LIGHT GROWTH RESPONSE AND AUXIN CURVATURES OF AVENA

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1. *Introduction, Method.*—In an earlier paper in these PROCEEDINGS (Van Overbeek 1936) it was shown that decapitated Avena coleoptiles to which auxin-a was applied unilaterally, curved less if they were continuously exposed to light than if they were kept in the dark. This paper presents a closer study of the phenomenon; when the relation of time to the auxin curvatures is considered. This was possible by using a device designed by Went (in press) with which it has become possible to record the curvatures of a large number of decapitated coleoptiles at any time desired, without exposing them to light. The principal points of this method are the following. The primary leaves of etiolated seedlings were pulled out and removed and a straw from Bermuda grass (Cynodon Dactylon) about 10 cm. long, was stuck about 2–3 mm. into the lumen of the coleoptiles. A small part near the tip of these straws was photographed by a small horizontal beam of light on a revolving drum to which bromide paper was attached. In this way a record is obtained showing for each of the plants every 6 minutes the distance the straw has moved from its original position. For small angles this distance is practically proportional to the angle of curvature of the coleoptile. The curvatures of the exposed plants were recorded in a similar way. These plants were placed between two mirrors which reflected the light from a 10-watt lamp above them on two opposite sides of the coleoptiles. Between the lamp and mirrors was a water layer of about 10 cm. to check the heat radiation from the lamp. The intensity of the light striking the plants was about 500 M.C.

2. *The Light Growth Response Demonstrated by Means of Auxin Curvatures.*—Avena plants were decapitated twice with an interval of about 2 to 3 hours between them. The leaves were pulled out and the straws were stuck 2–3 mm. into the lumen of the coleoptiles. Then agar blocks containing auxin-a were applied. The auxin was extracted from cornmeal (see Van Overbeek, 1936 a and b). About 10 minutes after the blocks were put on the first recording was made. Twenty-four minutes after the blocks were put on, the light was switched on in one set of plants in order to expose them. Figure 1 shows the results of such an experiment, in which three different concentrations of auxin were used. The curve marked 1 was obtained by application of the lowest concentration, which, in the standard Avena test (Went 1935), gave a curvature of about 3°. The other

sets of curves marked 2 and 4 were obtained by application of auxin concentrations which were, respectively, 2 and 4 times as high as the one administered in set 1. The standard test of these concentrations gave 7° and 17° curvature, respectively.

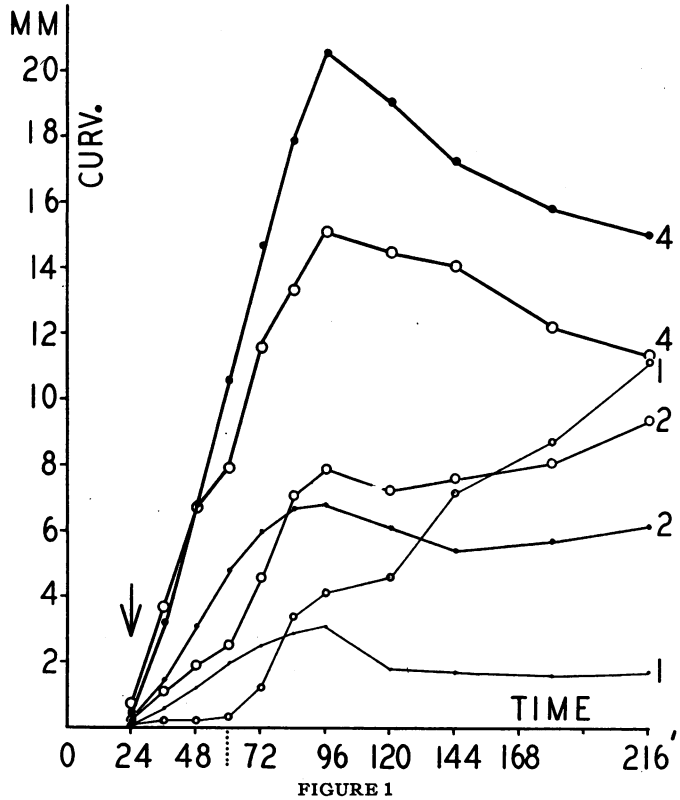

FIGURE 1

Auxin curvatures of exposed (open circles) and non-exposed (black dots) decapitated Avena coleoptiles. Abcissa: time after the block containing the auxin had been put on. Exposure to light started 24 minutes later (arrow). The vertical dotted line indicates the moment when the rate of curvature of the exposed plants begins to increase. Ordinate: curvature of the plants (in mm. deviation of the extended coleoptile from the vertical position). Mean values of 6 plants for each curve. Temperature: 20°C. Exp. number 60213.

