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George E. Ahlgren  
*University of Minnesota, St. Paul*

Theodore W. Sudia  
*University of Minnesota, St. Paul*

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# Distribution of Foliar Applied P-32 From the Leaves of Soybean at Various Ages<sup>1</sup>

GEORGE E. AHLGREN<sup>2</sup> and THEODORE W. SUDIA<sup>2</sup>

University of Minnesota, St. Paul

**ABSTRACT**—Transport patterns of phosphorus-32 from the cotyledons, primary leaves and the first five trifoliolate leaves of soybean were determined at various ages of these organs. The transport patterns studied indicate the same general pattern for each leaf. There is initially a bidirectional movement from the leaf that increases in its upward component as the leaf becomes older, followed by a sharp drop in the upward component and P<sup>32</sup> transport becoming essentially unidirectional downward in the stem. At fruit development, phosphorus-32 transport becomes quite specific for fruit at the axil of a particular leaf. Contiguity to sites of high metabolic activity seems to determine direction of phosphorus-32 transport.

Minerals are normally accumulated in leaves as a result of absorption by the plant's roots and subsequent movement through the xylem into the leaves. With some minerals, such as phosphorus, redistribution from the leaf can occur by movement of the minerals either up or down in the stem.

Radioactive phosphorus, when applied directly on a leaf, is absorbed directly, thus bypassing the normal route and affording an easy method of studying redistribution.

Using C<sup>14</sup>, the direction of transport and the accumulation sites of translocated organic assimilates from leaves has been studied intensively. It has been shown that the direction of transport is determined primarily by the relative contiguity of assimilates to high metabolic regions in the plant (Aronoff, 1955; Shiroya et al., 1961; Hale and Weaver, 1962). The same process seems to be true for phosphorous also as the direction of transport of radioactive phosphorous applied to leaves has been shown to be mostly downward from leaves in a lower position, bidirectional from leaves in a mid-position and mostly upward from leaves in a higher position Koontz and Biddulph, 1957; Colwell, 1942; Biddulph et. 1958).

## Materials and Methods

Seeds of soybean *Glycine max* L. (Merr.) var. Ottawa Mandarin were germinated between sheets of paper toweling. After five days, the seedlings were transferred to tanks containing complete Hoagland's solution. The plants were grown in the aerated nutrient solution in a controlled environment room set at 95° ± 2° F during a 12-hour light cycle, and 65° ± 2° F during a 12-hour dark cycle. Fluorescent and incandescent light provided 1500 foot-c illumination at plant level.

The P-32 solution used in the study was prepared by

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<sup>2</sup> B.S., Kent State University, Ohio; M.S. and Ph.D., Ohio State University. At present, Associate Professor, Department of Plant Pathology and Physiology. Interests are plant physiology and research on mineral transport.

<sup>3</sup> B.S. and M.S., University of Minnesota, St. Paul. Currently studying to complete requirements for Ph.D., and working on absorption of phosphorus by soybean leaves. Instructor and Research Fellow in Department of Plant Pathology and Physiology.

evaporating the solution in the stock bottle that was received from the Oak Ridge National Laboratory to dryness and redissolving the residue with 20mM NaH<sub>2</sub>PO<sub>4</sub> in a volume sufficient to bring the activity to 20 μc/μl. A portion of this solution was diluted further to 1 μc/μl at the time each treatment was made.

Applications of P-32 were begun on each leaf, i.e., the cotyledons, primary leaves and the first five trifoliolate leaves, as they first appeared, and continued at various time intervals throughout the life of the plant or until leaf senescence. Plants (four per treatment), were selected for uniformity of growth and were transferred for treatment to paper cold-drink cups that contained a nutrient solution. The cotyledon and primary leaves were treated by placing a 5 μl drop on the upper surface of each leaf for a total activity of 10 μc per plant. The trifoliolate leaves were treated by placing 10 μl (containing 10 μc) to the upper surface of the terminal leaflet. The isotope was applied in the morning of the treatment day approximately 3 hours after the light cycle had started.

