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Auxin Asymmetry during Gravitropism by Tomato Hypocotyls[1]

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ABSTRACT

Gravitropic asymmetry of auxin was observed in hypocotyls of tomato (*Lycopersicon esculentum* Mill.) soon after horizontal placement: the ratio of apically supplied [^{3}H]IAA collected from the lower sides to that from the upper sides was about 1.4 between 5 and 10 minutes. This was adequately early to account for the beginning of curvature. The auxin asymmetry ratio rose to about 2.5 between 20 and 25 minutes, and to 3.5 during the main phase of curvature. This compares reasonably well with the roughly 3.9 ratio for elongation on the lower side to elongation on the upper side that is the basis for the curvature. These data extend evidence that the Went-Cholodny theory for the mediation of tropisms is valid for dicot stems. Also consistent with the theory, an auxin asymmetry ratio of 2.5 was observed when wrong-way gravitropic curvature developed following application of a high level of auxin. In addition to reversing the asymmetry of elongation, the large supplement of auxin resulted in lower net elongation. Previous data established that ethylene is not involved in this decrease of growth as a function of increasing level of auxin.

A large body of evidence has accumulated in support of the Went-Cholodny theory that phototropism and gravitropism are mediated by lateral migration of auxin (22, 23). In particular, MacDonald and Hart (19) have recently consolidated evidence for applicability of the theory to gravitropically responding dicot hypocotyls. Nevertheless, further documentation of three aspects of the theory as applied to gravitropism of dicot shoots is desirable.

First, as discussed in the reviews cited above (19, 22, 23), doubt has been expressed about whether auxin asymmetries can be found at all in many dicots. In particular, Salisbury *et al.* have questioned whether such asymmetries develop in stems of soybeans (25), cocklebur, castor bean, and tomato (30).

Second, it has been questioned whether any auxin asymmetries which might be found develop early enough to cause curvature (6, 8). Many workers have indeed assessed asymmetry during relatively large time intervals, within which large gravitropic curvatures have already developed in controls. However, early development of asymmetry has been observed for corn seedlings: 5 or 10 min for coleoptiles (7, 15) and 3 min for mesocotyls (26, 27). These values may be viewed as heuristic evidence that lateral auxin asymmetry could develop early enough in corn seedlings to cause curvature, for all are minimal estimates of the earliness of asymmetry: during the interval of measurement, the asymmetry ratio must begin at 1.0 and increase to some final value, and the result is an integral over the entire period. In view of the continuing assertions that any development of auxin asymmetry may be secondary to curvature (6, 8, 30) it is important to extend such measurements to dicot hypocotyls, using methods of relatively high resolution.

Third, it has been questioned whether any auxin asymmetries which might be found are large enough to account for curvature (see reviews in Refs. 6, 8, 19, 22, 23). For corn coleoptiles it was shown that the gravitropic auxin asymmetry is in the range expected to elicit the observed curvature (9), but often auxin asymmetries have been presented without accompanying quantitation of how auxin controls growth, and often only small asymmetries have been reported. However, low ratios may be viewed as heuristic evidence that lateral asymmetry could be large enough to cause curvature, for in general auxin levels have been assessed for the entire upper and lower halves despite observations that (a) asymmetry ratios based on transport from downward *versus* upward oriented cut surfaces were higher than those based on net auxin in or transported basally out of the entire lower and upper halves (9, 14), and (b) it is the auxin available at the lower and upper epidermis and doubtless sometimes subepidermis that is most critical for the early stage of tropism (4, 17–19, 21, 28, 29 and references therein).

The present report compares the auxin available to the lowermost and uppermost sides of tomato hypocotyls for brief consecutive intervals during gravitropic stimulation. Although these measurements too are minimum estimates, any improvement in temporal resolution can provide a better basis for judging whether auxin asymmetries occur early enough and become large enough to account for the observed rate and extent of curving by the hypocotyls.

