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STUDIES ON THE PATH OF TRANSMISSION OF PHOTOTROPIC AND GEOTROPIC STIMULI IN THE COLEOPTILE OF *AVENA*

BY

HELEN ALICE PURDY

KØBENHAVN
HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL
BIANCO LUNOS BOGTRYKKERI
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A. Historical Survey.

Investigations on the transmission of a phototropic stimulus date from the latter half of the nineteenth century. Since the results of the earlier investigators have been discussed and cited more or less in detail in the literature of succeeding workers, I shall make no attempt at a complete historical survey but rather mention some of the more recent articles, having a direct relation to the special problem in question.

Boysen Jensen (1910, 1911, 1913) obtained a transmission of a phototropic stimulus from the unilaterally illuminated tip to the shaded base of the coleoptile of *Avena*, although direct contact between the plasma of the tip and base was broken. In the experiments of Boysen Jensen the tip of the coleoptile was removed with a sharp scalpel, a drop of a 10 % solution of neutralized gelatine was applied to the injured surface of the stump, the tip reset in the original position and the wound ringed with melted cocoa butter. On exposure of the tip to unilateral illumination, in the majority of cases a transmission of the phototropic stimulus to the shaded base was evidenced by a positive basal curvature, while the shaded control plants for the most part remained straight. A similar transmission of a geotropic stimulus was also accomplished by Boysen Jensen.

Later Paál (1914, 1918) investigated the probability of "Reizleitung über einen Schnitt" and arrived at the same conclusion as Boysen Jensen. Paál further demonstrated the transmission of a phototropic stimulus through an interposed gelatinous membrane of at least 0.05—0.10 mm in thickness. This point was established by placing a thin slice of *Calamus,* previously soaked in a 10 % solution of gelatine, between the severed tip and stump of the coleoptile.

The extensive experiments of Stark (1921) show that transmission of traumatropic and haptotropic stimuli may take place over a cut from the tip to the base of the coleoptile in *Avena* and also in other *Gramineae.* Also a positive response was produced in the base upon stimulation of the tip, not only when the tip was reset on the individual to which it belonged, but also when it was placed on the stump of another individual of the same species, a different species of the same genus, a genus of the same sub-family, or a genus of a different sub-family.

With the fact fairly-well established, that phototropic, geotropic, traumatropic and haptotropic stimuli can be transmitted over a cut from the stimulated tip to the base of the coleoptile, the question of the nature of transmission arises.

At present the balance of evidence seems in favor of one or more substances migrating between the stimulated tip and base of the coleoptile, with which the transmission of the stimulus is closely connected. In the following citation Boysen Jensen (1911, 24) expresses this view: "On n'a jamais pu constater de transmission de l'irritation à travers une incision lorsque les plantes d'experience se trouvaient sous l'eau. L'eau doit être en état d'empêcher cette transmission, ce qui ne peut s'expliquer que dans l'hypothèse où la transmission de l'irritation serait du à une migration de substance ou d'ions, qui se diffusent dans l'eau et ne peuvent plus agir."

The pertinent work of RICCA (1916) on *Mimosa* also lends support to this theory. RICCA inserted a small glass tube filled with water between the tip and the base of the upper portion of a shoot and upon excitation of the base he noted a green fluid exuding from its cut surface and diffusing through the water. When the volume of water was not too large, the spreading of the substance to the cut surface of the tip was observed and under that condition only a response in the leaflets followed. Thereupon RICCA inferred that the green fluid contained matter, which was carried along through the medium of water and was involved in the transmission of the stimulus.

From his experiments on the transmission of a phototropic stimulus through a gelatinous membrane PAÁL (1918, 431) concludes: "Dass . . . die phototropische Reizleitung durch die Gelatineschicht nicht durch elektrische Ströme, sondern durch diffundierende Stoffe vermittelt wird."

STARK demonstrated the existence of a relation between matter and tropic response in his final experiments. He placed a small cube of agar, containing an extract of the sap of injured coleoptiles, directly on the cut-surface of one side of a stump, while he used only pure agar in the control plants. The presence of the extract caused a marked increase in the number of individuals giving a response.

Since the association of the above-mentioned stimuli with diffusible matter seems to be generally conceded, let us consider the debatable issue, the probable path of transmission of the stimuli. Does transmission take place universally throughout the coleoptile or is the path restricted?

As the result of experimentation FITTING (1907) formulated the theory of transmission of a tropic stimulus universally throughout the living cells of the coleoptile.

In contradiction to FITTING, BOYSEN JENSEN demonstrated experimentally that transmission of the stimulus takes place mainly on the side of the coleoptile farthest from the light and on the lower side in geotropic experiments. As stated above, BOYSEN JENSEN obtained a transmission of a phototropic stimulus over a wound, therefore, his chief objection to the method employed by FITTING was that in the greater part of his experiments no steps were taken to prevent this transmission. BOYSEN JENSEN found that by inserting a mica plate in the cut, a transmission of the stimulus took place, when the incision was nearest to light, but when farthest, the transmission observed was practically negligible. Consequently, he drew the conclusion: "Für die Annahme, dass die Reizleitung sich allseitig fortpflanzen kann, sind noch keine Beweise vorhanden. Im Gegenteil spricht alles dafür, dass die Reizleitung in der *Avena*-koleoptile lokalisiert ist."

