Plant Physiol. (1969) 44, 1277–1284

Movement and Metabolism of Kinetin-^{14}C and of Adenine-^{14}C in Coleus Petiole Segments of Increasing Age[1]

Henk Veen[2] and William P. Jacobs
Department of Biology, Princeton University, Princeton, New Jersey 08540

Received November 12, 1968.

Abstract. **To see if polar movement was typical of growth-regulators other than auxins, the movement of adenine-8-^{14}C and of kinetin-8-^{14}C was studied in segments cut from petioles of increasing age. No polarity was found. In time-course experiments lasting 24 hr, kinetin showed a progressive increase of radioactivity in receiver blocks, while adenine showed a maximum at 8 hr with a decline thereafter. More kinetin moved through older segments than through younger ones. There was no difference in net loss as far as the position of the donor block is concerned. However, the loss of radioactivity from adenine donor blocks was much higher than the loss of radioactivity from kinetin donor blocks.**

The radioactivity in receiver blocks after 24 hr treatment with kinetin-^{14}C was still with kinetin, judging by location on chromatograms. By the same criterion, adenine and a smaller amount of some other compound were in receiver blocks after a 6 hr transport with adenine-^{14}C in the donors. By contrast, more zones of radioactivity were extracted from petiole segments to which kinetin or adenine had been added. For both purine derivatives the original compound represented no more than 20% of the total radioactivity extracted from the tissue after a transport period of 24 hr.

Polarity is a widespread phenomenon in the development of higher organisms. In vascular plants many manifestations of polarity can be explained as due to the action of polarly moving auxin (11). It is of obvious importance to discover if polar movement is limited to auxins, as was believed for many years (11). One might expect from analogy with the active transport systems studied in cell biology (32) that polar movement would be of more general occurrence among plant hormones.

As part of a broad program to investigate polarity in relation to movement of plant growth substances, we have been comparing the movement of various substances in the same system, namely, excised petiolar segments. Contrary to expectations from experiments run on different systems, we found that 2,4-D moves with a polarity similar to that of IAA (20). A close relation between auxin activity and polarity was found with 2,4,5-trichlorophenoxyacetic acid: shifting 1 chlorine atom, which caused the loss of most auxin activity, also caused the loss of most polarity of movement (12, 13).

The polar movement of abscisic acid has been reported recently (7). The 2 other classes of plant growth-substances that should be investigated are obviously the gibberellins and the cytokinins. Transport studies on gibberellic acid have been going on here for several years and will be published soon. The present paper reports on the movement of adenine and kinetin in the same system of aging petioles that we have used for our auxin and gibberellic acid studies. Adenine and kinetin were selected because: 1) they are analogous to the IAA and 2,4-D already studied in being endogenous and exogenous, respectively, and in showing a many-fold difference in activity; 2) they were both available with adequate specific activity from commercial sources; and 3) the literature on their movement is contradictory and confusing, as reviewed below.

Adenine was first shown to promote leaf-growth by D. Bonner and Haagen Smit (3). Skoog and Tsui (30) demonstrated what we would now call the real but relatively weak cytokinin effect of adenine on bud regeneration in sterile culture. No detectable movement of adenine through excised segments was found, even when high concentrations were added in donor blocks (2, 18). But small amounts of radioactivity, not running to the R_F of the adenine-^{14}C added in the donors, were found after 23 hr in the receiving blocks: more of this radioactivity was in the basal receivers (2).

[1] Research supported by United States Army grant to W. P. Jacobs and by funds provided by the Eugene Higgins Trust Fund and facilities made available by the Whitehall and John A. Hartford Foundations to the Department of Biology, Princeton University.

[2] Present address: Centre for Plant Physiological Research, Bornsesteeg 47, Wageningen, The Netherlands.

After Skoog and his co-workers isolated kinetin from autoclaved herring sperm DNA, it was soon discovered that kinetin acts like a "highly effective adenine" as does benzyladenine (22). Both these cytokinins have been tested for movement through excised segments, but with conflicting results. Osborne and co-workers noticed a basipetally polar movement of benzyladenine-^{14}C through *Phaseolus* petiole segments, and reported that "most, possibly all," of the ^{14}C found in receiver blocks was still with benzyladenine (2, 25). Fox and Weis (8), using longer counting times, a more sensitive counting system, and benzyladenine of higher specific activity, found movement in both directions but with no polarity in 4 species, including *Phaseolus* petioles. In every instance Fox and Weis found in the receiver blocks ^{14}C that ran to R_F-values other than that typical of benzyladenine. The percentage of ^{14}C in other zones was as much as 40 % of the radioactivity in the receiver blocks. Non-polar movement of benzyladenine was indicated by the low but essentially equal counts found in receivers on segments cut from *Lens* stems (28). In answer to Fox and Weis, Osborne and McCready reaffirmed the polar movement through *Phaseolus* petioles of ^{14}C from labeled benzyladenine (26), but *Xanthium* petioles showed very low counts in the receivers with no clear evidence of polarity. Using the same variety of *Pisum sativum* that Fox and Weis had used, they reported more counts in the basal receivers. Their *Pisum* data, however, show such low counts in both receivers that it is difficult to judge the validity of the differences in the absence of statistical tests of significance.

