Linford and Rhoades (9) reported a similar application, using the spinning tub of an automatic washing machine as a low speed centrifuge to remove excess surface H_2O from washed roots before determining moist weights. The differential centrifugation technique assumes that one can consistently remove a uniform fraction of the surface H_2O layer adhering to a root. Jeffrey (8) listed three basic assumptions that must be met for the technique to be accurate:

i. The surface tension and viscosity of surface H_2O films must be similar on roots to be compared;

ii. The centrifugal force generated at a given rpm will equilibrate with surface tension forces, leaving a uniform H_2O film adhering to the root surface; and

iii. H_2O can be removed from small capillary pores between root hairs.

Thus, if H_2O-saturated roots are centrifuged at a low force, followed by a higher force, the weight of H_2O spun off during the second centrifugation will be proportional to root surface area.

Root surfaces possess a net negative charge which attracts cations, but the charge density (charge per unit surface area) varies among plant species (6). Crooke et al. (5) found that the charge density of a root was highest at the root tip, possibly due to higher pectin content. They found that root sections from three segments above the root tip differed in CEC expressed on a dry wt basis but not on a surface area basis, which illustrates possible misinterpretations that can occur if the dry wt basis is used without caution. An accurate, reproducible means of estimating root surface area is needed to express root CEC on a surface area basis. The objectives of this experiment were:

1. To evaluate the differential centrifugation method of estimating root surface area; and
2. To evaluate the relationship between root CEC per unit of dry wt and root surface area index (RSAI = wt of H_2O removed from root surface/unit of root dry wt).

MATERIALS AND METHODS

Five forage legumes, alfalfa, sainfoin, yellow sweetclover, red clover and subterranean clover, and two check species, winter wheat and buckwheat, were pre-germinated on moist blotter paper for one day and transplanted to individual plastic test tubes (16 cm x 2.4 cm) filled with washed silica gravel. Seedlings were grown in a controlled environment chamber at 21±1C with a photoperiod of 16 hr at a photosynthetic photon flux density of 280 uEinsteins m^{-2} sec^{-1} provided by incandescent and fluorescent lights. Roots were harvested separately 35 days after germination of the forage legumes and 25 days after germination of winter wheat and buckwheat.

A gradient of P stress was established by differing levels of applied water-soluble and water-insoluble P. Each species was grown using 3 different P treatments in a randomized complete block design with 6 replications.

1) Three hundred forty mg of screened Idaho rock phosphate, provided by the J. R. Simplot Co., Pocatello, Idaho, were thoroughly mixed with washed silica gravel and the mixture added to each plastic test tube. Seedlings were watered every other day with a modified -P Hoagland's nutrient solution (7) containing, in mg/liter, N, 84(73 as NO_3 and 11 as NH_4); K, 68; Ca, 60; Mg, 12; S, 16; Cl, 0.8; B, 0.5; Mn, 0.5; Zn, 0.05; Cu, 0.02; Mo, 0.01; and Fe, 1.0 added as Fe.EDTA. The nutrient solution was adjusted to pH 6.0 using 1.0 N H_2SO_4 before use. The

gravel medium was flushed periodically with distilled water to avoid salt accumulation.

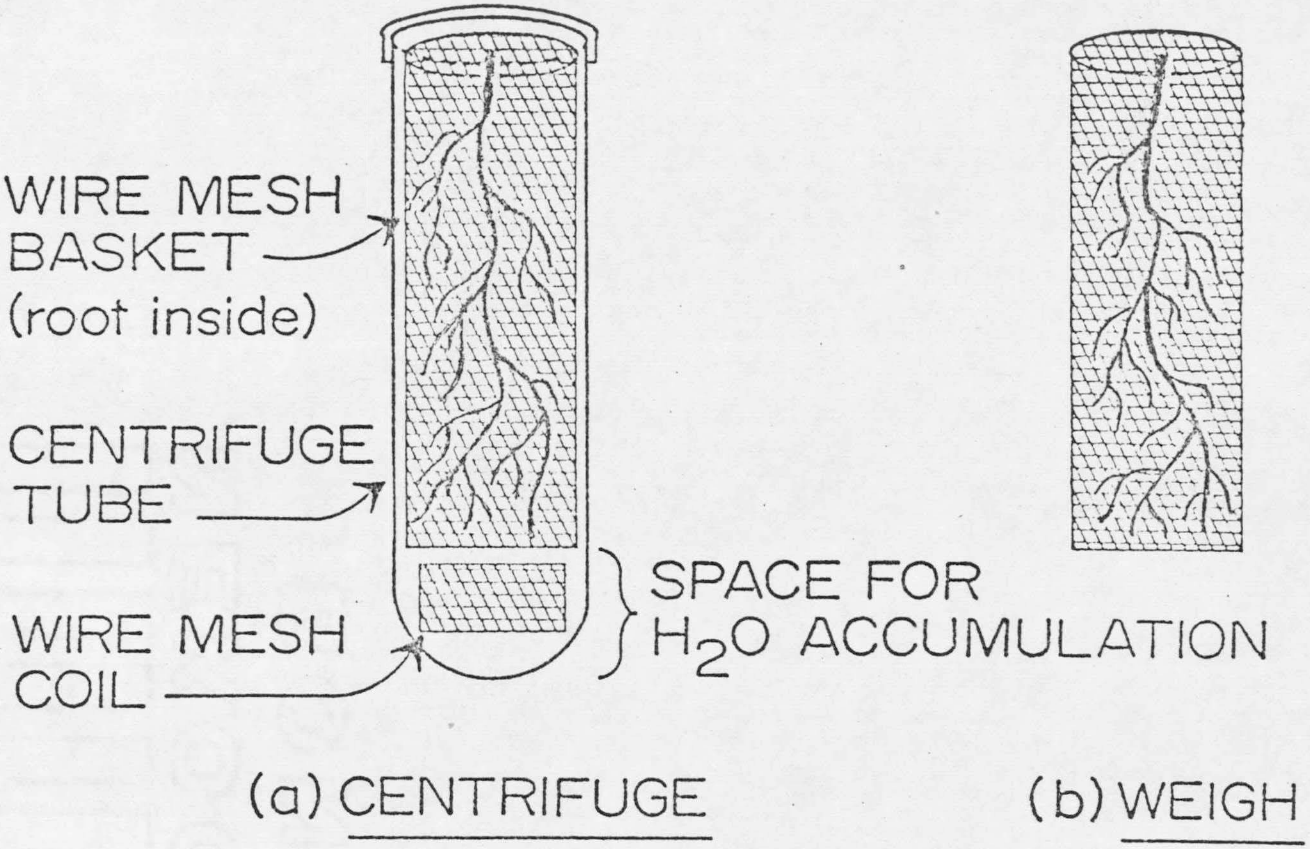
2) Seeds were planted in individual plastic test tubes filled with pure washed silica gravel and watered with the same nutrient solution as in treatment 1. No source of P was present.

3) Seeds were planted in individual plastic test tubes filled with pure washed silica gravel. Seedlings were watered with a complete nutrient solution including 8 mg/liter of water-soluble P in addition to the nutrients listed in treatment 1.

Root Surface Area

RSAI was determined as follows:

1. Wash roots gently with distilled H_2O to remove any adhering sand particles.
2. Equilibrate roots in distilled H_2O for 10 min.
3. Place roots in wire mesh basket in a 50 ml centrifuge tube (Figure I-1).
4. Balance tubes to constant wt by adding distilled H_2O and secure cap.
5. Centrifuge at 111 x g (center of tube) for 7 min.
6. Weigh wire mesh basket with roots inside on an analytical balance accurate to 0.1 mg.
7. Replace wire mesh basket in tube, secure cap, and centrifuge at 344 x g for 7 min.



(a) CENTRIFUGE

(b) WEIGH

Figure I-1. Diagram of differential centrifugation technique: (a) roots inside wire mesh basket are centrifuged in a 50 ml capped centrifuge tube, and (b) only wire mesh basket with roots inside are weighed after centrifugation.

8. Weigh wire mesh basket with roots inside again. Difference in two wts = mg H_2O spun off root which is proportional to total root surface area.

9. Oven dry roots at 70C and weigh to obtain dry wt.

10. Calculated RSAI. RSAI = mg H_2O spun off roots/mg root dry wt.

<u>Root CEC</u>

The acid-washing technique of determining root CEC (1) was modified for small sample sizes (100-500 mg moist wt) and used as follows:

1. Wash roots gently with distilled H_2O to remove any adhering sand particles.
2. Allow excess H_2O to drain off roots.
3. Acid-wash roots in 100 ml refrigerated 0.1 N HCl for 5 min and rinse with distilled H_2O.
4. Repeat acid-wash 3 times with a thorough rinsing after the last acid-wash.
5. Allow roots to drain of excess H_2O.
6. Place roots in 50 ml of neutral, 1.0 N KCl.
7. Titrate to pH 7 over a 5 min period with .001 N KOH.
8. Rinse roots with distilled H_2O.
9. Oven dry roots at 70C and weigh to obtain dry wt.
10. Calculate root CEC.

$$\frac{\text{ml titrant (KOH) x .001 N}}{\text{g root dry wt}} \times 100 = \text{CEC (meq/100 g dry wt).}$$

$$\frac{\text{ml titrant (KOH)}}{\text{RSAI}} = \text{CEC (meq/RSAI)}.$$

Root CEC and RSAI were measured on all samples. The order of measurement is not critical since neither measurement is influenced by small changes in metabolism that might occur during the experiment.

