Botany. — *"Further researches on the antiphototropic curvatures occurring in the coleoptiles of Avena."* By Dr. C. E. B. BREMEKAMP. (Communicated by Prof. F. A. F. C. WENT.)

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As I have shown in my former communication [1]), the conditions under which the coleoptiles of Avena produce an antiphototropic curvature, may be summed up in this way:

1st. At the end of the one-sided illumination the rate of growth should have about the same value at both sides of the coleoptile [2]). This result is only to be obtained with light of rather strong intensity. If this is provided for, the product of the intensity and the exposition-time should exceed a certain value.

2nd. After the close of the illumination, there should be a more rapid increase of the growth-rate, in the side that has received the greatest quantity of light. In this way it should reach here a higher value.

An explanation of the way wherein a difference in the rate of increase may come about, was given in my paper entitled: "Theorie des Phototropismus" [3]). After a previous diminution in consequence of the illumination, the rate of growth after some time increases again. This process commences probably the sooner, according as the diminution has been the greater. In this way the increase of the growth-rate in the side which has received the greatest quantity

[1]) C. E. B. BREMEKAMP. On antiphototropic curvatures occurring in the coleoptiles of Avena. Proceedings Kon. Akad. v. Wetensch. te Amsterdam. Vol. XXIV, p. 177. 1921.

[2]) In my previous work in stead of the expression "the rate of growth at the end of the illumination" I used the ampler expression "the rate of growth belonging to the grade of sensibility existing at the end of the illumination". In this way I reckoned with the possibility that it would give a latent period between the phototropical reaction i.e. the change of the rate of growth and the absorption of the light with its influence on the sensibility. However, a critical examination of the literature on this subject, has convinced me that the evidence in favour of the existence of this latent period, is not conclusive. The investigations of BOSE and others have made it very probable that the reaction follows the illumination almost immediately.

[3]) C. E. B. BREMEKAMP. Theorie des Phototropismus. Rec. d. trav. bot. Néerlandais Vol. XV. p. 123. 1918.

of light, may gain an advantage of that in the other side. This advantage will be the greater, according as there lies more time between the moment whereon the growth-rate in the anterior side has reached its lowest value, and the moment whereon this is the case in the posterior side. If it is sufficiently great, the rate of growth in the first-named side with the aid of it will reach at the end of the illumination or shortly afterwards a higher value. In any case the exposition-time should be long enough that an advantage of sufficient extent may be gained.

However, in my previous communication I showed that an antiphototropic curvature may come about also, if the expositiontime is very short. As in this case the explanation given above naturally fails, I suggested that the theory of BOSE[1]) might give us here the clue to get out of the difficulty.

According to this theory, a disturbance of equilibrium in the organism generally manifests itself in a local contraction (the direct effect) which is accompanied by an expansion in the adjoining tissue (the indirect effect). In the latter, the turgescence would be heightened by the water expelled from the contracted portion, and accordingly a temporary enhancement of the growth-rate would be the result. In this way a normal curvature in one part of an organ would always go together with an antitropic one in the adjoining region. Only if an increase of the rate of growth in that part, should be impossible, the antitropic curvature would remain out. In our case then, the origin of the antiphototropic curvature in the tip of the coleoptile might be connected with the origin of a normal phototropic curvature in the basal part.

To test the correctness of this supposition, I made a number of experiments wherein the phototropic reaction of coleoptiles exposed in the whole of their length, was compared with the reaction of coleptiles illuminated at the tip only, or illuminated also in the whole of their length, but after an exposition of the basal part to a two-sided illumination of rather great strength.

Before I enter into the details of these experiments, I will give a survey of the results which previous investigators have obtained in their researches on the influence of an illumination of one part, on the phototropic reaction of another.

First of all then, we have to consider the experiments on phototropism made by BOSE[2]) himself. They are rather few in number,

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[1]) J. C. BOSE. Plant Respose. London 1906.

[2]) J. C. BOSE assisted by Jyotiprakash Sircar. The transmitted effect of photic stimulation. Life Movements in Plants. Calcutta 1918/19. p. 362—377.

and form only a subordinate part in the general frame of his work. His experimental objects were seedlings of Setaria and roots of Sinapis.

