Effect of Inversion on Growth and Movement of Indole-3-acetic Acid in Coleoptiles

C. H. A. Little and Mary Helen M. Goldsmith

School of Forestry and Department of Biology, Yale University, New Haven, Connecticut 06520

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Summary. The effect of a 180° displacement from the normal vertical orientation on longitudinal growth and on the acropetal and basipetal movement of 14C-IAA was investigated in Avena sativa L. and Zea mays L. coleoptile sections. Inversion inhibits growth in intact sections (apex not removed) and in decapitated sections supplied apically with donor blocks containing auxin. Under aerobic conditions, inversion inhibits basipetal auxin movement and promotes acropetal auxin movement, whereas under anaerobic conditions, it does not influence the movement of auxin in either direction. Inversion retards the basipetal movement of the peak of a 30-minute pulse of auxin in corn.

The inversion-induced inhibition of basipetal auxin movement is not explained by an effect of gravity on production, uptake, destruction, exit from sections, retention in tissue, or purely physical movement of auxin. It is concluded that inversion (a) inhibits basipetal transport, the component of auxin movement that is metabolically dependent, and as a result (b) inhibits growth and (c) promotes acropetal auxin movement.

The displacement of an elongating organ from its normal orientation with respect to gravity causes longitudinal growth to be inhibited in a wide variety of species, including Avena sativa (1, 16, 31), Phaseolus multiflorus and Helianthus annuus (16, 26), Pharbitis sp. (3), coniferous tree species (20, 21, 28), and deciduous tree species (23, 29, 30). Koningsberger (19) and Bremekamp (4) demonstrated with Avena sativa as did Lyon (22) with Torenia fournieri and Lycopersicon esculentum that rotating plants on a horizontal-axis clinostat also inhibits growth. The well-known correlation between growth rates and auxin levels suggests the possibility that the inhibition of growth arising from a change in orientation with respect to gravity is due to an inhibitory effect of gravity either on the rate of auxin production or on the rate of auxin movement in the longitudinal direction (2). The purpose of the present work was to determine the effects of inversion on longitudinal growth and on the basipetal and acropetal movement of 14C-IAA in Avena sativa and Zea mays coleoptiles.

Basipetal auxin movement in oat coleoptiles is by both diffusion and transport, whereas under our conditions, acropetal movement involves diffusion but not transport (11, 12). In oats basipetal transport is eliminated under anaerobic conditions, hence under these conditions movement in both directions occurs only by diffusion (11). Both aerobic and anaerobic experiments were performed so that the effect of inversion on basipetal auxin movement could be determined both in the presence and in the absence of the transport component.

Materials and Methods

Plant Material. Seedlings of Avena sativa L. (var. Victory) were germinated and grown in vermiculite in darkness (11). Beginning at about 50 hours, seedlings were given 6 hours exposure to red light. After 4 days, the primary leaf was removed and sections 15 mm long (unless otherwise indicated) were cut 2 mm below the apex of coleoptiles 24 to 30 mm long. In all experiments involving the measurement of growth, sections were taken from coleoptiles whose lengths varied by less than 3 mm.

Etiolated coleoptiles of Zea mays L. (var. Barbecue) were grown in vermiculite as described previously (15). After 6 days, the primary leaves were removed, and 20 mm sections were cut 2 mm below the tip of coleoptiles 35 to 55 mm long.

Indole-3-acetic Acid. Both 14C-carboxyl-labeled IAA (New England Nuclear Corporation) and unlabeled IAA (Hoffman-LaRoche) were used. The 14C-IAA had a specific activity of 13.5 c/mole.

Donor blocks contained 10 μM IAA and in the experiments with corn 1% sucrose. Both donor and receiver blocks were made from 1.5% agar. The blocks had a volume of 60 and 36 μliter in the experiments with oats and corn, respectively.

Experimental Procedures. The classical system of donor, section, receiver was used to study the
effect of inversion on the basipetal and acropetal movement of $^{14}$C-IAA (32). Figure 1 gives the relative position of the donor and receiver blocks and the orientation of the sections in the different treatments. The adjectives apical, basal, acropetal and basipetal are used in a morphological sense.

