FACTORS AFFECTING ABSORPTION AND TRANSLOCATION OF FOLIAR APPLIED PHOSPHORUS^{1,2}

HAROLD KOONTZ 3 AND ORLIN BIDDULPH

DEPARTMENT OF BOTANY, STATE COLLEGE OF WASHINGTON, PULLMAN, WASHINGTON

Phosphorus is known to be exported from leaves of apple (8, 9, 10), bean (4, 6, 11, 12, 13), chrysanthemum (1, 2), corn (11, 12), tomato (12) and squash (7). The present work with bean plants compares export following application by spray, leaf vein injection (4) and droplet (13) methods. Other factors investigated which affect absorption and subsequent translocation of the spray-applied phosphorus include: 1) wetting agents, 2) phosphorus concentration of the spray, 3) leaf surface (upper vs lower surface), 4) different phosphorus compounds (pH and cation), 5) time, 6) hygroscopic agent, 7) size of area sprayed, 8) age and position of sprayed leaf, and 9) phosphorus level of the plant.

Methods

Red Kidney bean plants grown in one-half strength Hoagland solution under fluorescent lights on a 6:00 A.M. to 6:00 P.M. day were used throughout. The light intensity, temperature and relative humidity were 1000 ft-c (as measured half-way up the stem), $24^{\circ} \pm 1^{\circ}$ C and $60 \% \pm 4 \%$, respectively. At least two plants were used for each treatment. To obtain more uniform plants, the axillary buds were removed before vascularization was pronounced, 2 and 3 days before treatment.

The phosphorus solutions containing 0.2 ml of P³²-labeled phosphorus of known specific activity were sprayed onto the upper surface of the terminal leaflet of the first trifoliate leaf, unless stated otherwise, between 9:00 and 11:00 A.M. when the plants were 18 days old (12 days after the hypocotyls had straightened). To prevent contamination of the remainder of the plant the leaflet receiving the spray was enclosed in a clear plastic box which was removed several minutes after treatment. Except in the time course of uptake experiments, the plants were harvested and sectioned 24 hours after the application of the tracer. Usually each plant was sectioned into three parts: 1) the sprayed leaflet, 2) the remaining two leaflets and petiole of the first trifoliate leaf, 3) and the remainder of the plant. In some cases the remainder of the plant was divided at the node of the first trifoliate leaf to obtain the upward and downward movement. The amount of phosphorus applied was determined by summation. The percentage of applied phosphorus which moved into the nutrient solution was negligible (about 0.03%) and was not determined in most experiments.

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When autoradiograms were made from quickly dried, pressed whole plants using no-screen x-ray film, the exposure, development and reproduction were uniform so that direct comparisons could be made.

For radioactive assay the various plant sections were wet-ashed in nitric acid, made to volume and the activity determined on aliquots dried on porcelain counting discs using an end-window GM tube. The results were expressed in micrograms of phosphorus or in percentage of the applied phosphorus which was translocated from the sprayed leaflet. The activity applied per plant was between 5 and 20 μ c and was constant within each experimental run. P³² labeled phosphorus will be referred to as P^{*}.

RESULTS AND DISCUSSION

COMPARISON OF THREE APPLICATION METHODS: Leaf vein injection, droplet, and spray application methods were compared (fig 1) by using a recording rate meter in conjunction with a GM tube (5 mm^2) opening) positioned on the stem 2.5 cm below the node of the treated leaf. The volume of solution used, the number of microcuries of P³² employed, and the pH of the solution applied are given in the legend. Figure 2 shows an autoradiograph of treated leaflets (droplet application) from plants represented in tracings 14, 15, and 16. It is obvious that after entry the tracer was carried toward the periphery of the leaflet before entering the phloem for export. The droplet method, to be successful at all, required a pH of approximately 2.0, which produced necrosis at the place of application.

For routine use the spray application proved superior. It gave only a slightly lower concentration of tracer in the stem within a minimum migration period than the injection method, produced no visible injury (except at pH extremes), and it is the method which is best adapted for field use.