The idea that kinetin is relatively immobile in the plant came from results of kinetin application to the non-veinal part of leaf blades (16, 23) and to abscission explants (4–6, 9, 27). The only paper we could find on the movement of kinetin-^{14}C through petiole segments reported no detectable movement of radioactivity with cotton, non-polar movement with *Xanthium* and young *Phaseolus* petioles, and polar movement through petiole segments of old *Phaseolus* leaves (15). Although the radioactivity extracted from the receiver blocks could not be correlated with the R_F-value of kinetin-^{14}C because the activity was too low to give any response with a Geiger-tube scanner, the authors reported that "weak but positive" cytokinin activity was extracted from the 24-hr receiver blocks.

Materials and Methods

All material originated from the Princeton clone of *Coleus blumei* Benth., vegetatively propagated throughout the years. The plants were grown in the greenhouse under continuous light and were selected for uniformity by length of the number 2 leaf blade (the most recently formed leaf that was between 60 and 100 mm). Experiments were conducted using petiole numbers 3, 4, 7, and 8. Number 8 petioles were almost ready to abscise at the time of the experiment. Plants were assigned to the treatments within an experiment in a mathematically random manner.

Adenine-8-^{14}C was purchased from New England Nuclear Corporation, with a specific activity of 5.0 mc/mM. Kinetin-8-^{14}C was purchased from CalBioChem, with a specific activity of 10.0 mc/mM. A chromatographical analysis showed that 97 % of the total radioactivity was recovered on 1 spot in the case of adenine-^{14}C, the R_F-value of which was identical with adenine ("cold adenine", purchased from E. Merck, A. G.). In the case of kinetin-^{14}C, 82 % of the total radioactivity on the chromatogram was recovered on 1 spot, the R_F-value of which was identical with "cold kinetin" (from CalBioChem). This analysis was done on thin-layer plates of silica gel G (solvent system: distilled water). Stock solutions of these compounds were made with water and stored in the refrigerator. Kinetin was used at a concentration of 92 μM in the donor blocks, adenine at a concentration of 119 μM.

The experimental procedure during the transport experiments was similar to that developed by McCready (19). Segments were cut, 5 mm long, one from each petiole of a leaf-pair. The radioactive compound was applied in a donor block of agar gel to one end of the petiole segment, and the movement of the compound into a receiver block applied to the other end was estimated by assaying the radioactivity accumulated in it. From each pair of segments one was randomly assigned to basipetal movement, the other for acropetal. Donor, as well as receiver blocks, were assayed at the end of an experiment to be able to express the transport as a percentage of the amount lost by the donor blocks in the same period. Therefore fresh donor blocks which had not been in contact with petiole segments were also assayed.

All determinations of radioactivity were made with a liquid scintillation counter. Each donor and receiver block was counted in a separate vial containing 15 ml of fluid containing 25 % ethanol in Toluene-PPO-POPOP (24) for 10 min. As described earlier (34) identification of the radioactivity in donor and in receiver blocks as well as in tissue extracts was done by a combination of thin-layer chromatography, autoradiography and liquid scintillation counting. Immediately after the transport experiments, donor and receiver blocks were collected in small vials and stored in the refrigerator. Tissue segments were frozen in dry ice and stored at $-20°$. Subsequently blocks and tissue segments were extracted in 2 ml ethanol (95–99 %) at room temperature for 48 hr. According to Fox and Weis (8) the recovery of ^{14}C in *Coleus* was complete using this extraction technique. The ethanol extract was reduced in volume in a vacuum-oven and spotted on thin-layer chromatograms.

Thin-layer chromatography was done on cellulose plates impregnated with polyethyleneimine and supplied with a fluorescent compound. Before the samples were spotted, the plates were given a wash with distilled water. A 0.9 M NaCl solution was used as a solvent system. Such an anion-exchanger layer is especially suitable for the separation of nucleic acid derivatives (29). After development the chromatograms were covered with a "Saran Wrap" plastic sheet to avoid chemical reactions on the film plate. A Kodak medical X-ray film was then placed against the chromatogram for about 2 weeks. After developing the film, places on the chromatogram that had given blackening on the film were marked and the cellulose from each area was scraped off the glass and transferred to a counting vial. The scrapings then were suspended in 2 ml ethanol (50 % v/v) and after 24 hr a dioxane-naphthalene scintillation fluid (33) was added.

The total amount of radioactivity present in the tissue extracts was measured by taking aliquots and counting them in the liquid scintillation spectrometer. Quenching by chlorophyll was corrected for by the use of an external standard.

