LONGITUDINAL GRADIENTS OF P^{32} ABSORPTION IN ROOTS

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(WITH FIVE FIGURES)

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It is generally agreed that the greatest accumulation of ions occurs in the cells near the tips of the roots. PREVOT and STEWARD (**17**) observed that accumulation of bromide ions by excised barley roots was greatest in the apical centimeter; and STEWARD *et al.* (**20**) found that accumulation of potassium by roots of intact barley seedlings and of rubidium by excised roots 5 cm. in length increased progressively toward the tip and was greatest in the shortest segments analyzed (0.5 cm.). Experiments of OVERSTREET and JACOBSON (**16**) indicated that at 0° C maximum absorption of radioactive rubidium and phosphorus by apical segments of barley roots 1 cm. in length occurs within a millimeter of the tip. JACOBSON and OVERSTREET (**7**) later reported that maximum absorption of radioactive iodine and strontium occurs within 2 or 3 mm. of the root tip. STEWARD (**19**) has described in summary form work carried out in his laboratory in conjunction with Drs. R. Overstreet and S. M. Caplin. The accumulation of Cs^{137} in roots was studied by means of autoradiograms and by measuring the radioactivity of 1-mm. segments at intervals of 1 or 2 mm. from the apex to 10 cm. behind the apex. The published autoradiograms and counts show puzzling irregularities in accumulation along a single root and differences between roots from the same plant that could not be related to structure or physiological condition of the tissues.

While studying P^{32} absorption of pine roots, the authors obtained a number of autoradiograms. These showed that, as expected, there was usually heavy accumulation in the root tips and lower accumulation a few millimeters behind the root tip. Unexpectedly, however, a number of roots showed other regions of high accumulation extending some distance behind the tips. A typical example of this accumulation was shown in figure 2a of KRAMER and WILBUR (**9**). Since many examples of this unexpected pattern of accumulation were observed, further study was made to find how extensively it occurs. Efforts were also made to find what relations exist between dry weight, total nitrogen content, total phosphorus content, and radioactive phosphorus content of root segments at various distances behind the root apex.

Experiments and results

The pine roots used in this study were obtained from loblolly pine seedlings growing in pots in a cold frame. The tomato roots were adventitious roots produced on cuttings grown in aerated Hoagland's solution containing

no phosphorus. The barley roots were from seedlings germinated in half-strength Hoagland's solution lacking phosphorus.

AUTORADIOGRAMS

For preparation of autoradiograms root segments several centimeters in length were carefully freed of all foreign matter and immersed for one and one half to three hours in solutions of P^{32} having an activity of 200 to 300 μc. per liter. This solution was kept in shallow finger bowls at room temperature; and since considerable surface was exposed to the air and the liquid was quite shallow, no forced aeration was considered necessary. Most of the roots were detached from the plants, but the barley roots were left attached. At the end of the immersion period, the roots were washed in several changes of distilled water, rinsed in 0.01 N H_3PO_4, and quickly dried in an oven between layers of glass cloth. Glass cloth treated with Desicote (an anti-wetting agent) was used because root tips do not stick to it as they do to most materials. After the roots were dry, they were laid on a glass plate, or in later experiments on thick blotting paper, and covered with a sheet of aluminum foil or Pliofilm such as is sold in grocery stores. The photographic plate was brought into firm and uniform contact with the foil or plastic by means of rubber bands or by weights. The aluminum or plastic was inserted between the root and the plate to prevent any possibility of chemical action on the emulsion. The roots were left in contact with the photographic plates for periods varying from two to three hours to several days. The autoradiograms were made on Kodak M plates, except figure 1 A, which was made on a medium lantern slide plate.

Autoradiograms of a number of roots are shown in figure 1. It is quite apparent that considerable variation exists in distribution of radioactive phosphorus in different roots, even in those of the same species grown under identical conditions. Figure 1 A shows autoradiograms of two large roots of red pine (*Pinus resinosa* Ait.). They exhibit high accumulation of P^{32} in the tips. There is a well defined region of low accumulation beginning 2 or 3 mm. behind the apex which probably is in the region of rapid cell enlargement. The localized regions of high accumulation on the older parts of the roots are branch roots, either mycorrhizal or non-mycorrhizal. The four autoradiograms of figure 1 B are from small loblolly pine roots (*Pinus taeda* L.). The first and fourth roots show the same accumulation pattern as the red pine roots, but the second and the third roots show little accumulation in the tips. All four show heavy accumulation a centimeter or more behind the root tips.