EFFECT OF WETTING AGENTS: The following wetting agents were tested at a concentration of 0.05 %of the active ingredient, except where stated otherwise, with spray solutions of 10 mM NaH₂P*O₄: 1) anionic type, Igepon T-77 (sodium n-methyl-n-oleoyl taurate), Igepon T-78 (ester of sodium isethionate), Tergitol 7 (sodium heptadecvl sulfate), Vatsol OTB (dioctvl ester of sodium sulfosuccinic acid). Vatsol OS (isopropyl naphthalene sodium sulfonate) and 0.5% Dreft (sodium dodecyl sulfate); 2) cationic types; Vatsol C-61 (ethanolated alkyl guanidine amino complex); 3) nonionic types; Vatsol NI (nonyl phenol + 9 moles ethylene oxide) and 0.5 % Carbowax 4000 (polyethylene glycol). None increased and only two, Tergitol 7 and Vatsol OTB, significantly decreased the percentage of phosphorus translocated from the sprayed leaflet in the 24-hour interval.

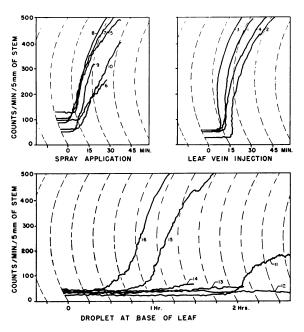


FIG. 1. Continuous rate meter recordings of P^{32} radioactivity in the stems of bean plants 2.5 cm below the node of the treated leaf. Treatment was by three methods described in the text. The volume, P^{32} radioactivity, and the pH of the solutions (adjusted with NaOH) for each curve are as follows: (1) 25 μ l, 92 μ c, pH 4; (2) 50 μ l, 121 μ c, pH 4; (3) 25 μ l, 167 μ c, pH 5; (4) 25 μ l, 100 μ c, pH 6; (5) 100 μ l, 318 μ c, pH 4; (6) 100 μ l, 318 μ c, pH 4; (7) 100 μ l, 288 μ c, pH 4; (8) 100 μ l, 450 μ c, pH 4; (9) 100 μ l, 336 μ c, pH 4; (10) 100 μ l, 336 μ c, pH 4; (11) 20 μ l, 3 μ c, pH 0.3; (12) 10 μ l, 48 μ c, pH 5; (13) 10 μ l, 48 μ c, pH 0.3; (14) 10 μ l, 46 μ c, pH 3; (15) 10 μ l, 42 μ c, pH 2.5; (16) 10 μ l, 46 μ c, pH 2.

These two latter wetting agents caused the spray solutions to spread very uniformly on the leaf surface and consequently to dry rapidly; three times faster than the controls or the wetting agents of poor spreadability.

Swanson and Whitney (13) found a 90 % reduction in the translocation of P^{32} from a foliar application when Tween 80 (polyoxyethylene sorbitan monooleate) was applied with the tracer. But Fisher and Walker (10) obtained a 7-fold increase in the apparent absorption of phosphorus by McIntosh apple leaves with the addition of Triton X-100 to the KH₂PO₄ spray solution. Apparently some wetting agents form a complex with some phosphate compounds.

Perhaps by using a wetting agent producing a uniform spread a higher concentration of phosphorus could be applied before injury from excessive phosphate occurred, but in many cases this would be more than offset by the smaller volume that could be retained on the leaf surface, by complex formation and by the rapidity of drying.

EFFECT OF PHOSPHORUS CONCENTRATION OF SPRAY: Solutions of 0.2 ml of NaH₂P*O₄ were applied at five different concentrations ranging from 0.3 to 30 mM. No leaf injury was noted. The amount of phosphorus translocated from the sprayed leaflet increased as the amount of applied phosphorus increased, but not in direct proportion (fig 3). The percentage of phosphorus translocated from the sprayed leaflet increased as the concentration of applied phosphorus increased from 0.3 to 10 mM, but no further increase was noted. The decrease with the 30 mM solution was within experimental error. The decrease in the percentage of phosphorus translocated from the treated leaflet at the low phosphorus concentration could be due either to a low rate of absorption or to a high percentage of retention of the applied phosphorus by the leaf tissues, or both.

Whether the 10 mM NaH₂P*O₄ spray was applied to the upper or lower leaflet surface made no significant difference in the percentage of applied phosphorus translocated from the leaflet in the 24-hour interval in spite of the difference in epidermal characteristics of the two surfaces, e.g., number of stomata, thickness and composition of the cuticle and pubescence. This is in agreement with the work of Bennett and Thomas (3) but opposed to Oliver (11).