The choice of the first-named object is not very happy, as the direct effect of the exposition of the coleoptile is not outwardly visible, and its existence therefore, as yet purely hypothetical. The indirect effect consists in an antitropic curvature of the axis. This curvature which appears almost immediately, is followed in about 25 minutes by a normal one. The latter should be the result of the propagation of the invisible direct effect. An illumination of the growing region gives a normal curvature.

That the antitropic curvature of the axis occurring with an exposition of the coleoptile should be the indirect effect of this illumination in the sense of Bose, is possible. It should be remarked however, that it is not proved. As yet, we don't know with certainty, if in this case the direct effect consists really in a contraction, as no sign thereof becomes outwardly visible.

The roots of Sinapis show a negative phototropism. At least this is the case, when both the tip and the growing region are exposed to the light. The curvature appears in the growing region, the tip always remaining straight. An exposition of the tip also gives a negative curvature of the growing region, but if this part itself is exposed to the light, there appears at first a positive curvature which only after some time is followed by a weak negative one.

Bose considers the negative curvature in the growing region produced by an exposition of the tip, as the indirect effect, the direct effect as in Setaria remaining concealed. That this curvature is not, as in Setaria, followed by a positive one, he explains by assuming that the intervening tissue would be practically unable to conduct the direct effect. In the case of an exposition of the growing region, the positive curvature is considered as the direct effect, whereas the negative curvature appearing a little later, is said to arise on account of transverse conduction of the direct effect under continued illumination.

However, this explanation is not very convincing. That a neutralisation of the curvature might come about by transverse conduction, is quite conceivable, but how a reversion of the curvature might be explained in this way, I fail to understand. Moreover, as a conductivity for the direct effect in the longitudinal direction is supposed to be absent, it is not readily admissible that is should be very efficacious in the transverse direction. Therefore, in this case the interpretation of Bose cannot be considered as sufficiently founded.

The explanations of these negative curvatures given by other investigators are, however, hardly more convincing.

Information about the influence of an illumination of the basal part on the reaction of the tip, is to be found in papers by VAN DER WOLK [1]), GUTTENBERG [2]) and ARISZ [3]), all dealing with the phototropism of Avena.

According to VAN DER WOLK the results of an illumination of the basal half of the coleoptile on the upper half, is to be seen in the fact, that an illumination of 12 MCS gives in these seedlings a curvature of the same strength as an illumination of 85 MCS in a wholly etiolated coleoptile. This greater curvability of the upper half might, perhaps, be explained by assuming that the contraction of the tissue in this part was facilitated by the decrease of turgescence in the basal half: the expulsion of the water would find here less resistance.

GUTTENBERG on the contrary, tried to show, that the curvability of the tip of the coleoptile is not altered by an illumination of the basal part. In his experiments three sets of seedlings were compared. They were all illuminated unilaterally with 22,2 or 33,3 MCS; but in the second and third set the basal part was exposed previously during one hour to an illumination with 11,1 MC; in the second set the seedlings rotated during this time round a vertical axis, whereas in the third set they stood still. In this case the after-illumination took place from the opposite side. GUTTENBERG found that the phototropic curvature in the third set was a little weaker than in the other two.

This result seems at first in flagrant contradiction to the statement of VAN DER WOLK cited above, but it should be remembered that in the experiments of VAN DER WOLK, the light was very strong, and the exposition only short, whereas GUTTENBERG used light of rather feeble intensity and a very long exposition. Therefore, in the seedlings of VAN DER WOLK the decrease of turgescence in the basal part, might have been greater, and consequently the effect on the curvability of the tip more important than in the seedlings of GUTTENBERG. This explanation would probably suffice, if there was no difference at all between the curvatures in the three sets. GUT-

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[1]) P. C. VAN DER WOLK. Investigations of the transmission of light stimuli in the seedlings of Avena. These Proceedings, Vol. XIV, p. 327.

[2]) H RITTER VON GUTTENBERG. Ueber akropetale Reizleiting. Jhrb. f. wis. Bot. Bd. 52 p. 333. 1913.

[3]) W. H. ARISZ. Untersuchungen über den Phototropismus. Rec. d trav. bot. Néerlandais. Vol. XII p. 44. 1915.