RESULTS AND DISCUSSION

Root Surface Area

Although fibrous-root systems are generally thought to have a larger root surface area/dry wt ratio than tap-root systems, the opposite may be true for seedlings. In this study, the five forage legumes and winter wheat were found to have higher RSAI than buckwheat (Table I-1). Most legume seedlings have a fine tap-root system during the first few weeks of growth. Winter wheat exhibits a fine fibrous-root system as a seedling, while buckwheat has a coarse fibrous system.

Abed and Hassan (1) reported that the average diameters of pea and clover roots were larger than corn and barley roots on plants sampled 35 days after germination. Surface areas calculated from length and diameter measurements at representative root segments appeared smaller per unit of fresh or dry wt for legumes than for grasses; however, differences between means were not tested for significance. My data show that legumes in general had higher RSAI than winter wheat and buckwheat during the seedling stage before a dominant tap-root was established (Table I-1). The discrepancy between their results and mine may be due to sampling technique. Root surface area is difficult to calculate since a large proportion of surface area is likely associated with very small lateral roots and root hairs, which are often ignored in calculating surface areas because of the difficulty involved in measuring them. I believe the differential centrifugation method is more reliable

TABLE I-1. ROOT SURFACE AREA INDEX (RSAI) AND ROOT CEC EXPRESSED PER UNIT OF DRY WT AND PER UNIT OF RSAI FOR FIVE FORAGE LEGUMES, WINTER WHEAT, AND BUCKWHEAT.

		Root CEC	
Plant[1]	RSAI	meq/100 g dry wt	meq/RSAI
Subterranean clover	4.14 a[2]	42.7 b	7.7 bc
Sainfoin	3.93 a	58.7 a	10.1 ab
Red clover	3.34 ab	33.1 c	8.3 ab
Yellow sweetclover	3.19 ab	31.8 c	8.8 ab
Alfalfa	2.45 bc	29.3 c	11.5 a
Winter wheat	2.57 b	13.4 d	4.5 c
Buckwheat	1.54 c	26.9 c	8.4 ab

[1] Plants were grown without nutrient stress.

[2] Values within a column followed by a common letter are not significantly different at the 5% level.

because the entire surface area of an intact root system is measured.

Although Jeffrey (8) reported large differences in total surface area of roots with evident morphological differences, he did not establish the validity of the differential centrifugation method used to measure root surface area. It is important that H_2O is removed only from the shell surrounding the root surface during the centrifugation and not from inside the epidermis. Roots that were centrifuged at increasing forces were examined for possible plasmolysis. With the higher centrifugal force used (344 x g), no plasmolysis or excessive drying of small roots occurred. The forces used removed only part of the H_2O shell surrounding a root without damaging it.

This method depends upon exact duplication of the technique for all samples being compared. All centrifugation and weighing steps must be timed and reproduced accurately. Centrifuge speeds must be repeated accurately since small changes in force applied will have large effects on the amount of H_2O removed from the surface of a root. An accurate tachometer should be used to duplicate speeds. Baskets with roots inside should be weighed as quickly as possible after removal from the centrifuge tubes since equilibration with the atmosphere occurs rapidly. Several procedural problems that may cause errors are:

1. Centrifuge tubes not balanced to constant wt.
2. Centrifuge speeds not accurately repeated. A strobe tachometer is helpful in reproducing speeds.

3. Centrifugation steps not accurately timed.
4. Inconsistency during weighing. For example, taking 30 sec to weigh one basket and only 10 sec to weigh another.
5. Comparing surface areas of roots that have large differences in size.

RSAI among roots within a plant species can be expected to vary because of differences in root morphology within a species. Comparisons of surface areas determined by this method are most valid within a species since chemical differences among roots of different species will affect such properties as surface tension and viscosity of surface H_2O films surrounding a root. Although no totally acceptable method of measuring root surface area has been developed, I believe that this method of measuring RSAI provides a meaningful indicator of root morphology and warrants further study.

Root CEC

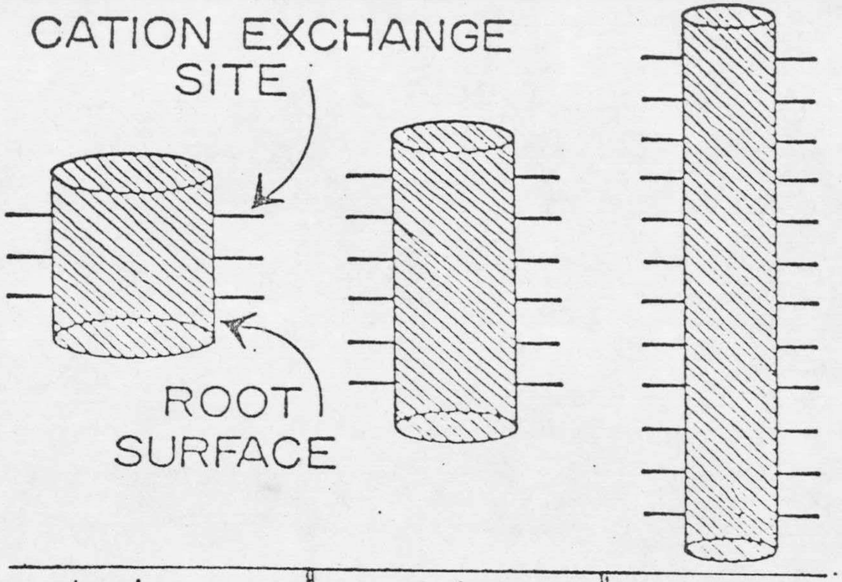
The amount of pectic material in cell walls at the root surface accounts for a large percentage of root CEC (5). Therefore, root CEC should be related to the density of carboxyl groups (potential exchange sites) arising from pectic material at the root surface. If the density of exchange sites is related to cell wall structure, then charge density per unit of root surface area would not be expected to vary much within a species unless cell wall structure is somehow appreciably changed. However, root CEC expressed per unit of dry wt often varies within a root system.

Root surface area/dry wt ratios change considerably throughout a root system. As the ratio increases, the number of cation exchange sites per unit of dry wt also increases if charge density per unit of surface area remains constant (Figure I-2). In other words, root CEC expressed per unit of dry wt will increase without a consequent increase in charge density per unit of surface area. If root CEC is to be used as an indicator of charge density, it should be expressed on a surface area basis. Root CEC expressed per unit of RSAI should truly indicate the density of potential exchange sites along a root surface.

The magnitude of values for root CEC depended on whether being expressed per unit of dry wt or per unit of RSAI (Table I-1). For example, root CEC per unit of dry wt for sainfoin was greater than that of alfalfa, but when expressed per unit of RSAI the reverse was true (Figure I-3).

In order to obtain roots within a species having a range of RSAI values, plants were grown under a gradient of P stress established by differing levels of applied soluble and insoluble P. Root CEC per unit of dry wt was significantly correlated with RSAI for all plants (Table I-2). Correlation coefficients were higher for the forage legumes than for winter wheat and buckwheat. Regression coefficients varied among species and were highest with red clover and lowest with subterranean clover.

The significant correlations between RSAI and root CEC per unit



DRY WT =	1	1	1
RSAI =	0.5	1	2
EXCHANGE SITES =	6	12	24
CEC/UNIT DRY WT =	0.5	1	2

Figure I-2. A hypothetical example illustrating the effect of root surface area index (RSAI) on root CEC expressed on a dry wt basis. Density of cation exchange sites along the root surface remains constant for all three examples.