Statistical methods for 't'-tests and linear regression calculations follow Snedecor (31). Each experiment was run 2 or 3 times unless otherwise specified.

Results

The average cpm in the receiver and donor blocks at various hours after kinetin-^{14}C or adenine-^{14}C was added to the petiolar segments are shown for a typical experiment in table I.

There was no sign of polarity of movement of either kinetin or adenine: for any 1 collection hr, the counts in the basal receivers for 1 substance were not significantly different from those in the corresponding apical receivers. A striking contrast between kinetin and adenine was apparent in the time-course. Kinetin treatment resulted in a steady increase of radioactivity in the receiver blocks, whereas adenine reached a maximum at 8 hr and declined thereafter. This is especially clear-cut with older petioles. (The value in table I for kinetin basipetally moving through petiole number 3 at 12 hr is not significantly different from that at 8 hr, and such an apparent decline was not found in the other repeats of this experiment.)

Significantly more kinetin movement was found through older than through younger petiole sections, judging by counts in receivers (table I). Because there are big differences in cross-sectional area between younger and older petioles, differences may be expected in net loss from donor blocks on petioles of different ages. To correct for this, as well as for the different specific activities, concentrations, and absorption of the 2 cytokinins, the radioactivity in receiver blocks is presented in Fig. 1 as a percentage of the net loss from donor blocks. The greater movement of kinetin through older than through younger petioles is here accentuated, and shown to be not merely the result of greater uptake from the donors.

To estimate the velocity of movement of kinetin, linear regressions were fitted to the data for petiole number 7 in Fig. 1. The equation for acropetal movement was: $Y = 0.334 \times -0.789$. The equation for basipetal movement was: $Y = 0.336 \times -1.18$. Because the extrapolated intercepts were not significantly different from each other, there was no evidence that the velocity was different in the 2 directions. It averaged 1.7 mm/hr.

Table I. *Time Course of Basipetal and Acropetal Movement of Kinetin-^{14}C and Adenine-^{14}C Through 5-mm Petiolar Segments Cut From Young or Old Leaves*

Values are average cpm (corrected for background) ± SE from 3 agar receiver blocks. The background averaged 24 ± 0.5 cpm based on a sample of 24. The original donors averaged 98,492 ± 987 cpm (n = 12) for kinetin and 63,715 ± 614 cpm (n = 12) for adenine.

Hr	Petiole #3 (Young)		Petiole #7 (Old)	
	Basipetal	Acropetal	Basipetal	Acropetal
		Kinetin (92 μM)		
4	75 ± 62	182 ± 119	15 ± 6	23 ± 14
8	491 ± 195	450 ± 279	347 ± 238	387 ± 266
12	348 ± 95	563 ± 117	684 ± 204	751 ± 379
24	1190 ± 265	1155 ± 322	2198 ± 118	2151 ± 256
		Adenine (119 μM)		
4	20 ± 12	24 ± 16	9[1]	39[1]
8	151 ± 29	204 ± 106	81 ± 76	67 ± 35
12	62 ± 5	63 ± 28	50 ± 19	80 ± 42
24	29 ± 6	68 ± 18	34 ± 15	26 ± 8

[1] Only 1 block of the 3 gave any counts.

