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Polar Movement of Indole-3-acetic Acid-^{14}C in Roots of Lens and Phaseolus[1, 4]

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Abstract. A critical review of the few papers on IAA-^{14}C movement in roots revealed apparent contradictions, as well as flaws in experimental design that would be apt to cause artifacts. The movement of ^{14}C from IAA-^{14}C was studied in sections of *Lens* and *Phaseolus* roots, using a system 20 or more times as sensitive as any previously used. To make sure that our results with roots could be compared validly with published work on petioles and stems, we used the same techniques as we had earlier used for shoot structures. The results with *Lens* were similar in many ways to those for shoots: net movement into receiver blocks was very strongly polar, followed a linear course for several hours, and showed a velocity of the same order of magnitude as in shoots (and, in fact, very close in absolute value to that found in *Coleus* stem cylinders). Also, as with shoots, all the radioactivity in receiver blocks ran to the R_F of IAA. The time-course of loss of counts from donor blocks was similar to that found in shoots. The 2 most striking differences from shoots were 1) the very low percentage of added ^{14}C that was moved into the receivers (about one-tenth of the values for bean petioles), and 2) the fact that the polar movement was acropetal in roots, rather than basipetal as in shoots. Results with *Phaseolus* roots were similar to those for *Lens*, although an additional complication with *Phaseolus* roots was the indication of a transitory stage of weak basipetal polarity in the first few hours after excising the section. This stage was followed in a few hours by a stronger acropetal polarity.

In shoots of vascular plants the role of auxin and the properties of its movement have been quite thoroughly explored (*cf.* 13, 14, 17, 19, 27). Much less is known about the auxin relations of roots, and almost nothing about auxin movement through roots. It would be particularly interesting to know in what ways auxin movement through roots is the same as through shoots. Does it show strong polarity, as found for many, though not all, shoot structures? If so, in which direction is the movement polar—toward the apex of the root, or toward the base? (Shoots show basipetal polarity in all polar cases so far investigated.) Kinetic studies of auxin movement in shoots have given evidence that the basipetal accumulation of auxin in receiver blocks is linear for several hours after an initial non-linear portion (18, 20, 30, 32); the linear portion of the time course allows one to estimate quantitatively the velocity of auxin movement (9, 14, 21). Do roots show similar kinetics, and is the velocity of auxin movement the same in roots as in shoots? If indole-3-acetic acid (IAA) tagged with ^{14}C is added in donor blocks and results in ^{14}C accumulating in the receiver blocks on the opposite end of the root sections, is the transported material as consistently unchanged chemically as it seems to be for shoots (14)?

Published papers are apparently contradictory on several points. A critical reading of these papers makes clear that each of them contains potential or likely sources of error or of artifact sufficient to vitiate their conclusions about auxin movement in roots. These papers are reviewed, compared, and criticized below as an explanation of the need for a new investigation.

Of the few papers using IAA-^{14}C, one reported no movement into receiver blocks of agar (35), another said that the amount of radioactivity found in the receiver blocks was too small to use (2), while a third reported sizeable amounts in the receivers (26). Hertel and Leopold (10) said that they could not get enough counts in the receivers for a determination of velocity unless they cut the transport section down to 2 mm (from the 5+ mm more frequently used).

Based on counts of ^{14}C in the receiver blocks, Pilet reported a weak acropetal polarity (92 counts in the acropetal receivers compared to 44 in the basipetal) for *Lens* root sections. Because they could not get enough counts in their receiver blocks, Yeomans and Audus as well as Bonnett and Torrey counted the ^{14}C obtainable from segments of tissue at the opposite end of the transport section from the agar- or liquid-donor and assumed that this measured auxin movement. Because the tissue next

