THE UPTAKE OF ORTHOPHOSPHATE AND ITS INCORPORATION INTO ORGANIC PHOSPHATES ALONG ROOTS OF *PINUS RADIATA*

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Summary

An automatic scanning–recording method showed that relative incorporation of [^{32}P]orthophosphate along sterile pine roots into both the nucleic acid fraction and the phospholipid–phosphoprotein fraction was usually much greater in the apical 1- and 2-cm segments than in the remainder of the root. Relative incorporation into phosphate fractions was modified considerably by the phosphate uptake and phosphate status at different parts of the root. Relative incorporation into the readily acid-soluble fraction was greatest at sites of greatest phosphate uptake along the root, and was less with phosphate-deficient plants than with high-phosphate plants. Description of root behaviour as an average of the entire root is inadequate and is likely to lead to erroneous interpretation of nutrient uptake and use by roots.

Uptake of phosphate during 20 min from 5×10^{-6}M phosphate by 3-week-old *P. radiata* seedlings was more than two-and-a-half times greater with non-sterile than with sterile roots. Relative incorporation into the nucleic acid fraction of non-sterile and sterile roots was 15·5 and 6·1% respectively (significant at the 0·1% level). Relative incorporation of the phosphate into the fraction soluble in cold 0·1N perchloric acid was significantly less with non-sterile than with sterile roots. Mechanistic interpretations of kinetics of phosphate uptake and utilization by roots may be seriously in error by neglect of the microbial factor.

I. Introduction

It is probable that the phosphate available for translocation from different parts of a root will be affected considerably by the extent to which absorbed phosphate is incorporated into translocated and non-translocated compounds. However, detailed studies of the extent of incorporation of orthophosphate into organic compounds at different parts of roots have been severely hampered by the lack of a ready method to examine this. Indeed, previous detailed studies appear to have been confined to the apical few millimetres of the root (Holmes *et al.* 1955; Jensen 1958). Furthermore, in many previous studies of phosphate incorporation into roots it has not been recognized that this can be distorted by microorganisms superimposing their own properties on those of the root and by their affecting root metabolism (Barber 1966; Bowen and Rovira 1966, 1969; Barber and Loughman 1967; Lonberg-Holm 1967).

The present study: (1) provides a new method for readily studying phosphate incorporation into various phosphate fractions along roots, (2) demonstrates large differences in such phosphate utilization along sterile roots and the effects of previous

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phosphate nutrition on these differences, and (3) extends the findings of gross microbial distortion of phosphate uptake and utilization to a tree species. It also discusses the place of sterile and of non-sterile plants in studies of phosphate nutrition of plants.

II. Materials and Methods

(a) *Growth of Plants*

Seed of *Pinus radiata* was surface-sterilized with equal parts of 20-vol. hydrogen peroxide and ethanol for 20 min followed by washing with several changes of sterile water during 20 min. The seed was then germinated on agar and, when the radicles were 5–10 mm long, three sterile seedlings were placed on stainless-steel mesh immediately above 35 ml of nutrient solution in each of several 20- by 3-cm test tubes. Plants were grown for 3 weeks in a glasshouse before assessment of phosphate uptake ability and fractionation of phosphate. Asepsis was achieved by using cotton-plugged tubes and sterilizing the tubes plus nutrient solution before planting the sterile germinating seed. Sterility was verified at the end of the growth period by plating some of the growth solution to a nutrient agar. Where phosphate uptake and utilization by non-sterile plants was to be compared with that of sterile plants a wide range of microorganisms was introduced by adding 0·1 ml of a 1% aqueous suspension of soil (a red-brown earth) 1 week before the uptake experiment.

The high-phosphate ($2{\cdot}5\times10^{-4}$M) and phosphate-deficient nutrient solutions used throughout the studies were the complete and phosphate-deficient solutions designed by Hoagland and Arnon (1938) but at one-quarter strength. In some experiments "low-phosphate" plants were grown in phosphate-deficient solution to which phosphate was added at 1×10^{-6}M as potassium dihydrogen phosphate. At the end of the 3-week growth period 90% of the phosphate in this solution had been removed by the plants. The initial and final pH of all solutions was 6·3. Where plants were grown in the presence of ^{32}P continuously, this was added as orthophosphate to the nutrient solution at an initial activity of 60 μCi/l (less than 10^{-8}M).