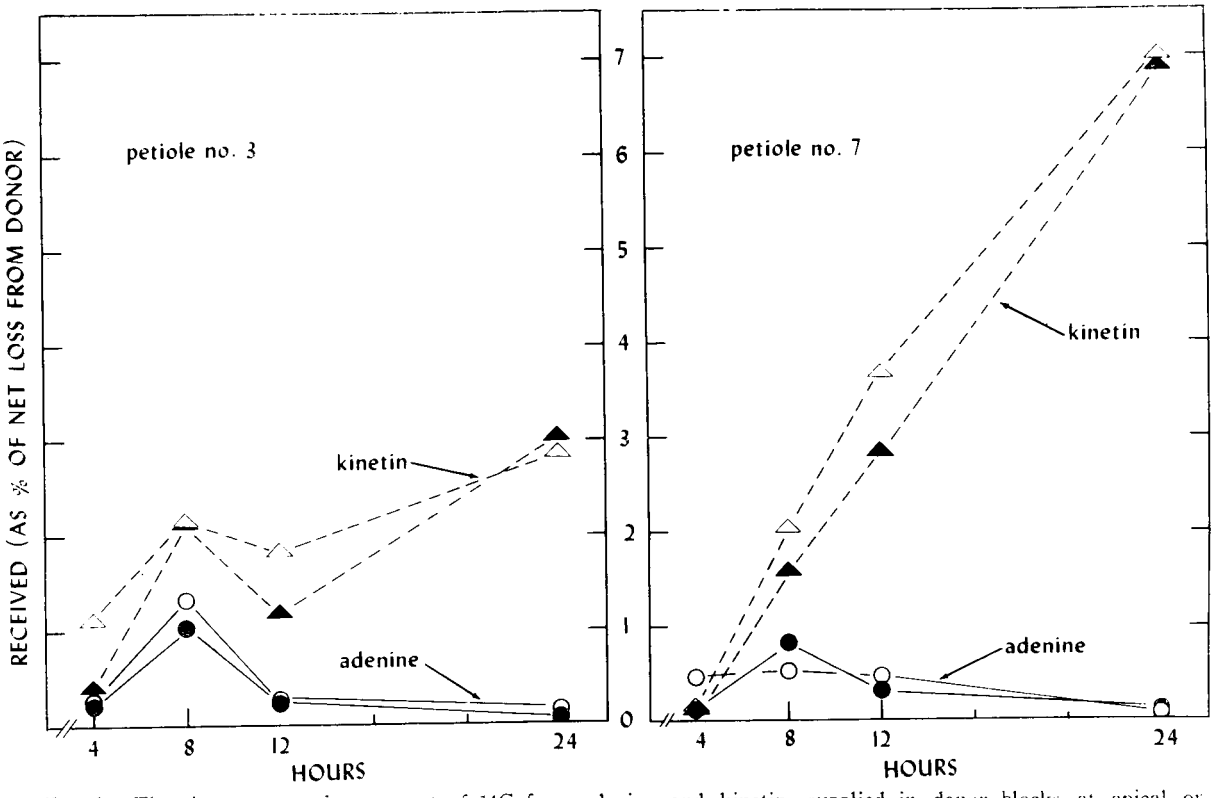

FIG. 1. The time course of movement of ^{14}C from adenine and kinetin, supplied in donor blocks at apical or basal end. Radioactivity in receiver blocks is expressed as a percentage of radioactivity lost from donor block. Based on data of table I. Adenine and kinetin were applied at an initial concentration of 119 μM and 92 μM respectively. ○——○, acropetal movement of adenine; ●——●, basipetal movement of adenine; △-----△, acropetal movement of kinetin; ▲-----▲, basipetal movement of kinetin.

The percent of the original donor gone from donor blocks was greater for adenine than for kinetin, particularly at 24 hr where the difference was highly significant (Fig. 2). This was true despite the fact that more kinetin was being moved into the receiver blocks. For either one of the compounds, net loss from basal donor blocks was the same as from apical donors at the same collection hour.

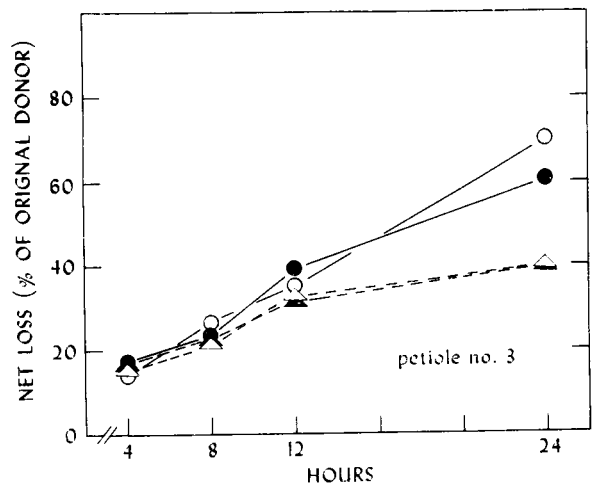

FIG. 2. The time course of loss of radioactivity from donor blocks at apical and basal ends. The net loss is presented as a percentage of the initial amount of radioactivity in donor blocks. Symbols as in Fig. 1.

The amounts of radioactivity present in the transport segments and extractable in ethanol were studied in relation to the transport period. Petiole numbers 4 and 8 were used for this study and gave similar results. The data of the experiment with petiole number 4 are plotted in Fig. 3. The amount of radioactive, ethanol-soluble material decreased with time in the adenine treatment, while the amount of ethanol-soluble material in the kinetin treatment remained nearly constant.

The identity of the radioactivity in receiver blocks was investigated by thin-layer chromatography. After adding kinetin for 24 hr, only kinetin could be identified in the 2 types of receiver blocks on petiole number 7, judging by the R_F-value (Fig. 4). An experiment with petiole number 3 gave the same result. After 24 hr of adenine treatment, the total amount of radioactivity in the receiver blocks was too small to give significant peaks on the chromatograms after extraction. However, in 1 experiment we extracted receivers after only a 6 hr transport period with adenine in the donor blocks; the TLC showed 2 zones with sizeable amounts of radioactivity.