![Diagram of setups](image)

Fig. 1. Arrangement of the setups. D = donor block; R = receiver block; A = morphological apical end of section; B = morphological basal end of section; (V) = basipetal movement in vertical (V) and inverted sections (I); (V-A) (I-A) = acropetal movement in vertical and inverted sections.

In aerobic experiments, sections and their donor and receiver blocks were threaded over fine glass rods anchored in pieces of paraffin. The glass rods were used to maintain close contact between sections and blocks throughout the translocation period. The sections were prepared and harvested under dim green light. During the period of translocation, the sections were in darkness in a chamber of high humidity.

In anaerobic experiments, the sections and their donor and receiver blocks were placed in appropriate holders in 100 ml airtight lucite chambers. The chambers were equilibrated with moist prepurified nitrogen by alternately evacuating and filling with nitrogen 5 times (11). Without opening the chamber, the sections were put in contact with their donor and receiver blocks after flushing with nitrogen for an additional 30 minutes. The orientation of the sections and the positioning of the donor and receiver blocks were the same for all sections in any particular chamber. The sections were prepared and harvested under ordinary room illumination, but during equilibration and translocation they were shielded from light by wrapping the chambers with black cloth.

At the end of both the aerobic and the anaerobic experiments, the length of the sections was measured to the nearest 0.1 mm on a micrometer scale. Each section then was cut transversely into smaller pieces with a razor-blade cutter. Unless otherwise indicated, corresponding blocks or pieces of sections from 10 different setups were pooled for counting.

Samples were counted in Bray's solution for at least 10 minutes (11) in an Alokon liquid scintillation spectrometer. All counting data were corrected for background. The efficiency of counting was 68%. The movement of radioactivity was presumed to reflect the movement of $^{14}$C-IAA, since several investigators have demonstrated that all of the radioactivity detected in receivers was recovered in the section translocation experiments is incorporated in IAA (14, 15, 17, 18, 24, 27).

An additional series of experiments was performed to investigate the effect of inversion on growth in sections from which the apex was not removed. The basal 1 to 2 mm of these 17 mm tips were pushed into 1.5% agar in small troughs. The troughs, containing 10 sections each, were placed with the sections either upright or inverted in darkness in chambers of high humidity. The final length of the sections was measured on a micrometer scale.

Results

**Effect of Inversion on Growth in Intact Sections (Apex Not Removed).** A 180° displacement from the normal vertical orientation results in a significant inhibition of longitudinal growth in sections of oats with intact apices. In 5 experiments of 24 hours duration, inversion inhibited growth an average of 30% (table I). The inverted sections respond geotropically. Twenty-four hours after the start of treatment their apices are oriented at about 30 degrees from the normal vertical position.

<table>
<thead>
<tr>
<th>Expt No</th>
<th>V*</th>
<th>Growth</th>
<th>% Inhibition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mm</td>
<td>mm</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>3.84 ± 0.42</td>
<td>4.57 ± 0.72</td>
<td>21.7</td>
</tr>
<tr>
<td>2</td>
<td>4.07 ± 0.45</td>
<td>2.50 ± 0.41</td>
<td>38.6</td>
</tr>
<tr>
<td>3</td>
<td>4.93 ± 0.58</td>
<td>3.59 ± 0.49</td>
<td>27.2</td>
</tr>
<tr>
<td>4</td>
<td>4.02 ± 0.86</td>
<td>2.52 ± 0.65</td>
<td>37.3</td>
</tr>
<tr>
<td>5</td>
<td>4.96 ± 0.42</td>
<td>3.62 ± 0.79</td>
<td>27.0</td>
</tr>
</tbody>
</table>

Mean 4.76 (A) 3.36 (B) 29.4

* Average growth for 10 sections ± 1 standard deviation.

**Effect of Inversion on Growth and Basipetal Auxin Movement in Decapitated Sections under Aerobic Conditions.** In sections supplied with exogenous auxin, inversion significantly inhibits longitudinal growth and also the absolute amount of $^{14}$C-IAA translocated into receivers. In 10 experiments with 15 mm oat sections, an average growth inhibition of 16% was associated with an average decrease of 67% in the amount of radioactivity in the receivers (table II). Inversion also inhibits both longitudinal growth and the basipetal movement of auxin into receivers for 7.5 mm oat sections and for 20 mm corn sections (table III).