An additional aspect of the Went-Cholodny theory in need of clarification is the means by which the direction of curvature is controlled. It has already been explained, to a first approximation, why net gravitropic bending is typically downward for roots although upward for shoots (5, 20). However, these basic orientations are subject to physiological and nonphysiological modulations many of which remain poorly understood (16, 19, 22). If valid, the Went-Cholodny theory must directly or indirectly account for such modulation. Toward this end, auxin asymmetry is described for one par-

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ticular test case in which hypocotyls carry out 'wrong-way' gravitropic curvature after loading with high levels of auxin.

Preliminary reports of these results have been presented (12, 13).

MATERIALS AND METHODS

Plants

Seeds of *Lycopersicon esculentum* Mill. cv Rutgers were grown in trays or narrow, 25-cm-long racks of potting soil under conditions described previously (10). Seedlings were used when the hypocotyls were 15 to 20 mm long and the cotyledons were about 15 mm long.

Gravitropic Curvature

Gravitropism was initiated by mounting the racks on end in a 24°C dark room at about 90% RH. Preliminary experiments showed that the high humidity was essential for fast response. A dim green lamp was used for the manipulation and also for shadowgraphs; it was checked that neither brief nor continuous unilateral exposure of plants to the lamplight induced phototropism. To subject plants to high levels of auxin, 20 min before stimulation a rack of plants was misted from a distance of 150 mm with 5 mL of 0.01% v/v Tween 80 containing a specified concentration of IAA. All curvatures were measured from the shadowgraphs with a goniometer, and are corrected for initial sag by subtracting the small value necessary to set curvature at the moment of horizontal placement equal to 0°.

Auxin Distribution

Thirty-five Ci mmol^{-1} [5-^{3}H]IAA was obtained from Research Products International (batch 683-1184). To measure breakdown products, it was purified no more than 6 weeks before use by dissolving in 50% v/v isopropanol and passing through a column of Sephadex LH20 beads. It was stored at 4°C and diluted into water immediately before use.

Intact seedlings were prepared for loading of radioactive IAA by dragging a sharp razor blade across the adaxial surface of the cotyledons, applying force sufficient to break numerous trichomes but not to gouge regular epidermal cells. A 1 × 3 mm strip of Whatman No. 1 filter paper was positioned on each abraded surface, and a 2 μL drop of 0.5 μM [^{3}H]IAA was applied to each strip. The solution was renewed 60 and 120 min later, and experiments were begun at 135 min. These parameters were selected on the basis of preliminary tests showing that under these conditions (a) by 135 min radioactivity was accumulating linearly with time at the base of the hypocotyl, and (b) the amount of auxin applied was two orders of magnitude below that required to cause nonlinearity of radioactivity transported to the base with respect to radioactivity loaded.

For each experimental unit, four shoots were excised 15 mm from the apex and the hypocotyls were abraded by lightly dragging a razor blade from each cotyledonary junction toward the base. The four hypocotyls were speared 10 mm from the apex, with abraded surfaces facing outward, on an insect pin of 0.3 mm diameter. They were positioned with axes about 3 mm apart, and mounted with the apical 6-mm portions between a pair of 1 × 6 × 12 mm blocks of 1% agar. The assembly, which was supported by a lucite holder, was maintained in a small chamber containing water-saturated air. The blocks were collected and replaced at specified intervals.

After collection, each block was placed in 4 mL of scintillation cocktail (Packard Opti-fluor) and equilibrated overnight at room temperature. Radioactivity was assessed with a Packard Tri-Carb model 3385 liquid scintillation spectrometer. Asymmetry was indexed as the ratio of radioactivity collected from the left (A) and right (B) sides of the hypocotyls. Initially, all assemblies were mounted with the hypocotyls oriented vertically; after a specified period of time, the experimental sets were rotated so that the hypocotyls were oriented horizontally with the right side (B) lowermost.

If plants were to receive a large step-up of auxin, a camel's hair brush was used to coat the still-vertical abraded surfaces with a film of nonradioactive 1-mM IAA; controls were treated with water.