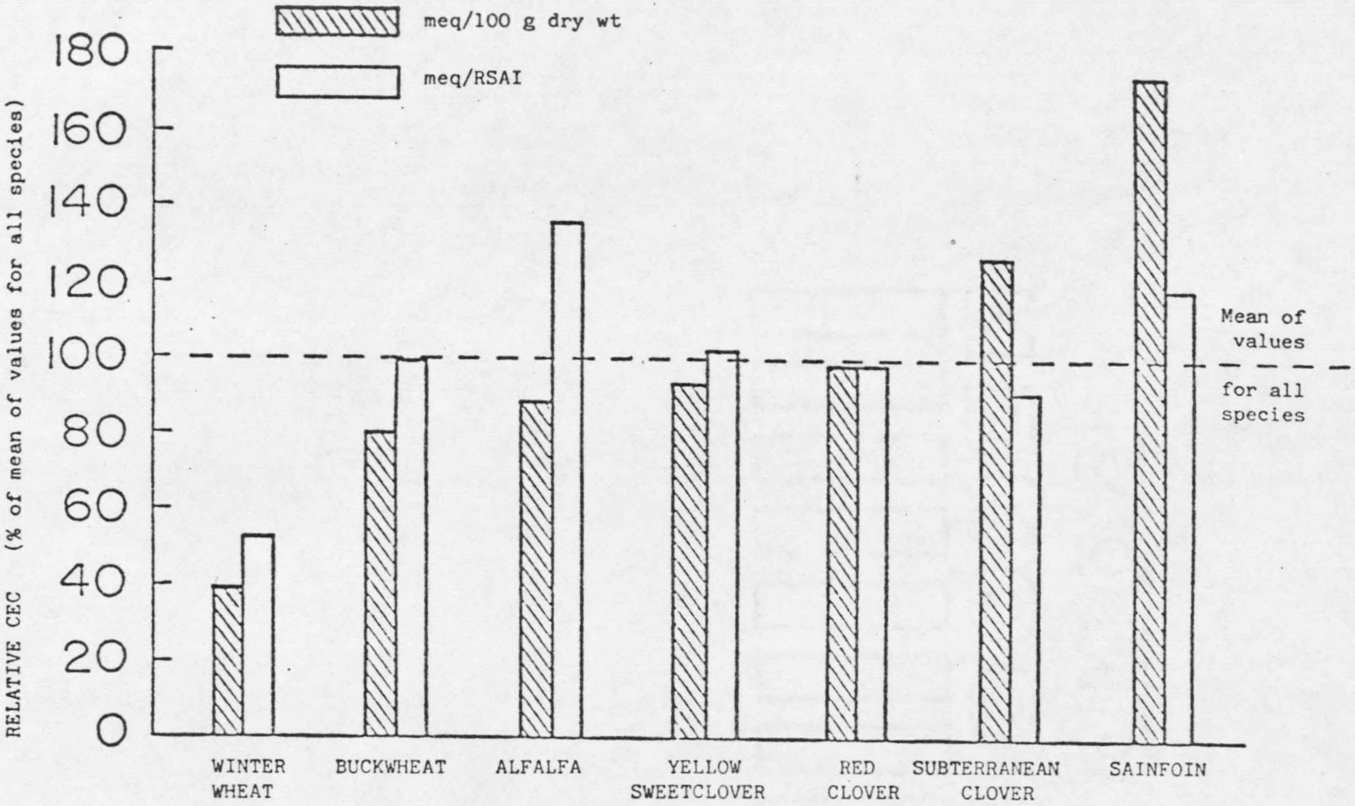


Figure I-3. Root CEC per unit of dry wt and per unit of root surface area index (RSAI) expressed as a percentage of the mean of values for all species for five forage legumes, winter wheat, and buckwheat.

TABLE I-2. SIMPLE CORRELATION AND LINEAR REGRESSION COEFFICIENTS OF THE RELATIONSHIP BETWEEN ROOT SURFACE AREA INDEX (RSAI) AND ROOT CEC EXPRESSED PER UNIT OF DRY WT (meq/100 g DRY WT) FOR FIVE FORAGE LEGUMES, WINTER WHEAT, AND BUCKWHEAT.

Plant[1]	r	b
Subterranean clover	.67**	3.05
Sainfoin	.71**	7.96
Red clover	.82**	8.55
Yellow sweetclover	.76**	5.27
Alfalfa	.83**	6.54
Winter wheat	.56**	6.82
Buckwheat	.56**	6.25
All species	.76**	8.27

[1] Plants are grown under a gradient of P stress established by differing levels of applied soluble and insoluble P.

**Significant at the 1% level.

of dry wt indicate that increases in root CEC per unit of dry wt likely did not result from increases in charge density along the root surface, but rather were a function of increased RSAI. Therefore, comparisons of different values of root CEC per unit of dry wt must be made with caution unless potential differences in RSAI can be ruled out.

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II. PHOSPHOROUS UPTAKE FROM FLUORAPATITE BY FIVE FORAGE LEGUMES, WINTER WHEAT, AND BUCKWHEAT

INTRODUCTION

The concentration of phosphate ions in soil solution is low enough in many soils that plants respond to P fertilization. Yet these soils may contain large reserves of total P, primarily in the form of insoluble phosphate minerals. Improving a plant's ability to feed on existing soil P sources would provide two obvious benefits. First, less P fertilizer would be needed, and second, the P uptake efficiency from applied fertilizer would likely increase since the amount of P absorbed from P fertilizers is usually restricted by precipitation of applied P before absorption occurs.

Plant species differ in their ability to absorb P from rock phosphate. The early work of Truog (23) and others (6, 7, 8, 11, 17, 22) established that legumes and dicotyledons, in general, utilize P from insoluble tricalcium-phosphate sources more efficiently than monocotyledons. Differences in feeding ability were often attributed to variations in the size of root systems until Fried (7) eliminated this possibility by determining L values. These values indicate the relative amount of P absorbed from rock phosphate when a labile pool of both soluble and insoluble P sources is present. Fried found that buckwheat and legumes absorbed more P from rock phosphate than grasses.

Many theories have been proposed to explain differences in P feeding ability. The solubilization of fluorapatite, a major constituent of rock phosphate, can occur as follows:

$Ca_{10}(PO_4)_6F_2 + 12H^+ \rightarrow 10Ca^{++} + 6(H_2PO_4^-) + 2F^-$. Therefore, the solubility of fluorapatite should increase with decreasing pH, and with decreasing concentrations of Ca^{++} and $H_2PO_4^-$ in soil solution (11). Any plant characteristic that enhances any of these conditions should increase the plant's P feeding power from fluorapatite. Several possibilities include a high root cation exchange capacity, excretion of organic acids or H^+ from roots into surrounding soil solution, absorption or adsorption of Ca^{++} by roots, mycorrhizal relationships, or chelate secretion by roots (6).

When P deficiency occurs, plants that are able to absorb P at low levels will have an advantage in soils low in soluble P simply by being able to lower the $H_2PO_4^-$ concentration in soil solution near the root surface by absorption (14). Consequently, the dissolution of insoluble P sources in the soil such as fluorapatite should increase because of the decreased $H_2PO_4^-$ concentration in solution near the root surface.

The dissolution of fluorapatite releases large quantities of Ca^{++} into solution (17). If the Ca^{++} concentration in solution becomes too high, reprecipitation of soluble P can occur. Therefore, plants that can remove large amounts of Ca^{++} from solution should enhance the dissolution of fluorapatite. Plants can remove Ca^{++} from solution by adsorption on the root exchange complex or absorption across a membrane. Johnston and Olsen (11) found the latter to be the most significant factor involved in the dissolution of fluorapatite by plant roots. Alfalfa, yellow sweetclover, and buckwheat often accumulate large quantities of Ca^{++} in their tops (15, 23), but sainfoin does not. Ross and Delaney (21) found that sainfoin has the unusual ability to accumulate large quantities of Ca^{++}, precipitated as $CaCO_3$, in the cortex of roots near the soil surface. As a result, sainfoin should also have the ability to lower the Ca^{++} concentration in solution near the root surface, allowing the dissolution of fluorapatite to continue.

Increasing the Ca^{++} concentration in solution often stimulates P absorption by legume roots when the $H_2PO_4^-$ concentration in solution is low enough to limit growth (19). However, this relationship may not be true for cereal grains. Leggett et al. (12) found that increasing the Ca^{++} concentration beyond 250 uM had no effect on P absorption in solutions containing 1 uM P for barley (Hordeum vulgare L.).

Brown et al. (5) observed differences in the response of grain sorghum (Sorgum bicolor L.) genotypes to P applications. They stressed the importance of knowing the P requirement of each genotype before making fertilizer recommendations that fully utilize the potential of soil tests. Roots of some genotypes were more efficient than others in making nutrient elements available in the soil. Both the soil and crop must be compatible before maximum yields and nutrient-use efficiency can be realized.

My interest in the ability of cultivated forage legumes to absorb P from insoluble soil sources resulted from observations that sainfoin, a forage legume grown in the Rocky Mountain region, seldom responds to P fertilization (16, 18). Quite often, on the same soil, alfalfa responds to P applications, but sainfoin does not. The lack of response by sainfoin indicated that it was absorbing P from existing soil sources. In the present study, growth responses, P uptake rates, and root to top translocation efficiencies of P were compared using fluorapatite as the soil source of P for five forage legumes, winter wheat and buckwheat. The latter two species were chosen because of the wealth of data already available regarding their P feeding power (6, 7, 11, 15, 22, 23).