VAN DER WOLK (1911) favors the opinion of FITTING that transmission of a phototropic stimulus takes place universally in living cells.

PAÁL and STARK have contributed considerable discussion of the subject but no decisive experimental work.

Since the path of transmission of a stimulus is a question of the utmost importance in the study of tropisms, and the results of experiments in this field require substantiation, I shall proceed to give a detailed account of my recent investigations treating the subject of transmission of both phototropic and geotropic stimuli in *Avena*.

B. Method.

The experiments were carried out on *Avena sativa* (var. "Gul Næsgaard") kindly provided by the Experimental Station at Lyngby. The grains were soaked for twenty-four hours in a shallow dish with just sufficient water to cover them. About twenty-five were planted daily in fresh, moist soil, contained in glass cylinders (10 cm in height and 2.5 cm in diameter). Germination took place in an electrically-heated thermostat at a temperature of 16—18° C. They were watered on the day of planting and on the following morning. This proved to be the most satisfactory course from the results of preliminary experiments, which showed that the degree of moisture greatly influenced the effectiveness of the experimental method. An excess of water frequently caused displacement of the foil, while dried out or freely-watered plants were only slightly sensitive. At the end of 4—6 days straight plants from 1.5—2.5 cm in length were chosen, all plants in which the hypocotyledonous stem had developed were discarded. The experimental work was carried out in a room completely darkened except for a dim, red, electric light.

The object of the experiments was to determine whether or not the position of the incision in relation to the source of illumination or gravity influenced the transmission of the stimulus. Therefore I exposed plants with the cut on the side of the coleoptile farthest or nearest in respect to the direction of the lighting, and above or below in regard to geotropic exposure. A quantitative determination of the response to the stimuli was made by actually measuring the curvature produced in the plants.

In general the experimental method employed was similar to that of Boysen Jensen. By means of a very sharp scalpel, I made an incision 3—5 mm from the tip and inserted a small rectangular piece of platinum foil. To prevent a possible transference of stimulatory substances from plant to plant, the pieces of foil were kept immersed in distilled water, when not in use, and the scalpel was carefully washed after making each incision.

The size of the curvature produced in the region of the coleoptile below the incision, was determined by the following method.[1] At the end of the period of exposure, the plants were uprooted and the foil removed. The curvature was then compared with arcs of circles having radii from 0.6—20 cm. When the concave side of the curvature was found to coincide with an arc, the length of the radius producing this arc was recorded (r), also the length of the shorter side of the curvature (l), measured with millimeter paper. The average thickness of the plants was obtained by measuring carefully with a micrometer several representative ones. The difference between the lengths of the shorter and longer sides of the curved base of the coleoptile (d) was

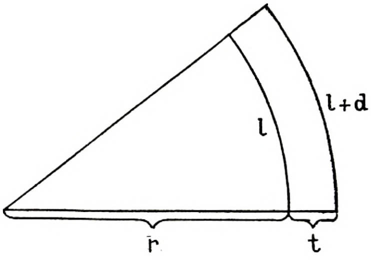

Fig. 1.

[1] A similar method is used by Sachs (1873, 392).

regarded as an indication of the response produced, being computed in this manner (cf. fig. 1):

$$\frac{r}{l} = \frac{r+t}{l+d}; \quad \frac{r}{r+t} = \frac{l}{l+d};$$

$$\frac{r}{t} = \frac{l}{d}; \qquad d = \frac{tl}{r}.$$ [1]

Since the incision made in the coleoptile produces a traumatropic response, the curvature resulting upon phototropic or geotropic stimulation is not solely due to the effect of light or geotropic influence. Therefore, a series of control experiments was run. In the phototropic experiments the controls consisted of plants completely shaded and placed between the experimental plants; in the geotropic experiments, plants stood in an upright position in the dark. The traumatropic response of the corresponding series was determined and added to or deducted, as the case required, from the curvature produced in the experimental plants.

The existence of these two simultaneous reactions[2] leads to uncertainty in the interpretation of the results. In order to avoid this complication, I repeated the above experiments with plants which had recovered from the traumatropic response occasioned by the incision.

Plants from 4—8 mm in length were cut late in the afternoon preceding the experiment. On the following morning the straight ones were selected for use.[3] The

[1] This equation can be found in Rothert (1894, 171).

[2] Van der Wolk in particular has objected to this complication involved in the above method.

[3] During the night if the plants had developed so that the incision in the inner leaf had grown beyond that in the side of the coleoptile, it was impossible to insert the foil securely. In this case, a second, slight

effectiveness of using recovered plants for the elimination of a traumatropic response from the results is clear on examination of the control plants. (cf. tables II & IV). Out of the ninety-five recovered plants, 95 % were straight at the end of the period of exposure.

