Gravitational Compensation and the Phototropic Response of Oat Coleoptiles[1]

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Summary. *Avena* seedlings were germinated and grown while continuously rotated on the horizontal axis of a clinostat. The coleoptiles of these gravity-compensated plants were phototropically more responsive than those of plants rotated on a vertical axis. When the plants were compensated after unilateral irradiation, phototropic curvature of the shoot progressed for the next 6 hours, with the rate of curving decreasing about 3 hours after irradiation. The decrease in rate was less in the plants gravity-compensated before irradiation than in those vertically rotated. In the period 70 to 76 hours after planting, the growth rate of the compensated coleoptiles was significantly less than that of the vertically rotated seedlings. The greater phototropic curvature, the decreased growth rate, and the slower rate of straightening of the curved, compensated shoot can be correlated with several consequences of compensation: an increase in sensitivity to auxin, a lowering of auxin content in the coleoptile tip, and possibly, from an interaction between compensation and phototropic stimulation, an enhanced difference in auxin transport between the illuminated and shaded halves of the unilaterally irradiated shoot.

The phototropic response of the vertically rotated seedling was significantly different from that of the vertical stationary, indicating the importance of vertically rotated controls in clinostat experiments.

Tropic curvature of an orthogeotropic organ is normally the expression of 2 stimuli. As soon as curvature commences in a vertical shoot responding to phototropic stimulation, the shoot is challenged by gravitational force. In *Avena*, this counter-stimulation could be expected when the tip axis departs as little as 1° from the vertical (19). Analogously, a geotropically curving organ is also concomitantly exposed to a continuously changing geostimulus.

Nullification of the subsequent geostimulus should facilitate characterization of the primary response. The clinostat enables such nullification by compensating the directional component of the gravitational force vector (12, 18, 24, 25). This paper describes the phototropism of *Avena* seedlings when the georesponse was removed by clinostat rotation. We will show that gravitational compensation results in an enhancement of phototropic sensitivity, and correlate this enhancement with auxin response, content and transport.

Materials and Methods

Planting. *Avena sativa* seeds (Victory I,

Svalof) were rinsed with tap water at 40°, allowed to soak for 2 and one-half hours and then rinsed again with warm water. (For the auxin studies, after hydration the seeds were kept in the dark at 4 to 6° for 20 hours before planting (P. Ray, personal communication); this cold treatment resulted in more uniform germination and growth. About 50 ml of hot 1.5 % agar in tap water were poured into the base section of a 150 ml Erlenmeyer flask, the top section of the flask having been cut away intact at about 3.5 cm from the base. Four hydrated seeds, embryos pointed inward, were planted 90° apart, near the center of the agar surface to minimize the effect of centrifugal force. Each seed was angled 45° to the agar surface so that the emerging shoots grew away from and at right angles to the agar surface, and the roots grew into the agar. A drop of warm agar was placed around each seed to help maintain its position and orientation during the experimental period. The flask-top was stoppered with a loose cotton plug, and sealed to the base with masking tape; removal of the top of the flask facilitated phototropic stimulation and subsequent shadowgraphing of the seedlings.

Gravity Compensation. Each flask assembly was clamped onto a multiple unit, single-axis clinostat (fig 1), and rotated at 2 rpm (22, 24) by a synchronous-motor drive. Larsen (22, 24) has shown that lower rates of clinostat rotation induce

continuous geotropic movement of plant organs. Rotational axes were horizontal for gravity compensation and vertical as a control for motion per se. Change in the position of the rotational axis was obtained by shifting the entire clinostat, using a spirit level for final adjustment. At 2 rpm, the maximum centrifugal force imposed on the seedling was about $5 \times 10^{-5} \times g$, a level about 2 orders of magnitude less than the range of force required for material geotropism of the *Avena* shoot (19, and unpublished data). Clinostat rotation began as soon as the flasks were set in place and, except as indicated, continued throughout the experimental period.

Growth Conditions and Phototropic Stimulation. Germinating seed were exposed to red light (General Electric Ruby Red tungsten filament lamps, 7.5 w, incident irradiance about 0.4 mw·cm^{-2}) for the first 24 hours after planting to inhibit mesocotyl elongation. The plants were then grown in the dark at 25°, a green safe-light (32) being used for illumination when required. Seventy hours after planting, 1 seedling from each flask was selected for experiment; the remaining plants were discarded. The average initial length of the shoots was approximately 20 mm; shoots deviating from the mean length by more than 3 mm were discarded. For phototropic stimulation, the seedlings were irradiated unilaterally with blue light, using incident energies of 3 to 13 kergs·cm^{-2} to obtain curvatures in the first-positive range (32). The preceding energies were based on unshielded thermopile readings at the irradiation locus, and

included the thermal emission from the glass-filter source. The irradiances were, respectively, 0.61 to 2.65 kergs·cm^{-2}, when the light source was shielded by an infrared reflecting filter (Corning IRR glass, ⅛″ thickness), correcting for the 30 % absorption by the IRR glass in the visible spectrum. Irradiance was varied by changing the voltage applied to the source; the exposure time was always 15 seconds. A temperature-compensated thermopile, calibrated against a standard lamp, was used for the determination of irradiances. Phototropic curvatures were measured on shadowgraphs taken periodically after stimulation. Phototropically inactive orange light (tungsten-filament lamp plus 3 layers of DuPont cellophane No. 3159, Tango) and Kodak Panalure F paper were used for shadowgraphing.

