Auxin Transport in Geotropic Curvatures of a Branched Plant [1, 2]

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Our present understanding of growth curvatures produced by negative geotropism is based on the concept of excess of auxin in the lower side. Dolk's (5) report of this imbalance of IAA in coleoptiles has been confirmed by refined techniques (7, 8). Evidence for a downward movement of auxin through other organs has also been obtained but it too was derived from the distribution of free auxin in juvenile structures rather than from measurements of auxin supply to the growth zones of established plants. Dijkman (4) obtained data from diffusible auxin in hypocotyls of *Lupinus* after a few hours in the horizontal position. Van der Laan (14) measured diffusible auxin in the upper and lower halves of *Vicia* epicotyls for periods up to 90 minutes. Brauner and Böck (2) used ethanol to extract IAA from hypocotyls of *Helianthus* after 45 minutes of gravity stimulus. Boysen-Jensen (1) extracted auxin from horizontal epicotyls of *Phaseolus* and *Vicia*.

Lateral transport by gravity within the tissues of typical branches and axial internodes is only a reasonable assumption from the evidence for seedling structures. The movement of auxin molecules has not been demonstrated in nonseedling tissues. The probability for such downward transport in a nonvertical stem is supported, however, by the appearance of full epinastic curvatures in branches (10) only when growth of the plant on a horizontal clinostat eliminates an apparent lateral transport effect of gravity.

This report presents direct evidence from dicotyledonous stems for a definite transport effect of gravity on exogenous IAA-2-C^{14}, based on the distribution of the compound and its reaction products within immature internodes after response to a geotropic stimulus had produced growth curvatures in them. The resulting imbalance of radioactive compounds between upper and lower sides closely resembles that of unaltered auxin in seedling organs.

Materials and Methods

The work was done with immature greenhouse plants from a clone of *Coleus blumei* Benth. They had been grown in pots of rich loam, kept well watered, and given supplementary light for 12 hours per day during the fall and winter months. Except for experiments with curvatures of the main axis, vigorous branching was induced by pinching out the apical buds when the plants were 20 to 30 cm tall.

Aside from a few tests with IAA supplied through 1 leaf per branch (fig 2), experimental plants were completely defoliated with a sharp blade and the tip of each branch (or axis) was cut back to the first firm node. Auxin was applied to this cut surface as a terminal cap of 1 % IAA-2-C^{14} in lanolin, approximately 1 mm thick, (or spread thinly on the lower epidermis of a young leaf). A chromatogram of the radiocarbon compound, furnished by New England Nuclear Corporation, showed no measurable radioactivity outside the zone of pure IAA.

Geotropic curvatures were initiated immediately after treatment, either by suspending each plant in an inverted position (5 experiments) or by laying the pot on its side with the main axis or its branches free to grow upward without touching anything (fig 1, 2). Groups of 12 to 15 plants were used for each experiment with branches and at least 25 plants for each test with unbranched stems. The plants were in darkness or briefly in very weak light while the IAA was moving into the stem tissues. The temperature range was 21° to 23° with a variation of no more than 1 degree for a single experiment.

Radioassay. The pattern for transport of the IAA within the geotropic curvatures was determined from the distribution of radiocarbon in extracts from the convex (lower) and concave (upper) sides of the curved parts of the branches or axes. These curved stem sections were excised, taken into a 4° cold room, and at once bisected manually into equal weights of lower and upper halves. The 2 lots of tissues were then diced finely and stored in a deep freeze.

A triple extraction of the radioactive material was later started in the same cold room by grinding the 2 lots of tissue in separate mortars with chloroform and enough 0.1 N HCl to make an aqueous liquid with pH 2.8 to 3.0. The macerated tissues were left overnight in the mortars with the 2 solvents, then ground further for at least 5 minutes each with 2 fresh portions of chloroform.