For the purpose of ascertaining the reaction of the plants to the injury resulting from the incision, 17 straight

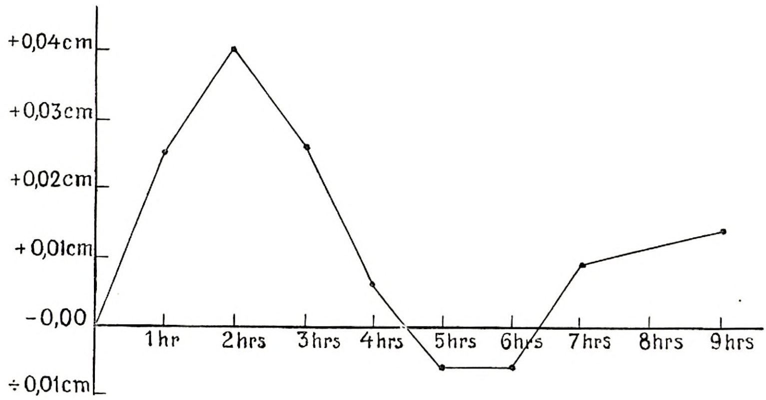

Fig. 2. Graph representing the traumatropic response of the seedlings of *Avena sativa* taking place during the nine hours following the making of the incision. The abscissae indicate the time in hours, the ordinates the mean **d** of the curvature.

plants from 1.0—1.4 cm in length were cut and observed at various intervals during part of the period of recovery. Complete measurements of the curvature taking place were made at each observation and the values for **d** computed. (cf. the table & fig. 2).[1]

cut was made in the leaf with the edge of the foil by drawing it back and forth a few times against the leaf. The dried out incision in these plants also lessened the probability of the displacement of the foil by water collecting in the cut.

[1] Although the number of plants used is insufficient to enable drawing a general conclusion, the results give an approximate idea of the response of the plants to the incision during the period of recovery.

Traumatropic response of the seedlings of *Avena sativa* (cf. fig. 2).

No. of plant	Period of Observation							
	1 hr.	2 hrs.	3 hrs.	4 hrs.	5 hrs.	6 hrs.	7 hrs.	9 hrs.[1]
1	+ .04	+ .04	+ .02	.00	.00	.00	.00	+ .03
2	.00	.00	.00	.00	— .03	— .04	— .04	.00
3	+ .06	+ .07	+ .02	.00	.00	.00	+ .02	.00
4	+ .06	+ .06	+ .06	+ .03	+ .02	+ .02	+ .06	+ .04
5	+ .04	+ .04	+ .02	.00	— .03	— .02	.00	.00
6	+ .05	+ .07	+ .08	+ .03	.00	.00	+ .06	+ .07
7	.00	+ .03	+ .02	+ 02	.00	.00	+ .04	+ .04
8	+ .03	+ .03	.00	.00	.00	.00	.00	.00
9	.00	+ .03	.00	— .04	— .04	— .04	.00	+ .02
10	+ .02	+ .04	+ .03	+ .02	.00	.00	.00	.00
11	.00	+ .03	.00	— .05	— .05	— .04	+ .02	+ .04
12	+ .04	+ .06	+ .04	+ .02	.00	.00	.00	.00
13	.00	+ .02	+ .01	.00	.00	.00	.00	.00
14	+ .02	+ .03	+ .03	.00	.00	.00	.00	.00
15	+ .03	+ .06	+ .06	+ .03	.00	.00	.00	.00
16	.00	+ .03	.00	00	.00	.00	.00	.00
17	+ .03	+ .04	+ .04	+ .04	+ .03	+ .02	.00	.00
Mean d	+ 0.025	+ 0.040	+ 0.025	+ 0.006	— 0.006	— 0.006	+ 0.009	+ 0.014 cm

To determine whether or not a slight traumatropic response might be produced in the recovered plants immediately after insertion of the foil, I observed at intervals of one hour a small number of plants, eigth in all, in which foil had been inserted. At the end of six hours no curvature was noted.[2]

In the phototropic experiments the method employed by BOYSEN JENSEN in shading the plants was followed. In every case a cover of black paper was used with a hole pierced in the center through which the tip of the coleop-

[1] No further observations were made until the following morning, when all the plant were straight.

[2] To prove that this result was not due to the fact that these seedlings had lost their sensibility, I placed them in a horizontal position with the incision on the upper side, and in one and one-half hours a strong, negative, geotropic response had begun to take place.

tile might pass. The plants were arranged in a row in a box with a glass front in air saturated by means of moist paper. The tip of the coleoptile was exposed in a temperature of 13—15° C. to unilateral illumination produced by an electric light bulb of 100 candle power about 2 meters distant. The bulb was enclosed in a wooden box having a circular opening in front 7 cm in diameter. In this manner a stream of light was directed to the row of plants in the opposite box. The periods of exposure of the tips of the coleoptiles include a range of $3^1/_2$—7 hours, the most favorable period being 5 hours.

Observations of preliminary experiments led me to make the incision, in the plants allowed to recover, less deep than in the plants used at once. My reason for doing this was that while the deeper incision seemed to produce less traumatropic response, it could not be used in the recovered plants, because during the long period of recovery a protrusion of the intersected leaf resulted, bending backwards and frequently breaking off the tip of the coleoptile. The incision in the recovered plants extended through about $^1/_2$ of the coleoptile and that in the plants used at once, about $^2/_3$. The same depth, of course, was used in cutting the individuals belonging to the same set of experiments. In the geotropic experiments a similar procedure was carried out.