After a 24-hour uptake period, the plants were separated into root and hypocotyl, internodes, leaves and, where they occurred, flowers and fruits. The plant parts were then placed into 30 ml beakers, dried, wet ashed with nitric acid and counted in a Geiger counter. Counts were corrected for decay to the date of treatment. The activity in cpm was totaled for P-32 transported up from the node of the treated leaf and P-32 transported down from the node of treated leaf. An additional plant was autoradiographed for visual evidence of direction of transport and site of accumulation. This was done by placing the plant between sheets of vinylidene chloride film (saran wrap) and either placing it on an individually wrapped x-ray film according to a method described by Sudia and Linck (1961), or placed on x-ray film in a metal cassette. In both methods, the plant and film were exposed in a freezer.

## Results

The P-32 activity detected in the morphological parts of the plant was totaled for parts above and below the node of the treated leaf. These activities in cpm were then calculated in terms of percentage of radioactive phos-

phorous moving upward and downward in the stem from the treated leaf.

The P-32 activity for each leaf, at each age treated, is represented by the bar graphs in Figs. 1-5. The zero on these graphs represents the node of the treated leaf; the percentage of total upward activity is represented by that part of the bar above the zero line and the percentage of downward activity, by that part of the bar below the zero line.

Transport from the cotyledons, Fig. 1, shows that

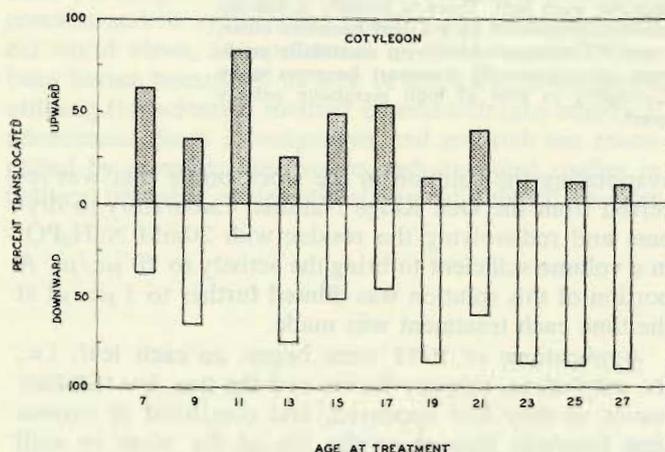


FIGURE 1. Percentage of P-32 translocated upward and downward in the stem of soybean from cotyledons treated with P-32 at different ages. Five  $\mu\text{C}$  P-32 were delivered in a five  $\mu\text{l}$  drop per cotyledon and the plants were harvested 24 hours after treatment.

initially the movement is essentially bidirectional. The seven-day-old plants translocated 63 per cent of the phosphorus 32 upward in the stem, followed by a decrease to 36 per cent in the 9-day-old plant, and up again to 83 per cent in the 11-day-old plant. A sharp decrease in upward movement ensued between the seventeenth and nineteenth days from 53 per cent to 13 per cent followed by a small increase, and then a decrease to a point where upward movement was quite small. This type of distribution was maintained in the older plants treated. The bidirectional aspect of the distribution pattern was maintained up to the seventeenth day, when the primary and first trifoliolate leaves were fully developed after which the movement of phosphorus was largely in a downward direction. Previous to this treatment the developing terminal portion and leaves above the cotyledons received increasing amounts of P-32.