Elongation

Beads of 0.4 mm diameter (Bio-Rex 9 analytical grade ion exchange resin, Bio-Rad Laboratories) were placed on the upper and lower sides of a 16- or 17-mm long hypocotyl of an intact horizontal seedling to demarcate an apical 6-mm interval and a subapical 6-mm interval. The assembly was viewed at about ×125 magnification on a Panasonic video monitor (WV5410). Bead separation was assessed by counting pixels (resolution: 250 × 240) 20 min and 80 min after initiation of gravitropic stimulation; the difference was multiplied by a conversion factor to determine elongation in mm.

Standard Errors

Standard errors of the mean are shown for the means in the table and for the data points in each graph (unless the width of the symbol exceeds that of the error).

RESULTS

Gravitropism with Normal Levels of Auxin

Auxin Asymmetry Develops Early

Figure 1 shows that auxin becomes asymmetrically distributed across the hypocotyl within minutes after a seedling is set horizontal. During the first 5-min interval of gravitropic stimulation the ratio of radioactivity measured between the lower and upper sides of hypocotyl assemblies was slightly greater than in any preceding interval, but *t* tests did not indicate statistical reliability of the difference. For the interval between 5 and 10 min, however, the ratio between lower and upper sides was 1.36, a value substantially greater than that for any preceding interval and one shown by *t* test to be significantly different from that of the immediately preceding interval with a probability $P < 0.02$, different from the last prestimulus measurement of the same assemblies with $P < 0.01$, and different from the averaged prestimulus values of the same assemblies with $P < 0.001$. Meanwhile, *t* tests showed that ratios for vertical controls remained statistically indistinguishable from 1.0.

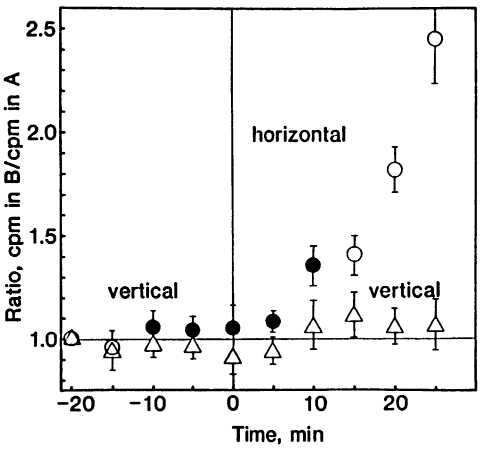

Figure 1. Ratio of radioactivity moving into laterally placed receiver blocks A and B during 5-min intervals prior to and following horizontal placement of seedling tomato shoots. The initial ratios were not precisely 1.0 because neither the loading of [^{3}H]IAA nor the collection into receivers was perfectly symmetric; therefore, the data for each of the averaged assemblies were normalized by adding or subtracting a value bringing the initial ratio (for −25 to −20 min) equal to 1.0. Open symbols show averages for 12 assemblies, and closed circles show data for 27 assemblies including the 12 shown by open circles.

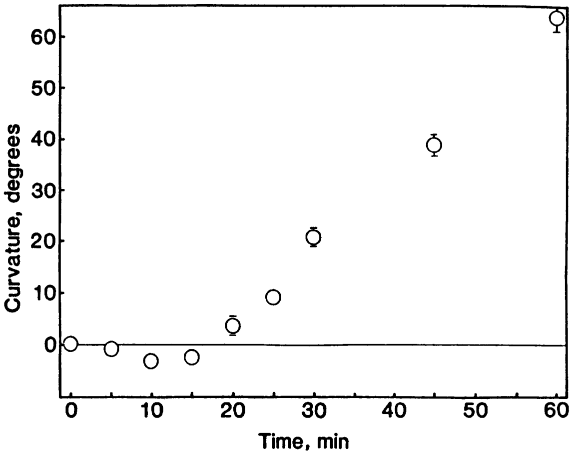

Figure 2. Time-course of gravitropic curvature by horizontally placed tomato seedlings (n = 37).

