Relationship Between Metabolism and the Lateral Transport of IAA in Corn Coleoptiles

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Abstract. The lateral movement of IAA in coleoptiles of Zea mays has been investigated under aerobic and anaerobic conditions. The IAA-1-14C was supplied asymmetrically to the apical end of the segment. The results were as follows: A) In air more 14C was found in the lower half of horizontal segments supplied with an upper donor than in the half opposite the donor in vertical segments. The enhanced lateral movement of 14C in geotropically stimulated segments of corn coleoptiles under aerobic conditions has thus been confirmed. B) This increased lateral movement of 14C in geotropically stimulated segments is greatly reduced, but is not completely abolished, under anaerobic conditions. C) The lateral movement of 14C in vertical segments is significantly less under anaerobic conditions than in air. D) Under anaerobic conditions, the lateral movement of 14C in horizontal segments can be reduced to the level found in vertical segments by pre-soaking the tissue in a 1 mM solution of the metabolic inhibitor sodium fluoride for 2 hours. The inhibitor has no effect on lateral movement of 14C in vertical anaerobic segments. E) In air, sodium fluoride has no effect on the lateral movement of 14C in either vertical or horizontal segments.

On the assumption that the movement of 14C reflects the movement of IAA, these results show that the enhanced polarized lateral movement of IAA observed in horizontal corn coleoptile segments is totally abolished only when both aerobic and anaerobic metabolism are arrested. In addition, there appears to be a small metabolically dependent component in the lateral movement of IAA in vertical segments supplied with an asymmetric donor in air.

More than 30 years ago Weber (15) and Navez and Robinson (13) established that the upward geotropic curvature of horizontal coleoptiles was due to an increase in the growth rate of the lower half of the organ and a decrease in the growth rate of the upper half. The problem of explaining the geotropic response of coleoptiles thus resolved itself into establishing the mechanism for the induction of different rates of growth of the 2 halves of the organ. In 1926 Cholodny (2) and Went (16) suggested independently that the differential growth underlying the geotropic response was due to the establishment of a lateral auxin concentration gradient across the coleoptile. The validity of this suggestion has been established experimentally in a number of investigations into the distribution of both naturally occurring auxins (3,4,13) and isotopically labeled 3-indolyl acetic acid (5,8,12) in horizontal and vertical coleoptiles. These studies have recently been reviewed by Wilkins (17). The most recent investigations have been made with coleoptiles of Zea mays and IAA-14C, and these must be briefly discussed again.

Gillespie and Thimann (5) supplied IAA-1-14C symmetrically to the apical end of horizontal Zea mays coleoptile segments in air and found that the ratio of 14C in the upper and lower halves of a split receiving block at the basal end of the segment was 30:70. The ratio of 14C in the upper and lower halves of the segment was 40:60. Virtually identical ratios were found for both the tissue and receiver blocks by Goldsmith and Wilkins (8). More recently Naqvi and Gordon (12) using symmetrical sources of IAA-2-14C at the apical end of the segment, found the ratio of 14C in the upper and lower halves of the segment to be 20:80. Since both Hertel and Leopold (9) and Naqvi and Gordon (12) have shown that IAA is the only radioactive molecule to emerge from the basal end of a Zea coleoptile segment, these experiments clearly show that IAA becomes asymmetrically distributed in geotropically stimulated corn coleoptiles. The data do not, however, provide any evidence that establishes by what mechanism the asymmetry arises. Several possibilities exist: A) lateral movement of IAA within the segment, as had been suggested by Cholodny (2) and by Went (16) in 1926, B) differential uptake, immobilization or secretion of IAA by the upper and lower halves of the horizontal segment and C) different rates of longitudinal basi-
petal movement of IAA in the upper and lower halves of the geotropically stimulated organ. Any one of these possibilities, or a combination of them, could result in an asymmetric distribution of IAA in the receiving blocks and the tissues of a horizontal segment taking up IAA from a symmetrically applied donor block.