All four of the autoradiograms of adventitious roots of tomato reproduced in figure 1 C exhibit high accumulation of P^{32} in the meristematic region, but their accumulation patterns are otherwise quite dissimilar. There was negligible accumulation in most of the older portion of the first root; noticeable accumulation occurred only in the first centimeter of the second root; but heavy accumulation occurred along the entire length of

the third root, except in the region of elongation. The fourth root showed variations in P^{32} accumulation in the older portion which cannot be related to root structure.

The autoradiograms of barley roots in figures 1 D and 1 E also show

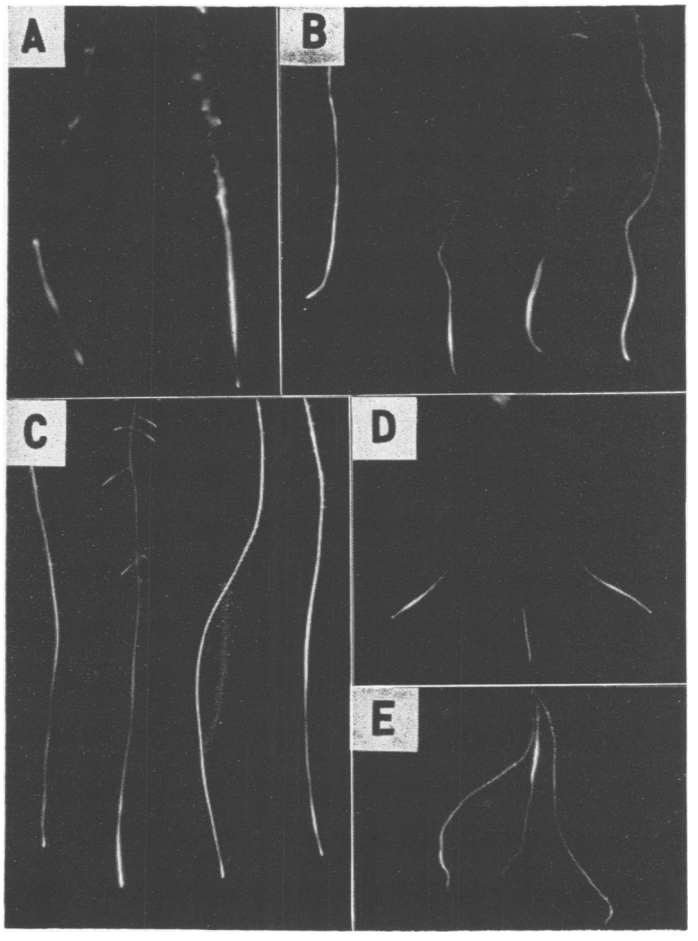

FIG. 1. Autoradiograms of roots of four species showing variations in absorption of P^{32}. A. Two large roots of red pine. B. Four small roots of loblolly pine. C. Four adventitious roots of tomato. D and E. Seedling roots of barley. Most autoradiograms show heavy absorption in the meristematic region, lower absorption in the region of elongation, and heavy absorption a centimeter or more behind the root tip. Many exceptions to this pattern occur, however, as shown by these autoradiograms, of which A and D might be regarded as typical while B, C, and E show variations from the typical pattern.

variability in respect to accumulation of P^{32}. The three roots of figure 1 D are similar in having high accumulation in the root tip, lower accumulation in the region of elongation, and very heavy accumulation a centimeter or more behind the apex where root hairs are well developed. The three roots