Auxin Asymmetry Becomes Large

The asymmetry ratios for the horizontal shoots in the experiment of Figure 1 increased over successive intervals, reaching almost 2.5 before the experiment was terminated at 25 min. At no time did the ratios for the vertically maintained control shoots significantly differ from 1.0 ($P > 0.2$).

Time-Course of Curvature

A preliminary assessment of gravitropic response (11) showed that intact, undisturbed seedlings grown and gravitropically stimulated under the specified conditions begin to curve slowly. In the experiment of Figure 2 the early phase of curvature is illustrated in more detail. Hypocotyls bent downward perhaps 3° at 10 min, on average, and did not attain an upward curvature until almost 20 min had lapsed. Upward bending then continued rapidly during the next 40 min; an hour after the beginning of stimulation, the plants had attained about 60° curvature.

In order to check whether the early net downward bending resulted from growth rather than sagging, seedlings were set horizontal for 5 min and then placed on a 3-rpm clinostat for development of curvature. Figure 3 shows that essentially the same amount of wrong-way curvature was seen at 15 min for plants on the clinostat as on the bench, confirming that the early downward curvature was in large part achieved actively rather than passively. Figure 3 also confirms that the plants were reasonably sensitive, for the 5-min stimulus induced an ultimate curvature of about 13°.

Almost no macroscopic curvature occurred during the first 5 min of gravistimulation, and the curvatures which occurred during the first 15 min were slight. Thus, to the extent that the plants in Figures 1 and 2 are comparable, it may be concluded that auxin and growth asymmetries begin to develop at closely comparable times.

Gravitropism with Elevated Levels of Auxin

Wrong-Way Main-Phase Curvature

Figure 4 compares the development of curvature by seedlings misted with 1 mM IAA and with a control solution. Although controls curved normally—even if a little slowly in comparison with the unmisted plants of Figure 2—the IAA-treated plants bent vigorously downward.

In a dose-response experiment, illustrated in Figure 5, misting with 1 μM IAA decreased the extent of gravitropism without changing its direction, but with 10 μM IAA the direction of response was reversed and with 100 μM IAA wrong-way gravitropic bending was about two-thirds as great as with 1 mM IAA.

Auxin Asymmetry in Auxin-Supplemented Plants

Figure 6 shows that the extent of gravitropic auxin asymmetry is diminished by misting plants with 1 mM IAA, but the direction of asymmetry is unchanged. Whereas the ratio

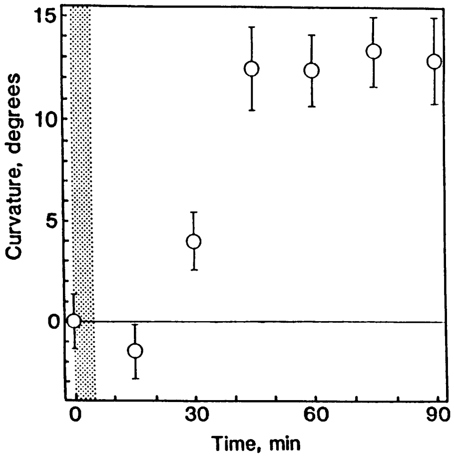

Figure 3. Demonstration that the early wrong-way gravitropic curvature seen in Figure 2 is active. Tomato seedlings were set horizontal for 5 min (stippled bar) and then rotated on a 3-rpm clinostat. (n = 22).