There has been only one unequivocal demonstration that an enhanced lateral movement of IAA from the upper to the lower half does occur in horizontal coleoptiles of *Zea mays*. Goldsmith and Wilkins (8) supplied coleoptile segments at their apical ends with an asymmetric source of IAA-1-^14^C and then orientated the segments either vertically, or horizontally with the donor block in contact with the upper half. Twice as much ^14^C was found in the half segment opposite the donor block in the horizontal segments as in the vertical ones. In addition, while in vertical segments more ^14^C was recovered in the receiving block applied to the same half segment as the donor, in horizontal segments the gradient was reversed; more ^14^C was recovered in the receiving block applied to the opposite half of the segment. Furthermore, the horizontal segments bent slightly towards the donor block (upwards), whereas the vertical segments developed large curvatures away from the donor. These ^14^C and curvature data, together with the reports of Hertel and Leopold (9) and Naqvi and Gordon (12) that all the ^14^C emerging into a receiving block at the basal end of a *Zea* coleoptile segment is confined to the IAA molecule, clearly establish that geotropic stimulation leads to an enhanced lateral movement of IAA in *Zea* coleoptiles.

Lateral movement may not, however, be the only process which gives rise to the asymmetric distribution of auxin in horizontal coleoptiles. Hertel and Leopold (9) originally found that the ability of vertical *Zea* coleoptile segments to transport IAA basipetally is affected by gravity and both Naqvi and Gordon (12) and Little and Goldsmith (10) have recently reported that less IAA reached a basal receiving block when the segments were inverted. The data of Little and Goldsmith (10) point to this phenomenon being due to inhibition of the basipetal movement of IAA rather than to inhibition of uptake or secretion of auxin by the segments. Of particular interest with regard to geotropic responses is the further finding of Naqvi and Gordon (12) that the upper and lower halves of horizontal *Zea* coleoptile segments appear to develop different longitudinal transport capacities. The lower half of a longitudinally totally split coleoptile transported to the receiving block 1.2 times the IAA-^14^C transported by the upper half. In partially split coleoptiles the ratio in the lower and upper receiving blocks was 3.2, thus confirming that in the intact segment another process, the lateral transport system, makes the major contribution to the establishment of the asymmetry of auxin distribution.

Naqvi, Dedolph, and Gordon (11) have examined the effect of anaerobic conditions upon the asymmetry of IAA-^14^C in the upper and lower receiving blocks at the base of a horizontal *Zea* coleoptile segment supplied with a symmetrical apical donor. They found the asymmetry to be even more marked in anaerobic conditions than in air. This result implies that the lateral polar movement of auxin is largely independent of aerobic metabolism. In the same paper (11) it is reported that anaerobic conditions have little effect on the longitudinal basipetal movement of IAA-^14^C by the segments. The latter finding has not, however, been confirmed; Goldsmith (6), Wilkins and Martin (18) and Wilkins and Whyte (20) have shown the basipetal longitudinal movement of IAA to be greatly reduced in coleoptile segments which have been deprived of oxygen, but that it remains slightly greater than acropetal movement. Wilkins and Whyte (20) have, however, shown that inhibitors of glycolysis, such as sodium fluoride, reduce the basipetal movement of IAA under anaerobic conditions to the level of acropetal movement. The basipetal polar flux of IAA is thus totally abolished in *Zea* coleoptile segments only when both aerobic and anaerobic metabolism are brought to a halt.

Since the lateral asymmetry of IAA in horizontal *Zea* coleoptiles arises principally from a lateral polar flux from the upper to the lower half of the organ the present investigation was undertaken to determine to what extent this flux is dependent upon aerobic and anaerobic metabolism.

**Materials and Methods**

Seeds of *Zea mays* L. var. Giant Horse Tooth, were soaked in tap water for 24 hours and sown in moist vermiculite. The seedlings were grown in total darkness at 25° for 7 days by which time the coleoptiles were approximately 35 mm long. Segments 5 mm and 10 mm in length were excised 1 mm below the apices of detached coleoptiles from which the leaves had previously been removed.