(b) *Uptake of Phosphate*

For short-term uptake experiments with ^{32}P, plants were removed from their tubes, and the roots pretreated in 5×10^{-4}M calcium sulphate for 1 hr before being placed for 20 or 30 min (20°C) in a solution of 5×10^{-4}M calcium sulphate and 5×10^{-6}M potassium dihydrogen phosphate with ^{32}P as orthophosphate at 600 μCi/l (less than 10^{-7}M). The pH was 6·3. After uptake, the roots were washed in rapidly running water for 5 min which removed free-space phosphate. As with previous studies using wheat (Bowen and Rovira 1967) it was shown that there was no appreciable movement of phosphate from sites of uptake over the experimental period. Uptake experiments were conducted with intact plants to avoid the marked decline in uptake which can occur upon excision of roots (Bowen and Rovira 1967) and tops were severed from the roots after the post-uptake wash.

(c) *Fractionation of Phosphate Compounds*

Phosphate fractions were obtained by the modification of the Ogur–Rosen method (Ogur and Rosen 1950) used by Loughman and Russell (1957), with the further modification that inorganic orthophosphate and readily acid-soluble esters (including sugar phosphates and nucleotide phosphates) were removed by a series of five freezings (at −70°C) and thawings of each root in 5 ml of 0·1N perchloric acid followed by three washings with distilled water at 1–2°C. The efficacy of such extraction was checked by subsequently grinding a number of ^{32}P-labelled roots in 0·1N perchloric acid followed by centrifuging at 4°C and counting the radioactivity of the supernatant. In one experiment with nine plants, freezing and thawing removed 96·7–98·0% (mean 97·3%) of the acid-soluble fraction. In this experiment the acid-soluble fraction contained 83·9% of the total ^{32}P. In a second experiment with 12 plants,

97·6–100·0% (mean 98·6%) of the acid-soluble ^{32}P in the apical 2 cm and 98·3–100·0% of the acid-soluble ^{32}P of 2-cm basal portions of the roots were extracted by freezing and thawing.

Nucleic acids were removed according to Loughman and Russell (1957), but because of doubt of the clear separation of DNA and RNA in such extraction (Hutchison and Munro 1961) a distinction between RNA and DNA is not made in the results below. The residue from these extractions contained phospholipid and phosphoprotein.

(d) Measurement of Radioactivity of Phosphate Fractions along the Root

The radioactively labelled roots were laid between two strips of thin polyethylene sheeting (40 μm thick), to prevent drying of the root, and attached lengthwise along 4-cm-wide Whatman No. 1 chromatography paper. Distribution of radioactivity along the root was recorded by passing the mounted root through a gas-flow chromatogram scanner–recorder (Nuclear-Chicago Actigraph III). Distribution of ^{32}P along the roots was obtained on each root initially and after each extraction. The amounts of each fraction in specified segments of the root were calculated by differences (on an area basis) between successive extractions.

With the levels of radioactivity in the roots in these experiments, initial scanning (i.e. total ^{32}P) of 12 replicate roots at optimum settings took up to 2 hr. Rescanning the first roots at the end of this period showed there had been no redistribution of ^{32}P. This time can be reduced considerably by increasing the radioactivity of the phosphate treatment solution and by reducing the number of replicate roots scanned in a series before commencing extraction. Rescanning the polyethylene after removal of the roots showed there was no residual phosphate. In preliminary experiments, not reported in detail here, it was shown that, as with wheat (Bowen and Rovira 1967), there was a high correlation between areas under successive 2-mm sections of scans and the radioactivity of the same portions of the root digested and counted with a liquid Geiger–Mueller tube, i.e. the resolution of the method is better than 2 mm and any self-absorption of ^{32}P radioactivity was uniform along the root.

III. Results

(a) Effects of Microorganisms

Phosphate uptake and incorporation over 20 min by sterile and non-sterile *P. radiata* seedlings grown for 3 weeks in different phosphate pretreatments are shown in Table 1.

The 263% greater uptake of phosphate per centimetre of root by non-sterile plants (significant at 0·1% level) was independent of root length, which was unaffected by microorganisms in each nutrient solution; low-phosphate and phosphate-deficient plants had significantly shorter roots than did plants grown in high-phosphate solutions.