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to the apical receiver showed more counts than the tissue next to the basal receiver, the authors of both papers concluded that there was more acropetal than basipetal movement of IAA-^{14}C. None of these authors corrected for the fact that the basal end of the transport sections would be expected to have a larger area than the apical end. With a larger area at the base, and with no active transport, one would expect more diffusion into the tissue from the basal donor than from the apical—giving, as an artifact, evidence for a weak acropetal polarity. Hertel and Leopold, using their short 2 mm sections, contrasted what they considered the active, polar movement of IAA through coleoptiles with the active, non-polar movement through roots. Their data on roots (conveniently seen in fig 11, in 19) are not, however, validly comparable to regular transport data for 2 reasons. First, they used much shorter sections for the root studies of their table I than for the shoot structures in the same table. Shorter transport sections habitually display weaker apparent polarity (*e.g.*, fig 3, in 6). Secondly, further on in the paper they report essentially no polarity for roots (with 90/100 as the counts in the acropetal compared to basipetal receivers). But these counts were obtained by applying receiver blocks to both ends of sections which immediately before had had donor blocks on both ends. Since uptake from donor blocks is both high and quite non-polar, so far as the tissue adjacent to the donor blocks is concerned (*cf.* fig 2, in 16), one would expect so much non-polar diffusion back into the immediately adjacent receiver blocks that any natural polarity of auxin movement would be obscured. This expectation has been directly confirmed for bean petiolar sections (table I, in 22).

The few studies of the kinetics of labeled auxin movement in roots are similarly contradictory. Hertel and Leopold assumed a linear relation to exist in roots, and by extrapolating from their 2-point determination of receiver blocks on 2 mm root sections, estimated the basipetal velocity to be 6 mm/hour. An acropetal velocity of 9 to 10 mm/hour was reported for IAA movement in cultured roots of *Convolvulus* by counting at increasing time intervals the ^{14}C in tissue slices 8 to 12 mm from the donor solution (2). Although the ^{14}C counts showed a 4-point linear increase with time (their fig 2), the acropetal velocity was identical with the classical basipetal velocity of auxin movement in the *Avena* coleoptile (9), and ether extracts of the tissue run on paper chromatograms showed a single peak of radioactivity that was at the R_F zone typical of IAA, one feels somewhat less secure about this as an estimate of IAA movement in *Convolvulus* roots after noting that the peak represented only 31 % of the ^{14}C in the slices. None of the other 3 papers gave evidence that the ^{14}C being counted was still in the IAA molecule after moving through the root sections. The only other kinetic study is that of Pilet (26). His figure 3 shows a steady increase in counts in the apical receivers. However, the straight line drawn through the points intersects the time axis at zero so that one cannot estimate velocity from it.

One other major question concerns the purity of the chemicals used. All the authors added IAA-^{14}C in their donor blocks or solutions. Judging by their descriptions, the purity of their IAA-^{14}C solutions was checked, if at all, with a Geiger-tube scanner. We have found that a small percentage of radioactive impurity in the donor (as judged by chromatography) is sufficient to give substantial amounts of apolar movement of the radioactivity (p 29 of 21). More recently, Werblin has found that a solution of IAA-^{14}C that was "pure" IAA by the criterion of Geiger scanning could contain enough impurity—detectable by the more sensitive liquid scintillation counter—to give apolar movement of the ^{14}C (unpublished senior thesis, 1966, Princeton University). Therefore, in all cases where workers report relatively apolar movement of "IAA-^{14}C", it is crucial to know if the original IAA solution was pure by a criterion as sensitive as liquid scintillation counting. None of the papers on IAA-^{14}C movement in roots meets this requirement.

As this brief survey makes clear, there is little agreement in the literature as to the properties of labeled auxin movement in roots. In addition to the sources of potential error described above, the contradictory results so far published could also result from: A) the very different IAA concentrations added in the donors by the various authors (ranging from 0.07–10 mg/l); B) the fact that each paper reports on a different genus; C) the portion of the root studied (3 papers used sections from near the root-tip, while Bonnett and Torrey used sections cut many centimeters back from the tip); and D) the most thorough paper used only roots that had been grown in sterile culture for 6 weeks (2). One cannot judge to what extent the results obtained with old portions of cultured roots are valid only for such material.

Accordingly, we thought that it would be worthwhile to investigate IAA-^{14}C movement in roots. Our plan was to use the same, relatively long, 5 mm sections that the Princeton group has been using regularly for shoots, and to apply the auxin in agar as we have been doing for petioles and stems. Any differences in results would then be unlikely to be the result of different techniques. Since the earlier workers, with the exception of Pilet, had such difficulty detecting any "transported IAA-^{14}C" in receivers, we increased the sensitivity of detection about 20-fold by using IAA-^{14}C of 10 times higher specific activity and by using a liquid scintillation counter. The latter has 2 to 8 times the sensitivity of Geiger tubes for counting agar blocks; for counting zones of paper chromatograms, its sensitivity is approximately 6 to 8 times as high.

Lens roots were selected because they had already been used for studies on auxin movement in roots (25, 26), and *Phaseolus* roots were used as part of our plan to investigate thoroughly the hormone transport of an entire plant (11, 12, 14, 16, 21, 22, 30).