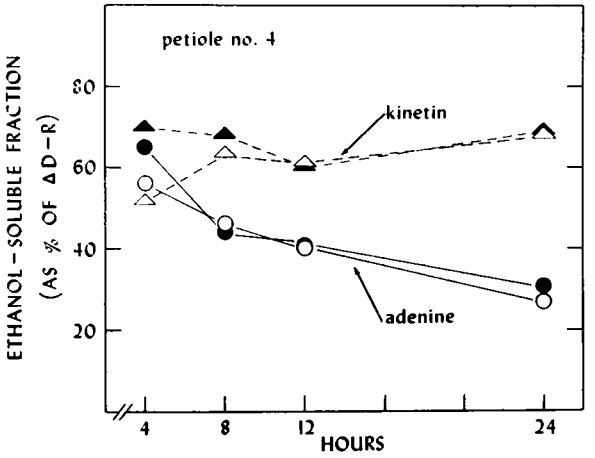

FIG. 3. The amounts of ethanol-extractable radioactivity present in petiole sections in transport experiments as a percentage of what has been lost by the donor block (ΔD) minus the radioactivity found in receiver blocks. Symbols as in Fig. 1.

the more active one having the same R_F as adenine (Fig. 5).

The same procedure was used to investigate the identity of the radioactivity in the ethanol-extract of the plant segments. In Fig. 6 the radioactivity is presented as a percentage of the total activity on the chromatogram, in relation to different R_F-values. Even extracts after 4 hr showed numerous zones of radioactivity, indicating that both compounds were quickly converted. For both compounds the original compound represented no more than 20 % of the total activity. A small shift of the R_F-value of adenine to lower values was observed if adenine was spotted on the thin-layer together with a plant extract. Thereby, the R_F-value of adenine in the extract did not correspond completely with the R_F-value of adenine from the stock solution.

Discussion

Polar transport of auxin is generally thought to involve a transport mechanism specific to auxin-

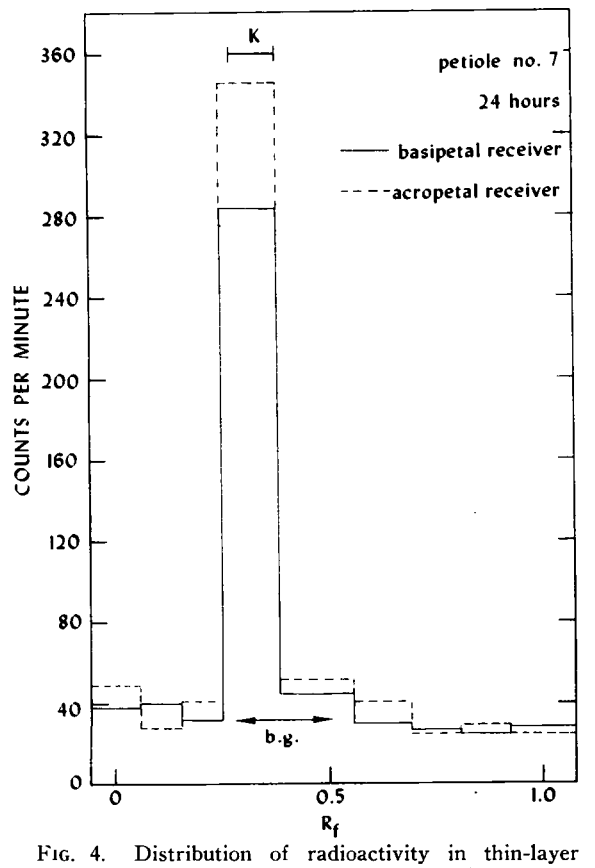

FIG. 4. Distribution of radioactivity in thin-layer chromatogram of extracts of receiver blocks from transport experiments in basipetal and acropetal direction, in which kinetin-^{14}C was supplied in the donor blocks. The R_F-value of kinetin is indicated in the upper part of the figure. Transport period: 24 hr. Background not subtracted.