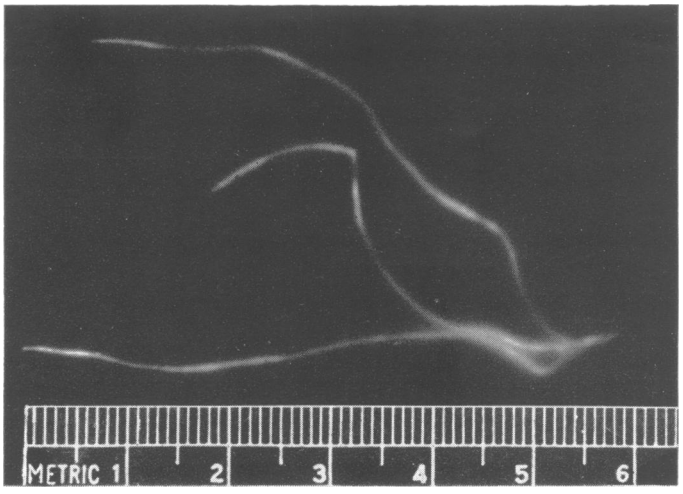

FIG. 2. Autoradiograms of barley roots, showing uneven distribution of P^{32}. The three roots originated from a single seed.

of figure 1 E show little accumulation in the tip and an irregular pattern of accumulation in the older parts of the roots.

Figure 2 is an enlargement of the autoradiograms of three barley roots produced from the same seed. The enlargements show a surprisingly irregular distribution of P^{32}, with alternating regions of high and low concentration. Comparison of the autoradiograms with the activity of 2-mm. segments cut from the same root, as measured by counting the individual segments, shows good general agreement between regions of high and low concentration as measured by the two methods (fig. 3) which seems to

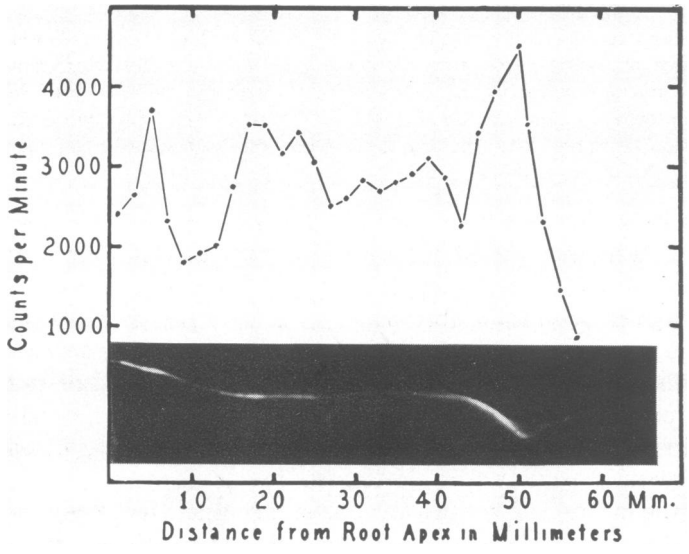

FIG. 3. Autoradiograms of a barley root, with concentration of P^{32} as determined by counting 2-mm. segments graphed above it.

eliminate any possibility that the various irregularities in distribution of P^{32} shown in the autoradiograms are artifacts produced during their preparation. Such artifacts might result from differences in diameter of the roots, differences in amount of flattening during drying, from bends in the roots, or from lack of uniform contact between the roots and the photographic plates.

Activity measurements

It is difficult to determine accurately small differences in relative activity from autoradiograms. Roots therefore were dried as previously described, cut into short segments, and the activity of each segment measured indi-