The percentage incorporation of phosphate into the nucleic acid fraction was two-and-a-half times greater with non-sterile than with sterile plants (significant at 0·1% level) and percentage incorporation into the acid-soluble fraction with non-sterile plants was significantly less (significant at 1% level) than with sterile plants. Although Table 1 shows trends for greater incorporation into the acid-soluble fraction with high-phosphate plants and a greater effect of microorganisms on incorporation with low-phosphate and phosphate-deficient plants, these differences were not significant due to considerable variability in the material. This variability was also encountered, particularly with non-sterile plants, by Bowen and Rovira (1966) in phosphate-uptake studies with tomato and subterranean clover seedlings. An indication of effects of plant nutrition on incorporation is given by the significantly greater percentage incorporation into the phospholipid–phosphoprotein fraction with low-phosphate and phosphate-deficient plants compared with high-phosphate plants.

(b) *Distribution of ^{32}P Fractions along Sterile Roots*

(i) *Short-term Labelling*

In this experiment a period of 2 hr after the 30-min uptake of [^{32}P]phosphate was allowed for further metabolism. Radioactive phosphate distribution along sterile pine seedling roots after successive extractions are shown in Figure 1.

Figure 1 is for a typical plant grown under conditions of high phosphate. In high-phosphate plants there was a sustained high uptake along the root (no significant

TABLE 1

PHOSPHATE UPTAKE AND INCORPORATION BY STERILE AND NON-STERILE PINE SEEDLINGS

Uptake during 20 min by 3-week-old plants from solutions containing 5×10^{-6}M KH_2PO_4, 5×10^{-4}M $CaSO_4$, and 600 μCi ^{32}P (pH 6·3) was measured

Culture Solutions	State of Seedlings	Root Length (cm)*	Uptake/Cm (counts/100 sec)	Percentage Incorporation into Fraction: Acid-soluble	Nucleic Acid	Phospholipid and Phosphoprotein
High phosphate	Sterile	37·3	199	92·0	5·2	3·0
	Non-sterile	35·7	621	85·8	10·5	3·3
Low phosphate	Sterile	26·6	388	91·1	4·8	4·0
	Non-sterile	25·1	771	72·9	20·0	7·0
Phosphate deficient	Sterile	30·0	248	85·6	8·3	6·2
	Non-sterile	22·9	802	77·3	16·1	6·5

Significant Differences between Means

Mean Values	L.S.D. (5% level)	Level of Significance
Root length High phosphate (36·5), low phosphate (25·9), phosphate deficient (26·5)	5·13	1%
Uptake per centimetre Sterile (278), non-sterile (731)	215	0·1%
Percentage incorporation into acid-soluble fraction Sterile (89·6), non-sterile (78·7)	5·52	1%
Percentage incorporation into nucleic acids Sterile (6·1), non-sterile (15·5)	3·68	0·1%
Percentage incorporation into phospholipids and phosphoproteins High phosphate (3·1), low phosphate (5·5), phosphate deficient (6·4)	2·50	5%

* Means of triplicate tubes each with three plants.

differences between segments) (Table 2) but in phosphate-deficient plants a high uptake in the apical 2 cm was followed by a low uptake along the rest of the root (difference significant at 0·1% level). Uptake in the apical 2 cm of the phosphate-deficient plants was approximately half that of the same portion of high-phosphate plants (Table 2), but other segments of phosphate-deficient plants had only one-third to one-fifth of the uptake of the segments of high-phosphate plants. The roots did

not have root hairs and except for the apical millimetre were of uniform diameter (0·9 mm) along their length. Marked differences occurred in distribution of ^{32}P along