Effect of Light and Compensation on Tissue Reactivity to Auxin. Seventy hours after planting, a solution of indoleacetic acid (IAA), sodium salt, in 0.1 % Tween-20 was applied symmetrically to the coleoptile tip of the intact seedling with a fine camel-hair brush. The controls for auxin treatment consisted of seedlings to which the Tween-20 solution, without auxin, was similarly applied. For irradiation, seedlings were illuminated equilaterally from above with the blue light for 15 seconds; the incident energy was 6.4 kergs·cm^{-2}. Immediately after auxin- or light-treatment or the combination of the 2, the seedlings were returned to their respective vertical or horizontal clinostats. Shadowgraphs were taken hourly during the 6 hours following treatment.
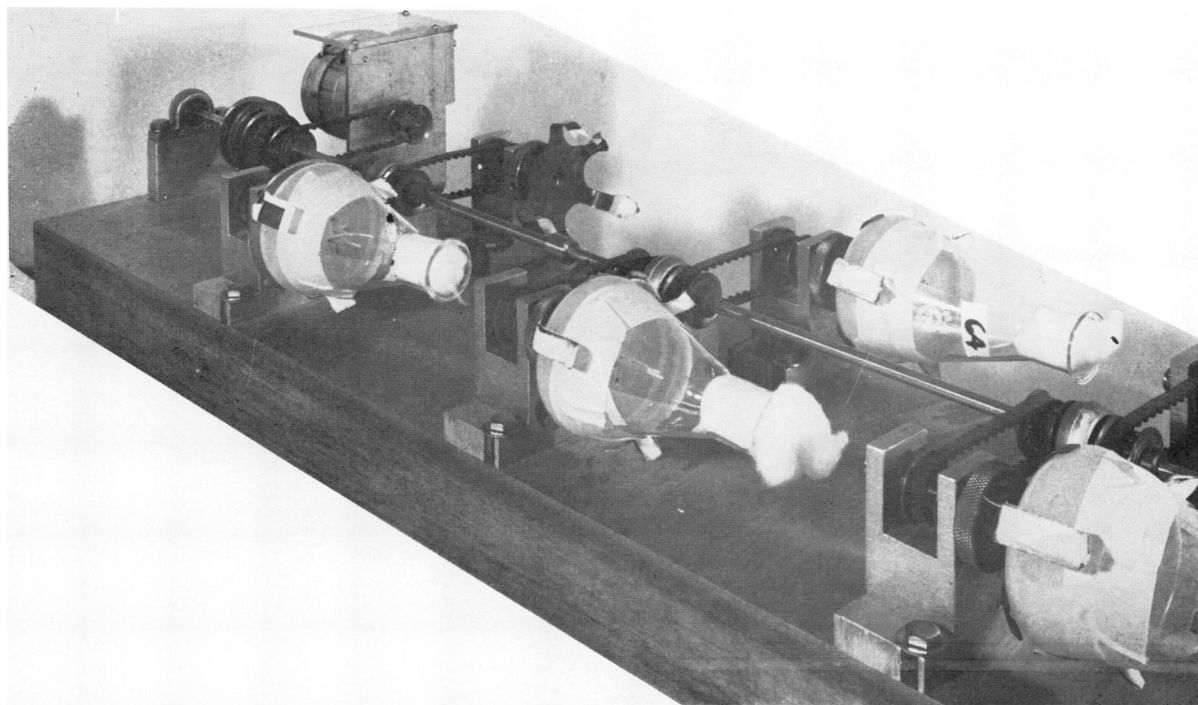

FIG. 1. Multiple unit, single-axis, clinostat assembly.

Auxin Content. Five-mm tips of 70-hour old seedlings, gravity-compensated or vertically rotated, were excised and their cut surface blotted with moist filter paper. The tips were then mounted vertically on a 1 × 8 × 11 mm agar block (1.25 % agar in tap water). Thirty tips were mounted on 1 block. A thin film of water, about 10 μl, was spread on the block to facilitate tissue-block contact. Tip-block assemblies were kept in the dark for 3 hours in a water-saturated atmosphere at 25° for auxin diffusion, and then disassembled. The blocks were kept in a moist atmosphere for several hours to equilibrate. They were then divided into 12 smaller blocks for assay by the *Avena* curvature test (23).