The 3-indolyl (acetic acid-1-^14^C) (IAA) of specific activity 32.1 c/mole was applied at a concentration of 25 µM in blocks of 1.5% agar to one-half of the apical cut surface of coleoptile segments. A block of plain 1.5% agar was applied to the other half of the apical cut surface. Receiver blocks were not applied to the bases of the segments in this investigation.

The arrangement of the apparatus is shown in figure 1. Two agar blocks (B and C) (size 14 × 2 × 1 mm³) were placed 1 on either side of a razor blade (D) held perpendicular to a perspex base (A) and secured in the base by a perspex wedge. One of these blocks (B) contained IAA-^14^C. Four coleoptile segments (E) per donor block were supported on the razor blade which finally projected 2 mm into the segment when the segment and donor were in contact. All manipulations were carried out...
Fig. 1. Arrangement of the coleoptile segments (E) on the razor blade (D) which separates the asymmetric donor block containing IAA-1\(^{14}\)C (B) and a plain agar block (C). The perspex base (A) holds the razor blade in place. The evacuation chamber (G) used to achieve anaerobic conditions in the tissues is shown in outline in this figure, but details have been given by Wilkins and Martin (18). The piston (F) is used to press the segments on to the donor blocks after the oxygen has been removed from the chamber.

out with segments in the vertical position. The apparatus supporting the segments was placed either vertical or horizontal, and in the latter position the donor block containing the IAA was always applied to the upper half of the apical cut surface of the segments. In all experiments the segments were maintained in an environment of high humidity, diffuse daylight and at 25°. There were duplicate samples of 4 coleoptiles each for all the treatments in individual experiments.

In experiments performed under anaerobic conditions, unless it is otherwise stated, the segments were mounted on the razor blade in such a way that they were supported by it, but were not in contact with the blocks on either side of the razor blade. Anaerobic conditions were attained with the apparatus and evacuation chamber (G) described in detail by Wilkins and Martin (18). When using 10-mm segments, the height of the chamber was increased by inserting a specially constructed perspex ring between the top and bottom parts. The perspex base (A) supporting the coleoptile segments (fig 1) was placed in the lower half of the gas-tight chamber. The latter was then closed, sealed and flushed with oxygen-free, water-saturated nitrogen, which continued to flow through the apparatus for the duration of the experiment. During the first half-hour of the 1-hour flushing period, the chamber was evacuated to 100 mm of mercury, and refilled with nitrogen 6 times at 5-minute intervals to ensure the removal of oxygen from the coleoptile cavity. At the end of the flushing period, the coleoptile segments were brought into contact with the donor blocks by lowering the piston (F) without admitting air to the chamber. One chamber was then orientated so that the segments were horizontal, and the other so that the segments were vertical.

Three experimental procedures were used: A) IAA was applied apically to vertical and horizontal 5-mm segments for 2 hours in air, or 3 hours in nitrogen. B) IAA was applied apically to vertical and horizontal 10-mm segments for 3 hours in air or 4 hours in nitrogen. C) IAA was applied apically for 1 hour in air to vertical 10-mm segments, and then for 4 hours in nitrogen with the segments either vertical or horizontal. When segments were transferred from air to nitrogen, their contact with the donor block of IAA was not broken.

A longer transport period was used in the case of the anaerobic segments to obtain enough \(^{14}\)C in the various parts of the segment to make a reliable measurement. Anaerobic conditions reduce the uptake of IAA-\(^{14}\)C from an apical donor block by approximately 70% (18, 20). Prior to the third procedure some of the segments were soaked for 2 hours in water, or in a solution of the metabolic inhibitor sodium fluoride at a concentration of 1 mM. At the end of the soaking period the solution was blown from the central cavity with a micro-pipette and the segments were surface dried on filter paper.

At the end of the experiments the coleoptile segments were marked with India ink on the side to which IAA had been applied, and bisected longitudinally along the cut originally made by the supporting razor blade. The 10-mm segments were also bisected transversely to give 4 portions for analysis. The corresponding portions of the 4 coleoptile segments from a single treatment were combined for radio-assay.