The curves of the non-exposed plants show that the coleoptiles start to curve about 20 minutes after the blocks were put on. This is probably due to the fact that the topmost part of the coleoptile is not able to curve because the straw in that part prevents it from doing so. Then after the coleoptiles start to curve the curvature is almost directly proportional to

the time until about 72 minutes after the blocks were put on. At 96 minutes after the blocks are put on the curves start to go back. These figures have only approximate value; a detailed study of these curvatures of non-exposed coleoptiles is made by Went and is not presented here.

The curves showing the course of the curvatures of the exposed plants are quite different from the ones, just described, of the non-exposed coleoptiles. In all light-curves, but most markedly in the curves 1 and 2, two parts can be distinguished. (1) A part from the moment the exposure began until 36 minutes later, in which the rate of curvature of the exposed plants is less than in the non-exposed controls. (2) A part following the first part immediately, showing that 36 minutes after the exposure began the rate of curvature increases again. In many cases (possibly depending upon the concentration of the auxin) the rate of curvature in the second part of the curve is even higher in the light than in the dark. This is the case in the curves 1 and 2 of figure 1, and also in the two lowest concentrations of an experiment partly presented in table 1. Figure 2 shows the rates of curvature (in 0.1 mm. horizontal deviation of the straw per 12 minutes) of exposed plants as compared to non-exposed plants. This figure is calculated from the curve 2 of figure 1. Similar results are given in table 1 (column: dark-light). The horizontal dotted line in figure 2 indicates the place in the graph where the rate of curvature is the same in the dark as in the light. Below this line the rate of curvature is smaller in the light than in the dark; and above the dotted line the rate of curvature is larger in the light than in the dark.

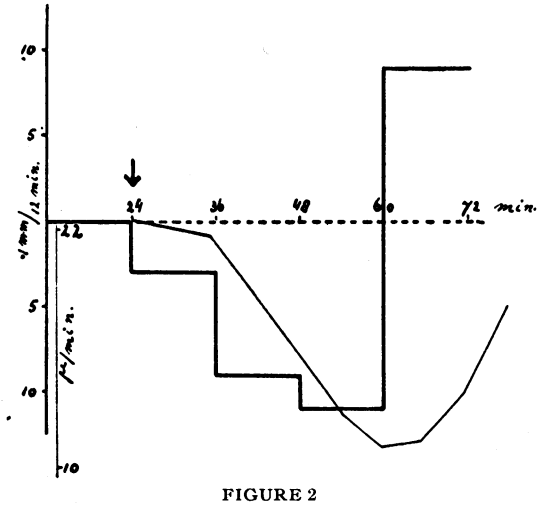

FIGURE 2

The effect of exposure to light upon the rate of curvature (heavy line) and upon the growth rate (thin line; after Koningsberger). Abcissa same as in figure 1. Ordinate: rate of curvature in the dark minus rate of curvature in the light; and (thin line) growth rate. Further explanation in text.

Table 1 shows the results of a similar experiment represented by the curves of figure 1. The relative concentration of the auxin and the curvature obtained in the standard Avena test are shown in the first column. The third and fourth columns show the increase in curvature in dark and

light during periods indicated in the second column. The fifth column shows the differences in rate of curvature between dark and light. The sixth column shows the ratio of the increase in curvature, during the first 36 minutes after the exposure to light began, of the non-exposed plants and the exposed ones (dark/light).

TABLE 1

RATES OF CURVATURE OF EXPOSED AND NON-EXPOSED AVENA COLEOPTILES. TEMPERATURE, TIME EXPOSURE STARTED, ETC., THE SAME AS IN FIGURE 1. AVERAGE VALUES OF 8 PLANTS. EXP. NUMBER 60130.