Auxin Transport. ^{14}C-Methylene labeled IAA, 12.6 C_i/mole, was stored in purified (36) acetonitrile. An aliquot of this solution was resolved by paper chromatography before use (17). The eluted ^{14}C-IAA was dissolved in aqueous 0.1 % Tween-20. For transport determinations, a 3 mm length of electrical "spaghetti" tubing (1 mm i.d.) was slipped over and supported by the tip of the intact coleop-

tile (fig 2). About 9 mμg of ^{14}C-IAA in 6 μl solution was introduced into the tubing lumen using a No. 30 hypodermic needle. Working with 3 flasks at a time, fitting and filling of the tubing involved removal of the seedlings from the clinostat for no more than 3 minutes. The donor tubing was allowed to remain on the seedling at 24° in the dark. At hourly intervals for 5 hours, assemblies were separated into the following parts to determine the distribution of ^{14}C-activity: 1) tubing + rinse of the coleoptile tip with water-saturated scintillation solvent, 2) apical 5-mm of the coleoptile tip, 3) next lower 15 mm, 4) remainder of the shoot, 5) residual seed, and 6) roots. Occasionally leakage from an ill-fitting donor tube was observed: this was readily detected as a glistening reflection from the tissue beneath the tubing when each flask was held up to the safelight for inspection. Such assemblies were discarded. Levels of radioactivity were determined by liquid scintillation counting, the various parts being equilibrated in the scintillation solvent [Liquifluor, 25x: toluene: absolute ethanol, 4: 71: 25, v/v/v, (33)] for at least 2 hours at 25° before counting.
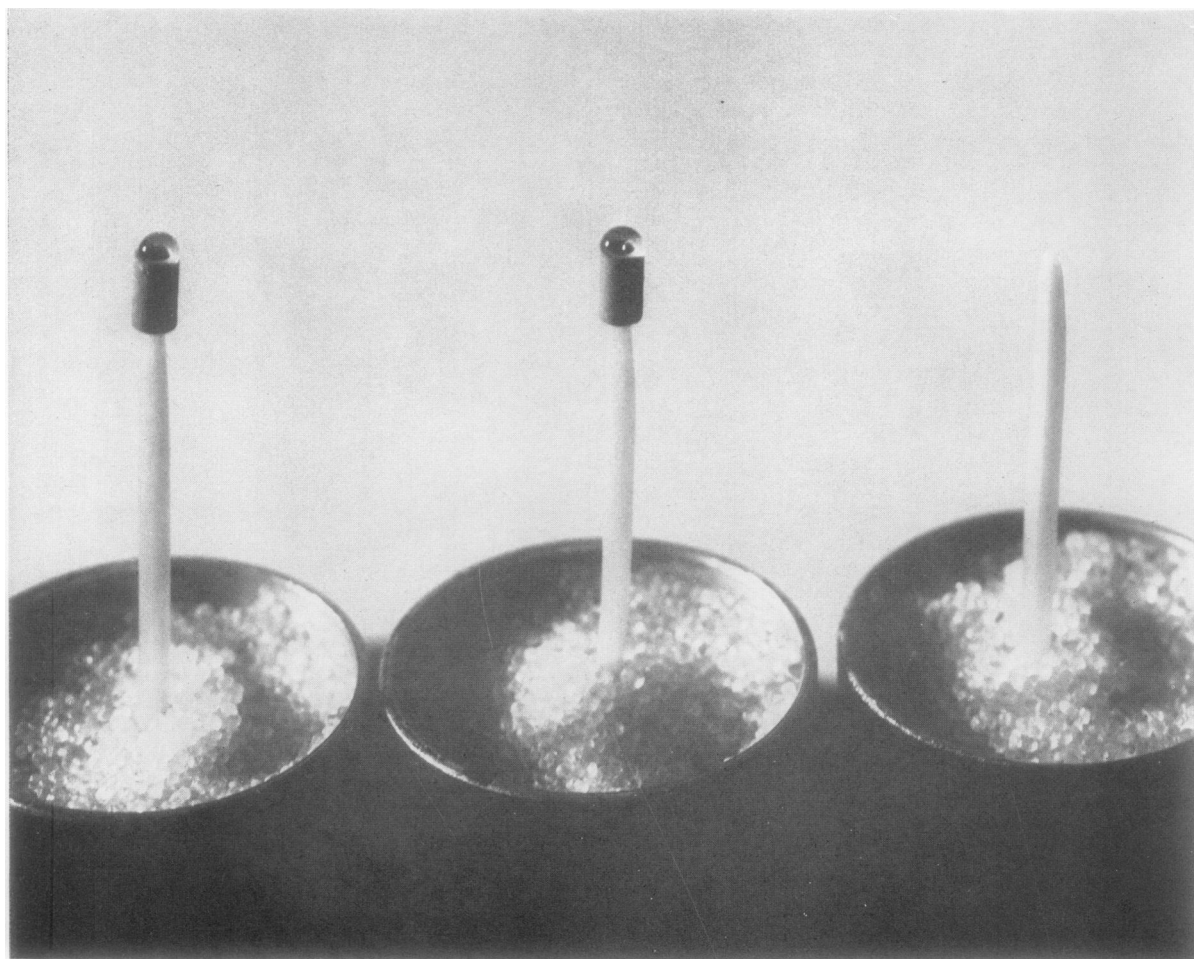

FIG. 2. Donor-tube seedling assemblies used for measuring IAA transport.

We considered that part 1, the residual donor solution and rinse of the tip, would be in error by the amount of radioactivity adhering to the surface of the tip tissue. To obtain an estimate of this residue, typical transport assemblies were made in replicate. Immediately after supply of the ^{14}C-IAA solution to each assembly, the tubing was removed and the coleoptile rinsed with water-saturated scintillation solvent. The tip was then excised from the coleoptile and its radioactivity determined. Residual radioactivity on the tip surface was found to be (2.4 ± 0.9) % of the total ^{14}C-IAA applied. All mean counts for the tip tissues in the transport experiments were corrected by the above factor.