Materials and Methods

Seedlings of *Lens culinaris* Medikus, from the seeds of Pilet's stock, were grown in Petri dishes in a dark incubator at 25 ± 1° according to the methods of Pilet (28). Three days after soaking, when the roots were 16 to 22 mm in length, the lengths reported by Pilet (24) to contain the largest amount of auxin, the roots were matched, in pairs, by length. Each root in a pair was assigned a treatment, acropetal or basipetal, in a mathematically random manner, with each treatment consisting of 4 to 15 roots. A section 5.1 mm long was cut with a double-edged cutter starting 3.2 mm from the root cap (avg of 10 individuals). The length and location of the section follow Pilet (26). The excised root sections for acropetal and basipetal transport were placed horizontally in a large Petri dish, 1 Petri dish being used for each hour. Application and removal of the agar blocks, each of which took about 1 minute per root, were done in laboratory light. Once all the agar blocks were applied, the Petri dishes were placed in the dark incubator at 25 ± 1° for transport. [Pilet (24) reported that there was more extractable auxin from roots grown in the dark than from those in light.] Hourly collections were run concurrently to minimize possible diurnal rhythms in transport (*i.e.*, a 6 hr transport would run from 9:00 AM–3:00 PM while the 4 hr transport would run from 10:00 AM–2:00 PM). In several experiments, at the end of transport, the roots were divided into five 1 mm transverse slices for an estimation of the distribution of IAA-^{14}C in the roots.

Seeds of *Phaseolus vulgaris* "Red Kidney" shell beans were surface sterilized with 6% sodium hypochlorite before soaking and the seedlings were used 4 days later.

Indole-3-acetic acid, labeled with ^{14}C in the carboxyl group of the side chain, was applied at concentrations of 2.5 to 3.0 mg/l in 1.5% agar blocks to the apical or basal end of the root section, with a plain agar receiver at the opposite end, essentially as described in our earlier papers (*e.g.*, 15). This concentration level was selected because it was close to that used by Pilet (2.2 mg/l), by Hertel and Leopold (1.8), and to some extent by Bonnett and Torrey; also, it was close to the 2 mg/l that we had often used for shoots. By using IAA-^{14}C of the highest specific activity available (33 mc/mM) and by counting in a Nuclear Chicago Mark I liquid scintillation counter with 84 to 85% efficiency, individual blocks could be counted. To improve the counting statistics, in some experiments 3 blocks or 3 tissue-slices from like treatments were placed in the same glass vial. In all cases, Naqvi scintillation fluid (25% ethanol in toluene-PPO-POPOP) was used (23). Each donor block gave about 20,000 cpm at the start of the experiment. All samples were routinely counted twice for 10 minutes each time, plus a 1 minute count for the external standard. Important samples with relatively low counts were counted for much longer periods (usually to 10,000 total counts) to improve the precision of the determinations. The scintillation counter was calibrated for each counting period by using a standard containing ^{14}C in Naqvi-solution, as well as background determinations. Vials being reused were checked after washing for contamination. Comparisons of the channel ratios (using ^{133}barium as external standard) with detailed quench-correction curves showed that there were no significant differences in quenching among the various samples being counted.

The stock solution of IAA-^{14}C in acetonitrile was kept in the refrigerator for 4 months, during which time the purity was checked 4 times by paper chromatography in an isopropanol-ammonia-water solvent (80:10:10 v/v), with subsequent counting of the zones of paper in the liquid scintillation counter (following Naqvi, 23). The stock solution was also checked 2 times with Ehrlich's reagent. There was no sign of any impurity during the entire period.

Statistical methods follow Snedecor (31).

When comparing our results with others', we have selected the published values which were most validly comparable in terms of original donor concentration, time, *etc.*

Results and Discussion

Lens *Roots.* When IAA-^{14}C at 2.8 mg per liter was added in donor blocks to 1 end of 5.1 mm long sections and the donor and receiver blocks were collected at various intervals, the average counts in the receivers were as shown in figure 1. There was very strong acropetal polarity. At 6 hours, an average of 33 times more radioactivity was found in the apical than in the basal receivers (200/6 counts). This is much stronger polarity than previously reported in any roots. (Pilet's ratio for 5 mm *Lens* root sections at 4 hrs was 2/1.) The polarity is comparable in strength to that found in shoots by the same techniques (15, 21). The apical receivers showed a steady increase in counts, the data of 3, 4, and 6 hours being obviously linear. (By contrast, there was no indication that the counts in the basal receivers are increasing during the period sampled. At 6 hrs, each basal receiver block averaged only 2 cpm above the background.) A 't' test of the 6 hour values showed the acropetal counts to be significantly greater than the basipetal counts at the 2% level.