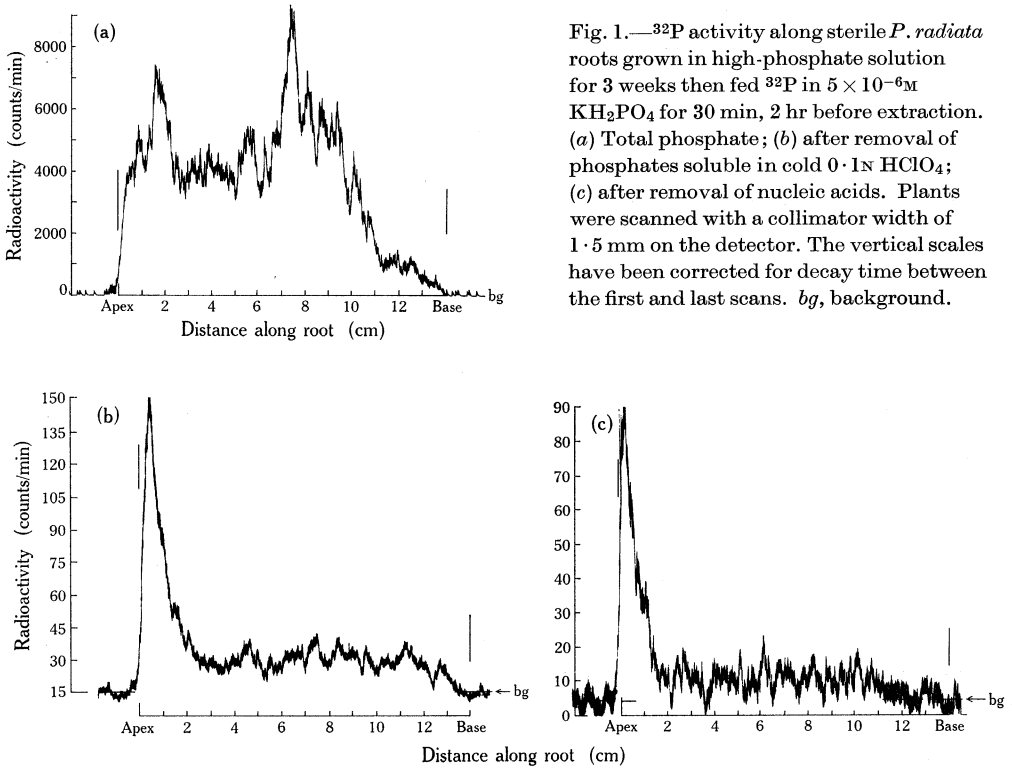


Fig. 1.—^{32}P activity along sterile *P. radiata* roots grown in high-phosphate solution for 3 weeks then fed ^{32}P in 5×10^{-6}M KH_2PO_4 for 30 min, 2 hr before extraction. (*a*) Total phosphate; (*b*) after removal of phosphates soluble in cold 0·1N $HClO_4$; (*c*) after removal of nucleic acids. Plants were scanned with a collimator width of 1·5 mm on the detector. The vertical scales have been corrected for decay time between the first and last scans. *bg*, background.

TABLE 2

PHOSPHATE UPTAKE ALONG ROOTS OF PINE SEEDLINGS

Uptake over 30 min from 5×10^{-6}M KH_2PO_4 in 5×10^{-4}M $CaSO_4$ was measured. Results for phosphate-deficient plants are means of 10 replicates, and those for high-phosphate plants are means of 12 replicates

Growth Solution	Phosphate Uptake (p-mole/cm) into Root Segments (cm from apex):							L.S.D. between Segments		
	0–1	1–2	2–3	3–4	4–6	6–8	8–10	5% Level	1% Level	0·1% Level
Phosphate deficient	87	72	41	32	28	23	27	14	19	25
High phosphate	137	145	157	157	136	135	126	42	56	87
Level of significance of differences	1%	1%	0·1%	0·1%	0·1%	0·1%	0·1%			

the root after removal of acid-soluble phosphates, particularly between the apical 2 cm and the rest of the root and with the high-phosphate plants.

Calculated incorporation of phosphate into the different fractions with different root segments of plants grown in high-phosphate solutions and in phosphate-deficient solutions are given in Tables 3 and 4. The "apical peak" data of Table 3 were calculated from the peak uptake occurring in the apical 5–10 mm of the root. Data for the various segments and for others not included in the statistical analyses are shown in Figure 2.

TABLE 3

PHOSPHATE UTILIZATION BY PINE SEEDLING ROOTS UNDER SHORT-TERM LABELLING CONDITIONS

Data from phosphate-deficient plants are means of 10 replicates, and those from high-phosphate plants are means of 12 replicates. PL, phospholipid; PP, phosphoprotein

Growth Solution	Root Length (cm)	Percentage Phosphate Incorporated at Apical Peak*		
		Acid-soluble Fraction	Nucleic Acid Fraction	PL and PP Fraction
Phosphate deficient	10·2	89·0	6·0	5·0
High phosphate	11·3	97·4	1·3	1·3
Level of significance of differences	n.s.	0·1%	0·1%	0·1%

* Defined in text—peak activity in 0–1 cm segment.