Procedures used for preparation of material for radio-assay were those described by Wilkins and Martin (18). Radioactivity was estimated using a thin window, low background, Nuclear-Chicago automatic gas flow counter. Background was 2 to 3 cpm, and samples were counted for 10,000 counts or 10 minutes. Self-absorption by the tissue was estimated by the method of Goldsmith and Thimann (7) and the \(^{14}\)C data in this paper are given on a per coleoptile basis corrected for both background and self-absorption.
Total uptake of IAA from the donor block was calculated as the total number of cpm in the tissue at the end of the transport period. The percentages of the total cpm in the various pieces of the segments are shown in the tables and figures. Standard errors of all the mean values have been calculated and significant differences determined by ‘Students’ ‘t’ tests. Differences have been regarded as significant if the calculated value of ‘t’ exceeded the table values at the 0.05 probability level. The number of individual experiments contributing to the mean values shown are indicated in the tables and figures.

Results

Lateral Movement of IAA in Horizontal and Vertical 5-mm Segments. Donor blocks were supplied asymmetrically to vertical and horizontal segments which, after a transport period of 2 hours in air or 3 hours in nitrogen, were split longitudinally for analysis. The results are shown in figure 2.

In both horizontal and vertical segments anaerobic conditions markedly reduced the total $^{14}$C taken up from the donor block. Of the total $^{14}$C taken up in air, 13.5% was found in the half segment opposite the donor in vertical segments whereas 29.5% had moved laterally in the horizontal segments. The corresponding values reported by Goldsmith and Wilkins (8) were 10% and 25% respectively. Of the total $^{14}$C taken up under anaerobic conditions, 10% was found in the half segment opposite the donor in vertical segments, and 12% in the lower half of the horizontal segments.

Anoxic conditions thus drastically reduce the lateral polar movement of $^{14}$C in horizontal coleoptile segments from 29.5% to 12% of the totals taken up from the donor block. The increased lateral polar flux of $^{14}$C found in horizontal segments in air does not appear to be totally abolished in an atmosphere of nitrogen, because in all the individual experiments under these conditions slightly more $^{14}$C is found in the lower half of horizontal segments than in the opposite half of vertical segments. However, the difference between mean values shown in figure 2 for the percentage of the total $^{14}$C reaching the opposite half of the horizontal and vertical anaerobic segments did not quite reach the level of statistical significance.

In vertical segments, anaerobic conditions significantly reduce from 13.5% to 10% the proportion of the total $^{14}$C taken up from an asymmetric donor reaching the opposite half of the segment, despite the fact that the segments in anoxic conditions had had a longer transport period in which diffusion could have occurred. Thus in vertical segments supplied with an asymmetric donor block of IAA-$^{14}$C there appears to be a small metabolically dependent component involved in the movement of $^{14}$C to the opposite half of the segment.

Lateral Movement of IAA in Horizontal and Vertical 10-mm Segments. A more detailed examination of the lateral movement of $^{14}$C in horizontal and vertical coleoptile segments was made using 10-mm segments and dividing them at the end of the experiment into the 4 portions A, B, C, and D as shown in table I. The transport period was 3 hours for segments in air and 4 hours for those in nitrogen. The data show the total $^{14}$C taken up by the segments, the proportion of the total taken up moving laterally into portions C and D, and the gradient of $^{14}$C across the basal 5-mm half of the segment (D/B).

In air, the proportion of the total $^{14}$C found to have moved laterally was 16.5% in vertical segments and 29.3% in horizontal segments. The gradient across the basal 5-mm of the segments in air was 0.45 for vertical tissue and 1.5 for horizontal tissue. Thus in the basal 5-mm, the concentration of $^{14}$C was greater in the half under the donor in vertical segments, but greater in the half opposite the donor in horizontal segments.

Of the total $^{14}$C taken up under anaerobic conditions, 11.2% moved laterally into the opposite half of the vertical segments, and a significantly higher...
Table I. The Effect of Anaerobic Conditions Upon the Total Uptake and Lateral Movement of IAA 14C by Horizontal and Vertical 10-mm Segments of Zea Coleoptiles Supplied With an Asymmetric Donor

Mean data of 10 individual experiments. For experimental details see text. Transport periods: 3 hours in air, 4 hours in nitrogen.