MATERIALS AND METHODS

The P feeding ability of 5 forage legumes, alfalfa, sainfoin, yellow sweetclover, red clover, and subterranean clover, and 2 check species, winter wheat and buckwheat, was studied in 2 separate experiments.

Growth Chamber Experiment

P uptake from both soluble and insoluble sources was studied in a controlled environment chamber at a temperature of 21±1C with a photoperiod of 16 hr at a photosynthetic photon flux density of 280 uEinsteins m^{-2} sec^{-1} provided by incandescent and fluorescent lights. Six replications of all species were grown with each of the following 4 treatments in a randomized complete block design.

1) ^{32}P treatment - Thirty-two g of pure fluorapatite ground to a fine powder and labelled with 60.5 mCi of ^{32}P were prepared for our use by the Tennessee Valley Authority, National Fertilizer Development Center, Muscle Shoals, Alabama. The fluorapatite was thoroughly mixed with washed silica gravel using a rotary tumbler. Individual plastic test tubes (16 cm x 2.4 cm) were filled with the mixture, each tube containing approximately 340 mg of ^{32}P-fluorapatite. Seeds of each species were pre-germinated on moist blotter paper for 1 day. Three germinated seeds were transplanted to each test tube and thinned to 1 per tube after establishment. All seedlings were watered every other day with a modified -P Hoagland's nutrient solution (9) containing, in mg/liter, N,84(73 as NO_3

and 11 as NH_4); K,68; Ca,60; Mg,12; S,16; Cl,0.8; B,0.5; Mn,0.5; Zn,0.05; Cu,0.02; Mo,0.01; and Fe,1.0 added as Fe·EDTA. The nutrient solution was adjusted to pH 6.0 using 1.0 N H_2SO_4 before use. The gravel medium was flushed periodically with distilled water to avoid salt accumulation.

2) RP treatment - Three hundred forty mg of screened Idaho rock phosphate, provided by the J. R. Simplot Co., Pocatello, Idaho, were thoroughly mixed with washed silica gravel and the mixture added to each plastic test tube. Seeds of each species were planted and watered with the same nutrient solution as in treatment 1.

3) -P treatment - Seeds were planted in individual plastic test tubes filled with pure washed silica gravel and watered with the same nutrient solution as in treatment 1. No source of P was present.

4) +P treatment - Seeds were planted in individual plastic test tubes filled with pure washed silica gravel. Seedlings were watered with a complete nutrient solution containing 8 mg/liter of water-soluble P in addition to the nutrients listed in treatment 1.

Roots and tops were harvested separately 29 days after germination for all species. Roots were thoroughly washed with distilled water to remove any adhering gravel or fertilizer. The surface area of each intact root system from the ^{32}P treatment was estimated using a modified differential centrifugation method (10) as described in Chapter I. All roots and tops were dried in a forced air oven at 70C and weighed. Representative samples of both roots and tops from the ^{32}P treatment were ground, weighed, pressed into a thin layer in a planchet, and assayed for ^{32}P activity using an end-window Geiger Mueller tube and scaler.

Greenhouse Experiment

Plant species were grown in sand culture in the greenhouse using a randomized complete block design with 5 replications. Seedlings were grown at greenhouse temperatures and supplemented with artificial light to provide a 16-hr photoperiod. Three different P treatments were used.

1) RP treatment - An identical rate by volume of screened Idaho rock phosphate as that used in the preceding experiment was thoroughly mixed with washed silica sand. The sand-rock phosphate mixture was added to 1800 ml plastic pots. Seeds of each species were pre-germinated on moist blotter paper for 1 day. Ten germinated seeds were transplanted to each pot. After establishment, the seedlings were thinned to 6 per pot. All seedlings were watered every other day with the same -P nutrient solution used in the preceding experiment. The sand medium was flushed periodically with tap water to avoid salt accumulation.

2) -P treatment - Seeds were planted in pots filled with pure washed silica sand and watered with the same -P nutrient solution as in treatment 1. No source of P was present.

3) +P treatment - Seeds were planted in pots filled with pure washed silica sand. Seedlings were watered with a complete nutrient solution containing 8 mg/liter of water-soluble P in addition to the nutrients present in the -P nutrient solution.

Roots and tops were harvested separately 28 days after germination of winter wheat and buckwheat, and 42 days after germination of the forage legumes. The longer growth period for legumes was required to permit their roots to spread profusely throughout the sand medium. Roots were thoroughly washed with distilled water to remove any adhering sand or fertilizer. All roots and tops were dried in a forced air oven at 70C, weighed, and ground. Representative samples of both roots and tops were analyzed for P content using the molybdovanadophosphoric acid method (1) modified for small sample sizes. Seeds of each species were also dried at 70C, weighed, ground, and analyzed for P content using the same method.

RESULTS AND DISCUSSION

Growth Chamber Experiment

With the exception of sainfoin and buckwheat, all species produced more dry matter with water-soluble P in the nutrient solution than when P was absent (Table II-2). Both sainfoin and buckwheat are large-seeded species, and P stored in their seed may have been adequate for growth during the experiment (Table II-1). However, seed size cannot be the sole reason for the lack of response to P by these species. Both winter wheat and subterranean clover responded to water-soluble P (Table II-2). These 2 species also have large seed and stored P in their seed is similar to that of sainfoin (Table II-1). Dry matter production for all species except sainfoin and winter wheat was the same for the 2 insoluble sources of P. Sainfoin produced more dry matter and winter wheat less dry matter with rock phosphate than with ^{32}P-fluorapatite (Table II-2).

An increase in root:top ratios often accompanies severe P stress (2). All forage legumes except red clover had higher root:top ratios without P than with water-soluble P in the nutrient solution (Table II-2). Buckwheat and winter wheat did not differ in root:top ratios for the same 2 treatments. Some plants appear to have an inherent ability to divert more dry matter production into roots rather than tops when severe P stress occurs.

A striking difference in root:top ratios occurred between the 2 insoluble P sources. Ratios were twice as great for the RP treatment

TABLE II-1. DRY WT AND P CONTENT PER SEED FOR 7 PLANT SPECIES.

Plant	mg dry wt	P content	
		% P	Total ug P
Sainfoin	20.5	0.29	59.5
Yellow sweetclover	2.5	0.35	8.6
Alfalfa	2.4	0.30	7.3
Subterranean clover	11.9	0.46	54.7
Red clover	1.9	0.35	6.6
Buckwheat	35.5	0.23	81.5
Winter wheat	33.1	0.17	56.2

TABLE II-2. PLANT GROWTH CHARACTERISTICS AS INFLUENCED BY DIFFERENT SOURCES OF P IN THE GROWTH CHAMBER.

Plant	Plant growth	P treatment			
		+P	RP	^{32}P	-P
Sainfoin	mg dry wt/day	6.06 b[1]	8.0 a	5.8 b	6.8 ab
	Root:top ratio	0.83 b	1.06 a	0.47 c	1.20 a
Yellow sweetclover	mg dry wt/day	5.8 a	6.2 a	5.4 a	2.9 b
	Root:top ratio	0.60 b	0.66 b	0.36 c	0.87 a
Alfalfa	mg dry wt/day	6.4 a	7.1 a	6.5 a	2.6 b
	Root:top ratio	0.60 b	0.57 b	0.35 c	0.83 a
Subterranean clover	mg dry wt/day	8.1 a	5.1 b	5.4 b	3.8 c
	Root:top ratio	0.68 b	0.82 a	0.41 c	0.90 a
Red clover	mg dry wt/day	5.2 a	3.0 b	2.8 b	1.2 c
	Root:top ratio	0.66 bc	0.94 a	0.62 c	0.82 ab
Buckwheat	mg dry wt/day	15.6 bc	17.5 ab	19.0 a	14.2 c
	Root:top ratio	o.32 a	0.29 ab	0.22 b	0.34 a
Winter wheat	mg dry wt/day	13.9 a	7.9 c	10.1 b	7.4 c
	Root:top ratio	0.99 b	1.31 a	0.57 c	1.05 b
All species	mg dry wt/day	8.7 a	7.8 a	7.9 a	5.5 b
	Root:top ratio	0.67 b	0.81 a	0.43 c	0.86 a

[1] Values within a row followed by a common letter are not significantly different at the 5% level.

than for the ^{32}P treatment for some species (Table II-2). These unexpected differences in root:top ratios were possibly due to differences in particle size of the 2 compounds. The ^{32}P-fluorapatite was ground finer than the rock phosphate, and thus had a smaller particle size. A decrease in particle size of such compounds facilitates their breakdown and dissolution in water. Therefore, the ^{32}P-fluorapatite was likely more easily dissolved, and its P consequently more available to plant roots. With increased solubilization, the Ca^{++} content of the bathing solution around the roots could increase dramatically (11), possibly accounting for the large differences in root:top ratios observed between the 2 treatments.