Since inversion influences neither total uptake nor the relative distribution of $^{14}$C-IAA recovered in the section...
Table II. Effect of Inversion on Growth and Basipetal Auxin Movement in Decapitated Oat Sections

Sections, 15 mm long, supplied with 14C-IAA for 8 hours. V = sections oriented vertically (see fig 1); I = sections inverted; S = section; R = receiver; D = donor. Means of V and I are significantly different at the 5% level when underwritten by a different letter.

<table>
<thead>
<tr>
<th>Expt No</th>
<th>Growth</th>
<th>% Inhibition</th>
<th>cpm In R</th>
<th>% Decrease</th>
<th>cpm in V</th>
<th>S+R</th>
<th>V**</th>
<th>I**</th>
<th>cpm in R × 100</th>
<th>cpm in D at end of translocation period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>V*</td>
<td>I*</td>
<td>S+R</td>
<td></td>
<td>V**</td>
<td>I**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>mm</td>
<td>mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1.98</td>
<td>1.74</td>
<td>12.1</td>
<td>231</td>
<td>85</td>
<td>63.2</td>
<td>25138</td>
<td>22290</td>
<td>0.9</td>
<td>0.4</td>
</tr>
<tr>
<td>2</td>
<td>2.40</td>
<td>2.01</td>
<td>16.2</td>
<td>458</td>
<td>128</td>
<td>72.1</td>
<td>25902</td>
<td>23215</td>
<td>1.8</td>
<td>0.6</td>
</tr>
<tr>
<td>3</td>
<td>3.16</td>
<td>2.50</td>
<td>16.8</td>
<td>349</td>
<td>90</td>
<td>74.2</td>
<td>20820</td>
<td>23909</td>
<td>1.2</td>
<td>0.4</td>
</tr>
<tr>
<td>4</td>
<td>3.16</td>
<td>2.50</td>
<td>20.9</td>
<td>795</td>
<td>135</td>
<td>83.0</td>
<td>22099</td>
<td>20373</td>
<td>3.5</td>
<td>0.7</td>
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<tr>
<td>5</td>
<td>3.11</td>
<td>2.58</td>
<td>17.0</td>
<td>340</td>
<td>116</td>
<td>65.9</td>
<td>23491</td>
<td>26700</td>
<td>1.5</td>
<td>0.4</td>
</tr>
<tr>
<td>6</td>
<td>2.66</td>
<td>2.30</td>
<td>13.5</td>
<td>332</td>
<td>126</td>
<td>62.0</td>
<td>20767</td>
<td>23405</td>
<td>1.6</td>
<td>0.5</td>
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<td>7</td>
<td>2.99</td>
<td>2.54</td>
<td>15.0</td>
<td>260</td>
<td>137</td>
<td>47.3</td>
<td>20615</td>
<td>19910</td>
<td>1.3</td>
<td>0.7</td>
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<tr>
<td>8</td>
<td>3.03</td>
<td>2.58</td>
<td>14.9</td>
<td>344</td>
<td>126</td>
<td>63.4</td>
<td>22458</td>
<td>22493</td>
<td>1.5</td>
<td>0.6</td>
</tr>
<tr>
<td>9</td>
<td>2.17</td>
<td>2.00</td>
<td>7.8</td>
<td>596</td>
<td>162</td>
<td>72.8</td>
<td>20126</td>
<td>23228</td>
<td>3.0</td>
<td>0.7</td>
</tr>
<tr>
<td>10</td>
<td>2.62</td>
<td>1.98</td>
<td>24.4</td>
<td>292</td>
<td>102</td>
<td>65.1</td>
<td>24061</td>
<td>23348</td>
<td>1.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Mean</td>
<td>2.64</td>
<td>2.22</td>
<td>15.9</td>
<td>400</td>
<td>121</td>
<td>66.9</td>
<td>22637</td>
<td>22887</td>
<td>1.8</td>
<td>0.5</td>
</tr>
</tbody>
</table>

** Average of 10 sections.
** * Total for 10 sections.
*** Difference between means of V and I significant at 0.1% level.