In the geotropic experiments the plants were placed horizontally in a box where the air was saturated by means of moist black paper and a temperature of 13—18° C. was maintained. The periods of exposure varied from 3—7 hours, the most favorable period apparently being 4 hours. In these experiments not the tip alone but the entire plant was exposed to the stimulus.

C. Results.

a. Phototropic Experiments.

Experiment I (cf. table I).

Plants with incision made just before exposure.

a. Incision on side of coleoptile farthest from light.

Out of 47 plants, 5 individuals were curved in a positive phototropic direction, 6 in a negative while 36 were straight. The mean value for **d** = — 0·002 cm ± 0·003 cm.[1]

b. Incision on side of coleoptile nearest light.

Out of 52 plants, 51 individuals were curved in a positive direction, 1 was straight. The mean value for **d** = + 0.085 cm ± 0.007 cm.

c. Control plants completely shaded, placed between the experimental plants, some with incision farthest from light, others nearest.[2]

Out of 49 plants, 29 individuals curved in a positive traumatropic direction, 1 in a negative, while 19 were straight. The mean value for **d** = + 0.018 cm ± 0.004 cm.

In the plants with the incision nearest the light the curvature produced should be regarded as a combination of the phototropic and traumatropic responses, occurring simultaneously. Therefore, to obtain a value for **d** in these plants, which may be attributed to the phototropic stimulus

[1] These figures represent the mean error which was computed for each series of experiments. The method employed was that described in Johannsen (1913, 54).

[2] The results show that the response given by the control plants is unaffected by the position of the incision in relation to the source of illumination. Therefore the two lots will be considered as a whole in the computation of the results.

Table I. Phototropic Experiments — Fresh cuts.

a, represents values for **d** in plants with incision farthest from light; **b**, nearest light; **c**, control plants, (1) incision farthest from light, (2) incision nearest.

a	b	c (1)	c (2)
.00	+ .10	+ .02	+ .03
+ .05	+ .11	+ .02	+ .03
.00	+ .16	+ .03	+ .10
.00	+ .07	.00	+ .08
.00	+ .12	.00	+ .03
.00	+ .08	.00	.00
.00	+ .11	.00	+ .00
.00	+ .05	+ .00	+ .04
.00	+ .05	+ .00	.00
.00	+ .12	+ .00	.00
.00	+ .00	+ .00	+ .00
+ .02	+ .09	.00	+ .05
.00	+ .08	.00	.00
.00	+ .09	+ .03	+ .04
.00	+ .14	.00	.00
+ .00	+ .07	+ .05	+ .00
.00	.00	.00	.00
+ .04	+ .07	.00	.00
.00	+ .03	+ .03	+ .00
.00	+ .00	+ .00	.00
.00	+ .09	+ .04	+ .08
+ .00	+ .10	+ .04	.00
.00	+ .12	+ .09	+ .00
.00	+ .20	+ .08	.00
.00	+ .20		— .02
.00	+ .11		
.00	+ .08		
.00	+ .09		
.00	+ .05		
.00	+ .06		
.00	+ .06		
.00	+ .09		
.00	+ .00		
.00	+ .04		
.00	+ .03		
.00	+ .05		
.00	+ .11		
.00	+ .13		
.00	+ .09		
.00	+ .07		
.00	+ .03		
— .01	+ .11		
— .03	+ .16		
— .05	+ .09		
— .06	+ .15		
— .05	+ .10		
— .00	+ .06		
	+ .07		
	+ .11		
	+ .16		
	+ .09		
	+ .00		
Mean **d** = — 0.002 cm.	+ 0.085 cm.	+ 0.018 cm.	
Mean error = ± 0.003 cm.	± 0.007 cm.	± 0.004 cm.	

Table II. Phototropic Experiments—Recovered plants.

a, represent values for **d** in plants with incision farthest from light; b, nearest light; c, control plants, (1) incision farthest from light, (2) incision nearest.

a	b	c	
		(1)	(2)
.00	+ .05	+ .07	.00
.00	+ .05	.00	.00
.00	+ .07	.00	.00
.00	+ .08	.00	.00
.00	+ .04	.00	.00
.00	+ .04	.00	.00
.00	+ .04	.00	.00
.00	+ .03	.00	.00
.00	+ .07	.00	+ .00
.00	+ .07	.00	.00
.00	+ .11	.00	.00
.00	+ .11	.00	.00
+ .05	+ .08	.00	.00
.00	+ .11	.00	.00
.00	+ .10	.00	.00
.00	+ .07	.00	.00
.00	+ .04	+ .06	.00
+ .06	+ .07	+ .00	.00
.00	+ .07	.00	.00
.00	+ .07	.00	.00
.00	+ .08	.00	.00
+ .07	+ .06	.00	
.00	+ .12	.00	
.00	+ .06		
.00	+ .07		
.00	+ .05		
.00	+ .05		
.00	+ .05		
.00	+ .09		
.00	.00		
.00	+ .11		
.00	+ .07		
.00	+ .05		
+ .00	.00		
.00	+ .06		
.00	+ .07		
.00	+ .04		
.00	+ .03		
+ .07	+ .08		
.00	+ .12		
.00	+ .00		
+ .06	+ .05		
.00			

	a	b	c
Mean **d**	= + 0.007 cm.	+ 0.064 cm.	+ 0.003 cm.
Mean error	= ± 0.003 cm.	± 0.005 cm.	± 0.002 cm.

alone, it is necessary to subtract the mean **d** in the control plants of this experiment from the mean **d** of the experimental plants with the incision nearest light.