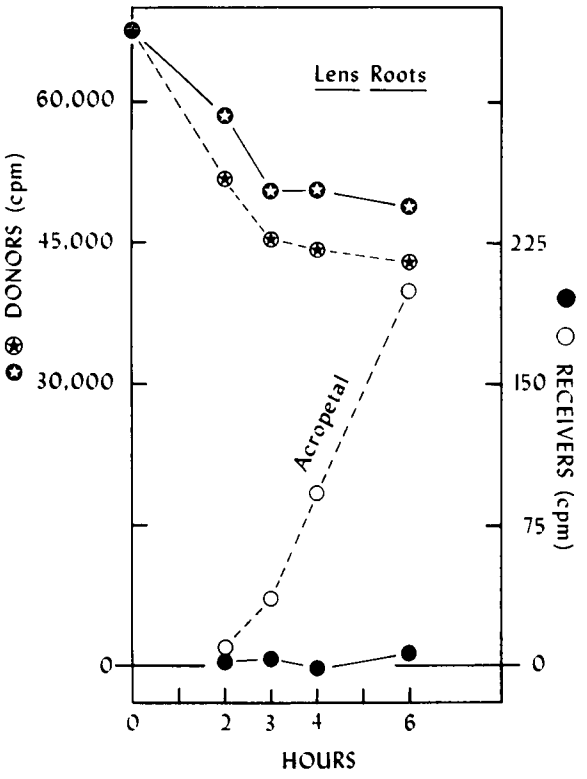

FIG. 1. The time course of movement of ^{14}C from indoleacetic acid supplied at an initial concentration of 2.8 mg/l to *Lens* root segments. At the top of the figure are counts in 3 donors (legend on left), at the bottom are counts in 3 receivers (legend on right). (The linear regression equation for counts in acropetal receivers at 3, 4, and 6 hours is: $Y = 54.55X - 127.50$). In all figures solid symbols with continuous lines refer to basipetal movement, and hollow symbols with dashed lines refer to acropetal.

Calculation of the regression for the linear portion of the acropetal curve showed the intercept with the time-axis to be 2.34 hours. Hence, the calculated acropetal velocity was 5.1 mm per 2.34 hours, or 2.2 mm/hour. This velocity is within the 2.1 to 3.3 mm/hour range found by the same techniques for basipetal velocity of IAA-^{14}C in *Coleus* stem cylinders (15). It is somewhat smaller than those previously reported for roots (see Introduction), as well as smaller than the 5.7 mm/hour found for IAA-^{14}C velocity in bean petioles (fig 6 of 21) or the 6.4 mm/hour from *Lens* stems (27).

The net decrease with time in counts in the donor blocks is shown at the top of figure 1. There was more net loss from basal than from apical donors. We might expect this from earlier work on shoots (15, 21), where the donors supplying auxin for the direction of strongly polar movement (in that case, the apical donors) also showed more net loss than the others. In *Lens* roots at 4 hours, 25.2 % of the counts were gone from the apical donors, 34.6 % from the basal. [In our 2 repetitions of this experiment, the loss from the basal donors was 30 % and 38 %—all 3 values being higher than the 16 % reported by Pilet (26) for the same material.] When a similar IAA-^{14}C concentration of 20 μM was added to bean petiolar sections of similar length (5.4 mm), we found a similar difference between the counts in the 2 types of donors at 5 hours (13 % of the original donor count), the apical donor showing a net loss of 49 % (fig 4 of 21). Apical donors applied to stem cylinders of *Coleus* showed a 32 % net loss of their original 5 μM by 4 hours (15). These comparisons indicate that roots are much like shoots in donor-loss relations.