Percentage incorporation into the acid-soluble fraction was less with root segments of phosphate-deficient plants than with the corresponding root segment

TABLE 4

PHOSPHATE UTILIZATION ALONG THE ROOTS OF PINE SEEDLINGS UNDER SHORT-TERM LABELLING CONDITIONS

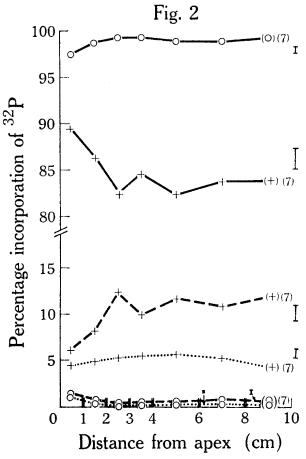
Data are means for the number of replicates given in Table 3. All differences between corresponding segments of phosphate-deficient and high-phosphate plants are statistically significant at the 0·1% level. PL, phospholipid; PP, phosphoprotein

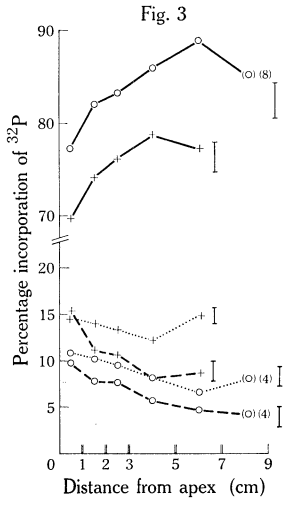
Fraction	Percentage Phosphate Incorporated into Root Segments (cm from apex):						L.S.D. between Segments		
	0–1	1–2	2–3	3–4	4–6	6–8	5% Level	1% Level	0·1% Level
Acid-soluble									
Phosphate deficient	89·6	86·9	82·5	84·6	82·1	83·7	2·3	3·0	4·0
High phosphate	97·5	98·8	99·3	99·2	98·9	98·7	0·6	0·8	1·0
Nucleic acid									
Phosphate deficient	6·1	8·2	12·2	9·9	11·9	10·9	1·8	2·5	3·3
High phosphate	1·4	0·7	0·5	0·5	0·6	1·0	0·4	0·6	0·7
PL and PP									
Phosphate deficient	4·4	4·9	5·3	5·5	5·7	5·4	1·1	1·4	1·9
High phosphate	1·0	0·5	0·3	0·3	0·4	0·4	0·2	0·3	0·4

of high-phosphate plants. Percentage incorporation into nucleic acids was 7–10 times greater with phosphate-deficient plants than with high-phosphate plants and

percentage incorporation into the phosphoprotein and phospholipid fraction was 5–19 times greater with phosphate-deficient than with high-phosphate plants. All differences were significant at the 0·1% level.

Highly significant differences also occurred between segments of the same root. In general the 0–1 cm (apical) segment differed from the 1–2 cm segment and both differed from the rest of the root. In the apical 2 cm of the high-phosphate plants, the relative incorporation into nucleic acids, phospholipids, and phosphoprotein was greater, and that into the acid-soluble fraction was smaller, than in the remainder of the root. With phosphate-deficient plants these patterns were reversed, but the total counts in the nucleic acid and phospholipid–phosphoprotein fractions were still highest in the apical 2 cm.





Figs. 2 and 3.—Relative incorporation of [^{32}P]phosphate along roots of sterile 3-week-old *P. radiata* seedlings which had been fed with [^{32}P]orthophosphate for 30 min (Fig. 2) or continuously (Fig. 3). For short-term labelling (Fig. 2) plants were fed 5×10^{-6}M KH_2PO_4 with ^{32}P for 30 min, and incorporation was allowed to proceed for a further 2 hr at 20°C before extraction. Data in Figure 2 are means of 10 (phosphate-deficient) and 12 plants (high-phosphate), and those in Figure 3 are means of 11 and 10 plants respectively, except where indicated by points and numbers in parentheses. Vertical bars indicate least significant differences at the 5% level. ○ High-phosphate plants. + Phosphate-deficient plants. ——— Phosphate soluble in cold 0·1N $HClO_4$. — — Phosphate incorporated into nucleic acids. • • • Phosphate incorporated into phospholipids and phosphoproteins.