The combined chloroform solutions (1 lot for each lot of tissue) were separated from the acid-water extracts, evaporated to volumes of about 0.5 ml, and measured to the nearest 0.01 ml. The aqueous solutions were evaporated and measured with the same

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accuracy. Finally threefold extractions of the tissue residues were made in the mortars with absolute ethanol. These 2 alcoholic solutions were likewise evaporated to small volumes, measured, and held in a refrigerator with the other 4 extracts for radioassay. Tests of the extracted tissues showed retention of about 10 % radiocarbon in both upper and lower halves of the stems.

Measurements of radioactivity in the extracts were made with small aliquots, using a Nuclear-Chicago liquid scintillation counter and glass vials of a dioxane-base fluid (3) that accepted all extraction solvents. The data for radiocarbon were adjusted later for a 0.50 ml volume of each concentrated extract. The standard errors of the measurements were reduced to less than 5 % by suitably high counts in the order of thousands for each sample.

To identify and assay the unaltered IAA that dissolved in the chloroform under the conditions of the extraction method (13), the chloroform extracts from each set of experiments (see table I) were combined into 2 solutions. Each of these mixtures, one from upper and one from lower tissues, was fractionated by washing with an aqueous solution of 0.1 M $NaHCO_3$ at pH 8.0, evaporated to a small, measured volume, and used for chromatograms after assay for total radiocarbon.

Chromatography. Standard methods of paper chromatography were used for partition of the radioactive compounds in the 6 alkaline extracts each of tables III and V. At least 2 and in many cases 3 solvents were used to separate the compounds in each alkaline solution. Solvent A was isopropanol, ammonia, and water (10: 1: 1 by volume); solvent B was *n*-butanol, acetic acid, and water (10: 1: 2 by volume); solvent C was *n*-butanol, benzene, methanol, and water (2: 2: 4: 1 by volume).

Salkowski's reagent was used to locate a marker spot of authentic IAA on the dried paper after partition. The bands of radioactive substances on other R_F zones of the paper, in amounts too small for color tests, were located with a counting tube designed by Fuller (6). Lack of knowledge of compounds other than IAA in the alkaline extract limited the analysis to the radiocarbon within the IAA zone of the paper and in lesser amounts elsewhere on each strip. The radioactivity in elutions of the 2 groups of material was measured with the scintillation counter.

Experimental Results

Curvatures. The location of a geotropic curvature was as shown in each of the 6 branches on the representative plant in figure 1. In many cases, as evident here, the asymmetric growth after change in the plant's position was made chiefly in the middle internode of a branch of this length. This zone of continued elongation contained the oldest immature tissue of a *Coleus* branch. The younger internode just under the cap of 1 % IAA in lanolin remained nearly straight and was held erect in some of the branches. In a branch so oriented that its base was near the upper side of the horizontal axis, the young-

Table I. *Radioactivity from Geotropic Curvatures Supplied with IAA-2-C^{14}*

Expt. no.	Hours of growth	Wt of tissue g	Tissue from	Cpm in 0.050 ml each of 3 conc extracts*		Ratio L/U
				Lower half (L)	Upper half (U)	
10	44.0	16.75	Brs. on sides	432.7	300.2	1.441
11	47.0	35.48	" " "	1,684.2	993.2	1.696
12	45.5	26.05	" " "	452.5	331.1	1.367
14	44.0	31.81	" " "	1,011.4	584.3	1.731
16	45.5	45.16	" " "	936.4	558.4	1.677
						M = 1.582 ± .111
1	18.5	20.37	Brs. inverted	444.8	303.9	1.464
2	18.5	17.25	" "	325.8	193.6	1.683
3	21.5	21.93	" "	367.0	294.2	1.247
4	17.0	15.57	" "	309.2	234.0	1.321
5	21.0	18.80	" "	243.7	164.8	1.479
						M = 1.439 ± .111
6	21.0	11.86	Axes horizontal	15.7	9.2	1.702
7	21.0	12.39	" "	24.1	16.2	1.485
13	46.5	17.56	" "	59.5	37.8	1.574
15	47.0	20.06	" "	198.7	121.0	1.642
17	46.5	23.00	" "	141.4	116.9	1.209
						M = 1.522 ± .129
18	47.0	23.10	Brs.; axis erect**	564.8	559.8	1.009
19	47.0	23.00	" " "	457.0	447.1	1.022
20	47.0	19.38	" " "	405.8	419.5	0.967

* Activity of IAA-2-C^{14} was 1.1 × 10^5 cpm/mg for experiments 1 to 7 and 4 times as great for the other experiments.
** No geotropic curvatures produced.

est internode was not erect because the extra auxin delivered to the originally upper side of the branch (10) produced a slight epinastic curvature in the branch (see fig 1).