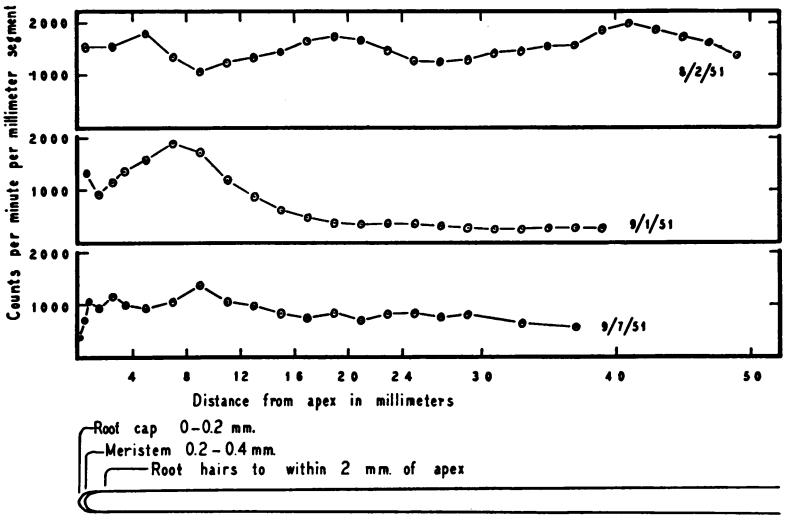

FIG. 4. Graphs showing the amount of P^{32} absorbed by various regions of barley roots, expressed as counts per minute per millimeter segment, also a diagram showing some features of barley root anatomy. The roots were cut into segments 2 mm. in length for counting, except at the tips where the segments were 1.0 mm. long for the series of September 1 and 0.2 mm. for that of September 7. The curve for August 2 is the average of three roots, that for September 1 the average of six roots, that for September 7 the average of four roots.

vidually with a Geiger-Muller counter. For this purpose the older portions of the roots were cut into 2-mm. segments, but the tips were cut into segments only 1.0 or 0.2 mm. in length to permit more accurate localization of the regions of high and low absorption. The averages of three sets of such measurements are summarized graphically in figure 4. Below the counts is shown a diagram indicating the approximate location of various regions of a barley root. This diagram is based on observations of the experimental roots and agrees in general with results of a detailed study of barley root anatomy recently published by HEIMSCH (**6**).

While the location of various structural regions of the barley roots varied but little, the autoradiograms and counts of activity shown graphically in figure 4 indicate that the pattern of P^{32} concentration varies appreciably.

The root tips of the experiment of August 2, 1951 (fig. 4), showed high accumulation throughout the first 50 mm. with regions of high accumulation 5, 18, and 42 mm. behind the tip. In the experiment of September 1, 1951, maximum accumulation was 9 mm. behind the tip, and in that of September 7, 1951, there was a region of high accumulation at 1 to 3 mm. and another at 9 mm. from the tips. The series of September 7 was the only one in which the root cap was counted separately, and in this series very little accumulation was found in the root cap. Differences in location of the region of heavy accumulation near the tip might possibly be related to differences in rate of growth of the roots immediately preceding and during the period of exposure to P^{32}. It seems that their past history has considerable effect on the accumulation pattern of the roots, and this probably accounts for the differences among the three groups of roots.

The results of the experiments indicate that the heaviest accumulation of P^{32} by barley roots generally occurs in the root hair zone. There is a suggestion that variations in accumulation along the older regions of the roots is related to variations in number and condition of root hairs. In pines, root hairs are less common and there is a tendency for the epidermal cells to slough off. Nevertheless, in pine, as in barley, maximum accumulation of P^{32} often occurs some distance behind the apical meristem.

Chemical analyses

An effort was made to see if any correlation existed between chemical composition of various regions of the root and the amount of P^{32} accumulated by cutting roots into segments and analyzing them for total nitrogen and total phosphorus. For the analyses the apical centimeter of each root was cut into 2-mm. segments, a segment was removed 20 mm. behind the apex and another about 50 mm. behind the apex. The corresponding segments of 4 to 10 pine roots, depending on their size, and 50 barley roots were pooled to provide samples large enough for analysis.

Fresh weight and oven-dry weight of the samples were obtained by weighing on a micro balance. For analysis of total nitrogen and total phosphorus, the samples were digested in hot sulphuric acid and cleared with 30% hydrogen peroxide, then diluted to 5 ml. and aliquots removed. Total nitrogen and total phosphorus were determined colorimetrically by essentially the same methods described by Lindner (10).

The results of the analyses of barley roots are summarized in figure 5. The apical segments of the barley roots, which included the root cap and the meristematic region, were low in fresh weight, relatively high in dry weight, and, although smaller in volume, contained about twice as much total nitrogen and total phosphorus per segment as any other part of the root. The fresh weight increased basally, as would be expected, because of an increase in water content in the region of cell enlargement and the increase in dry matter in the region of differentiation. The high dry weight and high nitrogen and phosphorus contents of the apical segment conform

with the view that it consists largely of protoplasm in which the vacuoles occupy a relatively small volume. The abrupt decrease in dry weight behind the apical segment doubtless is the result of the rapid enlargement and increased volume of vacuoles of cells in this region, accompanied by