Data Analysis. Duncan's new multiple range tests (16) were used for statistical analysis of tables I and III, and the "t" test for paired differences for table II. The method of least squares was used for the fitted curves of figure 5.

Results and Discussion

Phototropic Response. To determine the effect of gravity treatment on first-positive phototropic response, compensated (C) and stationary (S) seedlings were irradiated unilaterally with various radiant densities. The response curves are shown in figure 3. These results show, first, that compensation after photoexposure increases the tropic response, here about 2-fold (compare CC and SC to SS and CS). This increase can be ascribed to
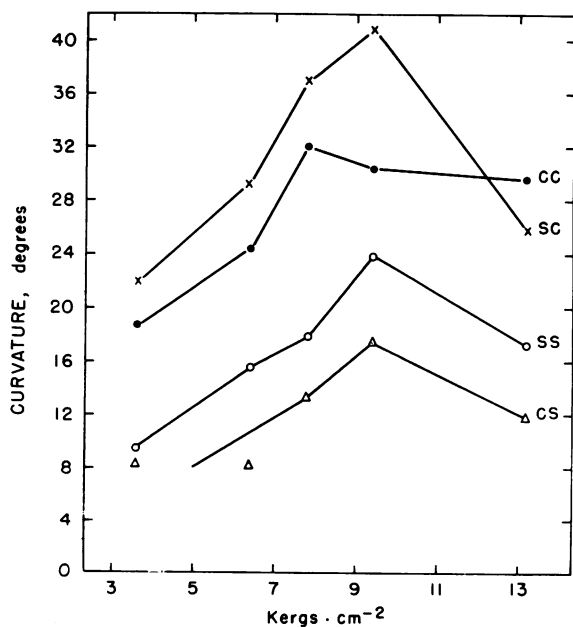

Fig. 3. Phototropic response curves for compensated and normal stationary *Avena* coleoptiles. Curvatures were determined 2 hours after phototropic stimulation. The first letter at each curve denotes the gravity treatment before, and the second after, photoexposure. C-compensated (rotational axis horizontal); S-vertical, stationary.

Table I. *Group Mean Phototropic Curvatures of* Avena *Coleoptiles Gravi-Compensated (CC), Vertically Rotated (RC) and Stationary (SC) Before Photostimulation and Compensated Afterwards*

The data are the means of 6 successive hourly measurements of curvature in 4 separate experiments, with 6 to 9 plants per experimental variant.

| | Exposure, kergs · cm^{-2} | | | |
| | 6.4 | 7.8 | 9.4 | |
Treatment		Degrees*		Row mean
CC	57.8$_a$	64.4$_a$	57.8$_a$	60.0
RC	51.0$_b$	62.4$_a$	56.9$_a$	56.8
SC	55.6$_a$	72.6$_b$	61.8$_b$	63.3
Standard error**	±1.1	±2.0	±0.3	±0.9

* For each radiant density, values with dissimilar subscripts differ significantly at the 1 % level. For the Row Means, all values differ significantly at the 5 % level, and SC from RC at the 1 % level.

** Significance of difference determined by Duncan's studentized range tables (16).

absence of the geotropic stimulus that is experienced by a vertically-oriented curving shoot. Second, compensation does not materially change the energies at which maximum response occurred. Third, seedlings that were oriented vertically and were stationary during the growth period before photoexposure curved more than those that were compensated (compare SC to CC and SS to CS).

Compensation involves 2 conditions with respect to orientation and motion not experienced by a stationary seedling. The treatment of rotation on a vertical axis (designated R) was therefore introduced as a control for the motion component of compensation. In combination with the 3 gravity treatments, seedlings were irradiated unilaterally at 3 levels of radiant density and then placed under compensation. Curvatures were determined hourly for the following 6 hours. The group means for the 3 radiant exposures are given in table I, and the time course of curvature development after the least photoexposure is shown in figure 4. Rotation per se apparently decreases the phototropic response since curvatures of both the horizontally- and vertically-rotated plants (CC and RC) are less than those of plants kept in a vertical stationary (SC) position before exposure (table I). However, comparison of the curvatures of plants previously rotated horizontally (CC) to their vertically rotated controls (RC) indicates that gravity compensation enhances the phototropic response. This enhancement is greatest at the lowest radiant density and decreases toward the saturating radiant exposures.