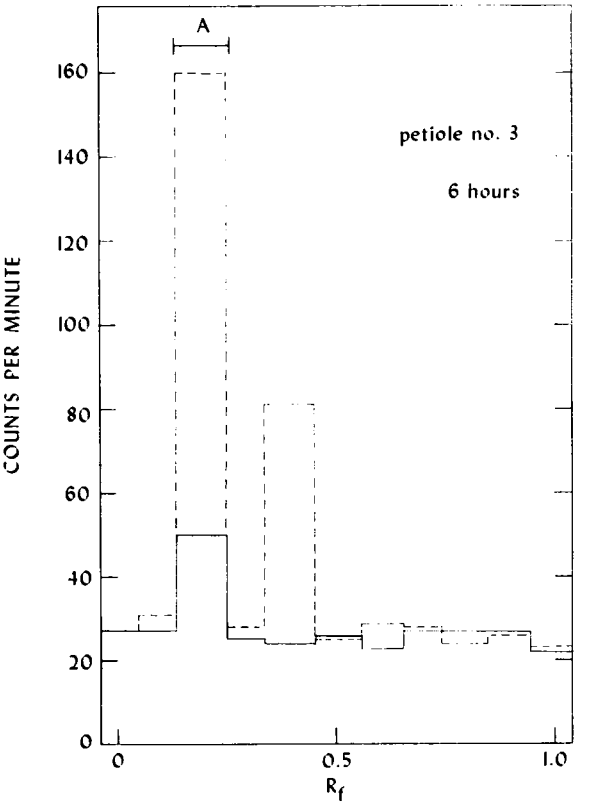

FIG. 5. Distribution of radioactivity in thin-layer chromatogram of extracts of receiver blocks from transport experiments in basipetal and acropetal direction, in which adenine-^{14}C was supplied in the donor blocks. The R_F-value of adenine is indicated in the upper part of the figure. Transport period: 6 hr. Background not subtracted. A smaller aliquot was used for the chromatogram of basipetal receivers (solid line) than for the acropetal ones (dashed line).

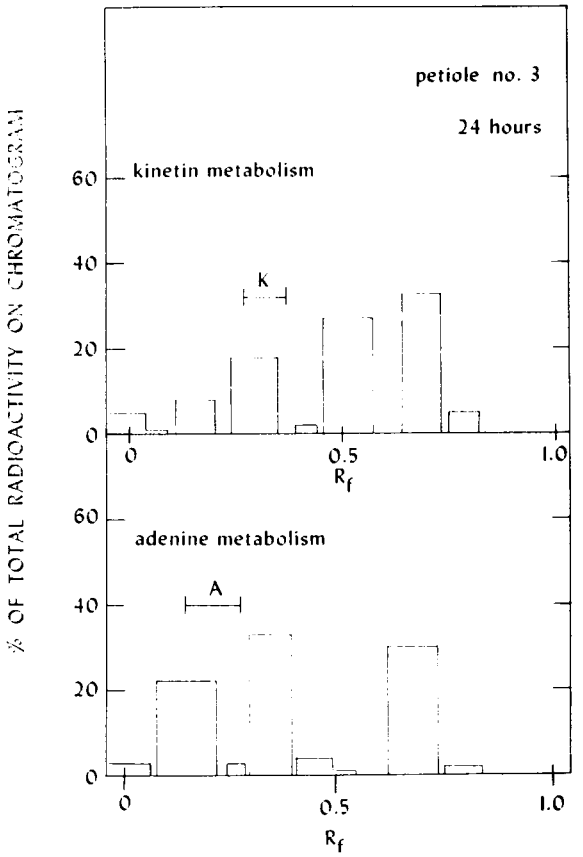

FIG. 6. Distribution of radioactivity in a thin-layer chromatogram of tissue extracts made from sections used for transport experiments with adenine and kinetin in donor blocks. The data of petiole number 3 are shown after a transport period of 24 hr. The radioactivity is presented as a percentage of the total radioactivity present on the chromatogram. Total corrected cpm were 3926 for kinetin, 2393 for adenine.

(17). The question is still open as to whether other growth-regulators will move with polarity or will compete with auxin in the same system (13).

We found that the movement of adenine and kinetin through *Coleus* petiole segments was non-polar whether the segments were cut from younger or older leaves (Fig. 1). More kinetin moved through segments from old than from young petioles [confirming the impression from earlier data (15) that were not corrected for different amounts of uptake]. Time-course experiments revealed that kinetin continued to increase in the receiver blocks up to 24 hr (the longest period observed), whereas radioactivity from adenine-^{14}C reached a maximum at 8 hr and declined thereafter. This parallels the results obtained under similar conditions with 2,4-D and IAA, respectively (12, 20, 24): for both the auxins and the cytokinins the net movement into receivers of the non-endogenous substances 2,4-D and kinetin continued steadily through 24 hr, while the endogenous substances IAA and adenine showed a decline after 8 to 12 hr. There was also a parallel in the time-course of the net loss from donor blocks, with the endogenous substances showing more net loss than the exogenous ones (20, and Fig. 2).

Even the maxima observed in the receiver blocks when 2,4-D or kinetin were added to the donor blocks were very close, being 7 % of the net loss of kinetin from the donor blocks at 24 hr and 8 % for 2,4-D. This comparison may be complicated by the higher concentration of kinetin than 2,4-D in the donor blocks because it has been a frequent observation with auxin movement that a smaller percentage of the added auxin is transported as the donor concentration is increased—*e.g.*, p. 32 of (20).

The velocity of movement of kinetin in older petiole number 7 calculated from extrapolated linear regressions was 1.7 mm/hr. No significant differences were found between the velocity of basipetal or acropetal movement, agreeing with data on IAA movement through old bean petioles (Fig. 15 of 12). The velocity with which kinetin moved was similar to that found for 2,4-D (14) and benzyladenine (2), and slower than that for IAA (12, 20). The same chromatographic purity found with transported auxins in receiver blocks (12) has been found here for kinetin movement also (Fig. 4).