For *Lens* roots, only 0.30 % of the radioactivity added in the original donor at 2.76 mg/l (= 15.8 μM) actually reached the apical receiver by 6 hours. If we use net loss from donors as an estimate of potentially absorbed radioactivity, we can calculate the amount reaching the receiver as a percentage of the amount gone from the donors by that same time. Such a calculation shows that only 0.81 % of the net loss appeared in the apical receivers by 6 hours. This is only one-eighth of the 6.9 % found with young bean petiolar sections at 5 hours when 20 μM IAA-^{14}C was added to their apical ends (21). It is a similarly small percentage when compared to the values for cylinders cut from older *Coleus* internodes (fig 3, in 15). (Pilet reported values for *Lens* roots that were an order of magnitude larger than we found. His table I shows 5.8 % of the radioactivity in the original donor to be in his receivers after 4 hrs.)

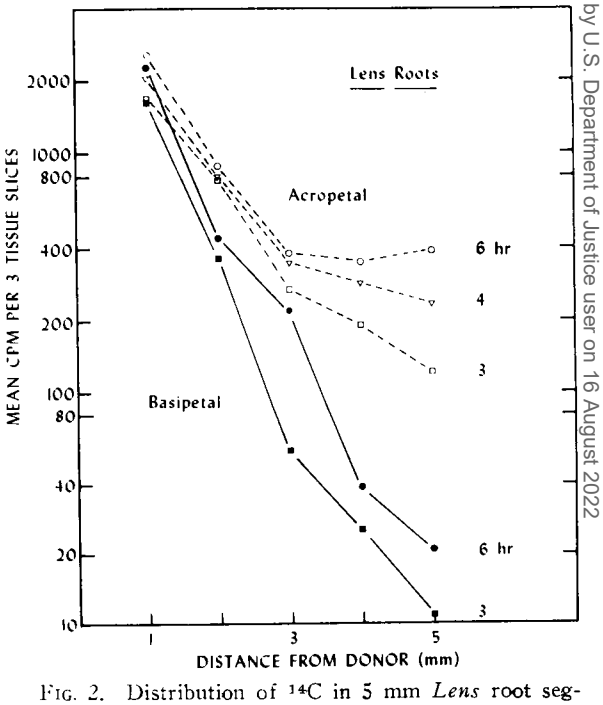

FIG. 2. Distribution of ^{14}C in 5 mm *Lens* root segments treated for 3, 4, and 6 hours with IAA-^{14}C at the apical ("Basipetal") or basal ("Acropetal") end. Symbols as for figure 1. Same experiment as figure 1.

It seems likely that this strikingly lower ability of roots than of shoots to move absorbed IAA-^{14}C into receiver blocks can account for the inability of all earlier workers except Pilet to find sufficient ^{14}C in their receivers to count. The similarity of the time course of net loss from donors in both *Lens* roots and the earlier investigated shoot sections would explain why ground-up tissue, to the contrary, would provide adequate counting levels (as found by Yeomans and Audus, or Bonnett and Torrey).

Since we found such strikingly polar movement of ^{14}C from IAA (in contrast to the weaker polarities reported by earlier workers), it was not so crucial as we had expected to determine the areas of the apical and basal cut surfaces. However, with an ocular micrometer and a dissecting microscope we measured the diameter of 10 apical and 10 basal cut surfaces. The diameters averaged 1.22 mm for the basal, and 0.94 mm for the apical cut. Assuming that the roots were circular in transsection, we calculated areas to be 1.169 and 0.694 mm^2, respectively. The area of the apical cut surface of these *Lens* root-sections was, by this criterion, only 59.4 % of the basal 1. Our suggestion that weak acropetal polarities might be explained by more diffusion through the larger area on the basal cut surface is supported.

To see if counts of tissue slices (2, 35) gave the same estimate of polarity as counts of receiver blocks (10, 26) when the same material was used, the distribution of counts in the root sections was followed by cutting transport sections transversely into five 1-mm slices and counting them as soon as the donor and receiver blocks had been removed. In figure 2 are shown the average values from slices of the same transport sections used in figure 1. The acropetal polarity, manifested in the counts of receivers, was reflected also in these counts from the tissue slices. At 3 hours the slices that were touching the donors showed little difference in counts between acropetal and basipetal transport sections, but there was a sizeable difference in counts at the opposite, receiver, end of the transport section. With 122:11 as the ratio of counts from the latter acropetal:basipetal slices, the counts from the corresponding 3 hour receivers was 35:3. Obviously, at that early period of ^{14}C movement into the receiver blocks, the counts from the immediately adjacent tissue slice gave essentially the same measure of polarity as did the receivers. But by 6 hours the slices touching the receivers gave 387:21 for the acropetal:basipetal counts. This ratio of 18:1 indicated a weaker polarity of auxin movement than that based on counts of the receivers (33:1 at 6 hr). There are 2 obvious reasons why counts from tissue slices would suggest weaker polarity: 1) although counts from receivers show chromatographically pure auxin (15), counts from transport tissue would be expected to show other metabolites, too (1, 34); 2) the polarity of auxin movement as measured by counts in receivers is progressively less in the shorter sections (6), hence the tissue slices would be expected to indicate less polarity than would the receiver blocks adjacent to them but still somewhat farther from the donors. As figure 2 shows, the use of slices of tissue that represented an even larger percentage of the section-length than one-fifth would suggest even less polarity. (Bonnett and Torrey counted the upper half or upper third of their transport sections.)