EFFECT OF DIFFERENT PHOSPHORHS COMPOUNDS (PH AND CATION): The effects of pH and cation on the absorption and translocation of phosphorus from the sprayed leaflet were determined at a concentration of 10 mM phosphorus. $H_3P^*O_4$ and the following three series of phosphorus compounds were used: 1) NaH₂P*O₄ · H₂O, Na₂HP*O₄ · 7 H₂O, Na₃P*O₄; 2) KH₂P*O₄ , K₂HP*O₄, K₃P*O₄; and 3) NH₄H₂-P*O₄, (NH₄)₂HP*O₄. The results with the sodium and potassium compounds are shown in figure 4. The 10 mM H₃P*O₄ solution injured the sprayed leaflet and only 4.7 % of the applied phosphorus was exported. About 6.0 % of the phosphorus was exported with both ammonium compounds. A second sodium

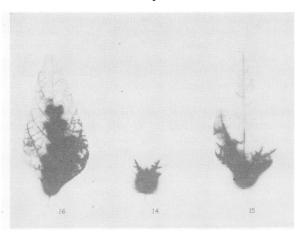


FIG. 2. An autoradiogram of the treated leaflets of the plants represented in tracings 14, 15 and 16 of figure 1. The leaflets were severed from the plants at the times indicated by the termination of their respective tracings.

series, in duplicate, at 0.3 mM phosphorus gave the following average translocation percentages: $H_3P^*O_4$, 6.0; $NaH_2P^*O_4$, 2.6; $Na_2HP^*O_4$, 0.6; $Na_3P^*O_4$, 2.1. No injury from $H_3P^*O_4$ was evident at this lower concentration.

It seems unlikely that the rather large variability in individual plants can be attributed to chance differences in the distribution of the spray from the same sprayer. It is more likely that plants differ individually and from time to time in their ability to translocate phosphorus.

The results with 0.3 mM phosphorus are similar to those obtained by Swanson and Whitney (13). They attributed the increased effectiveness of absorption and translocation at the lower pH to a suppression of the dissociation of phosphoric acid, and to a possible direct effect on the permeability of the adjacent cells. But they worked only with sodium phosphates, and when the potassium curve of figure 4 is taken into consideration it is evident that their explanation is not tenable. The translocation of phosphorus from the $H_2PO_4^-$ form of the sodium and potassium compounds exhibited striking differences. KH₂P*O₄ yielded the lowest and NaH₂P*O₄ the highest translocation in their respective series. The differences in absorption and translocation cannot be explained as being due to pH since the cation had considerable effect.

It was observed that NaH₂PO₄ and K₂HPO₄, the two compounds from which translocation was highest, did not crystallize on the leaflet as rapidly as KH₂PO₄, Na₂HPO₄, Na₃PO₄, NH₄H₂PO₄ and $(NH_4)_2HPO_4$. The assumption was made that their effectiveness in supplying phosphorus was due to their effective retention of moisture. Two experiments were performed to test this assumption. The moisture retention of the sodium and potassium compounds was determined as follows. Known duplicate quantities of each of the compounds were dissolved in a small amount of water in individual containers and then reweighed after drying 24 hours. The values obtained were plotted in figure 5, together with the average values for the percentage of phosphorus translocated from the previous experiment. The amount of phosphorus translocated parallels the moisture retention in all cases with the exception of K_3PO_4 . K_3PO_4 had the greatest moisture retention but failed to support a corresponding efficient translocation, probably because of its high pH.

In order to test the effects of a hygroscopic agent, glycerin, ethylene glycol and propylene glycol were added to ten 1 mM solutions of KH_2P*O_4 and K_2HP*O_4 which, in turn, were used in translocation studies as above. The results are shown in figure 6. The moisture retention was determined in the same manner as before, except that one drop of the additives was included after the initial weighings. Moisture retention was greatly increased with glycerin but essentially unaltered with the glycols. Glycerin raised the percentage of phosphorus translocated from KH_2P*O_4 solutions from 2 to 14 but reduced the percentage translocated from $K_2HP^*O_4$ solutions from 10 to 4. The glycols did not increase translocation significantly and were not hygroscopic.

The results with glycerin and $\text{KH}_2\text{P*O}_4$ are in agreement with the results of Fisher and Walker (10) who observed that absorption of $\text{KH}_2\text{P*O}_4$ by apple leaves was more than doubled with the addition of glycerin and more than tripled by rewetting the sprayed areas 3 times in the 24-hour period.

