

**Botany.** — "*Phototropical curvatures of seedlings of Avena which appear when reaction of the distal side is excluded.*" By H. RAMAER.  
(Communicated by Prof. F. A. F. C. WENT.)

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The phototropical curvatures which appear when seedlings of *Avena* are illuminated unilaterally with different quantities of light, have been carefully studied by ARISZ (1). He found that a positive curvature appears with 1.4—4000 M.C.S., a negative curvature with 4000—70000 to 120000 M.C.S. and a second positive curvature with still greater quantities of light.

It has been tried in several different ways to explain the phototropical curvatures by a difference in the rate of growth between the illuminated and unilluminated sides of the coleoptile.

BOYSEN JENSEN (2) thought that he could conclude from his investigations about the locality of the conduction of the phototropical stimulus that the positive curvature is the result of an increase in the rate of growth of the unilluminated side. This increase would be induced by substances, formed, owing to the unilateral illumination, in the unilluminated side of the tip and diffusing through the distal side to the growing zone.

PAAL (3) showed that *Coix* under normal circumstances always forms growth-accelerating substances in the tip and he explained the positive curvature by a decrease in the rate of growth of the illuminated side as a result of a onesided decrease in the production of growth-accelerating substances.

BLAAUW (4) sought connection between the phototropical curvatures and the lightgrowth-responses studied by him.

According to his theory, every part of a phototropically sensitive organ is able to show a growth-response to the quantity of light it receives, so that a phototropical curvature may be the result of the combinations of these growth-responses.

Bij means of this theory VAN DE SANDE BAKHUYZEN (5), later VAN DILLEWIJN (6) more accurately, could wholly explain the curvatures determined by ARISZ.

In consequence of a recent publication of BOYSEN JENSEN and NIELSEN (7), in which they again bring forward arguments in favour of the theory of BOYSEN JENSEN, I want to compare the three theories with each other and discuss them in connection with some recent investigations of C. VAN DILLEWIJN and F. W. WENT and with the results I obtained by the method of BOYSEN JENSEN and NIELSEN.

In their first experiment they made a median section in the tip of a coleoptile and placed a little screen in the cut. Round the base they placed

a small tube and then illuminated one half of the tip with an intensity of 25 M.C. for an indefinite period (2—3 hours). They found no curvature, but when the light fell in the direction of the screen a curvature appeared. Evidently the wound had no effect on the sensibility of the tip.

This result was an argument in favour of the theory of BOYSEN JENSEN. The same can be said of the following. The tip of a coleoptile was cut off and replaced by two sidely placed tips, between which a small screen was put. When one of the tips was illuminated unilaterally ( $2\frac{1}{2}$  hours  $\times$  25 M.C.) the base showed a negative curvature which necessarily was the result of an increase in growth of the proximal side induced by the distal side of the illuminated tip.

I repeated both experiments, although chiefly the first, because the second can afford too many mistakes, for instance individual differences in the production of growth-accelerating substances, the one tip perhaps drying up more rapidly than the other, the contact with the base being unequal etc.

The tip was cut into two by putting a needle through the plant a few m.m. below the tip and then moving it upwards. With a little practice the tip can be accurately split into two in this way. In the cut a little black screen was placed.

The results with onesided illumination were as follows :

1. After onesided continuous illumination of the one half of the tip with 25 M.C. for four hours, the base shows a positive curvature.

This curvature is very slight which may be due to the action of the wound, because plants with a cut but without a screen and illuminated for the same time show the slight curvature while intact plants, as a control experiment, show a maximal curvature in the direction of the light.

As working with continuous illumination appeared to me to be an objection, because so little is known about the allsided continuous illumination, I decided to illuminate with certain definite quantities of light.

2. An allsided illumination with 800 M.C.S. causes a decrease in growth.

If I illuminated the plants unilaterally with 800 M.C.S. after they had been kept in the dark for five hours after the operation (in order to loose the effect of the wound) a positive curvature appeared which reached its maximum after two hours (fig. 1).

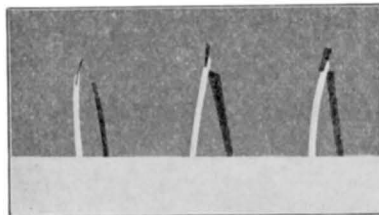


Fig. 1. Curvature after illuminating with 800 M.C.S. (10 sec.  $\times$  80 M.C.) from the right hand side. By means of a little screen light is prevented from reaching the base.

This curvature was shown by 80 % of the plants while 20 % remained straight.