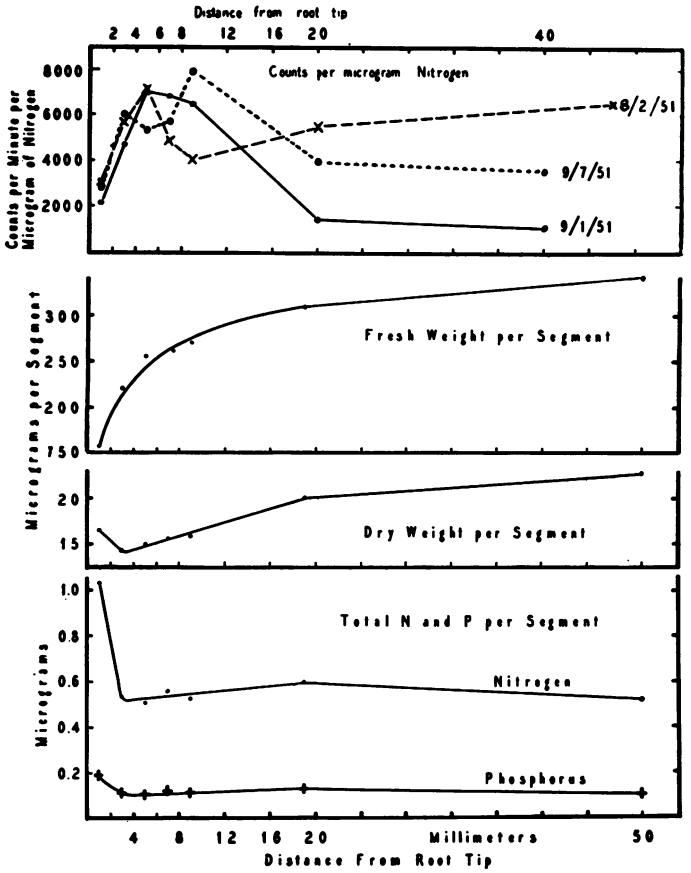

FIG. 5. Analyses of barley roots. The data for fresh and dry weight, total nitrogen, and total phosphorus represent the averages of five groups of 50 roots each. The tip centimeter was cut into segments 2 mm. in length, a 2-mm. segment was cut 18 to 20 mm. behind the tips, and another 48 to 50 mm. from the tips. The upper graph shows the amount of P^{32} absorbed per microgram of nitrogen for each 2-mm. segment. Although considerable variation occurred in the amount of P^{32} absorbed by the older portions of the roots, all three groups show low absorption per unit of nitrogen in the meristematic region and high absorption 3 to 10 mm. behind the tip. Compare with figure 4, showing uptake of P^{32} per segment by the same groups of roots.

little increase in dry matter. Further back, cell walls become thickened and dry weight increases. Both total nitrogen and total phosphorus show little change per segment behind the apex. This observation suggests that little new protoplasm is synthesized in the region of these roots 5 to 50 mm. from the apex and the increase in dry weight must be largely cell wall material.

The analyses of pine roots showed essentially the same gradients in all constituents, except for a decrease in fresh weight in the 48 to 50-mm. segments, caused by suberization and death of epidermal and cortical cells in this region. The curves showing the amount of P^{32} accumulated per microgram of nitrogen will be discussed later.

These analytical results are in general agreement with those reported for onion roots by NORBERG (**14**) and NORRIS (**15**). BROWN and BROADBENT (**4**) measured the dry weight, protein nitrogen, cell number, and cell volume in pea roots. When measured on a segment basis, dry weight and protein nitrogen were highest 2 mm. from the tip and decreased in segments 4 and 5 mm. behind the tip. On a cell basis, however, dry weight increased rapidly from the apex to 5 mm., then increased gradually, while protein nitrogen reached a maximum at 5 mm. from the apex and decreased slightly in segments from 5 to 10 mm. from the apex.