In the second group of experiments as reported in table I, the plants were suspended in the inverted position and the epinastic effect coincided with the geotropic curvatures. The growth responses in the horizontal axis (third group) were similar to those in branches. The erratic curvatures in figure 2 are discussed below.

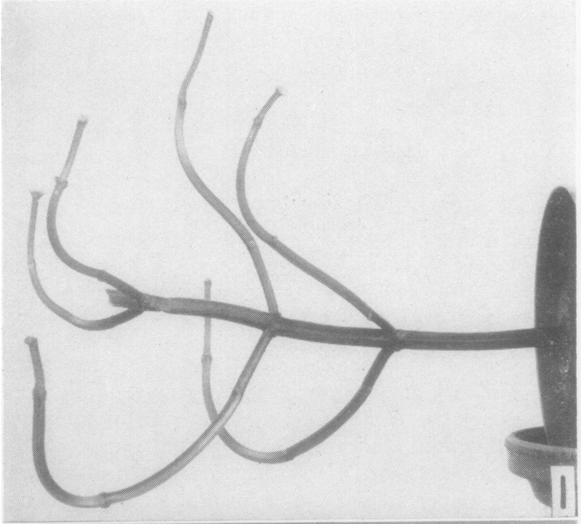
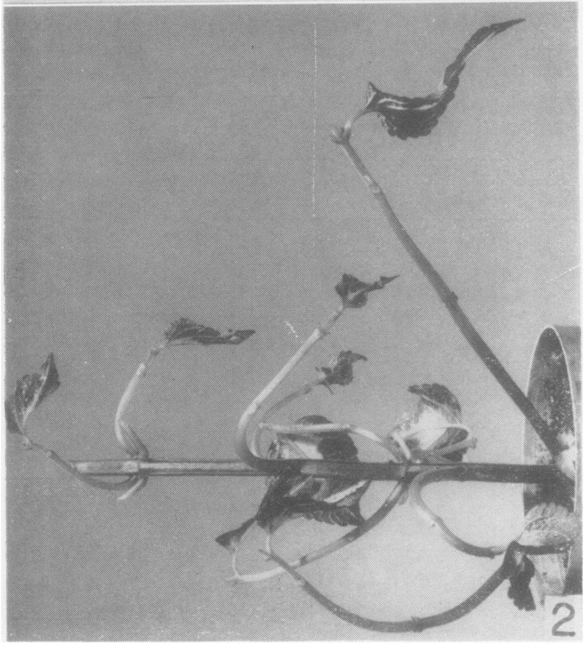

FIG. 1, 2. Geotropic responses of *Coleus* branches to 1 % IAA in lanolin after 24 hours with axis horizontal. FIG. 1. Normal curvature from auxin supplied in terminal caps. FIG. 2. Geotropic curvatures weak or absent from auxin applied to leaves and partly degraded in them.

Within the internode that develops the strongest geotropic curvature, there is a complete sheath of cambium and young secondary tissue around the thick, succulent pith. The younger, straight internode also has some secondary, interfascicular growth but all immature zones of the branch are composed chiefly of parenchyma cells within a cylinder of schlerenchyma. As the auxin arrives in these immature internodes, probably by way of the vascular tissues (9, 11), there is nothing but thin-walled tissue through which it would move in lateral transport.