Data on the apical peak were substantially those of the 0–1 cm segment with the same differences between phosphate-deficient and high-phosphate plants (Tables 3, 4).

(ii) *Continuously Labelled Plants*

Incorporation data for various root segments of 3-week-old sterile seedlings grown in ^{32}P-labelled high-phosphate or phosphate-deficient solutions are given in Table 5 and Figure 3 (which also includes data on segments not included in Table 5).

Distribution of total ^{32}P along the roots was similar with both series of plants and was reasonably uniform along the root. The mean length of phosphate-deficient roots was 7·3 cm and that of high-phosphate roots was 10·0 cm (differences significant at 1% level). Over the 10–11 replicate plants in each treatment, radioactivity in the phosphate-deficient roots was approximately six times that of the corresponding segment of the high-phosphate roots.

As with the short-term-labelled plants, highly significant differences in percentage label in the various fractions occurred between the two groups of plants and between different segments of roots within groups. Phosphate-deficient plants had significantly greater relative incorporation in the nucleic acid (36–85% greater) and phospholipid–phosphoprotein fractions (39–125% greater) and significantly less in the acid-soluble fraction than did phosphate-rich plants.

TABLE 5

PHOSPHATE FRACTIONATION ALONG CONTINUOUSLY LABELLED PINE SEEDLING ROOTS

Plants were grown in the presence of [^{32}P]orthophosphate continuously. Results for phosphate-deficient plants are means of 11 replicates, and those for high-phosphate plants are means of 10 replicates. PL, phospholipid; PP, phosphoprotein

Fraction	Percentage Incorporation of ^{32}P into Root Segments (cm from apex):					L.S.D. between Segments		
	0–1	1–2	2–3	3–5	5–7	5% Level	1% Level	0·1% Level
Acid-soluble								
Phosphate deficient	69·7	74·1	76·1	78·7	77·1	3·5	4·6	6·1
High phosphate	77·4	82·0	83·2	86·0	88·9	3·6	4·8	6·4
Level of significance of differences	0·1%	0·1%	0·1%	0·1%	0·1%			
Nucleic acid								
Phosphate deficient	15·3	11·0	10·5	8·1	8·7	2·2	3·0	4·0
High phosphate	9·8	7·7	7·7	5·8	4·7	2·3	3·1	4·1
Level of significance of differences	0·1%	1%	5%	5%	1%			
PL and PP								
Phosphate deficient	15·0	14·0	13·4	12·3	14·9	1·9	2·6	3·4
High phosphate	11·0	10·4	9·6	8·2	6·5	2·1	2·8	3·8
Level of significance of differences	0·1%	1%	0·1%	0·1%	0·1%			

Gradients in phosphate fractions occurred along the roots, the apical centimetre and the 1–2 cm segments being markedly different from each other and from the rest of the root. Gradients were in the same direction with both the phosphate-deficient and high-phosphate plants, with greatest percentage label in the nucleic acid and the phospholipid–phosphoprotein fractions and least into the acid-soluble fraction in the 0–1 cm and the 1–2 cm segment than in other parts. Up to 109% difference occurred along the root in relative incorporation into nucleic acids and up to 69% difference in relative incorporation into the phospholipid–phosphoprotein fraction.

IV. Discussion

The markedly greater uptake of phosphate and its greater relative incorporation into nucleic acids with non-sterile roots of *P. radiata* seedlings confirms similar results obtained with wheat (Bowen and Rovira 1966; Rovira and Bowen 1966) and with barley (Barber and Loughman 1967). This microbial factor must affect the validity of interpretation of phosphate uptake kinetics and of studies on esterification of phosphate and of phosphate "pools" in roots in studies carried out by many previous workers. In studies of *mechanisms* of phosphate uptake and usage by the root itself, the inclusion of microorganisms is likely to lead to great difficulties in interpretation of data. Strict asepsis is preferable to the use of microbial suppressants in raising experimental material because of the possible effects of the suppressants on the plant.