In short, the 2 growth-regulators, kinetin and 2,4-D, move through petiolar segments with similar kinetics. The most striking difference is that the movement of kinetin is non-polar even through segments from young petioles, whereas 2,4-D movement is strongly polar in young petioles but progressively less so in older ones [table II of (21)].

Adenine-^{14}C added to petiolar sections gave results contrasting strongly with those from kinetin. In addition to the greater net loss from adenine donors and the earlier occurrence of maximum counts in the receivers, less of the absorbed adenine moved into the receivers (Fig. 1). Also, adenine was unique among the growth-regulators studied by us in showing a sizeable amount of radioactivity extracted from receivers running to another R_F than that typical of the donor growth-regulator (Fig. 5). Benzyladenine was reported to show such results in one of the earlier conflicting reports (8). The lack of any detectable adenine in extracts of receivers taken from bean petioles after 23 hr (2) seems likely to have been due to a secondary decline in counts such as we have observed with *Coleus* petioles (table I, Fig. 1).

The most likely hypothesis to explain the secondary decline of radioactivity in the receiver blocks when adenine-^{14}C is added to the donor blocks is that part of the radioactivity in receiver blocks is taken up again into the tissue because of a more intense metabolism of the adenine than of kinetin. The greater net loss of radioactivity from adenine donor blocks than from kinetin donor blocks can be explained in the same way. Evidence for this hypothesis is that more of the added adenine than of the

kinetin is incorporated into ethanol insoluble material (Fig. 3).

Another exogenous growth regulator, naphthaleneacetic acid (NAA) showed a time-course like that of IAA (10). A fast metabolic turnover of NAA was found, and it was suggested that this was the primary cause of the retention of the radioactivity in the segment (33). Andreae (1) showed that 2,4-D is not metabolized in pea roots within the first 24 hr; conversely, IAA and NAA showed a quick turnover in metabolic products. This difference was reflected in the transport of these compounds (12, 20, 34). The close resemblance in time course experiments among adenine, IAA and NAA, and between kinetin and 2,4-D, respectively, supports the opinion that a close relationship exists between the movement and metabolism of growth regulators (34). Further evidence for this view was found by comparing IAA movement and metabolism in young and old petioles (35).

One last difference between the auxins and these cytokinins in their movement through petiolar sections is the greater variability of the cytokinin data. As table I shows, the coefficient of variation is as much as 50 % for kinetin or adenine. For auxins it is more typically 10 %. Comparison of the records revealed that much of this extra variance was from responses of individual plants. If a given plant of the sample of 3 showed greater basipetal movement through 1 of its petioles, it would almost always show greater acropetal movement through the other sister petiole. Lagerstedt and Langston (15) in their study of kinetin movement reported "great variability," too, although the absence of variance data in their paper prevents us from knowing its exact size. Some hint comes from the fact that a mean cpm of 199 was not significantly different from 1 of 476 (their table III). If we found this much variance using our clonal stock, other workers might reasonably expect even greater variance from pooling data from non-clonal plants.

Acknowledgment

The authors are indebted to Miss Susan C. Kirk for technical assistance.