Auxin Distribution. Evidence for a movement of appreciable amounts of auxin from the symmetrical, terminal supply to the lower side of a *Coleus* branch or axis is included in table I. The lateral transport effect can be measured by the L/U ratios of C^{14} extracted from the lower (L) and upper (U) halves of stems with geotropic curvatures. Since the atoms of radiocarbon represent molecules of IAA supplied to the truncated end of the stem, their location after a period of growth records their transport under the influence of gravity. In general, the L/U ratios show that about 50 % more IAA and its metabolic products were extracted from the lower tissues.

This distribution of all the radiocarbon between the opposing sides of the curvatures, as shown in table I, is of major concern in tracing the movement of the IAA. The effectiveness of the method, in comparison with the practice of assaying only unaltered auxin, can be appraised in part by noting the distribution of the radioactivity among the 3 solvents used in the extractions. A typical example of results for individual experiments is shown by the first set of data in table II.

The measurements obtained for this example of the first 15 experiments in table I show the excess of C^{14} in extracts from the lower side of the stem but the ratios of C^{14} always varied widely from the ratio for total distribution in any one experiment. No ratio for a single solvent was a reliable index of partition of the radiocarbon and therefore of IAA before its degradation. The compounds extracted by the acid-water commonly carried more than half of the radioactivity while the alcoholic solution usually held more radiocarbon than the chloroform extract. Since the method provides for the unaltered IAA to be removed by the chloroform, the C^{14} in the other solvents must represent nonvolatile metabolic products of the auxin.

The difference in radioactivity between chloroform extracts of the lower and upper tissues is of special interest. These extracts can be used to measure the imbalance of residual IAA during or after geotropic curvature, in place of comparative bioassays that are subject to interference by inhibitors of growth during assay. The data in table III show that about two-thirds of the C^{14} extracted by the chloroform and removed from it by the alkaline water was still in IAA molecules. The L/U ratio of all C^{14} in the chloroform varied from 4.034 to

Table II. *Distribution of C^{14} in Solvents After Extractions of Branch Curvatures*

Expt. no.	Tissues extracted with	Cpm in 0.050 ml of extract		Ratio L/U
		Lower half (L)	Upper half (U)	
10*	Chloroform	53.4	42.6	1.254
	Water	256.5	168.9	1.519
	Ethanol	122.8	88.7	1.384
	Total	432.7	300.2	1.441
M**	Chloroform	84.3	81.5	1.034
	Water	2,764.5	6,332.0	0.437
	Ethanol	818.5	2,143.7	0.382
	Total	3,667.3	8,557.2	0.429

* For experimental conditions, see table I and text.

** Data are means from 3 experiments with IAA-2-C^{14} and derivatives supplied to each branch through a leaf for 22.5 to 23.0 hours.

0.798, with a mean of 1.638 ± 0.200 for the 15 experiments. This average is not significantly different (at the 5 % level) from any of the 3 mean ratios for total radiocarbon recovered in these experiments (table I) yet the average amount of C^{14} in the chloroform extract was only 14.2 ± 1.1 % of the total extracted.

The excess of auxin and its metabolic products in the lower tissues of strong geotropic curvatures proved to be 51.5 ± 4.4 %, with a mean percentage ratio of 39.8: 60.2 between the upper and lower tissues. In contrast, there was a balanced distribution of radiocarbon in the stem tissues of erect *Coleus* plants (experiments 18–20, table I), associated with an absence of new growth curvatures. There was no reason to expect a difference between auxin movement in the main axis and in branches on an axis placed horizontally. Geotropic response in inverted branches, however, might have resulted in a greater percentage of auxin in the lower side of the curvature through an additive effect of lateral transport by gravity and transport to the morphologically upper side by the unknown process shown (10) to be responsible for branch epinasty. No such effect can be seen in the data of table I, experiments 1 to 5, in comparison with the other 10 experiments. The 2 processes seem not to be additive when they act in the same direction.

Comparison with Seedlings. For comparison with measurements of auxin distribution in curvatures of seedling stems, usually reported by ratios of percentages, the 3 means of L/U ratios in table I have been thus computed and included in table IV along with ratios of residual auxin as reported for seedling curvatures.