Table III. Effect of Inversion on Growth and Acropetal Auxin Movement in Decapitated Oat and Corn Sections

The oat and corn sections, 7.5 and 20 mm long, respectively, were supplied with 14C-IAA for 8 hours. V = sections oriented vertically (see fig 1); I = sections inverted; S = section; R = receiver.

<table>
<thead>
<tr>
<th>Plant material</th>
<th>Expt no</th>
<th>Growth</th>
<th>% Inhibition</th>
<th>cpm in receiver</th>
<th>% Decrease</th>
<th>cpm in R × 100</th>
<th>cpm in S+R</th>
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<tbody>
<tr>
<td>Oats</td>
<td>1</td>
<td>2.27</td>
<td>2.09</td>
<td>1358</td>
<td>550</td>
<td>59.5</td>
<td>6.1</td>
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<tr>
<td></td>
<td>2</td>
<td>2.03</td>
<td>1.88</td>
<td>2067</td>
<td>627</td>
<td>69.7</td>
<td>10.0</td>
</tr>
<tr>
<td>Corn</td>
<td>1</td>
<td>5.06</td>
<td>4.31</td>
<td>6975</td>
<td>3290</td>
<td>52.8</td>
<td>14.7</td>
</tr>
</tbody>
</table>

** Average of 10 sections.
** * Total for 10 sections.

Table IV. Effect of Inversion on Growth and Basipetal and Acropetal Auxin Movement in Decapitated Oat Sections

Sections, 15 mm long, supplied with 14C-IAA for 4 or 8 hours. Experiments performed under aerobic conditions. See figure 1 for description of treatments.

<table>
<thead>
<tr>
<th>Expt No</th>
<th>Translocation period</th>
<th>IAA conc</th>
<th>Growth</th>
<th>cpm in receiver</th>
<th>I*</th>
<th>V-A*</th>
<th>I-A*</th>
<th>V</th>
<th>I*</th>
<th>V-A</th>
<th>I-A</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>hr</td>
<td>μM</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
<td>mm</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>1.98</td>
<td>1.82</td>
<td>0.27</td>
<td>0.35</td>
<td><strong>200</strong> (3.64)***</td>
<td>114 (2.26)</td>
<td>9 (0.48)</td>
<td>17 (1.29)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>2.17</td>
<td>2.00</td>
<td>0.35</td>
<td>0.71</td>
<td>298 (2.96)</td>
<td>81 (0.70)</td>
<td>19 (0.31)</td>
<td>58 (1.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>2.42</td>
<td>2.29</td>
<td>0.40</td>
<td>0.52</td>
<td>214 (0.98)</td>
<td>141 (0.70)</td>
<td>15 (0.12)</td>
<td>44 (0.47)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

** Average of 10 sections.
** * Total for 10 sections.
*** Percentage of the total uptake.
In the amounts of auxin translocated basipetally and acropetally is correlated with considerably greater growth in sections with basipetal movement (table IV).

Inversion promotes acropetal movement, in contrast to its inhibitory effect on basipetal movement (all expts, table IV; compare data for treatments V-A and I-A and for treatments V and I). Polarity of movement into receivers is reduced in inverted sections. The inversion-induced increase in acropetal auxin movement is reflected in the occurrence of somewhat greater longitudinal growth in these sections (I-A) than in vertical sections with acropetal movement (V-A, table IV).

Effect of Inversion on Growth and Basipetal and Acropetal Auxin Movement in Decapitated Sections under Anaerobic Conditions. No growth occurs and no radioactivity is detected farther than 6 mm from the source with any of the treatments (fig 4). The latter finding indicates that auxin movement is severely limited under anaerobic conditions. Since anaerobic uptake is proportional to the cross-sectional area of tissue in contact with the donor (11), acropetal uptake indicates that inversion does not directly inhibit exit from the base of the section to the receiver.

Inversion decreases the velocity of basipetal auxin movement. At the end of a translocation period of half an hour, no auxin is found in the receivers for inverted sections, whereas a significant amount is present in the receivers for control sections (fig 3A). The inhibitory effect of inversion on the flux into receivers increases with time. The rate of movement into receivers for vertical sections continues with little or no decline throughout the 8 hour experimental period, whereas after 2 hours the flux for inverted sections is about 0.14 that for vertical sections (fig 3A). Although the effect of inversion on longitudinal growth is not as great as on transport, this inhibition also tends to increase with time (fig 3B).