Although buckwheat absorbed the greatest total amount of P from the ^{32}P-fluorapatite, yellow sweetclover, a small-seeded legume (Table II-1), had the greatest % P in its dry matter (Table II-3). Sainfoin had a lower total P uptake from fluorapatite than both yellow sweetclover and alfalfa, and a lower % P in its dry matter than yellow sweetclover, but sainfoin produced more dry matter with rock phosphate than with a water-soluble P source (Table II-2). This result is difficult to explain, but is consistent with the lack of response by sainfoin to P fertilization on Montana soils (18). The efficiency of P utilization after absorption must also be considered.

Lindgren et al. (13) expressed the ratio of P in plant tops to total plant P as the translocation efficiency (T-eff); mg P in top/(mg

TABLE II-3. P UPTAKE FROM ^{32}P-FLUORAPATITE IN THE GROWTH CHAMBER AND ITS DISTRIBUTION IN THE PLANT.

Plant	Whole plant % P	% of total P		mg P absorbed from fluora-patite	T-eff[2]		RA-eff[3]	
		from fluora-patite	from seed		Total P basis	% P basis	Per unit dry wt	Per unit estimated surface area
Sainfoin	0.29 b[1]	87.5 d	12.5 b	0.43 de	57.0 b	38.4 a	8.0 c	2.9 de
Yellow sweetclover	0.45 a	98.8 a	1.2 e	0.70 b	54.2 b	29.8 b	16.8 a	5.8 bc
Alfalfa	0.30 b	98.7 a	1.3 e	0.57 c	52.3 b	27.7 b	11.8 b	7.7 b
Subterranean clover	0.24 c	85.3 e	14.7 a	0.32 ef	45.2 c	25.4 b	7.1 c	1.9 e
Red clover	0.30 b	97.2 a	2.8 e	0.24 f	35.3 d	25.3 b	7.7 c	6.1 bc
Buckwheat	0.22 c	93.0 b	7.0 d	1.11 a	65.6 a	29.5 b	11.3 b	10.5 a
Winter wheat	0.21 c	90.2 c	9.8 c	0.55 cd	17.2 e	10.6 c	5.1 d	4.7 cd

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[1] Values within a column followed by a common letter are not significantly different at the 5% level.

[2] T-eff
Total P basis = mg P in top/(mg P in top + mg P in roots) x 100
% P basis = % P in top/(% P in top + % P in roots) x 100

[3] RA-eff
Per unit dry wt = ug P absorbed from fluorapatite/mg root dry wt
Per unit estimated surface area = ug P absorbed from fluorapatite/unit of estimated root surface area (mg of H_2O spun off roots)

P in top + mg P in roots) x 100. Since root:top ratios vary considerably among plant species, T-eff should also be corrected for differences in dry wt to make comparisons between species. Therefore, T-eff was also expressed on a % P basis; % P in top/ (% P in top + % P in roots) x 100. On a total P basis, buckwheat had a higher T-eff than all other species (Table II-3), although buckwheat had a lower root:top ratio than the other species (Table II-2). When differences in dry wt between species were removed (% P basis), sainfoin had the greatest T-eff.

Winter wheat roots absorbed considerable P from fluorapatite (Table II-3), but were very inefficient in translocating this P to tops. As a consequence, dry matter production of tops was limited by the lack of P. Most cereal grains, such as winter wheat, do not accumulate large quantities of Ca^{++} in their tissue as legumes often will. The poor translocation of P observed with winter wheat might have been caused by excessive Ca^{++} accumulation in the root cortex occurring from the dissolution of fluorapatite. A high Ca^{++} concentration in or near the root cortex could have caused reprecipitation of soluble P before translocation occurred in the root vascular system.

Root absorption efficiency (RA-eff) is also an index of the ability of plant roots to extract soil P. RA-eff was measured on both a dry wt and estimated surface area basis and expressed as follows: total ug P absorbed from fluorapatite/ (mg root dry wt) or (unit of estimated root surface area [mg of H_2O spun off roots]). Yellow sweetclover had the highest RA-eff on a dry wt basis, and buckwheat on an estimated surface area basis (Table II-3).

Asher and Loneragan (2) carefully examined the relationship between P concentration of the root bathing solution and the rate of P absorption by plant roots in solution culture. They showed that plants grew at a maximum rate over a wide range of P concentrations. Some legumes, such as Western Australian blue lupin (*Lupinus digitatus* Forsk) absorbed P at very low concentrations and required only a low supply for maximum growth (4, 14). In this study, sainfoin achieved maximum growth at lower levels of P than the other forage legumes tested. At very low levels of P, the extent to which a plant can lower the P concentration in soil solution at the root surface is very important (3, 20). A diffusion gradient of P towards the root surface needs to be established before adequate P absorption can occur. Lindgren et al. (13), however, suggested that plant roots may absorb P rapidly and still not be able to translocate it efficiently. They found large differences in P absorption rates between lines of snap bean (*Phaseolus vulgaris* L.). Their results suggest that one could select plants adapted to soils normally low in soluble P.

Greenhouse Experiment

In contrast to the growth chamber experiment where most species responded to rock phosphate, only sainfoin showed a significant increase in the rate of dry matter production for the RP treatment over the -P treatment in the greenhouse (Table II-4). Since the same rate of rock phosphate by volume was used in both experiments, the difference in response appears to be related to container size. The density of roots per unit of growth medium was less in the pots used in the greenhouse than in the plastic test tubes used in the growth chamber. The restriction of roots in small containers presents a serious problem when one attempts to simulate field conditions with regard to nutrient uptake.

In this experiment, sainfoin was the only species exhibiting a greater T-eff on both a total P basis and % P basis for the water-insoluble (RP) P source than for the water-soluble (+P) P source (Table II-4). RA-eff on a dry wt basis was greatest for the +P treatment for all species as would be expected.

TABLE II-4. P UPTAKE AND DISTRIBUTION IN THE PLANT AS INFLUENCED BY DIFFERENT SOURCES OF P IN THE GREENHOUSE.

		Plant growth		Whole plant P content		T-eff[2]		RA-eff[3]
Plant	Treatment	mg dry wt/day	Root:top ratio	% P	mg P	Total P basis	% P basis	Per unit dry wt
Sainfoin	+P	6.1 a[1]	0.94 a	0.46 a	1.15 a	41.5 b	39.7 b	9.6 a
	RP	5.3 a	0.97 a	0.24 b	0.55 b	58.3 a	57.4 a	5.0 b
	-P	3.2 b	0.86 a	0.28 b	0.36 b	63.7 a	60.1 a	6.1 b
Yellow sweetclover	+P	4.2 a	0.27 b	0.50 a	0.90 a	79.5 a	51.5 a	24.1 a
	RP	1.2 b	0.49 a	0.23 b	0.11 b	49.0 c	31.7 c	7.2 b
	-P	0.8 b	0.43 a	0.21 b	0.07 b	61.0 b	39.8 b	7.4 b
Alfalfa	+P	2.4 a	0.31 c	0.54 a	0.54 a	78.8 a	53.2 a	23.4 a
	RP	0.6 b	0.77 a	0.16 b	0.04 b	52.9 b	47.2 a	3.9 b
	-P	0.5 b	0.54 b	0.16 b	0.03 b	57.2 ab	41.9 a	4.8 b
Subterranean clover	+P	4.3 a	0.48 a	0.55 a	0.99 a	66.6 a	49.3 a	17.3 a
	RP	1.8 b	0.60 a	0.14 b	0.10 b	54.7 b	41.3 b	4.0 b
	-P	1.2 b	0.59 a	0.16 b	0.08 b	60.6 ab	47.3 ab	4.6 b
Red clover	+P	1.1 a	0.50 a	0.54 a	0.24 a	72.8 a	57.0 a	16.5 a
	RP	0.3 b	0.58 a	0.22 b	0.03 b	54.6 a	44.9 a	6.1 b
	-P	0.3 b	0.52 a	0.17 b	0.02 b	65.2 a	59.6 a	4.3 b
Buckwheat	+P	19.4 a	0.21 a	0.31 a	1.65 a	86.1 a	57.6 a	17.8 a
	RP	10.6 b	0.24 a	0.20 b	0.58 b	67.5 b	34.6 b	10.2 b
	-P	6.7 b	0.27 a	0.19 b	0.35 b	78.2 a	49.7 a	9.2 b
Winter wheat	+P	7.6 a	0.48 b	0.36 a	0.75 a	77.8 a	64.5 a	11.3 a
	RP	3.5 b	0.76 a	0.17 b	0.16 b	51.4 b	44.4 b	4.0 b
	-P	2.8 b	0.81 a	0.15 b	0.12 b	66.5 ab	62.1 a	3.4 b
All species	+P	6.4 a	0.45 b	0.47 a	0.89 a	71.9 a	53.3 a	17.3 a
	RP	3.3 b	0.63 a	0.19 b	0.23 b	55.5 c	43.1 b	5.8 b
	-P	2.2 b	0.58 a	0.19 b	0.16 b	64.6 b	51.0 a	5.8 b

[1] Values within a column for each individual species followed by a common letter are not significantly different at the 5% level.