The decrease in phosphorus translocation when glycerin was included in the K_2HP*O_4 spray solution might be accounted for by the formation of a K_2HP*O_4 -glycerin complex. Evidence for this was obtained by chromatographic methods which indicated that a K₂HPO₄-glycerin complex, but not a KH₂PO₄-glycerin complex, may be formed. Anv complex would, of course, decrease the effective phosphorus concentration and thereby reduce phosphorus translocation. Silberstein and Wittwer (12) found growth to be less from the use of foliar applied potassium glycerophosphate than from H_3PO_4 , KH_2PO_4 or NH₄H₂PO₄ solutions. Support is thereby given to the idea that the hygroscopicity of a foliar applied fertilizer is of prime importance, but complex formation is to be avoided.

TIME COURSE OF UPTAKE: The course of uptake of phosphorus over a period of 96 hours was determined with equal quantities of 10 mM NaH₂P*O₄. Figure 7 shows both the percentage of phosphorus absorbed and translocated from the sprayed leaflet, and that retained in the sprayed leaflet. To obtain these values the unabsorbed phosphorus was washed from the sprayed leaflet at harvest time by a lowpressure jet of dilute HNO₃ containing a wetting agent (Tergitol 7) (10). The other essential value, the total amount of phosphorus actually applied, was determined by summation.

It is evident that after 30 hours, when about onehalf of the applied phosphorus had been absorbed, uptake fell off markedly. The phosphorus translocated from the leaflet continued to increase thereby actually reducing the amount retained within the leaflet. By the end of the 96-hour period 60 % of the applied phosphorus had been absorbed and more than half of this had been translocated away from the leaflet. Using the corresponding potassium salt at 14.7 mM, Fisher and Walker (10) found a 30%absorption in 4 days by apple leaves. Absorption appears to continue for some time after application (8, 9, 10, 11). The break in the absorption curve probably was due to drying of the spray to the point of crystallization. Rewetting of the sprayed area, raising of the relative humidity, or the presence of a hygroscopic agent might be expected to delay this break; the use of the corresponding potassium salt might hasten it.

In order to compare the amount of applied material moving upward and downward within the plants, they were divided at the node of the first trifoliate leaf at harvest time. It was found that within the first half hour more than 6 times more phosphorus

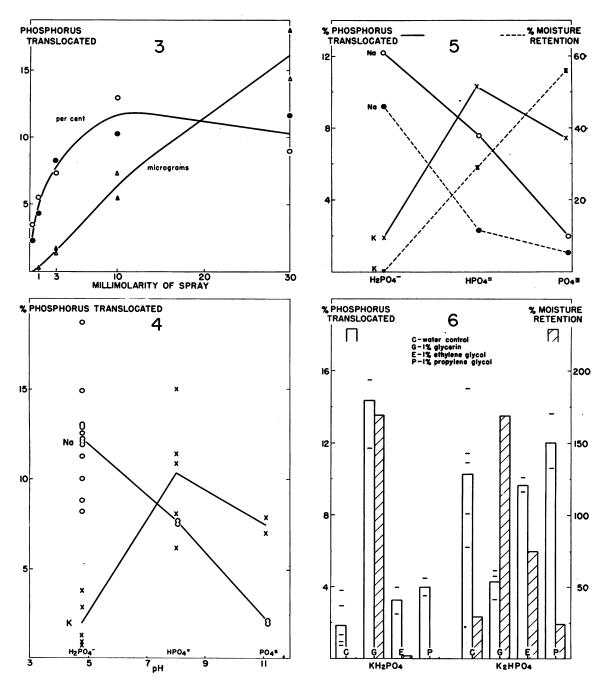
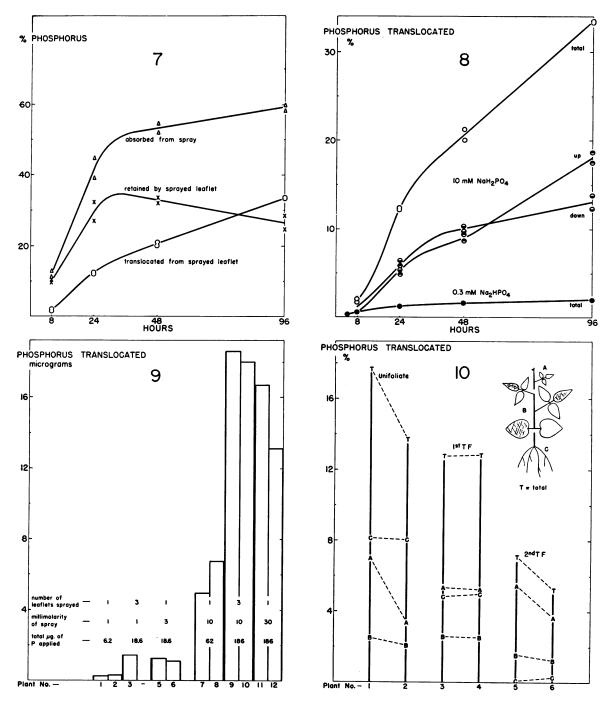