The meristematic region generally is regarded as a region of high metabolic activity. According to MACHLIS (**13**) (barley roots) and BERRY and BROCK (**3**) (onion roots) root respiration per segment and per unit of volume is highest near the apex. In corn roots, according to GODDARD and MEEUSE (**5**), most active respiration on a fresh weight basis occurs in the apical millimeter; but if based on total nitrogen, protein, or ribose nucleic acid content, respiration is lowest in the apical 1 or 2 mm. and most rapid respiration occurs 4 to 5 mm. behind the tip where cells are elongating. Brown and Broadbent found respiration per segment of pea roots to be highest at 1.2 mm. behind the apex and respiration per cell to be highest at about 5 mm. behind the apex, decreasing somewhat in cells between 5 mm. and 9 mm. behind the apex where measurement stopped. If respiration is calculated in terms of total nitrogen, as is often done, the high nitrogen content of the barley root tips modifies the respiration curve. When the oxygen consumption of barley roots, as measured by MACHLIS (**13**), is calculated in terms of the total nitrogen content of barley roots used in this investigation, it is slightly, but probably not significantly, higher in the 20-mm. region than in the apical region. BROWN and BROADBENT (**4**) found a close correlation between protein nitrogen and respiration in pea roots, except possibly for the apical 0.4-mm. segment, which appeared to have a high rate per unit of protein nitrogen.

BERRY and BROCK (**3**) suggested that the high oxygen consumption of root tips does not necessarily indicate a higher rate of respiration per unit of material but probably is merely the result of a larger quantity of respiring material per segment. This view seems to be supported by the data presented here and also by those of NORRIS (**15**), who reported that if respiration of onion root segments is calculated per unit of nitrogen, it is no higher in the apical 5 mm. of the root than in segments farther back. He did find a gradient if the rate of respiration was calculated in terms of phosphorus content, but this would not be true of the data of this investigation.

BERRY and BROCK (3) found respiration of the apical 5-mm. segment of onion roots to be inhibited more by cyanide than the respiration of older segments. This inhibition suggests that the meristematic region has a different type of oxidative metabolism from that found in older portions of the root. BERRY (2) found that respiration of the apical 5-mm. segments of onion roots is limited by oxygen, which is not true of older portions of the root.

The amount of P^{32} accumulated per segment of barley root in this study was calculated in terms of total nitrogen per segment, and the results are shown in the upper part of figure 5. As would be expected from the data presented in figure 4 and those for total nitrogen in figure 5, the concentration of P^{32} per microgram of nitrogen is lower in the apical segment than anywhere else in the terminal 50-mm. portion of the roots. These relationships are shown numerically in table I where it can be seen that the ratio of phosphorus to total nitrogen is not significantly different in the various root

TABLE I

RELATION BETWEEN TOTAL NITROGEN, TOTAL PHOSPHORUS AND RADIOACTIVE PHOSPHORUS IN SEGMENTS OF BARLEY ROOTS.

Distance from tip	Total N per root segment	Total P per root segment	Ratio total P to total N	Counts per minute per root segment	Ratio P^{32} to total P $\times .001$
mm.	*μg.*	*μg.*			
0 to 2	.514	.0985	.192	1360	13.8
2 to 4	.269	.0535	.199	1470	27.5
4 to 6	.255	.0515	.202	1650	32.1
6 to 8	.279	.0540	.194	1610	29.9
8 to 10	.264	.0570	.216	1620	28.5
18 to 20	.294	.0625	.212	1070	17.1
48 to 50	.260	.0500	.192	965	19.3

segments. The ratio of radioactive phosphorus to total phosphorus is only half as great in the apical segment as it is in segments located 2 to 10 mm. behind the root tip. Evidently accumulation of radioactive phosphorus is not directly correlated with the concentration of total phosphorus. Neither is it directly correlated with the synthesis of protein which presumably is occurring most rapidly in the meristematic region located in the apical segment.

In the roots studied, accumulation of P^{32} seemed to be greater per unit of nitrogen in cells which are enlarging and differentiating than in cells which are dividing. Accumulation also was high, at least in some instances, in epidermal cells which are not even capable of differentiation. SANDSTROM (18) suggested that selective absorption of ions is localized in the epidermis. While the methods employed did not permit exact localization, autoradiograms of cross-sections of roots show the P^{32} to be concentrated near the surface; and none could be found in the central part of the apical meristem. This unexpected situation is being investigated further.