Similarly, the slight response in the plants with the incision farthest from light may be considered the result of a partial compensation of the opposing phototropic and traumatropic reactions. In this case then, the value for **d** should be subtracted from the mean value for **d** in the control plants considering both values positive.

The result of the above computation gives a value for **d** in the plants with the incision farthest from light of $+ 0.016$ cm ± 0.005 cm, in the plants with the incision nearest to light $+ 0.067$ cm ± 0.008 cm.

The above final results show that in the plants with the incision nearest to light a positive curvature has taken place, which is more than four times as great as that in the plants with the incision farthest from light.

Experiment II (cf. table II).

Plants with incision made on day preceding exposure.

a. Incision on side of coleoptile farthest from light (cf. fig. 3).

Out of 43 plants, 6 individuals were curved in a positive phototropic direction, 0 in a negative, while 37 were straight. The mean value for **d** $= + 0.007$ cm ± 0.003 cm.

b. Incision on side of coleoptile nearest light. (cf. fig. 4).

Out of 42 plants, 40 individuals were curved in a positive phototropic direction, 2 were straight. The mean value for **d** $= + 0.064$ cm ± 0.005 cm.

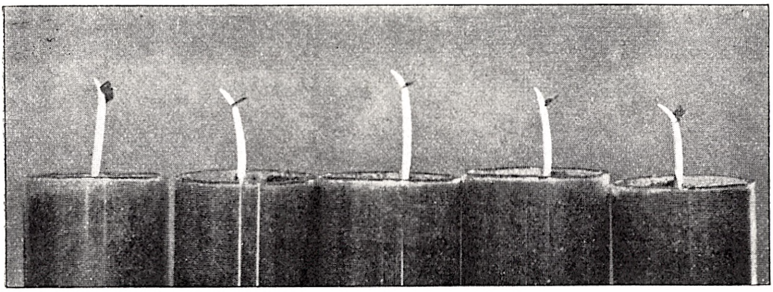

Fig. 3. Plants with incision farthest from light.

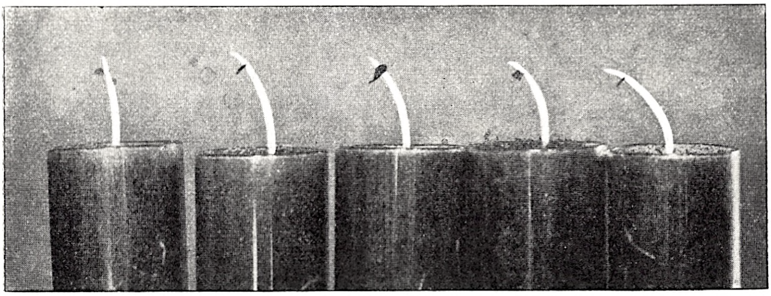

Fig. 4. Plants with incision nearest light.

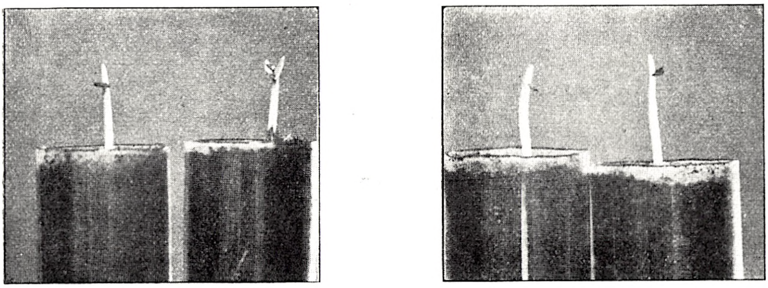

Fig. 5. Control plants.

Table III. Geotropic Experiments. — Fresh cuts.

a represents values for **d** in plants with incision on lower side of coleoptile; **b**, on upper side; **c**, control plants.

a	b	c
.00	— .12	.00
.00	— .11	+ .04
.00	— .15	+ .02
.00	— .17	+ .06
.00	— .09	+ .08
.00	— .14	+ .04
.00	— .12	+ .09
.00	— .18	+ .04
.00	— .24	.00
.00	— .19	+ .00
.00	— .14	.00
.00	— .25	+ .06
.00	— .18	+ .10
.00	— .21	+ .05
— .11	— .23	+ .08
.00	— .16	+ .14
.00	— .05	.00
.00	— .15	+ .05
.00	— .13	+ .00
.00	— .04	+ .11
.00	— .09	.00
.00	— .20	.00
.00	— .21	+ .05
— .04	— .15	+ .10
— .04	— .23	.00
.00	— .10	.00
— .06	— .20	+ .14
.00	— .21	.00
.00	— .14	+ .06
.00	— .19	.00
— .00	— .12	.00
— .00	— .13	+ .05
— .00	— .14	+ .04
.00	— .32	.00
— .10	— .21	+ .00
.00	— .19	+ .00
.00	— .14	.00
.00	— .39	.00
.00	— .35	+ .04
.00	— .32	+ .04
— .06	— .35	+ .05
— .03	— .10	.00
.00	— .22	.00
.00	— .30	.00
.00	— .32	.00
— .08	— .03	.00
— .06	— .03	.00
	— .05	+ .00
	— .07	.00
	— .07	.00
	— .16	
	— .18	
	— .25	
	— .24	
Mean **d** = — 0.012 cm.	— 0.175 cm.	+ 0.031 cm.
Mean error = ± 0.004 cm.	± 0.012 cm.	± 0.006 cm.