Fig. 2 shows the distribution of P-32 from the primary leaf of soybeans treated at various ages. Initially phosphorus movement is primarily downward but in treatments given to older plants upward movement into the developing terminal bud and immature trifoliolate leaves continued to increase up to the 18-day-old plant, at which time 74 per cent of the phosphorus translocated had moved upward. Two days later, the direction of transport shifted downward after which only 23 per cent had been transported upward in the 21-day-old plant. Upward transport of P-32 continued to decrease up to the 36-day-old treatment. At this time, upward movement

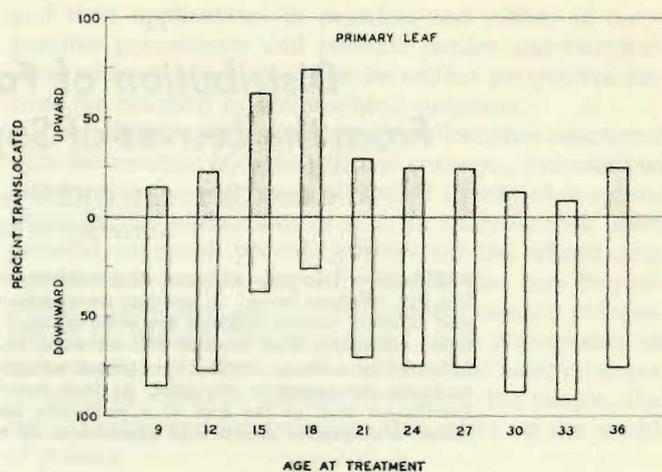


FIGURE 2. Percentage of P-32 translocated upward and downward in the stem of soybean from primary leaves treated with P-32 at different ages. Five  $\mu\text{C}$  P-32 were delivered in a five  $\mu\text{l}$  drop per primary leaf and the plants harvested 24 hours after treatment.

increased as a result of the formation of fruits with a corresponding movement into these structures. Radioautograms showed that much of the P-32 moved upward into the immature trifoliolate leaves. Some movement into these leaves continued even after maturity but was sharply reduced. At maturity of the first trifoliolate leaf, P-32 movement was predominantly into the terminal bud and developing second trifoliolate leaf. At maturity of the second trifoliolate leaf the greatest movement was into the terminal bud and the developing third trifoliolate leaf. At this stage, however, the total upward movement of P-32 had already been sharply reduced.

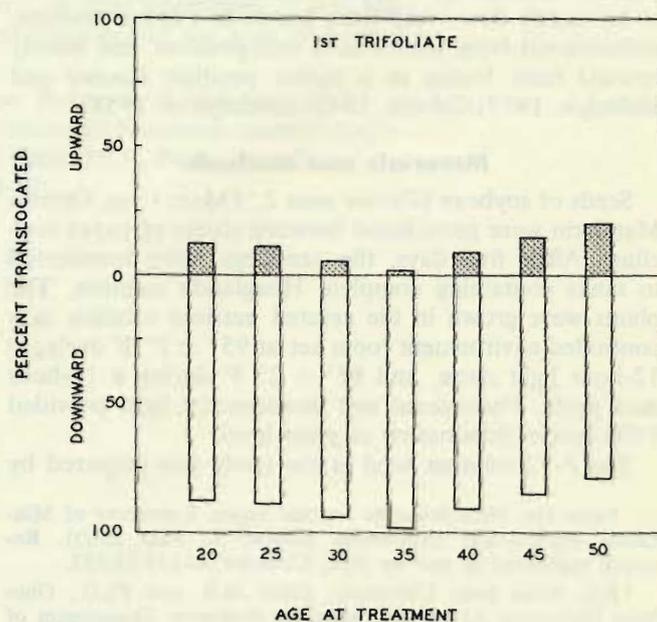


FIGURE 3. Percentage of P-32 translocated upward and downward in the stem of soybean from first trifoliolate leaves treated with P-32 at different ages. Ten  $\mu\text{C}$  P-32 were delivered in a 10  $\mu\text{l}$  drop applied to the terminal leaflet. The plants were harvested 24 hours after terminal leaflet. The plants were harvested 24 hours after treatment.

As is shown in Fig. 3, the percentage of total P-32 translocated upward into the stem from the first trifoliolate leaf was considerably less than that from cotyledons or the primary leaves.