The changing distribution of counts along the transport section is of interest, particularly in comparison with the somewhat similar investigation of basipetal movement made by Goldsmith and Thimann in the *Avena* coleoptile (their fig 7–8, 8). They reported that ^{14}C from IAA showed a logarithmic distribution in 20-mm sections of the coleoptile, starting at 1 hour and lasting to 12 hours. "Some departure from the logarithmic distribution is often noted at the base of the section, where a low level of activity somewhat greater than predicted by extrapolation of the logarithmic curve may appear", they noted. This can be seen in the most basal determination of their figure 7, but not in their figure 8. Our ^{14}C distribution data for acropetal movement in roots provide evidence for a similar logarithmic decrease in the 3 basal slices (the 3 mm closest to the donors), the slope of the line also remaining quite stable as the absolute values increase with time. By contrast, the most apical 2 slices—those farthest from the donors—showed a striking change from logarithmic linearity (fig 2). These counts increased more and more above the logarithmic relation, with the counts in the most apical 1-mm slice even increasing over those in the adjacent slice that was nearer to the donor. This seems much more extreme than the change from logarithmic relation found in *Avena*. However, Goldsmith and Thimann were cutting up their coleoptiles into slices 4 + mm long, in contrast to our 1 mm slices. If one applied the greater discrimination of 1 mm slices to the coleoptile also, the "somewhat greater" level "often" noted in basal slices 4 to 8 mm long might turn out to be an averaging of a process much more like that shown in our figure 2. (This experiment was run twice, once in dim green light.)

The data for ^{14}C distribution from IAA-^{14}C applied in the opposite, basipetal, direction do not provide strong evidence for this "upward" trend at the end opposite the donor (fig 2). The sample size was smaller, in this experiment, for the "basipetal slices" than for the acropetal ones, hence, the less regular pattern for basipetal slices probably was due partly to less adequate sampling. But it looks as if the decline in counts was logarithmic for the apical 3 slices (as it was for movement in the opposite direction) and that the most basal 2 slices showed some of the increase over logarithmic linearity that was so striking for acropetal move-

ment. (Counts of "basipetal slices" of *Lens* was run only once.)

To see if the ^{14}C in the apical receivers was still with IAA, 25 apical receiver blocks from *Lens* roots were collected at 4 hours and extracted 3 times with ethanol. The reduced extract was spotted on paper chromatograms and run with isopropanol-ammonia-water solvent. Counts of the various zones of the chromatograms showed only 1 peak, which was at the R_F zone to which IAA-^{14}C runs. The receiver blocks were counted after being extracted and showed only 2% of their original counts. A repeat of the experiment gave similar results.

Phaseolus *Roots*. To compare *Lens* with bean, sections were cut at the same distance from the root-tip of *Phaseolus* and were treated in the same way with donor and receiver blocks. The time-course revealed a clear and strong acropetal polarity (fig 3). At 8 hours the acropetal values were significantly larger than the basipetal ones by the 't' test. A secondary decline in net counts in acropetal receivers occurred between 8 and 10 hours, recalling the similar declines of still longer transports in *Phaseolus* petioles and *Coleus* stems (21, 23). The counts in the 2 types of donors showed the expected sizeable divergence once the acropetally polar movement into the receivers was well established.