c. Control plants completely shaded, placed between the experimental plants, some with incision farthest from light, others nearest.[1] (cf. fig. 5).

Out of 44 plants, 4 curved in a positive traumatropic direction, 40 were straight. The mean value for **d** = + 0.003 cm ± 0.002 cm.

It is noteworthy that a traumatropic response following the insertion of the foil occurred only in about 9 % of the plants. However, as in Experiment I, it is necessary to eliminate this reaction from the results by adding the mean **d** of the control plants to that of the plants with the incision farthest from light and subtracting the same from the mean **d** of the plants with the incision nearest light.

The result of the above computation gives a value for **d** in the plants with the incision farthest from light of + 0.010 cm ± 0.004 cm, in the plants with the incision nearest to light + 0.061 cm ± 0.005 cm.

The above final results show that in the plants with the incision nearest to light a positive curvature has taken place, which is almost six times as great as that in the plants with the incision farthest from light. An examination of table II also reveals the fact that in the case of the plants placed in the latter position only about 14 % reacted in a positive phototropic direction as contrasted with about 95 % in the former.

b. Geotropic Experiments.

Experiment III (cf. table III).

Plants with incision made just before exposure.

a. Incision on lower side of coleoptile.

[1] Cf. foot-note 2 page 13.

Out of 47 plants, 12 individuals were curved in a negative geotropic direction, 35 were straight. The mean value for **d** = — 0.012 cm ± 0.004 cm.

b. Incision on upper side of coleoptile.

Out of 54 plants, the entire number curved in a negative geotropic direction. The mean value for **d** = — 0.175 cm ± 0.012 cm.

c. Control plants set in an upright position.

Out of 50 plants, 28 curved in a positive traumatropic direction. The mean value for **d** = + 0.031 cm ± 0.006 cm.

In order to obtain relative values for the geotropic curvature taking place in the plants, it is necessary to eliminate the traumatropic response from the above results.

The result of the computation gives a value for **d** in the plants with the incision on the lower side of the coleoptile of — 0.043 cm ± 0.007 cm, in the plants with the incision on the upper side — 0.144 cm ± 0.013 cm.

These final results show that in the plants with the incision on the upper side of the coleoptile a negative geotropic curvature has taken place, which is about three and one-half times as great as that in the plants with the incision on the lower side.

Experiment IV (cf. table IV).

Plants with incision made on day preceding exposure.

a. Incision on lower side of coleoptile. (cf. fig. 6).

Out of 51 plants, 43 individuals were curved in a negative geotropic direction, 8 were straight. The mean value for **d** = — 0.074 cm ± 0.007 cm.

Table IV. Geotropic Experiments. — Recovered plants.

a represents values for **d** in plants with incision on lower side of coleoptile; **b** on upper side; **c** control plants.

a	b	c
— .11	— .14	.00
— .06	— .13	.00
— .11	— .23	.00
— .08	— .18	.00
— .17	— .20	.00
— .16	— .21	.00
— .12	— .16	.00
— .09	— .15	.00
— .11	— .22	.00
— .12	— .25	.00
— .18	— .20	.00
— .17	— .28	.00
— .10	— .26	.00
— .02	— .20	.00
— .09	— .14	.00
— .11	— .11	.00
.00	— .13	.00
— .06	— .14	.00
— .11	— .16	.00
— .04	— .17	.00
— .14	— .16	.00
— .04	— .17	.00
.00	— .09	.00
— .03	— .20	.00
— .03	— .15	.00
— .07	— .16	.00
— .08	— .08	.00
— .04	— .18	.00
— .06	— .23	.00
— .10	— .27	.00
— .06	— .14	.00
— .15	— .25	.00
— .09	— .03	.00
.00	— .13	.00
— .03	— .06	.00
— .07	— .16	.00
— .05	— .20	.00
— .08	— .06	.00
— .03	— .20	.00
— .06	— .23	.00
— .12	— .25	.00
— .05	— .17	00
— .19	— .21	.00
— .06	— .19	— .00
.00	— .27	.00
.00	— .16	.00
.00	— .06	.00
.00	— .13	.00
.00	— .23	.00
— .09	— .14	.00
— .03	— .15	.00
	— .20	

	a	b	c
Mean **d**	= — 0.074 cm.	— 0.173 cm.	0.000 cm.
Mean error	= ± 0.007 cm.	± 0.008 cm.	