The agreement among the 10 sets of percentages from geotropic curvatures is reasonably close in spite of the different methods and plant materials. About 60 % of the auxin appears in the lower tissues where the growth rate is higher until the curvature has been completed. The immaturity of all the zones of growth seems to make different kinds of stems open to a similar lateral movement of part of the auxin by processes still unknown.

Transport Form. The probability that auxin moves in unchanged form was first tested in this study by identification and assay of IAA in the chloroform extracts from the opposing sides of the curved stems. The results are shown in table III that lists data for the IAA and associated compounds removed from the chloroform solutions by alkaline, aqueous washings. The small amount of radioactive compounds in the single experiments of table I made it necessary to combine the chloroform extracts of the 5 experiments in each group before fractionation.

It is clear from the data in table III that most of the C^{14} removed from the chloroform extracts was in unaltered IAA. The identities of the other com-

Table III. *C^{14} Distribution in Alkaline Extract**

Tissue extract from	Cpm in 0.050 ml of extract conc to 0.50 ml					
	Branches on sides		Branches inverted		Axes on sides	
	IAA**	Other	IAA**	Other	IAA**	Other
Upper half	30.7	19.9	26.5	17.8	10.5	3.5
Lower half	58.6	23.4	44.0	26.8	13.8	2.3
% Upper	34.4		37.6		43.2	
% Lower	65.6		62.4		56.8	

* Data are means of radioactivity eluted from at least 3 chromatograms each.

** Eluted from zone of IAA spot on papers; identified by cochromatography at R_F 0.32 to 0.34 with solvent A and at R_F 0.88 to 0.90 with solvent B and/or at R_F 0.42 to 0.52 with solvent C.

Table IV. *Ratios of Auxin in Geotropic Curvatures of Stems*

Author	Boysen-Jensen		Brauner and Böck	Dijkman		Van der Laan		Lyon		
Genus	*Phaseolus*	*Vicia*	*Helianthus*	*Lupinus*		*Vicia*		*Coleus*	*Coleus*	*Coleus*
Stem	Epicotyl		Hypocotyl	Hypocotyl		Epicotyl		Branch on side	Branch invert.	Axis of plant
% Upper	39	44	46.0	32.5	40.4	39	37	38.7	41.0	39.6
% Lower	61	56	54.0	67.5	59.6	61	63	61.3	59.0	60.4

pounds are unknown. The greater amount of IAA from the lower half tissues of each group of experiments (cf. table III) supports the concept that most if not all of the excess radiocarbon from the lower side in the table I experiments, regardless of its chemical form during extraction, was transported there in IAA molecules. The distribution ratios for IAA in the opposing sides (table III) agree well with ratios reported for gravity curvatures in general, as assembled in table IV.

A second test of downward transport of auxin as the IAA molecule was made by supplying the radioactive compound to *Coleus* stems by way of the lower epidermis of a leaf attached to its branch just below the severed tip (fig 2). At the start of the experiment, the attachment of these leaves was to the upper side of the growth zone as the plant was laid on its side with the lanolin paste spread on the lower side of the leaf.

The weak, dissimilar curvatures in figure 2 illustrate the geotropic responses of branches to which the auxin was supplied through leaf tissues. In branches attached to the sides of the horizontal axis, the mechanism of epinasty either prevailed over that of negative geotropism (second pair of branches above the soil) or combined with it to produce an angle of about 45° in the growth zone. Only the uppermost, young branch near the tip showed a geotropic curvature comparable to those in figure 1 during the first 24 hours. (Geotropic curvatures appeared in the other branches only after 2 or 3 days.)

These slow, uncertain responses to gravity suggested very small supplies of growth hormone to the lower sides of the branches. The data for radioactive compounds in the 3 extracts each from the opposing sides (experiment M, table II) confirmed this estimate. On the average, only 1 or 2 % of the IAA absorbed by the leaf and carried into the stem was present in either half of the branch in forms soluble in chloroform, and less than half of these radioactive solutes proved to be unaltered IAA (cf. table V). The percentage of C^{14} compounds, extracted in chloroform was much smaller than that for typical geotropic curvatures (cf. experiment 10, table II). The total radioactivity in the chloroform was about the same for the 2 sides but there was over 50 % more IAA in the extract from the lower side, as shown in table V.