REL. AUXIN CONC.	PERIOD OF TIME	INCREASE OR DECREASE(−) IN CURVATURE DURING 18-MINUTE PERIODS DARK	LIGHT	DARK-LIGHT	DARK/LIGHT
3 (about 11°)	24–42	29	18	11	63/25 = 2.51
	42–60	34	7	24	
	60–78	20	15	5	
	78–96	21	8	13	
2 (about 7°)	24–42	22	9	11	46/13 = 3.54
	42–60	24	4	20	
	60–78	14	21	−7	
	78–96	3	12	−9	
1 (about 4°)	24–42	11	−2	13	27/−1 = ∼
	42–60	16	1	15	
	60–78	−5	21	−26	
	78–96	8	18	−10	

If the rate of curvature at various times after exposure to light as discussed above is compared with the growth rates obtained by Koningsberger (1923, p. 260, Fig. 1) on straight growing intact *Avena* seedlings a striking resemblance is noticed (Fig. 2). Koningsberger exposed the plants to 400 M.C. at 20°C. and found that the growth rate dropped until after 35 minutes a minimum was reached. From this time on the growth rate increased again.

3. *The Ratio of the Curvatures of Exposed and Non-Exposed Plants and the Influence of the Concentration of Auxin upon it.*—In an earlier paper dealing with the light growth response of Raphanus hypocotyls (Van Overbeek 1933) it was found that a definite relation exists between the ratio of the auxin curvatures in the light and the ones in the dark and the concentration of the auxin applied. When the curvatures were plotted against the concentration, then in the dark a curve was found similar to the ones described by Went (1928) and Van der Wey (1931), viz., a so-called "Blackman curve." In the light, however, the curve had an S-shape (Van Overbeek, 1933, Fig. 27, p. 604). The relation between the ratio of the auxin curvatures in light and dark and the concentration of the auxin applied was found to be a hyperbola (Fig. 28, p. 605). In a recent article by Söding (1936) it is shown for Avena that the relation between curvature and concentration of auxin can be expressed by an S-shaped curve. Söding grew his

plants and performed his experiments in the daylight in contrast with Went's method. The curvatures, below the maximum angle, obtained by Söding's method, therefore, do not indicate directly the "strength" of an auxin preparation as they do when Went's test method is used.

The light growth response of Raphanus hypocotyls consists of a decrease in growth only. The first part of the light growth response in Avena (from 24 min. to the vertical dotted line in Fig. 1) can therefore, be compared with the response of Raphanus. If for this part of the light growth response the "dark/light" value is determined, the following figures are found: For concentration 3, 2 and 1 (table 1) the dark/light ratio is 2.51, 3.54 and ~, respectively. From figure 1 one can find for the concentrations 4, 2 and 1 respectively the following ratios: 1.42, 2.00 and 9.5. If these ratios are plotted against the concentration of the auxin a hyperbola is obtained (Fig. 3). This may indicate that the light growth response of Raphanus and the first part of the light growth response of Avena are of a similar nature. The increase in growth rate which is found in Avena apparently does not exist in Raphanus (see Van Overbeek, 1936b).

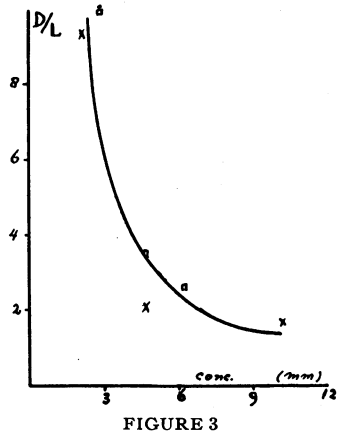

FIGURE 3

The ratio of the curvatures—36 minutes after the exposure started—of exposed and non-exposed coleoptiles as a function of the auxin concentration. Ordinate: dark/light. Abcissa: concentration. ×: obtained from experiment 60213. □: obtained from experiment 60130.

The typical increase in rate of curvature of the exposed plants to which auxin of low concentrations is applied (Fig. 1, light-curve 1) will not be considered here and is under investigation at present.

4. *Summary.*—The rate of curvature of decapitated Avena coleoptiles to which auxin is applied unilaterally shows a similar response to continuous exposure to light as the growth rate of the intact seedling does upon illumination (base growth response). The first part of the light growth response of the Avena coleoptile, which is a decrease in growth rate, is comparable to the light growth response of the Raphanus hypocotyl.

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