TENBERG stated however, that the curvature in the third set was smaller than in the other two, and explained this discrepancy by assuming a propagation of the basal curvature to the tip. In my opinion it might have its cause in the circumstance, that these seedlings were already slightly curved at the moment of the after-illumination. If this had been the case, the tip would have received here a smaller quantity of light and this moreover partly under a less favourable angle than in the other sets, and consequently, the phototropic curvature would not have attained the same value. It should also be mentioned, that a repetition of these experiments by ARISZ (l.c. p. 105) gave only doubtful results, the sources of error being very great. In any case, we dare not say, that the acropetal propagation of the basal curvature has been demonstrated, and for the solution of the question, whether an exposition of the basal part exercises any influence on the curvability of the tip, the experiments are not suitable, the intensity of the light being too weak.

Nevertheless, there are in the paper of GUTTENBERG a few indications, which seem to show that the illumination of the basal part influences the curvability of the tip, in the way described by VAN DER WOLK. On p. 341 one may read: "Ein deutlicher Unterschied zwischen den Krümmungswinkeln der beiden Serien war dabei nicht zu konstatieren; doch verhielten sich die allseits vorbeleuchteten Pflanzen zunächst etwas anders als die verdunkelten. Bei ersteren erfährt nämlich das oberste Drittel der Koleoptile eine etwas stärkere Krümmung als bei letzteren, dafür ist aber bei diesen die Krümmung bereits weiter nach unten fortgeschritten". That these differences were only very small (further data l.c. p. 437) and quantitatively very different from those observed by VAN DER WOLK, may find its explanation, as I have pointed out already, in the feeble intensity of GUTTENBERG's illumination.

ARISZ mentions (l. c. p. 103), that he has repeated the experiments of VAN DER WOLK, and describes his results in this way: „Wohl ist in vielen Fällen eine kleine Vergrösserung der Spitzenkrümmung beobachtet worden, welche auch etwas früher sichtbar wurde, aber so eklatant, wie VAN DER WOLK seine Resultate beschreibt, war es nicht". ARISZ therefore does not deny, that the illumination of the basal part enhances the curvability of the tip; only he awards this influence less importance than VAN DER WOLK does.

Summing up, we may state that our knowledge of the influence which an exposition of the basal part exercises on the tip, is far from complete. Moreover, it cannot be said that the available data are very valuable for our supposition, that the antiphototropic curvatures of Avena might find their explanation in this way.

In the experiments of ARISZ (l.c. p. 97), the exposition of the basal part gave a normal curvature [1]), which did not extend itself beyond the limits of the part exposed. As the occurrence of an antiphototropic curvature in the tip is never mentioned, we must assume that under the circumstances of these experiments, the tip remained perfectly straight. At first sight, this seems to clash with our supposition, but we should remember, that in these experiments the tip remained continually in the dark, so that its turgescence underwent no decrease. Now in consequence of this circumstance, an increase of the rate of growth might be difficult or even impossible.

In my own experiments I compared in the first place the reaction of coleoptiles exposed at the tip only, with the reaction of coleoptiles exposed in the whole of their length. The result was very clear. Whereas in the first case antitropic curvatures were never found, in the second case they could be obtained without difficulty.

The etiolated seedlings used for these experiments, were planted in a single row in oblong zinc boxes. Each box got about 15 seedlings, so orientated, that their plane of symmetry was parallel to the small side of the box. During the exposition, the boxes were placed perpendicular to the rays of light. The seedlings that should be exposed at the tip only, stood with their basal part behind a screen, so that only $2\frac{1}{2}$—3 mm. of the tip protruded. This screen was prepared in the following way. A feeble red light was placed just in front of the experimental lamp, and the silhouette of the coleoptiles caught on a piece of black paste-board standing just behind them. The place of the tip was marked thereon with the aid of a pencil. Above these marks the paste-board was cut away and then the screen pushed $2^1/_2$—3 mm. deeper in the earth. After that the box was turned round and the red light removed. During the illumination with the experimental lamp, in this way just $2^1/_2$—3 mm. of the tip was exposed.