The other measurements of radiocarbon in experiment M of table II show that the radioactive products of IAA metabolism did not accumulate in the lower tissues by the effect of gravity or through any other process. Except for the chloroform extracts, the radioactivity was far greater in the aqueous and alcoholic extracts from the tissues of the upper side.

Discussion

This strong imbalance of IAA derivatives in favor of the upper half of a branch when the IAA was not applied directly to the stem is contrary to the

Table V. *C^{14} Distribution in Fractionated $CHCl_3$ Extracts of Weak Curvatures*

Expt. no.	Curvature tissue	% Radioactivity			IAA
		NaHCO$_3$ solution*		Residual in $CHCl_3$ extract	% Upper / % Lower
		IAA**	Other		
1	Upper half	29.2	17.8	53.0	35.1
	Lower half	53.9	20.1	26.0	64.9
2	Upper half	29.8	27.2	43.0	41.6
	Lower half	41.9	15.6	42.5	58.4
3	Upper half	24.4	23.4	52.2	41.0
	Lower half	35.1	17.7	47.2	59.0
Mean	Upper half	27.8	22.8	49.4	38.9
	Lower half	43.6	17.8	38.6	61.1

* Data from means of radioactivity eluted from 4 chromatograms each.

** Eluted from zone of IAA spot on papers; identified by cochromatography at R_F 0.32 to 0.34 with solvent A and at R_F 0.88 to 0.90 with solvent B.

results for all the other experiments with geotropic curvatures. It was to be expected, however, if only IAA molecules are moved by gravity, since most of the C^{14} received from the leaves would be in compounds other than IAA. Measurements of such radioactive but unidentified substances, derived from the same IAA-2-C^{14} and collected from *Coleus* petioles after application of the same auxin supply to the lower leaf surfaces, were reported by us in 1963 (11). Radioactivity from unaltered IAA accounted for only a small fraction of the total C^{14} in the petiole extracts. The large amounts of metabolic products thus transported from an upper leaf in this study (cf. experiment M, table II), or derived in part from a small amount of IAA after its delivery to the branch, might well tend to remain in the side to which the radioactivity was delivered.

The IAA compound did show the effect of gravity on its distribution between the upper and lower tissues, even in minimal supply (table V). The result was the same percentage excess in the lower side of weak curvatures that has appeared in strong curvatures, whether measured by unaltered IAA (table III) or by total C^{14} from the IAA supply (table I). A ratio close to 40: 60 seems to characterize the results of a lateral transport of IAA by gravity in any physiological quantity.

The comparisons between IAA ratios for *Coleus* in table III and various ratios reported from seedlings (in table IV) are direct except for experimental methods, since only assays of residual IAA were made in studies of seedling curvatures. The agreement between the percentage ratios for *Coleus* stems in tables III and IV is indirect unless one assumes in advance that the ratios were established by the transport effects before the metabolic products included in the data of table IV were formed from the supply of radioactive IAA. The reasonably close agreement among the 3 distribution ratios for IAA in table III provides some evidence for the probability that a certain small fraction of the total supply of IAA to a growth zone remains intact and extractable while most of the auxin undergoes metabolic changes (12).

The 40: 60 distribution ratio for the results of IAA transport in different concentrations during the development of geotropic curvatures, the weak, slow curvatures of *Coleus* in figure 2, and the distribution of C^{14} in the extracts of a branch supplied with it through an upper leaf (experiment M, table II) combine to support the view that only the unaltered IAA responds to a transport effect of gravity. The distribution ratios for C^{14} in the metabolic products dissolved in water and alcohol were completely reversed in the opposing sides of the branch over the ratios in the typical experiments of table I. More than twice as much radiocarbon remained in the upper tissues in spite of anatomical structures whereby the vascular tissues of an upper *Coleus* leaf should deliver leaf products to a zone midway between the upper and lower sides of the horizontal branch. Only the unaltered IAA was found in excess on the lower side.