Treatments were begun to the trifoliolate leaves of 16-day-old soybean plants. P-32 moved from the leaf into the untreated leaflets and into the petiole but none moved out of the leaf. The leaf at this state "imports" but does not "export" phosphorus, a condition that has been described previously for P-32 in beans by Biddulph et al (1958), and for C-14 by Jones et al. (1959), Hale and Weaver (1962) and others. Because P-32 did not move into the stem, the first treatment made to the first trifoliolate leaf is not represented on the bar graph in Fig. 3. Movement out of the first trifoliolate leaf was predominantly downward in all subsequent treatments. In the plants 20 days after treatment 13 per cent of the P-32 moved upward; this decreased to only 2 per cent in 35-day-old soybeans. The increased upward movement in subsequent treatments was due primarily to the development of the flowers and fruits.

Phosphorus translocation from the second trifoliolate leaf is somewhat similar to that from the first trifoliolate leaf in that transport is primarily downward in all treatments except in the last one made to 46-day-old plants. In this treatment, transport of P-32 was primarily into the fruits at the node of the treated leaf, a very active "sink." Radioautographs of plants treated at the second and third trifoliolate leaves greatly resemble those of the first trifoliolate leaf.

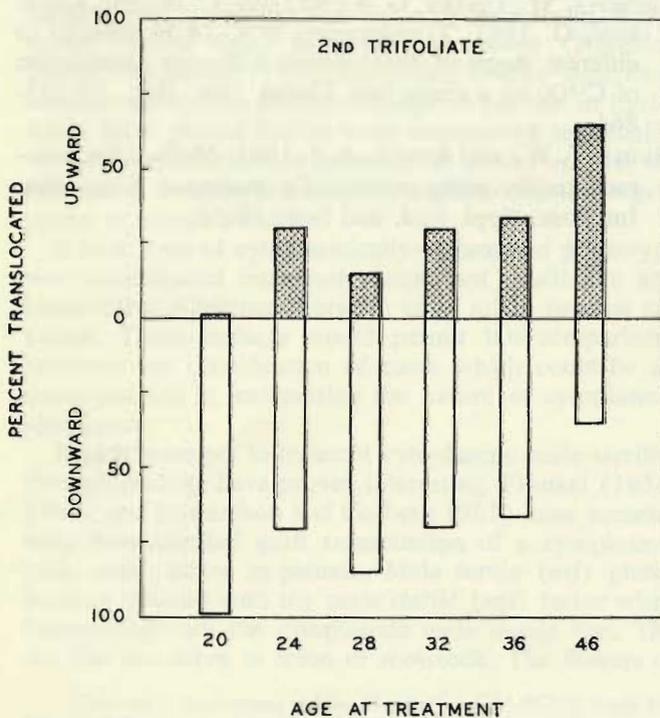


FIGURE 4. Percentage of P-32 translocated upward and downward in the stem of soybean from second trifoliolate leaves treated with P-32 at different ages. Ten  $\mu$ c P-32 were delivered in a 10  $\mu$ l drop applied to the terminal leaflet. The plants were harvested 24 hours after treatment.