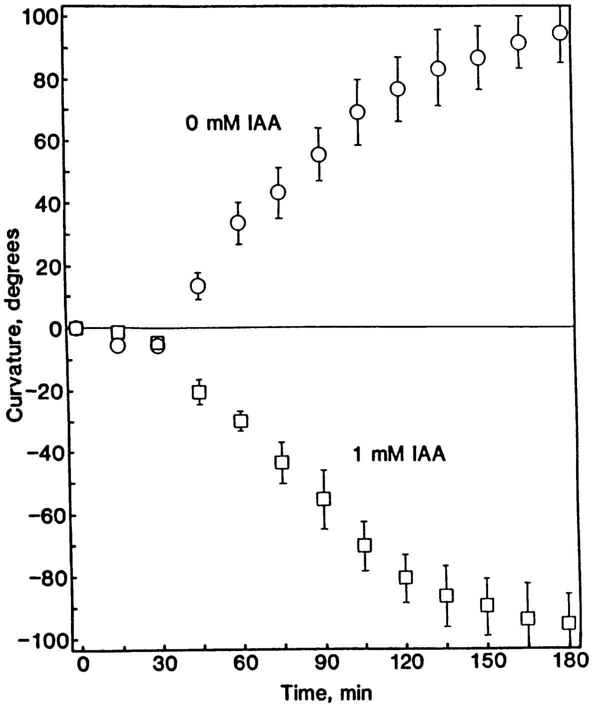

Figure 4. Reversal of the direction of gravitropic curvature by misting with 1 mM IAA (n = 15).

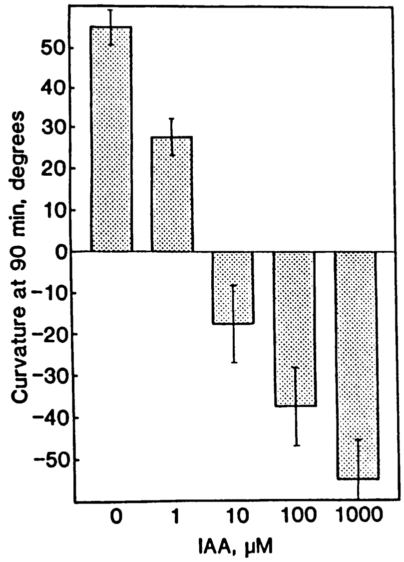

Figure 5. Extent and direction of gravitropic curvature as a function of the concentration of externally provided IAA (n = 16).

of radioactivity collected in lower *versus* upper receiver blocks reached about 3.5 for control seedlings, the corresponding ratio for misted plants was about 2.5. Thus, the wrong-way curvature of treated plants appears to result from response to high levels of auxin rather than to wrong-way transport.

Elongation

Table I shows that elongation in the apical 6-mm region of hypocotyls during the main phase of normal gravitropic curvature—between 20 and 80 min after the start of stimulation—was 4 times as great on the lower as on the upper side. Differential elongation also occurred in the basal zone.

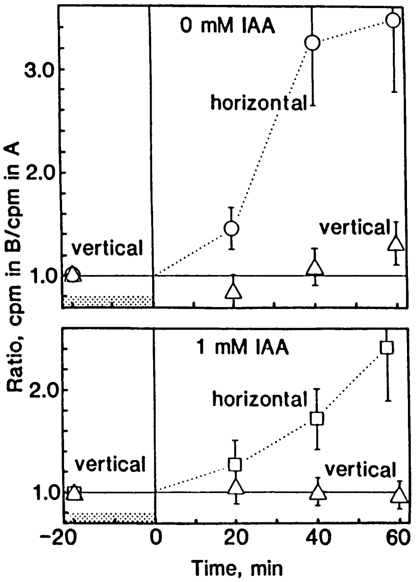

Figure 6. Diminution of gravitropic auxin asymmetry and maintenance of its vector by treating with 1 mM IAA. The initial ratios were not precisely 1.0 because neither the loading of [^{3}H]IAA nor the collection into receivers was perfectly symmetric; therefore, the data for each of the averaged assemblies were normalized by adding or subtracting a value bringing the initial ratio (for −40 to −20 min) equal to 1.0. The stippled zone marks the period in which test solution was applied to the plants. Twelve assemblies per treatment.

Table I. *Hypocotyl Elongation during the Main Phase of Gravitropic Bending (20–80 min after horizontal placement)*

n = 10.