The accumulation of other C^{14} compounds in these upper tissues raises the question of possible pathways of movement of IAA derivatives from petiole to branch. Some of them may be carried back in the phloem and thus reach tissues included within each half of the branch tissues to be extracted. Other molecules tagged with C^{14} may move through the nonvascular tissues of the petiole and into the upper, nonvascular tissues of the branch, since the data for our 1963 work with *Coleus* petioles (11) showed an abundance of metabolic products of IAA outside the vascular strands. Radioactivity of such an origin probably accounts for the excess of C^{14} in the upper halves of the weak branch curvatures, produced by auxin supplied through leaves. The excess of similar derivatives of radioactive IAA in the lower tissues of curvatures with a normal supply of auxin by way of the vascular strands indicates a lateral transport of auxin by gravity before destruction of most of the IAA.

Summary

Immature plants from a clone of *Coleus blumei* Benth. were used to trace the movement of indoleacetic acid-2-C^{14} during the development of geotropic curvatures in branches and the main axis, as determined by radioassay of the curvature tissues. The auxin was supplied either symmetrically to defoliated and detipped stems as terminal caps of 1 % IAA in lanolin or through a film of the paste on 1 leaf that was left on the upper side of the horizontal branch. In both cases the extractable, unaltered IAA was found to be distributed in a ratio of approximately 40: 60 in the upper and lower halves of the curvatures. Most of the radiocarbon was extracted in nonvolatile degradation products of the IAA but the same 40: 60 ratio held for the total radioactivity in the opposing sides of the stems when the C^{14} was supplied directly to the stem. The evidence supports the concept of downward transport of unaltered IAA as the basis for more rapid growth of the lower tissues in a geotropic curvature of a branch or main axis.

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Red light and the geotropic response of the Avena coleoptile [1, 2]

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Introduction

For many years red light was regarded as a safe light under which experimental manipulations in studies of plant tropisms could be conducted. This practice arose from the finding that light of wavelength greater than 520 mμ did not induce phototropic curvature. During the last few years, however, it has become clear that red light has a marked effect on both phototropic and geotropic responses of plant organs. The changes induced in the phototropic responses of coleoptiles have recently been reviewed by Briggs (9), and much of the literature describing effects of light on geotropism has been collated by Wilkins and Goldsmith (18).

Blaauw (3, 4) has investigated the effects of red and far-red light on the geotropic response of the *Avena* coleoptile. His findings on *Avena* differed from those of Wilkins and Goldsmith (18) on the coleoptile of *Zea mays* in 3 major respects: Firstly, the geotropic response of the *Avena* coleoptile was increased after exposure to red light whereas that of the *Zea* coleoptile was decreased. Secondly, the increased responsiveness to a geotropic stimulus in *Avena* was greatest when stimulation began 30 minutes after exposure to light and disappeared completely if this interval was 60 minutes. In *Zea* the decreased sensitivity did not develop until 6 to 8 hours after the light treatment but then lasted for at least 22 hours. Thirdly, far-red irradiation also elicited the short-lived increase in the sensitivity of the *Avena* coleoptile but did not reverse the effect of red light. In *Zea*, on the other hand, far-red irradiation alone had no effect on the geotropic responsiveness of the coleoptile but completely reversed the effect of red light. Since coleoptiles of *Avena* are rich in phytochrome (W. R. Briggs, personal communication, and 16), it is surprising that at least some reversal of the effect of red radiation was not observed.

The differences between the reported responses of coleoptiles of *Avena* and *Zea* to red light seemed sufficiently great to warrant further investigation, since they might reflect some fundamental differences in the growth and organization of the 2 tissues. The influence of red light on the geotropic response of the *Avena* coleoptile has therefore been reinvestigated with respect both to the short-lived effect described by Blaauw (3, 4) and to possible long-term effects similar to those found by Wilkins and Goldsmith (18), in *Zea*.

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