With investigations on the supply of phosphate to roots in soil and the subsequent use of phosphate by soil-grown plants, it is obviously necessary to include microorganisms in the test system. Even here, control over the composition of the microbial population is desirable for there are indications of microbial specificity in effects on phosphate uptake (Bowen and Rovira 1969). The present results confirm those of Barber and Loughman (1967) that microbial effects are large at low concentrations of phosphate. It is under this very condition that plant physiological studies are most relevant to a plant's growth in a soil situation, for the concentration of phosphate in soil solution is commonly 10^{-5}–10^{-6}M (Fried and Shapiro 1961) and often less. Microbial trapping of phosphate in soil–plant situations is likely to have greatest effect on plants in phosphate-poor soils, in which the low concentrations of phosphate in soil solution are not readily replaced from soil phosphate reserves.

With phosphate-deficient plants there was a much higher relative incorporation into the nucleic acid and the phospholipid–phosphoprotein fraction of roots than in phosphate-rich plants. Part of the reason for this with the short-term labelling experiment may be the lower uptake by phosphate-deficient plants in this experiment, as Barber and Loughman (1967) found somewhat increased retention of phosphate in the acid-soluble fraction of sterile barley roots with increased phosphate uptake. However, this is not the whole explanation, for in another short-term labelling experiment (not reported in detail here) uptake along phosphate-deficient roots was two to three times that along phosphate-rich roots, but relative incorporation into nucleic acids was some 67% higher with the phosphate-deficient plants (1·08% *v.* 0·65%) except for the apical centimetre in which relative incorporation was the same for each set (1·16%). The greater retention of phosphate in the acid-soluble fraction with high-phosphate plants is consistent with the greater translocation of phosphate to the tops found with such plants.

The data indicates the marked differences in relative incorporation into the various phosphate fractions *along* the pine root to be influenced by the level of uptake, the existing phosphate status, and the metabolic state of different parts of the root. There does not yet appear to be enough information available to analyse the individual importance of these factors—more detailed studies of selected parts of the root are required. However, it is clear that in studies of phosphate utilization

in the root, the phosphate status of the root, phosphate uptake during labelling, and the portion of the root studied must be specified.

The apical 1–2 cm obviously differs markedly in phosphate utilization from the rest of the root and this is not unexpected, as cell elongation (with its associated high metabolic activity) occurred over the apical 1·5–2 cm and was most marked over the apical 5 or 8 mm. Usually relative incorporation into nucleic acids, phospholipids, and phosphoproteins was greatest here, but in short-term labelling of phosphate-deficient plants relative incorporation into nucleic acids was least in the apical 2 cm. However, *total* radioactivity of the nucleic acid fraction was still greatest in the apical 2 cm. This apparent discrepancy arose from the high phosphate uptake in the apical 2 cm of such plants and the greater percentage retention of [^{32}P]phosphate in the acid-soluble fraction with increased uptake.

The differences in uptake at different parts of the root (Table 2; see also Rovira and Bowen 1968) and the differences between segments in phosphate incorporation into the various phosphate fractions emphasize that consideration of roots as uniform in behaviour along their length is erroneous, and interpretations of root behaviour derived from the averaging of data for the whole root is likely to lead to false conclusions. Rovira and Bowen (1968) have shown uptake of phosphate and other anions to increase very rapidly with the onset of lateral root production; the present paper shows large differences in the biochemical fate of phosphate between apical portions of roots and the older parts. If data are averaged for the whole root it is obvious that the extent of lateral root production under any particular experimental condition for the one species will have a large effect on whether the species is classified as a "high-flux" or a "low-flux" plant and as a "high-incorporation" or a "low-incorporation" plant. It is obvious that root morphology must be considered in interpretation of uptake data.

This study of biochemical utilization of phosphate at different parts of the root is part of a more detailed definition of the fate of phosphate entering different parts of the root. The results must be integrated into a more dynamic model of uptake, utilization, compartmentation, and translocation at different parts of roots. Studies on sites of translocation from pine seedling roots (Bowen, unpublished data) have shown all parts of the root to contribute to translocation, with rather less translocation occurring from the apical 5–10 mm. The greater relative incorporation of phosphate into the nucleic acid, phospholipid, and phosphoprotein fractions of the apical portions of roots is consistent with this. The method presented above allows the first step toward a ready examination of the biochemical fate of phosphate entering at many different parts of the root, as a preamble to more detailed studies of phosphate pools at different parts of the root.

V. Acknowledgments

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