A repetition of the 4 to 10 hour portion of this experiment gave qualitatively similar results, although the maximum value for acropetal movement and its subsequent decline occurred at 6 and 8 hours, respectively (rather than at 8 and 10 hrs).[5]

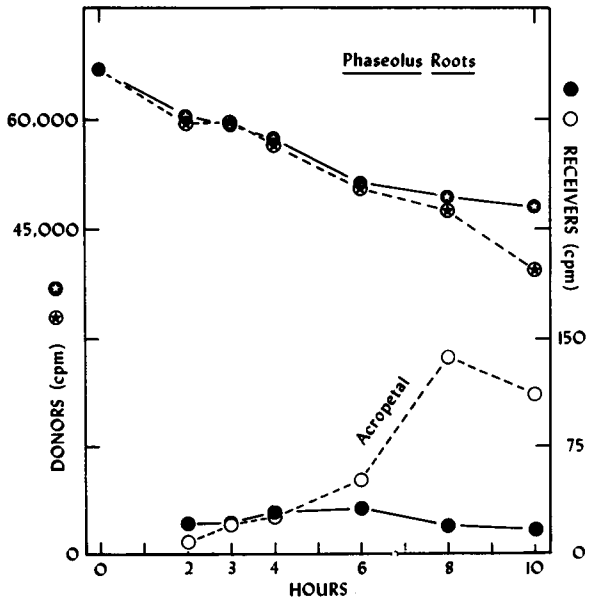

FIG. 3. The time course of movement of ^{14}C from indoleacetic acid supplied acropetally or basipetally to *Phaseolus* root segments. At the top of the figure are counts in donors (legend on left), at the bottom are counts in receivers (legend on right). (3 blocks per vial.)

During the first 2 to 3 hours of transport tests with sections from bean roots, we found evidence in 3 of the 6 experiments of a transitory stage of weak basipetal polarity. Evidence came from counts of both donor and receiver blocks, as well as counts of tissue-slices. This transient change in polarity is probably similar to the temporary reversal of polarity of movement of calcium and strontium induced in roots by wounding (33).

Conclusions

If sufficiently pure IAA is used, there is strongly acropetal polar movement of IAA-^{14}C through sections cut from the growing region of *Lens* and *Phaseolus* roots and into agar receiving blocks. The amount moved acropetally is so small, however, relative to the amount added in the donor blocks that an unusually sensitive detection system is required. The amount moving acropetally is a whole order of magnitude lower than found for shoot structures, using the same techniques. A transient period of basipetal polarity was often seen in *Phaseolus* roots in the first few hours after sectioning. This phenomenon is probably the cause of some difficulties experienced by earlier investigators of the auxin physiology of roots (*cf.* fig 20 of 7). It may explain the basipetal polarity reported for *Zea* roots after 1.5 hours of transport (10). Earlier experiments on the effects of excising the root tip on geotropism or on root-elongation should be reconsidered with the possibility of this transient shift in polarity being kept in mind. In other respects (such as velocity, linearity, net-loss from donors, chromatographic purity of the labeled material in the receivers), acropetal movement in roots showed very similar properties to the basipetal movement in shoots of which it is a logical extension.

If these results with isolated sections are applicable to the intact plant, auxin normally moves down the root axis toward the root tip. Such a conclusion fits various earlier findings: 1) Simon's neglected observation that xylem regeneration in roots is acropetal (29); 2) the acropetal development of cambial activity in intact roots (*e.g.*, 4);

[5] Such a secondary decline in counts in the acropetal receivers was also seen in our only *Lens* experiment run for 8 hours, as well as at 6 hours in the only *Lens* test that we ran completely in dim green light. [Pilet, all of whose tests were run in "dim green light", reported no such loss of counts through 16 hours (his table III, 26). Data from our experiment in green light did confirm his report that the slope of the line for counts in apical receivers was different enough from that shown in our dark-run experiment of figure 1 so that it looked as if it would intersect the time-axis at or near to zero.]

and 3) Camus' descriptions of the acropetal polarity of vascular differentiation in cultured pieces of root under the influence of grafted buds (5). Bonnett and Torrey (3) cited evidence for believing that acropetally moving auxin was the explanation for the polar regeneration of roots which they observed in their cultured root sections. (Their evidence would make even more sense if auxin movement were as strongly polar in their roots as it is in ours. It probably is. As shown by our comparison, counts of tissue slices give less apparent polarity than counts of receiver blocks.)

What could be the source of acropetally moving auxin in the roots of intact plants? It is unlikely that such auxin is merely from the downward moving stream of auxin that the shoot produces, because—judging by results with sections—there is a graded decrease in the amount transported down the bean hypocotyl to the point where little or none moves through sections from the stem-root transition region (11, 30). The point needs investigating, particularly with a critical appraisal of how accurately the results with sections apply to the intact plant.

Acknowledgments

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