[2] T-eff < Total P basis = mg P in top/(mg P in top + mg P in roots) x 100
% P basis = % P in top/(% P in top + % P in roots) x 100

[3] RA-eff = ug P absorbed from fluorapatite/mg root dry wt

CONCLUSIONS

My results show that yellow sweetclover absorbed more P and had a higher % P in its tissue than all other forage legumes tested when fluorapatite was the only source of P. The ability of yellow sweetclover to absorb P efficiently from insoluble calcium-phosphate compounds in the soil may partially explain its rapid establishment on recently disturbed land such as new road cuts or mine spoils when it is one of the first invaders. Sainfoin, although absorbing less P from fluorapatite than both yellow sweetclover and alfalfa, translocated P absorbed from fluorapatite from roots to tops most efficiently. Yellow sweetclover, alfalfa, and sainfoin produced maximum dry matter while feeding on either pure fluorapatite or rock phosphate in small, restrictive containers, but only sainfoin responded to rock phosphate when the root density was much less. Subterranean clover and red clover were the least efficient legumes in absorbing and utilizing P from pure fluorapatite or rock phosphate. My data, in agreement with other investigators, show that buckwheat absorbs P from rock phosphate very efficiently. Winter wheat roots absorbed considerable P from fluorapatite, but were very inefficient in translocating this P to tops.

Forage legumes differed in their ability to absorb and utilize P from insoluble soil sources. Thus, the potential exists to better match the proper forage legume with a soil, and to possibly increase P uptake and utilization within a species from insoluble soil sources.

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III. PLANT CHARACTERISTICS RELATED TO PHOSPHORUS UPTAKE FROM ROCK PHOSPHATE

INTRODUCTION

Plant species differ in their abilities to obtain P from unavailable forms of soil phosphate and survive on soils low in available P (4, 5, 7, 8, 12, 13, 15, 18). The ability of plants to grow successfully in less fertile situations is becoming increasingly more important because of the limited supply and high cost of fertilizer. Making better use of the less available forms of residual nutrients surviving from earlier applications of fertilizer by plants would decrease our dependence on repeated fertilization.

The dissolution of rock phosphate by plant roots has been attributed to numerous factors. Plants with high cation exchange capacity root systems usually obtain P more effectively from soil and rock phosphate than plants with low cation exchange capacity root systems (4, 5, 6). Truog (18) claimed that the increased Ca uptake by high exchange capacity roots caused greater mobilization of P in rock phosphate systems.

Recent investigations have shown that plants able to reduce the Ca^{++} concentration in the rhizosphere are the most effective feeders from rock phosphate (12, 13). Two mechanisms of removing Ca^{++} from solution are adsorption on the root exchange complex and absorption across root membranes. Therefore, plants such as forage legumes that have high root CECs, as well as high Ca^{++} bonding values (5), will adsorb more Ca^{++} on the root exchange complex. Buckwheat and most forage legumes can accumulate large quantities of Ca^{++} in their tops, or as sainfoin does, in the cortex of older roots near the soil surface (16). High root CECs and large quantities of Ca^{++} absorption are 2 important factors in allowing the dissolution of rock phosphate to continue before reprecipitation of soluble P occurring from high Ca^{++} concentrations can occur (Chapter II).

In early research, scientists often attributed variation in the feeding ability of different plant species for rock phosphate to differences in the size of their root systems. P uptake by plants is often limited by the rate of diffusion to the root surface. Plants having an extensive root system are often able to maintain a sufficient continuous uptake of P under limiting conditions (13). Since the dissolution of rock phosphate by plant roots is confined to a microenvironment near the root surface (12), increasing the amount of root surface area exposed in a soil should enhance the ability of a plant to feed on rock phosphate.

Soil P may also be present in the form of organic phosphates. Acid phosphatase activity at the surface of roots can cause the hydrolysis of organic phosphates to more available forms (13). Phosphatases are adaptive enzymes. Their activity increases with increasing P stress. McLachlan (13) obtained a strong inverse relationship between root exocellular acid phosphatase activity and plant production when available soil P was low. Phosphatase activities could prove useful in predicting plant species with potential for developing low available P soil situations.

Plant roots modify the pH of surrounding soil solution through the release of H^+ and OH^- or HCO_3^- ions into the rhizosphere when a differential uptake of cations and anions occurs (17). The dissolution of fluorapatite, a major constituent of rock phosphate, is a sensitive function of soil pH (12). Plants such as buckwheat that maintain a low rhizosphere pH are usually effective at causing the solubilization of rock phosphate (13).

Although factors such as mycorrhizal relationships (1) and root surface area are important in determining the feeding power of plants for rock phosphate, the belief that a chemical process occurring at the root-mineral interface facilitates the dissolution process has been well verified experimentally (7, 12, 13). It would be desirable to screen for plants possessing this capability.

The objectives of this study were to evaluate the responses of root cation exchange capacity, estimated root surface area, root exocellular acid phosphatase activity, and rhizosphere pH to different sources of P. Possible screening techniques which might be used to predict a plant's ability to survive and produce in low available P situations are also considered.

MATERIALS AND METHODS

Experiment 1

Five forage legumes, alfalfa, sainfoin, yellow sweetclover, red clover, and subterranean clover and 2 check species, winter wheat and buckwheat, were grown in gravel culture in a controlled environment chamber at a temperature of 21±1C with a photoperiod of 16 hr at a photosynthetic photon flux density of 280 uEinsteins m^{-2} sec^{-1} provided by incandescent and fluorescent lights. Six replications of all species were grown with each of the following 3 treatments in a randomized complete block design.

1) RP treatment - Three hundred forty mg of screened Idaho rock phosphate, provided by the J. R. Simplot Co., Pocatello, Idaho, were thoroughly mixed with washed silica gravel and the mixture added to plastic test tubes (16 cm x 2.4 cm). Seeds of each species were pregerminated on moist blotter paper for 1 day. Three germinated seeds were transplanted to each test tube and thinned to 1 per tube after establishment. All seedlings were watered every other day with a modified -P Hoagland's nutrient solution (9) containing, in mg/liter, N,84 (73 as NO_3 and 11 as NH_4); K, 68; Ca, 60; Mg, 12; S, 16; Cl, 0.8; B, 0.5; Mn, 0.5; Zn, 0.05; Cu, 0.02; Mo, 0.01; and Fe, 1.0 added as Fe·EDTA. The nutrient solution was adjusted to pH 6.0 using 1.0 N H_2SO_4 before use. The gravel medium was flushed periodically with distilled water to avoid salt accumulation.

2) -P treatment - Seeds were planted in individual plastic test tubes filled with pure washed silica gravel and watered with the same nutrient solution as in treatment 1. No source of P was present.

3) +P treatment - Seeds were planted in individual plastic test tubes filled with pure washed silica gravel. Seedlings were watered with a complete nutrient solution including 8 mg/liter of water-soluble P in addition to the nutrients listed in treatment 1.

Roots and tops were harvested separately 35 days after germination of the forage legumes and 25 days after germination of winter wheat and buckwheat. Roots were thoroughly washed with distilled water to remove any adhering gravel or fertilizer.

Each complete root system was assayed for exocellular acid phosphatase activity by adapting the colorimetric technique of Bessey et al. (3) to the measurement of acid phosphatase activity. Roots were immersed in 6 ml of 0.1 M acetate buffer, pH 5.0, in 25 ml test tubes covered with aluminum foil and equilibrated for 15 min in a 37C water bath. The reaction was initiated by the addition of 6 ml of p-nitrophenylphosphate disodium salt (50 mg/100 ml H_2O). Aliquots of 0.2 ml were taken at 15, 30, 45, and 60 min. The reaction of each aliquot was stopped by the addition of 3 ml of 0.1 N KOH. The amount of p-nitrophenol released was determined colorimetrically at 400 mu.

The cation exchange capacity of each complete root system was determined using the acid-washing technique (2) modified for small sample sizes. Root surface area was estimated using the differential centrifugation method (11). Both techniques are described in Chapter I. All roots and tops were dried in a forced air oven at 70C and weighed.

Experiment 2

Changes in rhizosphere pH induced by sainfoin seedlings were evaluated in solution culture. Seeds from a common source were germinated and grown in moist vermiculite for 5 days. The seedlings were watered with distilled water while in vermiculite. After 5 days, 45 uniform seedlings were transferred to 25 mm x 200 mm test tubes, 1 seedling per tube, covered with aluminum foil. The seedlings were supported by a layer of aluminum foil with a hole in the center. The test tubes were filled with the same complete nutrient solution as that used in treatment 3 (+P) of experiment 1. The nutrient solution was adjusted to pH 6.0 using 1.0 N H_2SO_4 before use. All solutions were aerated and mixed vigorously every 12 hr.