Effect of Inversion on Growth and Acropetal Auxin Movement in Decapitated Sections under Aerobic Conditions. Uptake is approximately twice as great from apical as from basal donors, but basipetal movement greatly exceeds acropetal movement both in the absolute cpm in receiver and in the percentage of the total uptake (table IV; compare data for treatments V-A and I-A with V and I).

Fig. 2. Effect of inversion on the amount of radioactivity translocated various distances through decapitated oat sections supplied with 14C-IAA for 8 hours. The sections, initially 15 mm long, grew approximately 3.0 mm during the translocation period. Translocation was calculated from the total radioactivity found in the section plus receiver below various distances from the donor (14). The difference of a few percent between vertical and inverted sections in the amount of radioactivity translocated each distance below the donor, although small, was observed consistently in replicated experiments. Each point on the graph is the average figure for 10 sections. O——O = Sections oriented vertically; X——X = sections inverted.

Fig. 3. Effect of inversion on basipetal auxin movement into receivers (A) and on longitudinal growth (B) in decapitated oat sections supplied with 14C-IAA. Each point on the graphs is the average figure for 2 experiments, with 10 sections in each experiment. O——O = Sections oriented vertically; •—• =
somewhat exceeds basipetal, but the distribution of auxin is similar in all treatments (fig 4). Under anaerobic conditions, inversion has no effect on either basipetal or acropetal auxin movement within the tissue.

**Effect of Inversion on the Basipetal Movement of a Pulse of 14C-IAA in Corn under Aerobic Conditions.** The pulse technique of Goldsmith (13) was adapted to study the effect of inversion on the basipetal movement of auxin. Donor blocks containing 14C-IAA were applied to the apical end of vertical 20-mm corn sections for a period of 30 minutes (treatment V, fig 1) and then replaced with 12C-IAA donors. After a further 20-minute period of translocation, one series of sections was harvested and subdivided into successive 2 mm pieces (treatment Initial, fig 5); other series were dismantled and then reassembled with half of the sections being oriented vertically and the other half being inverted (treatments V and I, respectively, fig 1). The same receiver and 12C-donor blocks were used before and after the reassembling. Translocation was allowed to proceed for an additional 30 minutes [treatments 30 mins (V) and 30 mins (I), fig 5] or 120 minutes [treatment 2 hrs (V, I), fig 5].

The peak of the radioactivity in the vertically-oriented sections is located 4 to 8 mm below the donor block at the end of the initial translocation period, and after an additional 30-minute period of translocation, the peak shifts to a point located 10 to 12 mm below the source [treatments Initial and 30 mins (V), fig 5]. The peak moves through the sections at about 8 to 12 mm/hour. Inversion retards the movement of the pulse and causes a symmetrical displacement of the entire pulse towards the donor end of the section [compare treatments 30 mins (V) and 30 mins (I), fig 5]. The difference in the location of the peak of the pulse is also observed in the inverted sections is significant at the 1% level. The data indicate that inversion slows down the movement of the peak by a few millimeters per hour.

Two hours after the initial translocation period has ended (fig 5), the amount of radioactivity in the receivers, as well as the level of activity remaining in the tissue, is similar for control and inverted sections. This indicates that inversion does not increase the retention of auxin by the tissue. Net movement into receivers is complete by 2 hours (13). At this time, nearly 40% of the activity taken up is in the receivers and the rest is distributed more or less evenly throughout the sections (fig 5).

**Discussion**

A 180° displacement from the normal vertical orientation inhibits longitudinal growth both in sections with intact apices and in decapitated sections supplied with IAA (tables I-IV). Similarly, Anker (1) demonstrated that a 90° displacement inhibits longitudinal growth in decapitated Avena sections even though the vertical and horizontal sections are supplied with the same amount of exogenous auxin. The growth inhibition is associated with a decrease in the amount of auxin appearing basipetally in the receiver (tables II-IV) and the basal end of the section (fig 2).