<table>
<thead>
<tr>
<th>Orientation</th>
<th>Total uptake of IAA 14C</th>
<th>% Of total 14C</th>
<th>Ratio D:B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>2649</td>
<td>29.3±1.5</td>
<td>1.3±0.1</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>1654</td>
<td>16.4±1.7</td>
<td>0.73±0.06</td>
</tr>
</tbody>
</table>

1 Standard error of mean.

Immediately after excision from the coleoptile, 10-mm segments were soaked for 2 hours in either water or 1 mM sodium fluoride. They were then surface dried, placed in the vertical position and supplied at their apical ends with the asymmetric source of IAA-14C for 1 hour in air. At the end of this time the segments contained approximately 80 cpm in portion B, and had a D:B ratio of approximately 0.32. The segments from each treatment group were then transferred to anaerobic conditions and divided into 2 batches, the one being placed horizontally and the other vertically for 4 hours. The asymmetric donor blocks originally supplied to the segments were left in place throughout the experiment.

The effect of sodium fluoride on the small amount of lateral movement of 14C that takes place in horizontal Zea coleoptile segments under anoxic conditions is shown in table II. The segments treated with sodium fluoride contained slightly less 14C than those which had been soaked only in water. This effect is undoubtedly due to the inhibition of uptake and basipetal movement of IAA by the segments during the 4-hour transport period under anaerobic conditions, previously reported by Wilkins and Whyte (20).

In the control experiment, the percentage of the total 14C moving laterally in horizontal and vertical segments was 16.6% and 12.8% respectively. These values were significantly different, and in close agreement with those reported in table I. Similarly, the value of the D:B ratio in horizontal segments (0.52) was significantly higher than that in vertical segments (0.36). In segments pretreated with sodium fluoride, however, neither the percentage of the total 14C moving laterally (13.5% and 12.2%), nor the values of the D:B ratio (0.41 and 0.40),

Table II. The Effect of Sodium Fluoride on the Total Uptake and Lateral Movement of IAA 14C by Horizontal and Vertical 10-mm Segments of Zea Coleoptiles Under Anaerobic Conditions

Mean data of 12 individual experiments. For experimental details see text.

<table>
<thead>
<tr>
<th>Orientation</th>
<th>Total uptake of IAA 14C</th>
<th>% Of total 14C</th>
<th>Ratio D:B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>1973</td>
<td>12.8±1.31</td>
<td>0.36±0.03</td>
</tr>
<tr>
<td>NaF</td>
<td>+</td>
<td>1516</td>
<td>12.15±0.66</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>+</td>
<td>2048</td>
<td>16.6±1.0</td>
</tr>
<tr>
<td>NaF</td>
<td>+</td>
<td>1887</td>
<td>13.5±0.8</td>
</tr>
</tbody>
</table>

1 Standard error of mean.
were significantly different in horizontal and vertical segments. Moreover, in table II, the percentages of \( {^1}^{14}C \) moving laterally in sodium fluoride treated vertical and horizontal segments were not significantly different from the corresponding values given for vertical control segments soaked only in water. Similarly, the values for the ratio D:B under anoxic conditions were the same in sodium fluoride treated vertical and horizontal segments and in anaerobic but otherwise untreated vertical segments.

The metabolic inhibitor sodium fluoride thus abolishes the enhanced polar flux of \( {^1}^{14}C \) which occurs in horizontal Zea coleoptile segments under anaerobic conditions.

**Effect of Sodium Fluoride on the Lateral Movement of IAA in 10-mm Segments In Air.** The segments were presoaked in sodium fluoride or in water for 2 hours and then, after being surface dried and orientated horizontally or vertically, allowed to transport IAA-\( {^1}^{14}C \) from an apically applied asymmetric donor block for 3 hours under aerobic conditions. The results are shown in table III. Data

![Image]

**Table III. The Effect of Sodium Fluoride on the Total Uptake and Lateral Movement of IAA-\( {^1}^{14}C \) by Horizontal and Vertical 10-mm Segments of Zea Coleoptiles Under Aerobic Conditions**

Mean data of 4 individual experiments. For experimental details see text.