Literature Cited

1. Andreae, W. A. 1967. Uptake and metabolism of indoleacetic acid, naphthaleneacetic acid, and 2,4-dichlorophenoxyacetic acid by pea root segments in relation to growth inhibition during and after auxin application. Can. J. Botany 45: 737–53.
2. Black, M. and D. J. Osborne. 1965. Polarity of transport of benzyladenine, adenine and indole-3-acetic acid in petiole segments of *Phaseolus vulgaris*. Plant Physiol. 40: 676–80.
3. Bonner D. M. and A. J. Haagen Smit. 1939. Leaf growth factors. II. The activity of pure substances in leaf growth. Proc. Natl. Acad. Sci. 25: 184–88.
4. Burrows, W. J. and D. J. Carr. 1967. Studies on the abscission of blue lupin leaves. II. Effects of kinetin and light on pulvinar and other types of explants. Planta 73: 369–75.
5. Carr, D. J. and W. J. Burrows. 1967. Studies on leaflet abscission of blue lupin leaves. I. Interaction of leaf age, kinetin and light. Planta 73: 357–68.
6. Chatterjee, S. K. and A. C. Leopold. 1964. Kinetin and gibberellin actions on abscission processes. Plant Physiol 39: 334–37.
7. Dörffling, K. and M. Böttger. 1968. Transport von Abscisinsäure in Explantaten, Blattstiel- und Internodialsegmenten von *Coleus rhenaltianus*. Planta 80: 299–308.
8. Fox, J. E. and J. E. Weis. 1965. Transport of the kinin N_6-benzyladenine: nonpolar or polar? Nature 206: 678–79.
9. Gorter, C. J. 1964. Studies on abscission in explants of *Coleus*. Physiol. Plantarum 17: 331–45.
10. Gorter, C. J. and H. Veen. 1966. Auxin transport in explants of *Coleus*. Plant Physiol. 41: 83–86.
11. Jacobs, W. P. 1961. The polar movement of auxin in the shoots of higher plants: its occurrence and physiological significance. In: Plant Growth Regulation. R. M. Klein, ed. Iowa State University Press, Ames, Iowa. p 397–409.
12. Jacobs, W. P. 1967. Comparison of the movement and vascular differentiation effects of the endogenous auxin and of phenoxyacetic weedkillers in stems and petioles of *Coleus* and *Phaseolus*. Ann. N. Y. Acad. Sci. 144: 102–17.
13. Jacobs, W. P. 1968. Hormonal regulation of leaf abscission. Plant Physiol. 43: 1480–95.
14. Jacobs, W. P., C. C. McCready, and D. J. Osborne. 1966. Transport of the auxin 2,4-dichlorophenoxyacetic acid through abscission zones, pulvini, and petioles of *Phaseolus vulgaris*. Plant Physiol. 41: 725–30.
15. Lagerstedt, H. B. and R. G. Langston 1966. Transport of kinetin-8-^{14}C in petioles. Physiol. Plantarum 19: 734–40.
16. Lagerstedt, H. B. and R. G. Langston. 1967. Translocation of radioactive kinetin. Plant Physiol. 42: 611–22.
17. Leopold, A. C. 1964. The polarity of auxin transport. Brookhaven Symp. Biol. 16: 218–33.
18. Libbert, E. and B. Kanter. 1966. Auxineinflüsse auf polare Erscheinungen bei Aufnahme, Transport and Metabolismus von Adenin in Hypocotylsegmenten von *Helianthus annuus*. Flora 157: 51–67.
19. McCready, C. C. 1963. Movement of growth regulators in plants. I. Polar transport of 2,4-dichlorophenoxyacetic acid in segments from the petioles of *Phaseolus vulgaris*. New Phytologist 62: 3–18.
20. McCready, C. C. and W. P. Jacobs. 1963. Movement of growth regulators in plants. II. Polar transport of radioactivity from indoleacetic acid-(^{14}C) and 2,4-dichlorophenoxyacetic acid-(^{14}C) in petioles of *Phaseolus vulgaris*. New Phytologist 62: 19–34

21. McCready, C. C. and W. P. Jacobs. 1963b. Movement of growth regulators in plants. IV. Relationships between age, growth and polar transport in petioles of *Phaseolus vulgaris*. New Phytologist 62: 360–66.
22. Miller, C. O. 1961. Kinetin and related compounds in plant growth. Ann. Rev. Plant Physiol. 12: 395–408.
23. Mothes, K., L. Engelbrecht, and O. Kulajewa. 1959. Über die Wirkung des Kinetins auf Stickstottverteilung und Eiweisssynthese in isolierten Blättern. Flora 147: 445–64.
24. Naqvi, S. M. 1963. Transport studies with ^{14}C indoleacetic acid and ^{14}C 2,4-dichlorophenoxyacetic acid in *Coleus* stems. Ph.D. Thesis, Princeton University.
25. Osborne, D. J. and M. K. Black. 1964. Polar transport of a kinin, benzyladenine. Nature 201: 97.
26. Osborne, D. J. and C. C. McCready. 1965. Transport of the kinin, N_6-benzyladenine: nonpolar or polar? Nature 206: 679–80.
27. Osborne, D. J. and S. E. Moss. 1963. Effect of kinetin on senescence and abscission in explants of *Phaseolus vulgaris*. Nature 200: 1299–1301.
28. Pilet, P. E., J. Guern, and E. Hugon. 1967. Sur le transport de la 6-benzylaminopurine. Physiol. Végétale 5: 261–70.
29. Randerath, K. 1964. Thin-layer Chromotography. Academic Press, New York.
30. Skoog, F. and C. Tsui. 1951. Growth substances and the formation of buds in plant tissues. In: Plant Growth Substances. F. Skoog, ed. University of Wisconsin Press. p 263–85.
31. Snedecor, G. W. 1956. Statistical Methods. Iowa State College Press, Ames, Iowa.
32. Stein, W. D. 1967. The Movement of Molecules across Cell Membranes. Academic Press, New York.
33. Veen, H. 1966. Transport, immobilization and localization of naphthylacetic acid-1-^{14}C in *Coleus* explants. Acta Botan. Neerl. 15: 419–33.
34. Veen, H. 1967. On the relation between auxin transport and auxin metabolism in explants of *Coleus*. Planta 73: 281–95.
35. Veen, H. and W. P. Jacobs. 1969. Transport and metabolism of indole-3-acetic acid in *Coleus* petiole segments of increasing age. Plant Physiol. 44. In press.