Treatment	Hypocotyl Elongation	
	Apical 6-mm zone	Subapical 6-mm zone
	mm	
Normal plants		
Upper zone	0.11 ± 0.08	0.00 ± 0.10
Lower zone	0.44 ± 0.09	0.52 ± 0.09
Lower/upper	4.0	Not defined
Plants misted with 1 mM IAA		
Upper zone	0.16 ± 0.09	0.35 ± 0.11
Lower zone	0.06 ± 0.08	0.14 ± 0.08
Upper/lower	2.7	2.5

In contrast, elongation was almost 3 times as great on the upper as on the lower side of the same apical zone of plants carrying out gravitropism after misting with 1 mM IAA. The elongation on the upper side of the misted plants was similar to that for normal plants (0.16 ± 0.09 *versus* 0.11 ± 0.08) but respective values for the lower sides were in the ratio of 6.3. As in the normal plants, differential elongation also occurred in the basal zone.

DISCUSSION

Auxin Asymmetry Develops Early Enough to Plausibly Account for Curving

The experiment of Figure 1 unequivocally shows that auxin has become laterally asymmetric within 5 to 10 min of initiation of gravitropic stimulation. This is as early as a macroscopic curvature response is seen in most dicot seedling stems; although stems may possibly begin bending at a very slow rate within a minute or two after horizontal placement (24), in general, bending is not rapid for at least 5 to 20 min (*cf.* 3). Assuming that the elongation response to gravitationally developing auxin asymmetries may sometimes begin after a lag of a minute or so and is well underway in perhaps 10 min (for review see Ref. 24) the time of appearance of statistically unequivocal auxin asymmetry in tomato hypocotyls is generally consistent with the Went-Cholodny theory that such asymmetry mediates the curvature response.

Enhancing this argument, there are two reasons the ratios of auxin diffusing out of the abraded lower *versus* upper epidermis of tomato hypocotyls during the early phase of gravitropism in Figure 1 provide outside limits on the earliness of asymmetry: (a) there is a diffusional lag between development of asymmetry in the tissue and in the blocks contacting the abraded epidermis, and (b) the auxin collected is the integral of diffusion over an entire 5-min interval; auxin collected during the early part of the interval when the asymmetry is relatively low will tend to swamp any asymmetry which may have developed during the late part of the interval. Thus, the occurrence of a ratio as high as about 1.4 during the 5 to 10 min interval after horizontal placement suggests that asymmetry was beginning to develop during the 0 to 5 min interval. Consistent with this interpretation, the asymmetry ratio for the 0 to 5 min interval is slightly higher than that for any of the intervals preceding stimulation.

Specifically comparing the development of auxin asymmetry and curvature for tomato hypocotyls, it appears that auxin asymmetry in the abraded hypocotyls of excised shoots (Fig. 1) developed at least as early as the initial, very small curvature response by unabraded hypocotyls of intact plants (Fig. 2). From the present data, however, it cannot be determined whether the transient early downward (wrong-way) bending seen in the first quarter hour of gravitropism is a transient response to a sudden right-way shift in auxin concentration and its consequences, or whether a transient initial wrong-way transport of auxin might occur in the unabraded hypocotyls of intact seedlings. It is well established that the direction of early curvature depends on seedling pretreatment (15). Excision of hypocotyls from the root system, abrasion of upper and lower surfaces, and mounting between agar blocks might each influence the pattern of initiation of gravitational response. Hypocotyls sandwiched between agar blocks in the auxin transport assemblies did carry out gravitropic curvatures, but in three large experiments on the time-course of gravitropism by abraded hypocotyls (data not shown), the wounded plants sagged much more than controls, suggesting desiccation, and their apical zones developed little if any curvature during the first 90 min of gravitropic exposure. However, preliminary experiments suggested that auxin collection could not be accomplished without altering the cuticular barrier. Of course, any comparison between auxin asymmetry and curvature is somewhat equivocal if mechanical stimulation and wounding are not identical for the two kinds of measurement, but the problem is of particular concern for the early, variable phase of gravitropic curvature.