FIG. 3. Percentage and micrograms of phosphorus translocated from the terminal leaflet of the first trifoliate leaf in 24 hours by the spray application of 0.2 ml of five different concentrations of NaH₂P*O₄. Open circles and triangles, expt 1; solid circles and triangles, expt 2.

Fig. 4. Percentage of applied phosphorus translocated from the terminal leaflet of the first trifoliate leaf in 24 hours by the spray application of 0.2 ml of a complete series of sodium (O) and potassium (X) phosphates. The pH's and anions of the spray solutions are shown on the abscissa.

FIG. 5. Relation of the percentage of phosphorus translocated (average values from figure 2) from a leaflet sprayed with 0.2 ml of 10 mM NaH₂P*O₄, Na₂HP*O₄, Na₂P*O₄, KH₂P*O₄, K₂HP*O₄, or K₃P*O₄ solutions to the percentage of moisture retention of similar solutions.

FIG. 6. Relation of the percentage of phosphorus translocated in 24 hours from a leaflet sprayed with 0.2 ml of 10 mM KH₂P*O₄ or K₂HP*O₄ solutions containing no additive, 1% glycerin, 1% ethylene glycol, or 1% propylene glycol to the percentage of moisture retention of similar solutions. The short horizontal lines represent experimental values, and the vertical bars represent averages.



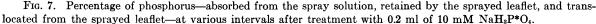


FIG. 8. Percentage of applied phosphorus translocated from the sprayed leaflet into the remainder of the plant (total), the portion of the plant above the first trifoliolate node (up), and the portion below this node (down) at various intervals after treatment with 0.2 ml of either 10 mM NaH₂P*O₄ or 0.3 mM Na₂HP*O₄.

FIG. 9. The micrograms of phosphorus translocated in 24 hours from the terminal leaflet or from all three leaflets of the first trifoliate leaf when sprayed with 0.2 ml of 1, 3, 10, or 30 mM NaH_2P*O_4 . The object was to compare translocation with the area (number of leaflets) treated.

FIG. 10. Percentage of phosphorus translocated from leaves of different positions on the stem into three plant sections, A, B, and C, as indicated in plant diagram. Plants 1 and 2 are duplicates and received 0.2 ml of NaH_2P*O_4 on a unifoliate leaf. The terminal leaflet of the first trifoliate leaf of plants 3 and 4, and the second trifoliate leaf of plants 5 and 6 received similar amounts of tracer.

from the spray was found below this node than above it. This ratio was decreased to 2.5 at the 8-hour interval, and after 96 hours more phosphorus from the spray was found above this node than below it (fig 8). The same relationship was observed in both experiments, i.e., with 0.3 mM Na₂HP*O₄ and with 10 mM NaH₂P*O₄ where the percentage exported in the 96hour period was 2.0 % and 34.5 %, respectively.

EFFECT OF THE SIZE OF AREA SPRAYED: To determine the relationship between the translocation of phosphorus and the leaf area treated, the spray was applied to either the terminal leaflet or all three leaflets of the first trifoliate leaf. Concentrations of 1, 3, 10 and 30 mM phosphorus were used in the experimental design selected to show this relationship. The design and the results are shown in figure 9. Each spray treatment involved 0.2 ml of solution.

The lateral leaflets appeared comparable to the terminal leaflet in translocation since three leaflets together translocated about three times as much as one leaflet when using 10 mM phosphorus. Within the concentration range used, the area sprayed seemed to make little difference. The amount of phosphorus applied appeared to be more important than the area of treatment, however the area factor is not without its effect when more concentrated solutions were used since one leaflet sprayed with 30 mM phosphorus exported slightly less phosphorus than three leaflets sprayed with 10 mM phosphorus.