From this result a few very important conclusions may be drawn.

First, that one half of the coleoptile is in itself able to show a light-growth-response, which corresponds with the decrease in growth, found by VAN DILLEWIJN, after all-sided illumination with 800 M.C.S. and therefore wholly in accordance with the theory of BLAAUW.

Further, that PAAL was right when he assumed this positive curvature to be the result of a decrease in growth of the proximal side. I must draw attention here to a recent research by WENT (8) who showed convincingly that the production of growth-accelerating substances in the tip decreases considerably with quantities of light of 800 M.C.S.

Finally the theory of BOYSEN JENSEN has been shown to fail in the area of the first positive curvature.

Besides, how could it be possible, as the latter assumes, that the distal side shows an increase in growth when the tip has been illuminated unilaterally with 800 M.C.S.? In this case illumination of both sides, and also all-sided illumination with 800 M.C.S. would have to cause an increase in growth of the whole coleoptile which is a flat contradiction of the facts.

3. With his last experiments VAN DILLEWIJN (9) found an increase in growth with 80000 M.C.S.

At the same time WENT found that with 100000 M.C.S. the production of growth-accelerating substances increases considerably in the tip.

When I illuminated the seedlings which had been treated in the above mentioned manner, unilaterally with 80000 M.C.S., 90 % showed a negative curvature after one hour (fig. 2).

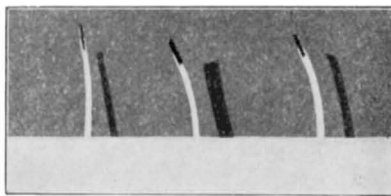


Fig. 2. Curvature after illuminating with 80000 M.C.S. (100 sec.  $\times$  800 M.C.) from the right hand side.

This time corresponds with that after which takes place an increase in growth after all-sided illumination with 80000 M.C.S.

When we discuss shortly the acquired state of affairs then it is proved here that when a coleoptile is illuminated unilaterally with 800 M.C.S. and reaction of the distal side is excluded, the first positive curvature appears through a decrease in growth of the illuminated side.

This corresponds with the theory of PAAL but not with that of BOYSEN

JENSEN, while the results are wholly in accordance with the theory of BLAAUW.

Along three different lines, namely by the lightgrowth-responses, by the research about the production of tipsubstances as well as by the above described experiments it has now been proved that the first positive curvature is the result of a decrease in growth of the illuminated side.

Besides, in the same way it has conclusively shown that with 80000 M.C.S. one half of the coleoptile independent of the other half may give an increase in growth.

Are there circumstances under which the distal side of coleoptile shows an increase in growth, while at the same time the proximal side grows in such a way, that a positive curvature results?

VAN DILLEWIJN has shown that these circumstances are indeed realized in the area of the second positive curvature.

From this it is therefore evident that the theory of BOYSEN JENSEN is valid for the second positive curvature.

So each of the theories of PAÁL and BOYSEN JENSEN has been proved to be correct for a certain area, while both now fit in the theory of BLAAUW, which explains the phototropic curvatures by the difference in lightgrowth-response of the proximal and distal sides.

#### LITERATURE CITED.

1. ARISZ, W. H., Untersuchungen über Phototropismus. Rec. d. Trav. bot. néerl. **12**, 1915.
2. BOYSEN JENSEN, P., Bull. de l'Acad. roy. des sciences et des lettres de Danemark 1911.
3. PAÁL, A., Über phototropische Reizleitung. Jahrb. für wiss. Bot. **58**, 1918.
4. BLAAUW, A. H., Licht und Wachstum I; Zeitschr. f. Bot. **6**, 1914.  
" " " " II; " " " **7**, 1915.
5. BAKHUYZEN, H. L. VAN DE SANDE, Analyse der fototropische stemmingsverschijnselen, Diss. Utrecht 1920.
- 6) VAN DILLEWIJN, C., The connection between lightgrowthresponse and phototropic curvature of seedlings of *Avena sativa*.
7. BOYSEN JENSEN, P., und NIELSEN, N., Studien über die hormonalen Beziehungen zwischen Spitze und Basis der *Avena coleoptile*. Planta. Archiv für wissenschaftliche Botanik **1**. 1925.
8. WENT, F. W., On substances accelerating the growth of the coleoptine of *Avena Sativa*. This Academy's "Zittingsverslagen" **35**, 723. 1926.
9. VAN DILLEWIJN, C., The lightgrowthresponses in different zones of the coleoptile of *Avena sativa*. This Academy's "Zittingsverslagen" **35**, 600, 1926.

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