The complete nutrient solution was changed in each test tube at 8 and 10 days after germination. Starting at day 11, the pH of nutrient solution in each test tube was measured every 24 hr for 3 days. Solutions were mixed vigorously before each pH reading. After pH readings were taken on day 13, the solutions in each test tube were replaced by the same -P nutrient solution used in treatment 1 and 2 of experiment 1. The pH of all solutions was again measured every 24 hr for 3 days. After pH readings were taken on day 16, the solutions were replaced with -P nutrient solution again. Three more pH readings were taken every 24 hr. The average of solution pH readings for all 45 test tubes was calculated for each time of measurement. Maximum and minimum pH readings were also compiled for each time of measurement.

RESULTS AND DISCUSSION

Experiment 1

Sainfoin, yellow sweetclover, alfalfa, and buckwheat all grew well with rock phosphate as the only source of P (Table III-1). Sainfoin and buckwheat actually produced more dry matter with rock phosphate than with a water-soluble source of P. Root:top ratios generally increased with increasing P stress.

Increasing the amount of root surface area exposed for P uptake to occur would be advantageous in low available P situations (13). In this study, total estimated root surface area for most species decreased as P stress increased (Table III-2). This would be expected since dry matter production also decreased when P stress occurred. Root surface area index (RSAI) generally increased as available P became more limiting for the forage legumes, but not for buckwheat and winter wheat. Roots appeared thinner and more lateral root branching occurred as RSAI increased. The magnitude of change in RSAI appeared to be more a function of the amount of available P in solution than a response to the presence of insoluble P.

The level of P nutrition may influence the cation exchange capacity of roots (10). McLean et al. (14) observed that the influence of plant nutrition upon root CEC was most notable in plants having low root exchange capacities. For all forage legumes except sainfoin in this study, root CEC expressed per unit of root dry wt increased with decreas-

TABLE III-1. PLANT GROWTH CHARACTERISTICS AS AFFECTED BY DIFFERENT SOURCES OF P.

Plant	Plant growth	P treatment		
		+P	RP	-P
Sainfoin	mg dry wt/day	6.1 b[1]	7.4 a	6.1 b
	root:top ratio	0.47 b	0.49 b	0.66 a
Yellow sweetclover	mg dry wt/day	9.8 a	8.8 a	4.0 b
	root:top ratio	0.32 a	0.39 a	0.43 a
Alfalfa	mg dry wt/day	10.2 a	8.1 b	2.2 c
	root:top ratio	0.36 a	0.38 a	0.40 a
Subterranean clover	mg dry wt/day	6.5 a	3.1 b	3.1 b
	root:top ratio	0.41 b	0.51 a	0.47 ab
Red clover	mg dry wt/day	8.0 a	2.2 b	1.0 c
	root:top ratio	0.43 a	0.47 a	0.51 a
Buckwheat	mg dry wt/day	10.9 b	12.8 a	11.0 b
	root:top ratio	0.21 b	0.20 b	0.29 a
Winter wheat	mg dry wt/day	9.3 a	6.6 b	6.3 b
	root:top ratio	0.57 a	0.51 a	0.53 a
All species	mg dry wt/day	8.7 a	7.0 a	4.8 c
	root:top ratio	0.40 b	0.42 ab	0.47 a

[1] Values within a row followed by a common letter are not significantly different at the 5% level.

TABLE III-2. TOTAL ESTIMATED ROOT SURFACE AREA AND ROOT SURFACE AREA INDEX (RSAI) AS AFFECTED BY DIFFERENT SOURCES OF P.

	P treatment			P treatment		
Plant	+P	RP	-P	+P	RP	-P
	--Total mg H_2O spun off roots[2]--			--mg H_2O spun off/mg dry wt[3]--		
Sainfoin	257.2 ab[1]	249.3 b	334.4 a	3.93 a	2.97 b	4.14 a
Yellow sweetclover	264.2 a	275.2 a	169.2 b	3.19 b	3.16 b	4.26 a
Alfalfa	215.8 a	221.4 a	110.6 b	2.45 b	2.87 b	4.93 a
Subterranean clover	253.1 a	114.1 b	158.1 b	4.14 ab	3.20 b	4.62 a
Red clover	278.2 a	111.6 b	48.2 c	3.34 b	4.35 a	4.40 a
Buckwheat	71.5 a	87.0 a	73.5 a	1.54 ab	1.61 a	1.21 b
Winter wheat	214.7 a	94.4 b	112.5 b	2.57 a	1.68 b	2.02 b
All species	222.1 a	164.7 b	143.8 b	3.02 b	2.83 b	3.65 a

[1] Values within a row followed by a common letter are not significantly different at the 5% level.

[2] Total mg H_2O spun off roots = total estimated root surface area.

[3] mg H_2O spun off roots/mg root dry wt= root surface area index (RSAI).

ing levels of available P (Table III-3). RSAI also increased as available P decreased (Table II-2). If root CEC is expressed per unit of RSAI, the resulting value should be a good estimate of the density of exchange sites along a root surface (Chapter I). With severe P stress (-P treatment), the density of exchange sites decreased dramatically for yellow sweetclover, alfalfa, subterranean clover, and red clover. Sainfoin showed no significant difference in the density of exchange sites between the P treatments, indicating that severe P stress did not occur. If total dry matter production (Table I-1) is compared with root CEC expressed as meq/RSAI (Table III-3), a strikingly similar pattern of response is evident for all species except buckwheat.

The response of root exocellular acid phosphatase activity to different sources of P is reported in Table III-4. An inverse relationship between phosphatase activity and dry matter production (Table III-1) was evident for most species. This is in agreement with other data (13) showing an increase in phosphatase activity with decreasing levels of available P.

Experiment 2

Since the dissolution of rock phosphate is a sensitive function of the pH of surrounding solution (12), I examined changes in rhizosphere pH induced by sainfoin seedlings. If sufficient variation exists among a species, then rhizosphere pH measurements might be used as a screening technique to select plants adapted to low available P soil situations.

TABLE III-3. ROOT CATION EXCHANGE CAPACITY (CEC) EXPRESSED PER UNIT OF DRY WT AND RSAI AS INFLUENCED BY DIFFERENT SOURCES OF P.

	P treatment			P treatment		
Plant	+P	RP	-P	+P	RP	-P
	--meq/100 g dry wt--			--meq/RSAI--		
Sainfoin	58.7 a[1]	42.9 b	46.4 ab	10.1 a	12.3 a	10.4 a
Yellow sweetclover	31.8 b	35.8 ab	39.8 a	8.8 a	9.8 a	4.0 b
Alfalfa	29.3 b	34.7 b	46.4 a	11.5 a	9.5 a	2.2 b
Subterranean clover	42.7 a	42.8 a	45.6 a	7.7 a	5.3 ab	3.4 b
Red clover	33.1 b	44.2 a	46.7 a	8.3 a	2.5 b	1.2 c
Buckwheat	26.9 a	27.1 a	23.0 b	8.4 b	9.2 ab	12.5 a
Winter wheat	13.4 a	10.4 b	10.8 b	4.5 a	3.5 ab	2.9 b
All species	33.7 a	34.0 a	37.0 a	8.5 a	7.5 a	5.2 b

[1] Values within a row followed by a common letter are not significantly different at the 5% level.

TABLE III-4. ROOT EXOCELLULAR ACID PHOSPHATASE ACTIVITY AS INFLUENCED BY DIFFERENT SOURCES OF P.

Plant	P treatment		
	+P	RP	-P
	--uM PNP[2] (g dry wt)$^{-1}$ (hr)$^{-1}$--		
Sainfoin	0.44 a[1]	0.33 a	0.37 a
Yellow sweetclover	0.32 b	0.34 b	0.73 a
Alfalfa	0.25 b	0.31 b	0.94 a
Subterranean clover	0.58 b	0.82 ab	0.91 a
Red clover	0.38 b	0.97 b	2.78 a
Buckwheat	2.02 a	2.10 a	2.31 a
Winter wheat	0.40 a	0.53 a	0.49 a
All species	0.58 b	0.72 b	1.18 a

[1] Values within a row followed by a common letter are not significantly different at the 5% level.

[2] PNP = p-nitrophenol

A wide range of pH readings in response to P stress among 45 sainfoin seedlings was obtained (Figure III-1). At days 13 through 19 after germination, using a -P nutrient solution, pH values tended to drop below the initial pH of 6.0 during the 1st day, and increase during the 2nd and 3rd days after a solution change. The range of pH values increased with increasing plant age. Sufficient variation in rhizosphere pH values existed among sainfoin seedlings to warrant further investigations into the use of rhizosphere pH as a possible means of identifying plants adapted to low available P soil situations.