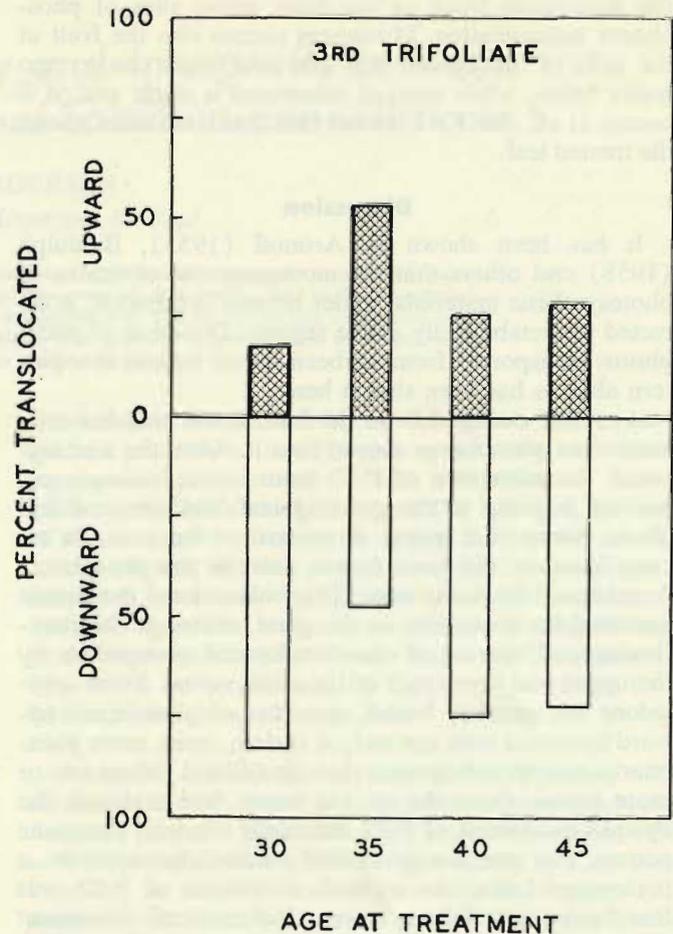


FIGURE 5. Percentage of P-32 translocated upward and downward in the stem of soybean from third trifoliolate leaves treated with P-32 at different ages. Ten  $\mu$ c P-32 were delivered in a 10  $\mu$ l drop applied to the terminal leaflet. The plants were harvested 24 hours after treatment.

Fig. 5 shows a marked increase in the upward movement of phosphorus from the third trifoliolate at the 35-day treatment. In 30-day-old plants 17 per cent moved upward, and in 35-day-old plants 54 per cent moved upward. This increase is a result, primarily, of the movement of phosphorus-32 into the developing leaves above the third trifoliolate leaf and the beginning of fruit formation at that node. Subsequent treatments, however, result in less upward movement although fruit formation continues at that node.

Upward movement of P-32 from the fourth trifoliolate leaves increased from the first treatment at 3 per cent to the last treatment at 40 per cent. Again, this is primarily due to pod formation at that node. Initial movement upward is small, which is surprising since, at that time, there are upper leaves that are still immature and metabolically active; however, the bulk of the plant body is below the treated leaf. Additional leaf formation in the plants grown under the conditions imposed in these experiments ceases and reproductive growth, i.e., formation of fruit, begins to predominate over vegetative growth. This is borne out by radioautograms that show

the developing fruits as the most active sites of phosphorus accumulation. Movement occurs into the fruit at the axils of the treated leaf and into fruits one to two nodes below, while upward movement is slight and, if it occurs at all, the P-32 moves into fruits at nodes above the treated leaf.

### Discussion

It has been shown by Aronoff (1955), Biddulph (1958) and others that the movement out of leaves of photosynthetic materials, under normal conditions, is directed to metabolically active regions. Direction of phosphorus transported from soybean leaves follows this pattern also, as has been shown here.

As a leaf emerged from the bud, it was metabolically active and phosphorus moved into it. After the leaf matured, the movement of P-32 from it was bidirectional, part of it going to the growing leaf and terminal bud above, some of it going downward to the root. In no case, however, did lower leaves share in the phosphorus translocated down the stem. This bidirectional movement persisted for some time in the plant, although the partitioning and sharing of the translocated phosphorus by the upper and lower part of the plant varied. From cotyledons and primary leaves, transport of phosphorus upward increased with age and, at certain times, more phosphorus was moved upward than downward. When two or more leaves above the treated leaves had matured, the upward movement of P-32 decreased sharply. The same pattern was true for every leaf studied; however, on a percentage basis, the upward movement of P-32 was less from the trifoliolate leaves. Bidirectional movement of P-32 occurred until fruit development, after which the upward movement declined sharply as the leaves above matured. Most of the phosphorus moving out of the trifoliolate leaves, except when fruit formation occurred, was transported downward.

After fruit development the transport was altered and movement into the developing pods at the axil of the

treated leaf predominated with some movement also into pods at one or two nodes below the treated leaf. Specificity of phosphorus from fruit borne at the axil of a treated leaf has been previously known to occur in pea plants by Linck and Swanson (1960).

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