If compensation were the sole variable affecting the photoresponse, there should be no difference in response between rotated and stationary plants when both are vertically oriented. That there was a difference in tropic curvature between these 2 control groups in the present experiments indicates
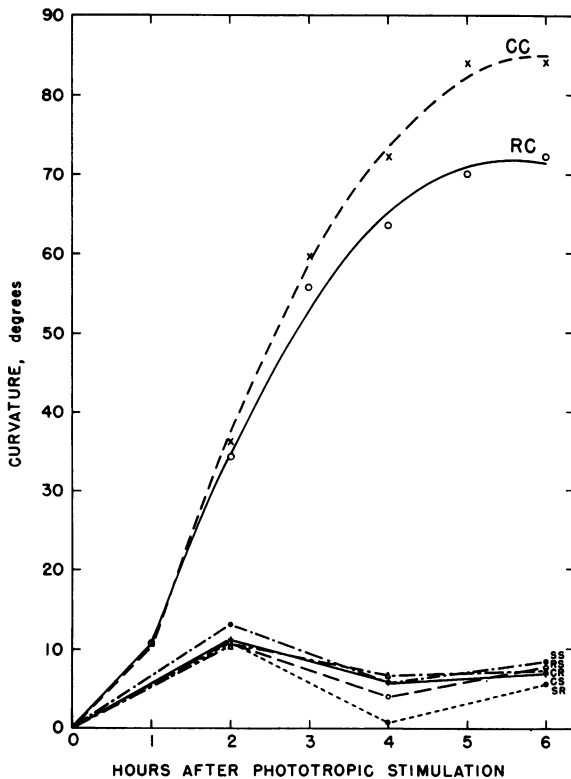
FIG. 4. Time-response curves of unilaterally irradiated *Avena* coleoptiles given various combinations of gravity treatment (R, vertically rotated control). Radiant exposure, 6.4 kergs · cm^{-2}.

a physiological effect of either motion per se or the technique utilized to obtain that motion. The rotational rate of the seedlings was 2 rpm and their maximum rotational radius was about 1 cm. As pointed out under methods, the geotropic stimulation from centrifugal force may therefore be disregarded.

It is possible that vibrational acceleration contributed significantly to the tropic response. Vibrational displacements were determined at various points on both horizontal and vertical clinostats during operation, using a piezo-electric accelerometer (General Radio Type 1560-P51). The frequency range of 2 to 1200 hertz was examined. There was a peak, non-persistent, acceleration of about $10^{-2} \times g$ in all of the clinostats. Since discontinuous accelerations are additive (25, 28), a recurrent force of the above magnitude could be above the threshold range of tropic perception by the coleoptile. It may be suggested, therefore, that clinostat experiments require a motion-control with a vertical axis of rotation, unless it is demonstrated that this treatment yields plants whose responses do not differ significantly from comparable stationary plants.

Figure 4 illustrates strikingly the effect of the geotropic stimulus when shoots are not compensated after unilateral irradiation. There was about a

10-fold greater curvature in response plateaus in the post-irradiation compensated seedlings. These plateaus occur at about 5 to 6 hours after phototropic stimulation with, and 1 to 2 hours after stimulation without, post-irradiation compensation. Similar observations were made by Arisz (2), who also noted that the time required for maximum curvature varied with the magnitude of the phototropic stimulus.

The time course of shoot curvature development shown in figure 4 follows the sigmoid response described by Lundegardh (26) for geotropism of the *Pisum* root (a rate demarcation that could not be distinguished by Larsen (24) with roots of *Artemesia*) : a starting phase with increasing rate, a "eumotorial" phase with a positive almost constant rate, and finally, an end phase in which the rate decreases and the organ eventually straightens. In the present study with compensated *Avena* coleoptiles, the phase of almost constant rate occurred approximately 1 to 3 hours after irradiation; the end phase occurs, as observed by Arisz (2), at about 5 to 6 hours.

Brauner and Hager (8) found that the terminal reduction in the rate of curvature development (end phase) in geostimulated shoots of *Helianthus* occurred more slowly when the plants were subsequently rotated on a horizontal clinostat. In *Avena*, we find this phenomenon not only with post-irradiation compensation (fig 4, compare upper and lower sets of curves) but also with compensation which takes place before photoexposure (compare CC with RC, fig 4). The prolonging of the phototropic reaction is thus not solely a removal of the geotropic stimulus by compensation, but also involves a change in tropic reactivity at non-saturating radiant densities. Though the phototropic response to treatment CC differs significantly from that to RC (table I), the difference arises during the later stages of curvature development (fig 4). De Witt (38) has associated the end-phase reduction in rate of curving with auxin content: the higher the auxin level in the organ, the more rapid the reattainment of linear form. Therefore, it seemed possible that the compensated plants contained less auxin than did those that were vertically rotated. Observations directly in support of this hypothesis will be considered later in this paper.

Auxin Studies. The phototropic response is greater, and subsequent straightening is delayed, in the compensated seedlings compared with their vertically rotated controls. Since tropism is classically associated with differences in auxin content, the following, not mutually exclusive, possibilities may be considered: compensation alters the amount of auxin supplied by the tip, changes the hormonal imbalance induced by unilateral irradiation, or changes the reactivity of the tissues to the hormonal imbalance.