The intensity of the illumination was in all experiments 750 MC;

[1]) In two experiments out of a very great number, ARISZ mentions to have obtained antitropic curvatures in the part exposed. In one case (illumination during 1 minute with 330 MC), the curvatures are stated to have been feebly normal or antitropic, in the other case (illumination during 1 minute with 200 MC), they were antitropic or absent. As these cases, however, stand wholly isolated among the rest of his results, it seems probable that these antitropic curvatures are due to some experimental error.

the exposition-time 12, 15, 18 and 21 seconds. The temperature varied between 15° and 20° C., but in each series of experiments it remained nearly constant. After the illumination the boxes came on the clinostat.

With an exposition of 12 seconds (light-quantity 9000 MCS), after $3^1/_2$ hours the coleoptiles exposed in the whole of their length, were feebly antitropic (S-shaped), the coleoptiles exposed at the tip only, feebly curved in the normal way.

With an exposition of 15 seconds (light-quantity 11250 MCS), the results were nearly the same.

With an exposition of 18 seconds (light-quantity 13500 MCS), after $3^1/_2$ hours the coleoptiles exposed totally, were clearly antitropic (feebly S-shaped), the coleoptiles exposed at the tip only, nearly straight.

With an exposition of 21 seconds (light-quantity 15750 MCS), after $3^1/_2$ hours the coleoptiles were all nearly straight.

The experiment with the exposition-time of 15 seconds, was repeated 5 times, always with the same result. That in this case, the occurrence of an antitropic curvature at the tip of the totally exposed coleoptiles, is dependant upon the exposition of the basal part, cannot be doubted.

The results of the experiments wherein the basal part of the coleoptiles was previously exposed to a very strong illumination, and where, therefore, the unilateral after-illumination of the whole coleoptile did not give a normal curvature in the basal part, demonstrate the significance of this influence also clearly.

In these experiments, I compared the result of an unilateral illumination of the whole coleoptile after a twosided exposition of the basal part, with that of an unilateral illumination of seedlings previously kept in the dark. During the fore-illumination two screens of the same shape were used, one in front of the coleoptiles, and one behind them. They were prepared in the same way as those used in the previous experiments, the only difference being that in this case, the basal part of the paste-board was for the greater part cut away. In this way during the illumination, at the tip of the coleoptiles a piece of $2^1/_2$—3 mm. remained in the dark. The fore-illumination lasted 60 seconds, and during this time, every 10 seconds the box was turned round. At the end of the fore-illumination the box was turned round for the last time, then the screens ware taken away, and the seedlings once more exposed to the same light. This time the illumination lasted 12 or 15 seconds. The intensity of the illumination was always 750 MC. The result of these experiments was, that the coleoptiles, whereof the basal part was previously exposed, remained straight, whereas the others showed the usual antiphototropic curvature.

In my former communication I admitted that in coleoptiles previously submitted to an omnilateral illumination of a definite value, an antiphototropic curvature might, perhaps, be obtained with the aid of a rather weak after-illumination. This seems now not very probable, as under these circumstances, the occurrence of a normal curvature in the basal part, may hardly be expected. Therefore, in this case neither of the causes hitherto discovered, by which an antiphototropic curvature may be produced, is present.

The relative importance of the two causes is as yet wholly unknown, but that the cause discussed in this paper, must be very efficient, follows from the experiments described in my former communication (l.c. p. 182). The antiphototropic curvatures produced by an illumination with a given quantity of light, showed but little difference if the exposition-time varied between 1 and 256 or between $^3/_4$ and 192 seconds. Now, as we have seen that with a very short exposition-time, the presence of the cause discussed in my earlier work, is wholly excluded, we must conclude that its influence in the experiments with a longer exposition, was here also rather weak.

S U M M A R Y.

The antiphototropic curvature which appears at the tip of the coleoptile of Avena with a very short exposition, does not show itself, if the illumination is limited to the tip, or if the basal part has previously been exposed to a rather strong illumination.

Therefore we should assume, that with an unilateral illumination of the whole coleoptile, the rate of growth of the tip, is enhanced by an influence proceeding from the basal part. This influence must be greatest in the side, which underwent the greatest contraction, that is to say in the side, which during the exposition faced the lamp. The origin of an antiphototropic curvature of this kind is, therefore, always connected with the origin of a normal curvature in the basal part.