EFFECT OF THE AGE AND POSITION OF THE SPRAYED LEAF: From figures 10 and 11 it can be seen readily that the age and position of the sprayed leaflet determined the amount and direction of translocation from the treated leaf. The results can be summarized as follows: 1) the amount of phosphorus translocated from a leaf was proportional to its age, and therefore to its position; the older leaves translocated the most phosphorus while the young immature leaves high on the stem failed to export phosphorus (Because of its size only 0.1 ml instead of the usual 0.2 ml of spray was used on the small, third trifoliate leaflet.); 2) the amount of phosphorus translocated from a leaf to the root was proportional to the proximity of the leaf to the root; 3) all leaves exporting phosphorus, regardless of age or position, contributed approximately equal amounts of phosphorus to the immature leaves at the stem apex. It should be stressed that these were young vigorous plants, and there was no sign of senescence of the primary leaves.

Most of the variability between duplicate plants in the percentage of applied phosphorus translocated can be attributed to section A, the stem tip where rapid growth was occurring. This is in agreement with work of Biddulph (5). Section A of plants 1 and 5 had lower dry weights than plants 2 and 6.

Steaming the petiole of the sprayed leaf completely blocked the passage of the P^{32} from the leaf. The xylem was still functioning as the leaf did not wilt during the 24-hour interval. The phloem, then, was the tissue involved in the exportation of the phosphorus as S. F. Biddulph (6) has shown by means of microautoradiograms.

EFFECT OF THE PHOSPHORUS LEVEL OF THE PLANTS: In all previous experiments the plants were grown in nutrient solutions with a 0.5 mM phosphorus level. If the level was reduced to 0.05 mM, there was no appreciable change in the amount of applied phosphorus translocated from the sprayed leaflet in 24 hours, and the foliage was comparable in appearance to the plants grown at the higher level, but the roots were slightly darker. However, plants grown without phosphorus in the nutrient solution were darker green in color, much smaller and translocated only one-fifth as much of the applied NaH₂P*O₄ as plants grown at the higher phosphorus levels. From this it is apparent that phosphorus translocation is impaired in phosphorus deficient plants.

EFFECT OF DAILY SPRAYING OF FOLIAGE ON THE PHOSPHORUS CONCENTRATION OF ROOTS: Four plants were grown at each of three phosphorus levels, 0.50, 0.05 and 0.00 mM. Two plants at each level were sprayed daily for 10 days, from the 9th to the 18th day, with unlabeled 30 mM NaH₂PO₄. Both the upper and lower surfaces of every leaf were sprayed

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INCREASE OF ROOT PHOSPHORUS FROM DAILY SPRAYING OF FOLIAGE OF PLANTS GROWN AT THREE PHOSPHORUS LEVELS

| P CONC OF NUTRIENT SOLN, MM | SAMPLE | Dry wt roots (mg) | | P in roots (mg) | | DIFF. | % Increase | % of spray |
|-----------------------------------|----------------|-------------------|-----------|-----------------|-----------|-------|------------|-------------|
| | | SPRAYED | UNSPRAYED | SPRAYED | UNSPRAYED | DIFF. | of root P | P in root * |
| 0.50 | 1 | 307 | 326 | 6.15 | 6.4 | | | |
| | 2 | 396 | 341 | 7.3 | 6.35 | | | • • • |
| | Av. | 352 | 334 | 6.7 | 6.4 | | | |
| 0.05 | 1 | 427 | 415 | 2.6 | 1.8 | | | |
| | $\overline{2}$ | 401 | 353 | 2.7 | 1.5 | | | |
| | Āv. | 413 | 384 | 2.65 | 1.65 | 1.0 | 61 | 14 |
| 0.00 | 1 | 361 | 391 | 1.4 | 0.78 | | | |
| | $\overline{2}$ | 313 | 305 | 1.3 | 0.61 | | | |
| | Āv. | 337 | 348 | 1.35 | 0.70 | 0.65 | 94 | 9.1 |

* Total of 7.2 mg of phosphorus applied per plant.