Since the rate of elongation of coleoptiles is normally limited by auxin, a difference in elongation might reflect a change in auxin content.
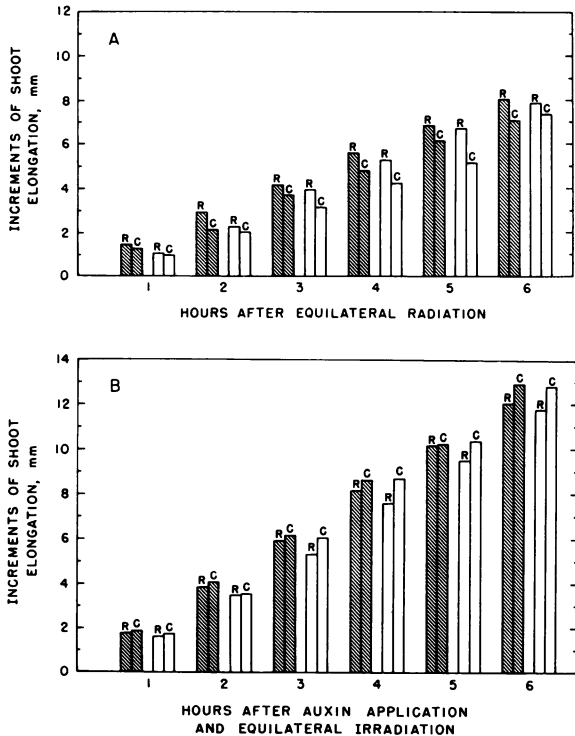
FIG. 5. Net elongation of intact 70-hour old *Avena* shoots as affected by gravity treatment, light and auxin. Shaded histogram = no irradiation; open histogram = equilateral irradiation, 6.4 kergs · cm^{-2} 70 hours after planting. A = no IAA; B = coleoptile apex moistened with IAA, 5 μg. The columns represent the means of 3 experiments. In each experiment, 8 plants in duplicate were used per treatment, and A and B were run simultaneously.

Previous studies of growth with clinostats reveal no uniformity of interpretation: influences of clinostat rotation on the growth rates of various organs have (4, 5, 6, 13, 14, 20, 22, 27, 30, 35) and have not (3, 9, 14, 15, 34) been observed. In our hands, when coleoptiles were measured 70 hours after planting, no significant difference in mean length was found between the compensated and vertically rotated plants. However, in the period between 70 and 76 hours, the coleoptile of the compensated seedlings grows materially slower than the vertically rotated control (fig 5A). This was found both for coleoptiles irradiated equilaterally and for those unirradiated. Furthermore, illumination itself resulted in a temporary reduction in growth rate (see also 29). Hence, for a portion of the growth of the coleoptile, compensation and light cause a significant decrease in rate of elongation. Conceivably these decreases could stem either from a decrease in sensitivity of the tissues to auxin or from a decrease in the amount of auxin available for growth.

Sensitivity to Auxin. The effect of compensation and light on tissue reactivity to exogenous auxin was then tested. First, concentration-growth responses of the intact *Avena* seedling to apically applied IAA (see Methods) were determined as an index of physiological concentration. The response curves are shown in figure 6. As with the section test, elongation is approximately proportional to the logarithm of the amount of auxin supplied. Here almost 5 orders of magnitude in amount of IAA did not saturate the response. Based on these results, 5 μg of IAA were applied to the coleoptile tips of compensated and vertically rotated seedlings at 70 hours after planting. The seedlings were then either irradiated equilaterally or not irradiated. Lengths of the coleoptiles were recorded over the next 6 hours. These measurements are shown as histograms in figure 5B. Comparison with figure 5A shows the overall enhancement of coleoptile elongation by the IAA. Auxin treatment of the coleoptile reversed the growth decrease induced by compensation, causing the growth rate of the compensated coleoptile to surpass that of its vertically rotated control. The group differences between the vertically rotated and compensated seedlings, either in the light or in the dark (figs 5A, 5B), are significant at the 1 % probability level. It may be concluded that compensation enhanced the response of the intact organs to applied auxin. Similar inferences have been drawn recently in 2 studies with cut tissues. Dedolph, et al., (14) observed that previous compensation of the intact seedling increased the curvature response of the decapitated *Avena* coleoptiles on whose stump IAA was applied unilaterally. And Brauner (7) found that the sensitivity of *Helianthus* hypocotyl sections to auxin is also increased by previous clinostat rotation of the plant on its horizontal axis. The maximum enhancement occurred after 3 hours of clinostat rotation. These enhancements of response by com-
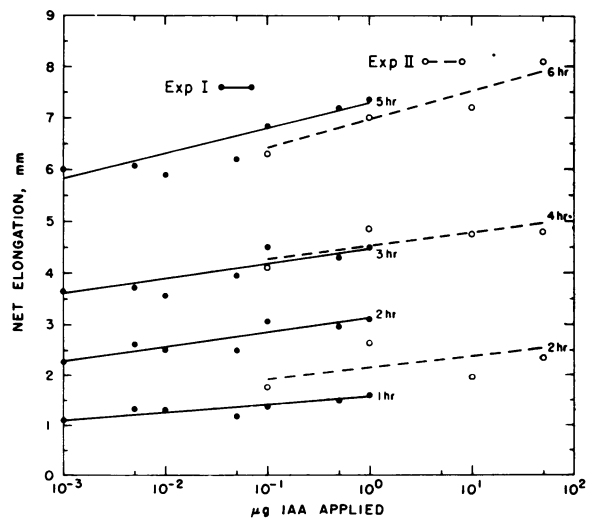

FIG. 6. IAA dosage-response curves for elongation of intact *Avena* shoots. Measurements made at the indicated intervals after apical application of the auxin. Each datum is the mean of 2 replicates, 8 and 10 plants per replicate, respectively, for Expt. I and II,

pensation may be associated with the higher metabolic activity of tissues that have been compensated or are undergoing compensation (11).