<table>
<thead>
<tr>
<th>Orientation</th>
<th>Conditions</th>
<th>Total uptake of IAA</th>
<th>% of total ( {^1}^{14}C ) in C+D</th>
<th>Ratio D:B</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Air</td>
<td>1113</td>
<td>16.7 ± 0.94 ( ^{1} )</td>
<td>0.56 ± 0.04</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Air + NaF</td>
<td>1082</td>
<td>16.6 ± 1.6</td>
<td>0.52 ± 0.04</td>
</tr>
<tr>
<td>D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>Air</td>
<td>1168</td>
<td>27.9 ± 3.3</td>
<td>1.37 ± 0.28</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>Air + NaF</td>
<td>1242</td>
<td>26.9 ± 3.0</td>
<td>1.23 ± 0.12</td>
</tr>
<tr>
<td>D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( ^{1} \) Standard error of mean.

for the horizontal and vertical segments which were presoaked in water confirm those shown in table I and the data for the segments presoaked in sodium fluoride were not significantly different from these. In both cases approximately 27% of the total \( {^1}^{14}C \) was recovered in the lower half of the horizontal segments and 16.5% from the half opposite the donor in the vertical segments. The ratio D:B for the vertical segments was approximately 1.3 in both the sodium fluoride treated and the untreated segments. Pretreatment with sodium fluoride had no significant effect upon the total uptake of IAA-\( {^1}^{14}C \) by the segments under aerobic conditions.

Sodium fluoride thus has no effect upon either the uptake or lateral movement of \( {^1}^{14}C \) by Zea coleoptile segments supplied with an asymmetric donor block containing IAA-\( {^1}^{14}C \) in air.

**Discussion**

In this discussion it is being assumed that the movement of \( {^1}^{14}C \) reflects the movement of IAA. While this assumption, as yet, lacks direct experimental verification, it is being made on the following grounds: A) In Zea coleoptile segments supplied apically with IAA-1-\( {^1}^{14}C \), all the \( {^1}^{14}C \) to enter the basal receiving block is confined to the IAA molecule (9. Parkes, personal communication); B) the gradient of \( {^1}^{14}C \) between the split basal receiving blocks in horizontal and vertical Zea coleoptile segments is closely reflected in the gradient of \( {^1}^{14}C \) across the basal portion of the segment itself (8); C) the net loss of \( {^1}^{14}C \) from IAA-1-\( {^1}^{14}C \) in the donor-block/receiver-block system is close to zero for Zea coleoptiles (5); D) in Zea mesocotyl segments supplied with IAA-1-\( {^1}^{14}C \) the only \( {^1}^{14}C \) molecule to be detected in the tissues themselves was IAA (14); E) in Avena coleoptile segments which have been supplied with IAA-1-\( {^1}^{14}C \) the whole of the bound and free \( {^1}^{14}C \) is confined to the IAA molecule (20).

Data presented in figure 1 and tables I and III show that when Zea coleoptile segments are supplied apically with an asymmetric source of IAA-\( {^1}^{14}C \) under aerobic conditions, approximately twice as much of the total IAA-\( {^1}^{14}C \) taken up moves laterally in horizontal segments as in vertical segments. These data thus confirm the findings of Goldsmith and Wilkins (8) that a lateral polar flux of IAA occurs towards the lower half of geotropically stimulated Zea coleoptiles. The enhanced lateral movement occurs in both 5-mm and 10-mm segments. The fact that the present data are closely similar to those reported by Goldsmith and Wilkins (8) shows that the absence of receiving blocks at the basal end of the segments in the present experiment does not significantly affect the ability of the segments to redistribute IAA. Receiving blocks were not used in this investigation for technical reasons associated with the application of the donor blocks after the segments had been thoroughly purged of oxygen. In tables I and III the ratio D:B, which represents the gradient of \( {^1}^{14}C \) across the basal 5 mm of the 10-mm segment was approximately 0.5 for vertical segments and 1.3 for horizontal segments. In the basal 5-mm of horizontal segments there is, therefore, more IAA-\( {^1}^{14}C \) in the lower half than in the upper half. The gradient of IAA-\( {^1}^{14}C \) across the basal half of vertical segments which have been supplied with an apical donor can thus be reversed by orientating the segment in the horizontal plane.