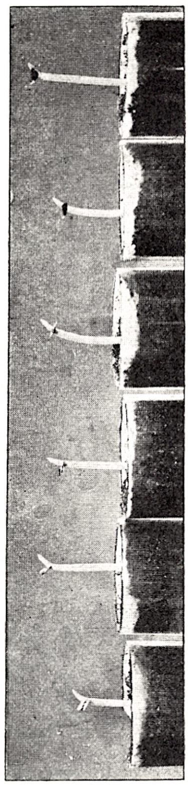

Fig. 6. Plants with incision on lower side of coleoptile.

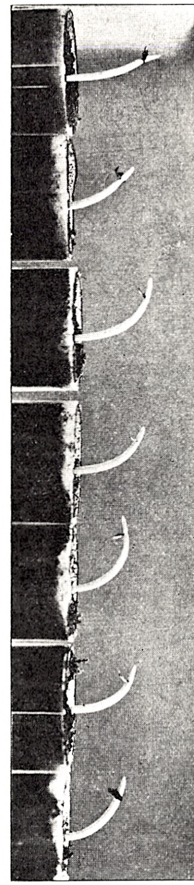

Fig. 7. Plants with incision on upper side of coleoptile.

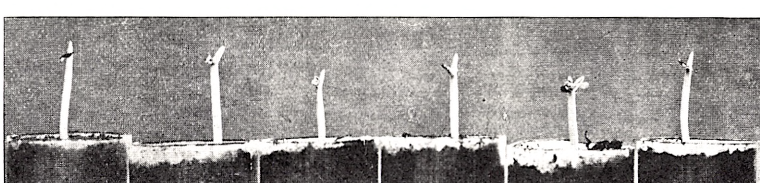

Fig. 8. Control plants.

b. Incision on upper side of coleoptile (cf. fig. 7).

Out of 52 plants, the entire number curved in a negative geotropic direction. The mean value for **d** = — 0.173 cm ± 0.008 cm.

c. Control plants set in an upright position. (cf. fig. 8).

Out of 51 plants, only 1 individual curved very feebly in a negative traumatropic direction, 50 remained straight. The mean value for **d** = 0.000 cm.

In this experiment the traumatropic response was practically eliminated.

The above results show that in the plants with the incision on the upper side of the coleoptile a negative geotropic curvature has taken place more than twice as great as that in the plants with the incision on the lower side.

A graphic representation of the results of the above experiments is given in fig. 9. The radius (r) of the mean curvature for the different series of plants was determined from the mean **d** by means of the equation:[1]

$$r = \frac{tl}{d}$$

where t = 0.14 cm, d = the mean d for a given series of plants, l = the approximate average length of all the plants of one set of experiments. The following drawings were constructed from the data obtained.

Since the curves a and b represent the mean response of the plants in the respective series to both traumatropic and phototropic or geotropic stimuli, that part of the reaction which may be considered as solely phototropic or

[1] cf. method for measurement of curvature page 8.

geotropic response is the angle through which the plant moves from right to left between the dash-and-dot arc *c* and the curves *a* or *b*.

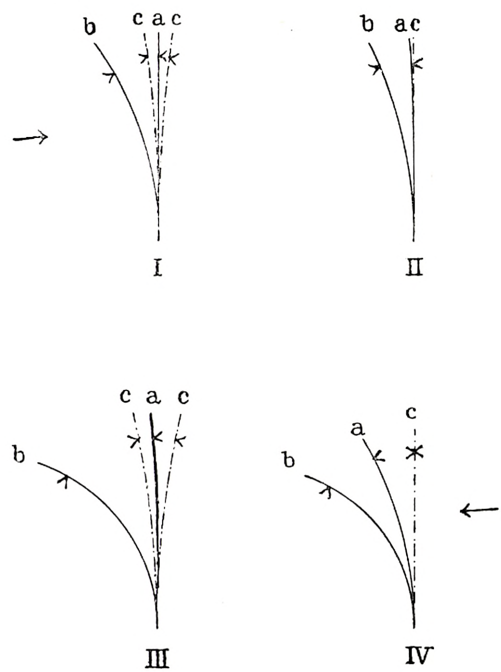

Fig. 9.

I represents the phototropic experiments with fresh cuts, II phototropic, recovered plants, III geotropic, fresh cuts, IV geotropic, recovered plants. *a* represents the curvature taking place in the plants farthest from light, or on the lower side in geotropic exposure, *b* plants nearest light or on upper side, *c* control plants. The carets indicate the position of the incision; the arrows the direction of the stimuli. Magnified 2 times.

D. Conclusions.

From the results of these experiments, considered both individually and collectively, the following conclusions may be drawn:

1. When the plants are placed with the incision on the side of the coleoptile either nearest

to the source of unilateral illumination or on the upper side in an exposure to geotropic stimulation, a marked transmission of the stimulus takes place from the tip to the base of the coleoptile.

2. When the plants are placed with the incision on the side of the coleoptile either farthest from the source of unilateral illumination or on the lower side in an exposure to geotropic stimulation, transmission of the stimulus from the tip to the base is only slight.

It should be borne in mind that the slight transmission of the stimulus taking place in the latter case may be due to the fact that it is not easy to effect an absolute prevention of transmission, since the cut sometimes fills with exuding sap.