Discussion

In these experiments, the initial activity of P^{32} in the external solution was usually 200 to 300 μc. per liter, the final activity considerably lower. In one experiment subjected to careful analysis, the final activity of the external solution was 280 μc. per liter, equivalent to a concentration of 3.1×10^{-11} moles of P^{32} per liter. The total phosphorus concentration of the solution was 8.1×10^{-7} moles per liter and the specific activity was therefore 3.8×10^{-5}. Specific activity is the concentration of P^{32} divided by the concentration of total phosphorus. After two hours in this solution, the P^{32} concentration in the roots on a volume basis was 1.2×10^{-8} moles per liter. Thus, the concentration of P^{32} in the roots was approximately 400 times as great as that of the external solution. The specific activity of P^{32} in the roots was only 1.1×10^{-6} moles per liter, or considerably less than in the solution. Since the amount of P^{32} in the roots is so small in proportion to the total phosphorus present, some question has arisen whether the uptake of P^{32} observed in these experiments can be regarded as true metabolic accumulation. Uptake of P^{32} might occur as the result of metabolic accumulation, it might occur as a result of exchange with phosphorus already present in organic compounds in the root, or by the non-metabolic exchange absorption of OVERSTREET and JACOBSON (**16**). The phosphorus might be precipitated as an iron or calcium salt on the surface of the root, or it might be absorbed in the meristematic region and then translocated upward. Perhaps all of these processes occur to a limited extent, but it is believed that most of them are of negligible importance in this study.

The possibility of upward translocation from the root tip to the root hair zone was studied by supplying P^{32} to restricted areas on barley roots through potometers. When P^{32} was supplied to the root tips for 10 hours, little upward translocation occurred. When it was supplied to the root hair zone, considerable translocation occurred downward to the tip of that root, upward to the seed and leaf, and even down into the tips of other roots of the seedling. It seems certain that upward translocation of P^{32} from the meristematic region cannot account for the large amounts of P^{32} found in the root hair zone, and it must have been for the most part absorbed in the regions where it was later found to be present.

In all of our experiments, the roots were washed in dilute acid, usually 0.01 N H_3PO_4, but in some instances in 0.005 N HCl, then rinsed in distilled water. This acid wash should have removed any P^{32} precipitated on the surface of the roots. Actually such washing removes little P^{32} and does not change the pattern of the autoradiograms.

There is little doubt that the major part of the P^{32} uptake observed in these experiments is controlled by metabolic activity. The uptake of P^{32} is about 10 times as great at 20° as at 3° C in both barley and pine roots. Perhaps the rate at 3° C is a measure of non-metabolic absorption. KRAMER (**8**) found that azide and fluoride at a pH of 4.7 to 4.8 reduced accumulation

of P^{32} by pine roots to less than 5% of the controls. He also found that dead pine roots absorbed less than 5% as much P^{32} as living roots. It seems that the possibilities of appreciable surface precipitation or translocation have been eliminated, and the amount of P^{32} accumulated is much greater than can be accounted for by non-metabolic absorption. Possibly exchange between P^{32} in the external solution and P^{31} in the cells is controlled by metabolic activity, but this seems improbable. Exchange with P^{31} existing in organic compounds within the cells should be greatest in the meristematic region where the highest concentration of P^{31} occurs and metabolic activity is rapid, but as shown in table I and figure 4 uptake of P^{32} is lower in this region than further back where the concentration of P^{31} is lower.

In tracer studies, it is difficult to prove that the path and manner of uptake of the radioactive isotope is an accurate indicator of the path and manner of uptake of the non-radioactive isotope. Such a similarity has not been proven in this study, but it has been shown that uptake of P^{32} is reduced by treatments which are known to reduce accumulation of ions. While more evidence would be desirable, it seems probable that the uptake of P^{32} observed in these experiments was really metabolic accumulation and probably is indicative of the manner in which phosphorus usually is absorbed.

It seems clear from the results of these studies that accumulation of P^{32} is not restricted to the meristematic region of roots but often occurs several centimeters behind the root tip. In contrast the non-metabolic absorption observed by OVERSTREET and JACOBSON (**16**) at 0° C is highest in the meristematic region. We have also observed highest accumulation in the meristematic regions of roots exposed to P^{32} at 3° C. JACOBSON and OVERSTREET (**7, 16**) question the role of root hairs in mineral absorption because in their experiments dealing with non-metabolic absorption with 1-cm. segments at 0° C most of the uptake occurred below the root hair zone. LUNDEGARDH (**11, 12**) reported that wheat seedlings with few root hairs absorb less salt than those with numerous root hairs. He regards root hairs as quite important in the absorption of ions and states that in wheat roots maximum absorption occurs 10 to 25 mm. behind the tip, where root hairs are well developed. There seems to be little doubt that extensive accumulation of P^{32} occurs in the root hair zone of both barley and tomato roots, and this P^{32} is translocated more readily than that accumulated in the meristematic region of roots.