Under aerobic conditions, inversion not only inhibits basipetal movement but also promotes acropetal movement. In both types of movement, a greater amount of auxin is translocated through the section and into the receiver when the donor block is above the receiver block (treatments V and I-A, fig 1, table IV) than when the position of the blocks is reversed (treatments I and V-A, fig 1, table IV).
This observation introduced the possibility that the effects of inversion are artifacts that depend on the direction of passive movement with respect to gravity. For example, the movement of $^{14}$C-IAA may always be greater when the donor is above the receiver than when it is below simply because the rate of flow of extracellular water may be greater in the downward than in the upward direction. However, under anaerobic conditions, which in oat coleoptiles totally inhibit the transport component of basipetal movement (11), neither the uptake nor the distribution of auxin are affected by the position of the donor with respect to the receiver (fig 4). These results indicate that the rate of any physical movement through sections is independent of the position of the source. This would, of course, be expected for diffusion but not necessarily for flow.

Since inversion has no effect on the uptake (table II), production (6, 7, 8, 9), destruction (table II) or retention of auxin (fig 5); it apparently does not decrease the total quantity of auxin available for transport by the section. Since effects on exit of auxin from the base of the section (fig 2) and physical movement (fig 4) are also absent, the remaining possibility is that inversion affects the transport; i.e., the component of movement that requires metabolizing cells (11, 12). The following observations provide support for this conclusion: a) Inversion retards the basipetal movement of a $^{14}$C-IAA pulse, which has been shown to move via the transport system (13). b) Inversion promotes acropetal movement. Since acropetal movement is opposed by basipetal transport recycling auxin to the base (12), inversion if it inhibits basipetal transport should also promote acropetal movement. c) Anaerobic conditions simultaneously eliminate basipetal transport and the effects of inversion on both basipetal and acropetal auxin movement. Similarly Naqvi et al. (25), showed that the inhibition of basipetal movement in horizontal Zea mays sections does not occur anaerobically. d) Inversion inhibits longitudinal growth. If transport, as is probable at an exogenous concentration of 10 $\mu$m (14), departs the optimal or somewhat supranormal concentration of auxin to the section, then inversion would be expected to inhibit transport to a greater extent than growth. The finding that the inhibition of growth occurs after (fig 3) and is less than the inhibition of transport (tables II–IV) is consistent with the concept that the growth inhibition is the result of the inhibition of transport.

The literature pertaining to the effects of inversion on auxin movement contains conflicting reports. Hertel and Leopard (17, 18) found that inversion inhibited basipetal movement slightly in Zea mays but had no effect on acropetal movement. Naqvi and Gordon (24) demonstrated that inversion decreased both the intercept and the slope for the time course of basipetal auxin movement in one variety of corn, but that for another variety, inversion had no effect on these parameters unless a pretreatment of 5 hours was given. Pilefz and Barber (26) observed that inversion had no effect on either basipetal or acropetal movement in Lepus culinaris. Van der Weij (32) demonstrated that inversion slightly decreased the amount of auxin translocated basipetally into receivers in Avena. However, Pfafeltz (cf. 2) was unable to confirm this observation.

Several investigators have studied the effect of horizontal placement on auxin movement. Their results are also conflicting. In some but not all experiments with horizontal Zea mays sections, Goldsmith and Wilkins (15) found that basipetal movement decreased gradually during a translocation period of 4 hours. Gillespie and Thimm (10) and Pilet (27) concluded that horizontal placement had no effect on the quantity of auxin moved basipetally in Zea mays and Lepus culinaris, respectively. Dedolph et al. (5, 6) showed that rotation on a horizontal-axis clinostat influenced neither the movement of auxin nor longitudinal growth in Avena coleoptiles, whereas at slower speeds of rotation Lyon (22) found that both basipetal auxin movement, in Phascolus vulgaris and Brassica oleracea, and growth, in Torenia fournieri and Lycopersicon esculentum were inhibited.

Obviously, the magnitude of the effect of gravity on auxin movement in the longitudinal direction varies with different species and as clearly shown here (fig 3) becomes increasingly prominent with the length of time after displacement from the vertical. Since the typical translocation experiments are only of relatively short duration, this may explain why the effect of orientation on movement has often been small or even indetectable. The variation of the inhibition as a function of auxin concentration, length of section, and degree of inclination from the vertical has not been evaluated and this may also help account for the apparently conflicting reports.

Acknowledgments

We are grateful to Professors Arthur Galston and Joseph Gall for the use of their scintillation counters.

Literature Cited