Another explanation which may be offered for the results leading to the second conclusion is that the side of the coleoptile in which the incision is made is perhaps rendered practically insensible in consequence of the injury. This argument is met by experiment V in which 30 plants were exposed to unilateral illumination with the incision placed on the side of the coleoptile farthest from the light. The entire coleoptile of 15 of these plants was exposed, the roots being shaded, while only that portion of the tip above the incision was illuminated in the remaining plants. The results (cf. table V & fig. 10) show a mean curvature, as determined by

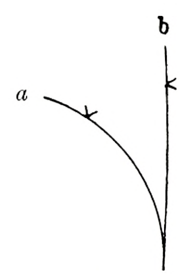

Fig. 10.
a represents the mean curvature of plants with entire coleoptile exposed, *b* plants with only tip exposed.

d, taking place in the former plants equal to about fourteen times as great as that in the latter.

Table V.

a	b
.00	+ .08
.00	+ .16
.00	+ .25
+ .00	+ .32
.00	+ .31
+ .04	+ .22
+ .05	+ .19
+ .11	+ .21
— .00	+ .18
.00	+ .16
.00	+ .20
.00	+ .21
.00	+ .09
.00	+ .16
.00	+ .03
Mean **d** = + 0.013 cm.	+ 0.185 cm.

E. Theoretical Considerations.

Fitting (1907, 241, 244) holds the following theory concerning the transmission of tropic stimuli in the coleoptile of *Avena*: "Durch die einseitige Beleuchtung wird in allen Teilen, wahrscheinlich in allen Zellen, des Perzeptionsorganes während oder infolge des Perzeptionsvorganges ein "polarer Gegensatz" geschaffen. Je nach der, allein vom Lichte abhängigen, Lage der Pole wird die "Reizstimmung" der Perzeptionszone und durch eine geradlinige oder quere Fortleitung, die ganz unabhängig ist von der Lage der Bahnen, auch die Stimmung der Reaktionszone verschieden. Die Stimmung entscheidet über die Richtung der Krummung." He also states, "Dass der polare Gegensatz, der in allen Teilen (Zellen) des Perzeptionsorganes durch den Aussenreiz induziert wird, sich auf lebenden Bahnen in die physiologisch radiär symmetrische, in seitlicher Richtung apolar gebaute Reaktionszone so ausbreitet, dass auch in ihr ebenso wie in den Zellen der Reizleitungsbahnen alle Teile in gleicher Weise 'polarisiert' werden."

If we are to agree with Fitting then we may suppose that on exposure of *Avena* to light the illuminated cells of the tip become "polarisiert", and this reaction spreads to the unilluminated cells through transmission not only in a straight line but also "um die Ecke", until a state of polarization is maintained throughout the cells of the coleoptile.

On the other hand, if transmission of the stimulus is to be attributed to the migration of one or more substances, it is obvious that since such an occurrence could not produce polarization of the cells, the theory of Fitting is entirely out of harmony. Since the most probable theory at the present time is the migration one, let us attempt on this ground to interpret briefly the results of the foregoing experiments. To produce a curvature a difference must exist not between the front and back of each cell but between the front and back of the unilaterally illuminated tip as a whole. This condition may be brought about by an unequal concentration of one or more substances. Furthermore it may be presumed that this difference is maintained by transmission of the stimulus to the base of the coleoptile. Only under these circumstances is it possible to conceive of a phototropic or geotropic curvature taking place.

Let us now consider the results of the recovered plants.[1] In view of the fact that a marked transmission of the

[1] Since the traumatropic response in this case need not be taken into consideration, these experiments were chosen.

stimulus occurs when the incision is placed on the side of the coleoptile nearest the light, and either no transmission or only a slight one is observed, when the incision is placed farthest from light, the conclusion of Fitting (1907, 237) "Dass die Reiztransmission keineswegs verlangsamt wird, wenn man eine longitudinale Reizübermittelung verhindert, woraus man schliessen muss, dass der Reiz sich ebenso gut in der Quer- wie in der Längsrichtung ausbreitet," must be erroneous. On the contrary the results[1] point out that the strongest tendency is for transmission of the stimulus to take place in a longitudinal direction, mainly localized in the side of the coleoptile farthest from light. Likewise in the geotropic experiments the results show that the greatest tendency for transmission of the stimulus is in the longitudinal direction, chiefly restricted to the lower side of the coleoptile. It is apparent, that this conclusion is in perfect harmony with the migration theory.

The above experiments, begun in the fall of 1920 and completed the following spring, were carried out in the Plant Physiology Laboratory of the University of Copenhagen. To Professor Johannsen, Director of the Laboratory, I wish to express my sincere appreciation of the courtesies of the laboratory extended to me, and of his stimulating and kindly interest in the work. To Dr. Boysen Jensen I

[1] Cf. also the results of the experiments of Stark, referred to in the text above, in which he placed cubes of agar containing an extract of one or more stimulatory substances on one side of the coleoptile directly on the cut surface. The curvature produced in this manner suggests the probability of migration of one or more substances in a more or less restricted path.

am deeply grateful for untiring and invaluable supervision of these investigations, inspired by the publication of his former research on the same problem.

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