Depriving horizontal segments of oxygen leads to a drastic reduction in the amount of IAA-\( {^1}^{14}C \) moving laterally into the lower half of the organ. The
lateral polar flux towards the lower half is not, however, totally abolished under anoxic conditions since significantly more IAA-14C moves laterally in horizontal segments than in vertical ones. If the segments are treated with the metabolic inhibitor sodium fluoride, which is known to block the operation of the Embden-Meyerhof-Parnas pathway by inhibiting enolase, the enhanced lateral movement of IAA-14C in horizontal, as compared with vertical, segments is totally abolished under anaerobic conditions. Under aerobic conditions sodium fluoride has no effect upon either the uptake or the lateral movement of IAA-14C by the segments. These findings are closely similar to those previously reported by Wilkins and Whyte (20) for the effects of sodium fluoride on the longitudinal basipetal movement of IAA under aerobic and anaerobic conditions. The results clearly suggest that under anaerobic conditions the operation of the Embden-Meyerhof-Parnas pathway provides the energy which maintains both the basipetal polar flux of IAA in the tissues, and the lateral polar flux of IAA in horizontal segments. Under aerobic conditions, an alternative pathway must provide the energy to maintain the polar flux in the presence of sodium fluoride.

The data of Goldsmith and Wilkins (8) and of Naqvi and Gordon (12) establish that the lateral transport system is in major part responsible for the establishment of the asymmetric distribution of IAA in horizontal Zea coleoptile segments. Since the present paper shows that the lateral transport system is greatly inhibited under anaerobic conditions, we are unable to account for the finding of Naqvi, Dedolph, and Gordon (11) that the asymmetry of IAA distribution between the receiving blocks at the base of a horizontal coleoptile segment supplied with a symmetrical apical donor is even greater under anaerobic conditions than in air. Several possible explanations exist: A) the uptake and longitudinal basipetal movement of IAA by the upper and lower halves of horizontal segments supplied with symmetrical donors may be differentially affected by anaerobic conditions; B) that some lateral transport of IAA occurred in the coleoptiles used by Naqvi et al. (11) due to residual oxygen being present in the central cavity; C) that the coleoptiles used by Naqvi et al. (11) adapted to anaerobic conditions more readily than did ours, and began to transport IAA at a higher rate than that found within the first few hours of being deprived of oxygen. Such a phenomenon has recently been found to occur in Zea roots (Wilkins and Scott, unpublished).

In vertical segments supplied with an apical asymmetric source of IAA, the proportion of the total IAA-14C taken up moving into the opposite half of the segment is significantly reduced by depriving the segments of oxygen. Under anaerobic conditions no significant further decrease could be effected by blocking anaerobic metabolism with sodium fluoride. These findings imply that in vertical segments having an asymmetric source of IAA, there is a small metabolically dependent component contributing to the net movement of IAA-14C into the opposite half of the segment in air. Cyclosis could obviously assist in this process and the inhibition of cyclosis under anoxic conditions, as reported by Botteiler (1) in *Avena* coleoptiles, is perhaps the most likely reason for the decreased lateral movement of IAA-14C found in the vertical coleoptile segments with our experimental procedure.

The occurrence of an enhanced lateral movement of radioactivity in horizontal segments as compared with vertical segments under anaerobic conditions shows that even in the absence of oxygen the tissues can perceive their orientation in a gravitational field. Whether they can perceive their orientation when anaerobic metabolism is also blocked is not known at present.

**Literature Cited**