Auxin Asymmetry Becomes Large Enough to Account for Curving

The 4-fold ratio between elongation on the lower and upper sides of the apical zone of the hypocotyls of horizontal seedlings for the 20 to 80 min interval (Table I) when gravitropic curvature is most rapid (Fig. 2) corresponds closely to the approximately 3.5-fold ratio of auxin collected at the lower and upper surfaces of the same zone of horizontal abraded hypocotyls of excised shoots during a comparable 20 to 60 min period (Fig. 6, top panel). In the normal range of auxin levels, over the short term, growth is ordinarily roughly linear with concentration and curvature is roughly linear with concentration difference (*cf.* 2, 9). The spatiotemporal distributions of both auxin and elongation are doubtless complicated, and the influences of secondary mediational asymmetries (22, 24) must be accounted for in any precise accounting of the control of growth. Thus, the rough correspondence between asymmetries of growth and auxin in tomato hypocotyls is adequate to support the Went-Cholodny theory for gravitropism.

Gravitropism with Artificially High Levels of Auxin Depends on Auxin Asymmetry

The direction of gravitropic bending is controlled both by the vector of auxin asymmetry and the graded responses of the cells to the local supply of auxin. Both factors are sensitive to internal and environmental conditions, and it appears that both may change during the course of gravitropic response (for review see Ref. 22). Presumably, changes in these two factors contribute to the counterreaction that straightens the apex of responding plants, shifting the locus of curvature toward the base and thereby stabilizing the plant. Regulation of these factors may also underlie the control of the angle of gravitropic equilibrium.

The observation that the direction of gravitropic curving by seedling tomato shoots misted with large amounts of auxin is downward rather than upward (Fig. 4) presented an opportunity for preliminary exploration of how increased levels of auxin might modulate the gravitropic response. This opportunity was of particular interest because it was previously shown (11) that in these seedlings the misting treatment does not stimulate ethylene formation; in contrast, effects of auxin on its own transport and on tissue response to its own levels are at least partially mediated by ethylene in many tissues (1).

Hypocotyls of tomato seedlings misted with 1 mM IAA developed an auxin asymmetry about 70% as large and with the same sign as those misted with a control solution (Fig. 6). While it is unclear how much IAA penetrated the cuticle, how rapidly it diffused into the core of the tissue, and hence how it diluted the radiolabeled IAA, the reversal of the direction of bending (Fig. 4) indicates that a significant amount of IAA entered the tissue controlling elongation. Evidently, the lateral transport system is heavily loaded but is not swamped by the extra auxin. Measurements of hypocotyl elongation (Table I) indicated that (a) in comparison to the controls, growth by seedlings misted with 1 mM IAA is relatively high on the upper side and low on the lower side, and (b) net elongation is considerably diminished. Although the relation between auxin levels and growth under these conditions has not been explored, it is noteworthy that the 2.5 ratio of auxin collected from the lower *versus* upper surfaces compares favorably in absolute magnitude with the 2.7 ratio of elongation in the apical zone on the upper *versus* lower sides. The simplest interpretation of the data is that the Went-Cholodny theory is operative for tomato hypocotyls even when auxin levels are increased far above normal, and that for these hypocotyls large increases in auxin shift the direction of gravitropism by their regulation of the growth response rather than by any major influence on the lateral transport system.

Insofar as ethylene appears to participate in the regulation of gravitropic responses of roots and leaves of tomato (1), caution is essential in comparing the present results with those for other organs even of the same plant.

Summary

Over the years, many kinds of evidence have been compiled to show that the Went-Cholodny theory is valid for the gravitropism of oat and corn coleoptiles; these have included demonstration of the early development of auxin asymmetry. New high-resolution time-courses for tomato show that gravitropic auxin asymmetry develops early enough and becomes large enough to account for gravitropic curvature in hypocotyls as well. A large auxin asymmetry also develops during an unnatural form of hypocotyl gravitropism. In the absence of any sound alternative explanation of the data, and considering their consistency with analyses of the development of gravitropic curvature in dicot seedlings summarized by MacDonald and Hart (19), they give reasonable confidence that gravitropism is mediated in much the same way in hypocotyls as in grass coleoptiles.

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