Exogenously supplied auxin did not reverse materially the growth impairment caused by light. Neither did light, at the radiant density employed, A) alter the slope of the curve of growth response to exogenous auxin, or B) affect the growth increment arising from the addition of auxin.

Auxin Content. Since compensation increases rather than decreases the sensitivity of the coleoptile to auxin, the alternate possibility that compensation decreases the amount of auxin available for growth was examined. As described under Methods, "diffusible" auxin contents were estimated by the *Avena* curvature test. The results are tabulated in table II. Gravity compensation of the seedling, compared to the vertically rotated controls, gives rise to a small (16 %) but nevertheless significant decrease in the amount of auxin diffusing from the coleoptile tip. In the present experiments the tips were removed from the clinostats for the period of diffusion. Dedolph (11) has shown that the respiratory rate of *Avena* seedlings under compensation drops when the plants were transferred to the vertical rotated position, reaching that of the rotated control within 2 hours. Therefore, the difference observed between the compensated and rotated seedlings (table II) might have been greater had the gravity treatments been continued during the 3-hour diffusion period. Trend differences similar to those shown in table II were indicated by the data of Dedolph et al. (14) where the amount of auxin diffusing from tips of compensated *Avena* coleoptiles was less than that from tips of plants vertically rotated. However, the

Table II. *Effect of Gravity-Compensation on the Diffusible Auxin of* Avena *Coleoptile Tips*

Each datum is the mean curvature of 12 test plants.

| Experiment | Gravity treatment | |
| | C | R |
	Degrees curvature	
I	12.5	14.1
	11.9	12.9
	9.4	11.0
II	9.4	10.2
	10.2	9.0
	6.6	12.7
III	12.0	14.7
	13.5	16.3
	...	14.5
Mean	10.7	12.8*
IAA (μg)/5mm tip**	5.1 × 10⁻⁷	6.0 × 10⁻⁷

* R is significantly greater than C at the 5 % level, standard error of difference ±0.74.

** Based on concentration-response curves for IAA simultaneously run in each experiment.

difference there noted was not significant statistically.

Though the IAA equivalents per 5 mm tip (table II) are less than those reported by Larsen (21), these results do support our hypothesis, based on de Witt's observations (38), that the difference in the straightening rate between the phototropically curved compensated and vertically rotated *Avena* coleoptile is caused by a difference in their auxin contents. The vertically rotated seedlings, with more auxin than the compensated, straighten more rapidly. Comparison between our results and those reported in the literature as to the effect of gravity nullification on auxin level is difficult. Brain (6) and Schmitz (31) found a higher content of diffusible auxin, respectively, in the hypocotyls of *Lupinus* and nodes of grasses grown on the horizontal clinostat. However, these workers did not run vertically-rotated controls.

Auxin Transport. The lesser amount of auxin diffusing from the tip of the compensated seedling than from the vertical rotated control might be the result of a compensation-induced reduction of auxin transport. The basipetal translocation of applied ^{14}C-indoleacetic acid (^{14}C-IAA) was therefore determined as an index of the effect of gravity treatment on auxin transport.

In preliminary experiments with ^{14}C-IAA applied apically to intact shoots, we found essentially no radioactivity in the seed or roots 5 hours after application of the labeled auxin. Measurements were therefore restricted to the tissue of the shoot. Data on the effect of compensation on auxin transport are shown in table III.

The ^{14}C-IAA applied to each seedling varied from 5 to 17 mμg. Since there was no correlation between the amount of auxin applied and the fraction absorbed (correlation coefficient, −0.23), replicate experiments were pooled to facilitate comparison between treatments. While compensation did not affect the auxin absorption by either the dark or equilaterally irradiated intact shoot, and did not affect the transport in the unirradiated tissues (table III), it appears to reduce the ^{14}C-IAA transport in irradiated seedlings. The 5 mm tips of the irradiated compensated shoot retain a small but significantly greater amount of IAA than those of the rotated controls. Although the ^{14}C-IAA activities are less in the lower portions of the compensated shoot than in the rotated controls, both in the irradiated and non-irradiated seedlings, the difference here is not significant statistically (5 % probability level).

These results suggest an interaction between the effects of light and gravity, and that compensation causes a reduction in the amount of IAA transported basipetally in the irradiated seedlings. Such interaction would explain the increase in phototropic response of the gravity compensated seedling as a result of an increased differential of auxin transport between the irradiated and the shaded

Table III. *Effect of Gravity Treatment on the* [14]*C-IAA Distribution in the Equilaterally Irradiated (6.4 kergs • cm*[-2])
and Unirradiated Shoot of the Intact Avena *Seedling*

Each datum is the mean of 3 replicates, 3 plants per replicate.