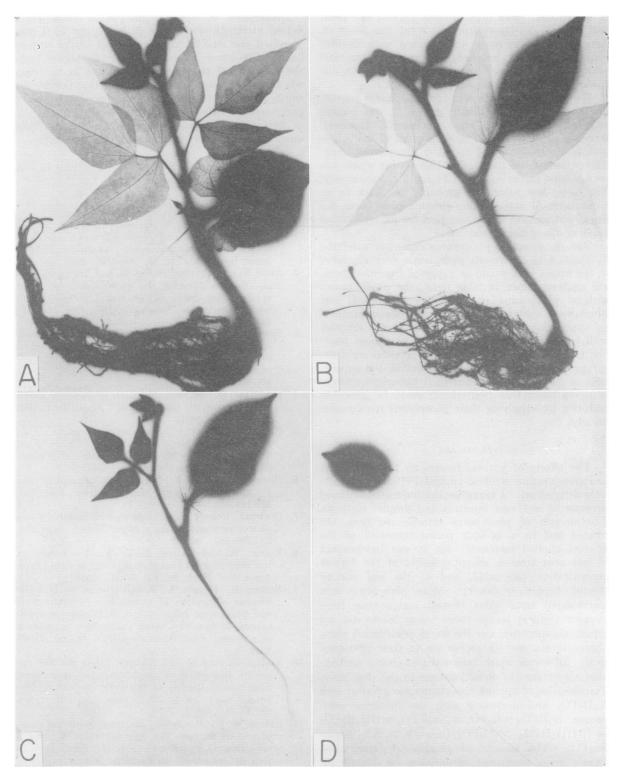


FIG. 11. Autoradiograms demonstrating the distribution of P^{32} in bean plants 24 hours after the spray application of 0.2 ml of 10 mM NaH₂P*O₄ to the following leaves: (A) a unifoliate leaf, (B) the terminal leaflet of the first trifoliate leaf, (C) the terminal leaflet of the second trifoliate leaf, (D) the terminal leaflet of the third trifoliate leaf. Axillary buds were not removed.

each morning. The total amount applied per plant was 7.2 mg. No injury from the spray was observed. After harvest the roots were washed with distilled water, oven dried, weighed, and analyzed for total phosphorus. The remainder of the plant was discarded. The results are shown in table I.

No significant increase in the phosphorus content of the roots of the plants grown at the normal (0.5 mM) phosphorus level was noted. However, increases of 61 % and 94 % were noted in root phosphorus at the 0.05 mM and 0.00 phosphorus levels. The percentage of the applied phosphorus which was translocated to the roots was 14 and 9.1, respectively. The latter low value was probably due both to an impairment of translocation through phosphorus deficient phloem and to the fact that the foliage utilized much of the applied phosphorus.

The symptoms of phosphorus deficiency exhibited by plants with inadequate phosphorus were alleviated to the extent that would be expected from the chemical analysis shown in table I, i.e., the plants grown without phosphorus in the nutrient solution, but which were sprayed daily with phosphorus, attained an appearance midway between the plants supplied with ample phosphorus and the plants without phosphorus either from the nutrient solution or from sprays. They were rapidly approaching the appearance of the plants at the normal phosphorus levels. It seems likely that bean plants could be grown to maturity by supplying their phosphorus requirement foliarly.

SUMMARY

The effects of various factors on the absorption and translocation of foliar-applied P³² in bean plants were determined. A spray application method proved superior to leaf vein injection and droplet methods. The amount of phosphorus translocated from the treated leaf in a 24-hour period increased as the amount applied increased; and it was independent of leaf area treated, except possibly at the highest concentration (30 mM), and of the leaf surface treated (upper or lower). More phosphorus was translocated from older (lower) leaves than from younger (upper) leaves (very young leaves did not export phosphorus), and the leaves contributed phosphorus to the root in proportion to their proximity to it. All leaves which exported phosphorus contributed approximately equal amounts to the stem apex. Translocation of applied phosphorus was greatest with NaH_2PO_4 and decreased with the following compounds: $K_2HPO_4 > K_3PO_4 \cong Na_2HPO_4 \cong NH_4H_2PO_4$ $\simeq (NH_4)_2 HPO_4 > H_3PO_4$ (injury) > $KH_2PO_4 \simeq$ Na₃PO₄. The amount of phosphorus translocated from a given compound appeared to be directly related to the drying time of the solution on the leaf. Glycerin increased the translocation from KH₂PO₄ to the level of NaH₂PO₄ but reduced the translocation from K_2 HPO₄, probably because a complex was formed.

Absorption of applied phosphorus (NaH_2PO_4) fell off markedly after about 30 hours, but 60 % was absorbed and 34.5 % translocated out of the treated leaflet in 96 hours. The amount of phosphorus from the treated leaf that moved downward in the stem was initially greater than the amount that moved upward, but after 48 hours accumulation in the upper part exceeded than in the lower.

Surface active agents (nonionic, anionic and cationic) were ineffective in increasing translocation.

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