It is difficult to explain variation in the region of maximum uptake of P^{32} among roots of identical past treatment. As STEWARD (**19**) stated with respect to Narcissus roots, these variations are not always explainable in terms of obvious features of root anatomy or development. Steward observed alternations in regions of high and low concentrations of Cs^{137} similar to those shown in figure 2 for P^{32}. Variations in growth during the preceding two or three days might produce differences in number and condition of root hairs and permeability of epidermal cells. LUNDEGARDH (**11**) mentioned the difficulty of producing uniform populations of roots and root

hairs, and OVERSTREET and JACOBSON (**16**) mentioned individual variations among barley roots. While the past history might explain variations in amount of salt accumulated and in regions of accumulation, it does not explain the bands of high and low concentration visible in figure 2.

It is generally supposed that salt accumulation occurs chiefly in cells which are actively growing, or at least in cells which are capable of growth and differentiation. While this probably is generally true, some exceptions were observed. Not only does appreciable uptake of P^{32} occur in regions of barley, pine, and tomato roots where little or no growth is occurring, but it also occurs in epidermal cells of pine which are sloughing off. In pine as described by ADDOMS (**1**) the epidermis near the root tip often begins to split off in long strips which remain alive for several days. Although such strips occasionally show limited elongation, they do not divide or differentiate and finally die; yet they absorb P^{32}. It may be debatable as to whether or not this is true accumulation, but the P^{32} activity of the tissue becomes several hundred times greater than that of the surrounding solution.

In conclusion, it appears that study of uptake of radioactive ions by individual roots is revealing individual differences not detectable by mass analysis of large numbers of roots. The available data indicate that there are much greater variations among roots of similar past history in respect to respiration and salt uptake than with respect to structure. While these variations complicate our studies, they may eventually add materially to our understanding of salt absorption.

Summary

Detached roots of pine and tomato and attached roots of barley were exposed to P^{32} solutions having an activity of 200 to 300 μc. per liter for one and one half to three hours at 22 to 28° C, and autoradiograms were made. Some of the roots were then cut into segments 0.2 to 2.0 mm. in length, and the activity of individual segments was measured with a Geiger-Muller counter. There was good agreement between the relative activity of segments of barley roots measured with a counter and their activity as indicated by the autoradiograms.

Considerable variation in distribution of P^{32} was found, even in roots grown under identical conditions. Some roots showed high uptake of P^{32} only at the tip; others showed little or no uptake at the tip but considerable uptake farther back. The most common condition was relatively high concentration in the root tip, a region of lower concentration a few mm. behind the tip which seemed to coincide with the region of elongation, and another region of high concentration 6 to 20 mm. behind the tip.

Absorption of P^{32} was not restricted to the meristematic region of the roots of any species studied. Heavy uptake occurred in the root hair zone of many barley and tomato roots and in epidermal cells of pine one or more centimeters behind the root tip.

Five groups of week-old barley roots about 50 mm. in length were cut into 2-mm. segments; and the fresh weight, dry weight, total nitrogen, and

total phosphorus content of each group was determined. The apical segments were low in fresh weight, relatively high in dry weight, and contained twice as much nitrogen and phosphorus per segment as any other region of the roots. Fresh weight increased basally from the apex, but the dry weight per segment was lower in segments 2 to 6 mm. behind the apex than in the segment 0 to 0.2 mm. from the apex. The dry weight increased gradually toward the base. Loblolly pine roots showed similar gradients in all constituents.

The uptake of P^{32} per segment was calculated in terms of total nitrogen content per segment and was found to be much lower in the meristematic region than in segments one or two centimeters behind the root tip. The highest uptake per unit of nitrogen appeared to be in the region where differentiation was occurring.

Although other processes may be involved, the uptake of P^{32} observed in this study is believed to represent principally metabolic accumulation because uptake is reduced to less than 10% of control by respiration inhibitors and by low temperatures.

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