Treatment		Time hr	NO IRRADIATION						EQUILATERAL IRRADIATION					
			1	2	3	4	5	Mean	1	2	3	4	5	Mean
Rotated Control	Tip 5 mm		80.8	65.5	58.9	56.6	48.3	62.0	74.5	60.2	53.0	59.5	56.5	60.7*
	Mid 15 mm		15.7	31.0	35.1	35.6	41.0	31.7	25.1	36.3	38.2	35.0	35.5	34.0
	Base		3.5	3.5	6.0	7.8	10.7	6.3	0.4	3.5	9.4	5.5	8.0	5.4
	% Absorption		35.6	42.9	48.8	46.2	39.0	42.5	36.7	38.6	27.3	47.7	37.6	37.6
Gravity Compensation	Tip 5 mm		79.6	67.8	57.0	58.9	56.2	63.9	80.5	68.5	56.8	57.2	60.6	64.7*
	Mid 15 mm		20.0	29.0	38.0	34.2	35.5	31.3	19.3	28.0	37.4	34.7	33.2	30.5
	Base		0.4	3.2	5.0	6.9	8.2	4.8	0.1	3.5	5.8	8.1	6.2	4.8
	% Absorption		38.5	32.3	42.2	44.5	35.4	38.6	36.0	40.1	51.3	50.7	40.9	43.8

* In the equilateral irradiation treatment, the tip-5 mm of the gravity-compensated treatment retains significantly more ^{14}C-IAA than the comparable rotated control [5 % probability level, standard error ±1.36 (16)].

half. This interpretation parallels Anker's (1) speculation about the observations of Bremekamp (10). Bremekamp found that horizontal clinostat rotation of *Avena* coleoptiles would increase geotropic curvature (cf. also 11, 13). Anker suggested that an impairment of auxin transport by the clinostat treatment would lead to an accumulation of auxin in the tip. And de Witt (38) found that the geosensitivity of a seedling is dependent upon the auxin content of the tip: within limits, the higher the auxin content, the greater is the response.

The transport differences noted above, as well as the effect of compensation on the amount of auxin diffusing from the tip (table II), and the growth differences between the compensated and vertically rotated shoot (fig 5), are of small magnitude. These differences are, respectively, about 7, 16, and from 10 to 20 % of the rotated-control measurements. Are they sufficient to account for the alterations in phototropic response? It should be borne in mind that tropism is a consequence of difference in auxin limited elongation between proximal and distal tissues in the plane of stimulus direction. And that relatively small elongation differences are involved in producing curvature of the organ. This is illustrated by the relationship of curvature to difference in length between the shaded and irradiated sides of an unilaterally irradiated coleoptile (fig 7). The lengths of the convex and concave surfaces of the shadowgraphed coleoptile were approximated by measurement with a flexible ruler. Since profiles were measured, the figure is derived from maximum differences in length between the 2 sides of the organ. Even so, a lateral difference that is less than 2 % of the length of the coleoptile may be associated with curvatures of about 10°. A 90° curvature involves a longitudinal difference of only about 10 %. The curve also illustrates the direct proportionality of the angle of curvature to the lateral differences in elongation (cf. 37).

Compensation results in an increase in phototropic curvature, a decrease in growth rate, and

a slower rate of straightening of the curved coleoptile. These responses can be associated with the following consequences of compensation: A) an increase in tissue sensitivity to auxin, B) a decrease in the amount of auxin supplied by the tip, and
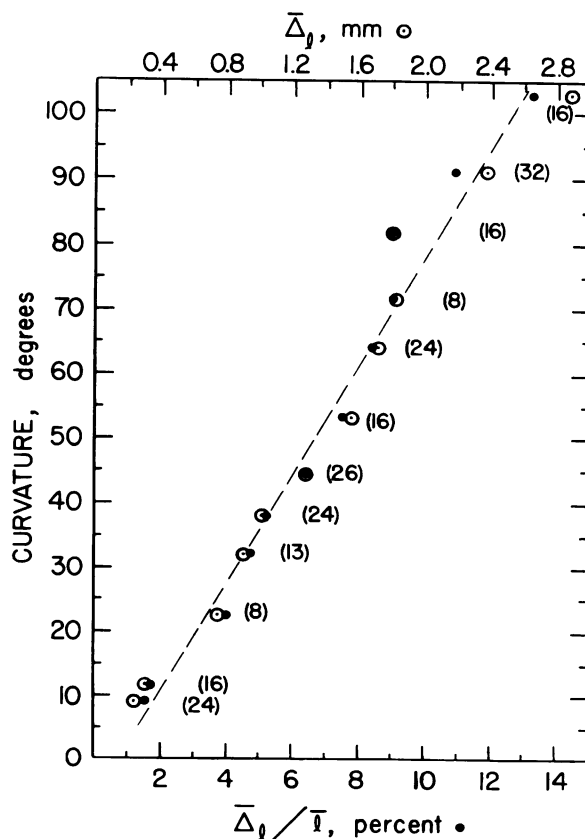

FIG. 7. Relationship of curvature to difference in length between the shaded and irradiated sides of the compensated *Avena* coleoptile at various times after unilateral irradiation. The number of coleoptiles sampled for each datum is shown in parenthesis. Δ_1: mean lateral difference in length; 1: mean length.

possibly, from the interaction between compensation and light, C) a greater difference in the auxin transport between the illuminated and shaded half of the phototropically stimulated shoot.

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