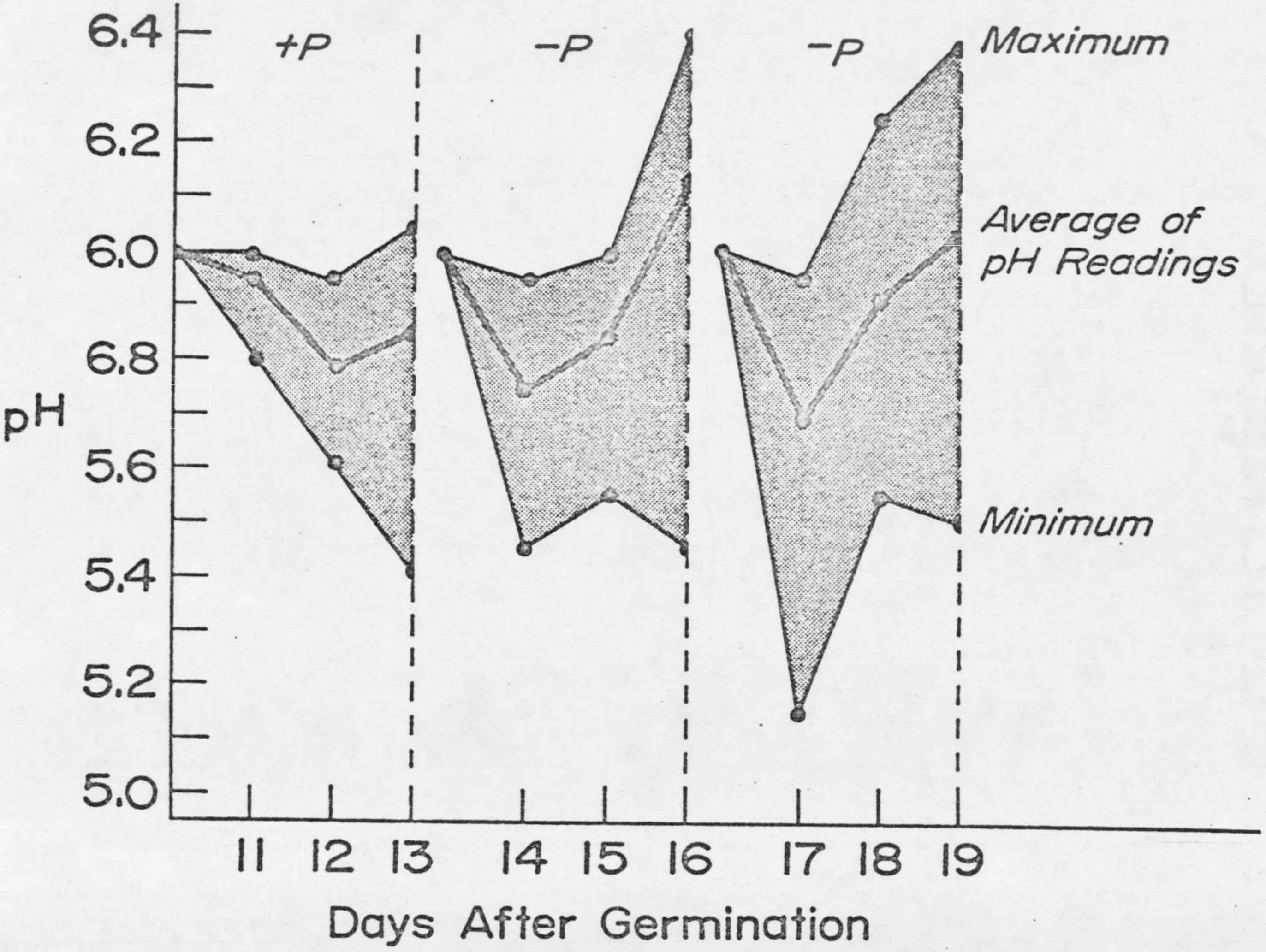

Figure III-1. Changes in rhizosphere pH induced by sainfoin seedlings. The vertical dotted lines indicate solution changes.

CONCLUSIONS

Root CEC expressed per unit of dry wt increased as the levels of available P decreased for all forage legumes except sainfoin. The density of cation exchange sites along the root surface decreased for yellow sweetclover, alfalfa, subterranean clover, and red clover, but not for sainfoin, when grown for 35 days with no source of P. Estimated root surface area per unit of dry wt (RSAI) generally increased as available P became more limiting for the forage legumes, but not for winter wheat and buckwheat. Root exocellular acid phosphatase activity was inversely related to total dry matter production for most species. A wide range of rhizosphere pH values for 45 sainfoin seedlings was obtained when the plants were subjected to P stress. The most promising indicators of a plant's feeding power for rock phosphate appeared to be rhizosphere pH changes in response to P stress and Ca^{++} accumulation by plants from insoluble calcium-phosphate compounds.

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SUMMARY AND CONCLUSIONS

The dissolution of fluorapatite, a major constituent of most rock phosphate reserves, can occur as follows: $Ca_{10}(PO_4)_6F_2 + 12H^+ \rightarrow 10\ CA^{++} + 6(H_2PO_4^-) + 2F^-$. Theoretical considerations predict that the solubility of fluorapatite should increase as the H^+ concentration increases (decreasing pH), and as Ca^{++} and $H_2PO_4^-$ concentrations in soil solution decrease. Any plant characteristic which enhances any of these conditions should increase a plant's P feeding power from fluorapatite.

To initiate the dissolution of fluorapatite, plant roots apparently lower the pH of rhizosphere soil solution. The release of H^+ from plant roots may be a hormonal response to P stress. As the pH of rhizosphere solution decreases, though, 2 antagonistic phenomena would be taking place; the dissolution of fluorapatite due to decreasing pH and the reprecipitation of soluble P due to increasing Ca^{++} concentration. Therefore, plant roots must also remove a significant amount of Ca^{++} from solution to allow the dissolution of fluorapatite and release of soluble P to continue.

Plant roots can remove Ca^{++} from soil solution by adsorption on the root cation exchange complex or by absorption across root membranes. Therefore, plants possessing high root cation exchange capacities and the ability to accumulate Ca^{++} in their tissue should be good P feeders from rock phosphate.

The absorption and utilization of P from insoluble tricalcium-phosphate compounds by alfalfa, sainfoin, yellow sweetclover, red clover, subterranean clover, winter wheat, and buckwheat were studied in gravel culture in a controlled environment chamber. Yellow sweetclover absorbed more P and had a higher % P in its tissue than the other forage legumes tested when ^{32}P-fluorapatite was the only source of P. Sainfoin translocated P absorbed from fluorapatite most efficiently from roots to tops. Yellow sweetclover, alfalfa, and sainfoin produced maximum dry matter while feeding on either pure fluorapatite or rock phosphate in small, restrictive containers, but only sainfoin responded to rock phosphate when the root density was much less. Subterranean clover and red clover did not absorb and utilize P from fluorapatite or rock phosphate as efficiently as yellow sweetclover, alfalfa, and sainfoin. Buckwheat was an efficient P feeder from rock phosphate. Winter wheat roots absorbed considerable P from ^{32}P-fluorapatite, but were very inefficient in translocating this P to tops.

Plant characteristics that allow plants to adapt to low available P soil situations include high root cation exchange capacities, excretion of organic acids or H^+ from roots into surrounding soil solution, absorption or adsorption of Ca^{++} from solution by roots, root exocellular acid phosphatase activity, increased root surface area, chelate secretion by roots, and mycorrhizal relationships. The responses of root cation exchange capacity, root exocellular acid phosphatase activity, root surface area, and rhizosphere pH to different sources of P were evaluated in this study. The density of cation exchange sites along the root surface decreased dramatically for yellow sweetclover, alfalfa, subterranean clover, and red clover, but not for sainfoin, when grown for 35 days with no source of P. An inverse relationship between root exocellular acid phosphatase activity and dry matter production occurred for most species. Estimated root surface area per unit of dry wt (RSAI) generally increased as available P became more limiting for the forage legumes, but not for winter wheat and buckwheat. A wide range of rhizosphere pH values was obtained among 45 sainfoin seedlings when subjected to P stress in solution culture.

Both Ca^{++} adsorption and absorption by plant roots are important to the continued dissolution of rock phosphate in the rhizosphere. If they do not occur, high levels of Ca^{++} in solution can cause reprecipitation of soluble P. To initiate the dissolution process, though, it is likely that plant roots must lower the pH of soil solution in the rhizosphere. Therefore, rhizosphere pH changes in response to P stress and Ca^{++} accumulation from insoluble calcium-phosphate compounds by plants appear to be the most promising indicators of a plant's P feeding power from rock phosphate.

Jacques, R. M.
Phosphorus uptake from insoluble soil sources by five forage legumes
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