Huygens Institute - Royal Netherlands Academy of Arts and Sciences (KNAW)

Botany. — *"Photo-growth reaction and disposition to light in Avena sativa"*. By H. L. VAN DE SANDE BAKHUIJZEN. (Communicated by Prof. F. A. F. C. WENT).

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Of late years our knowledge of the influence of light on the longitudinal growth of plants has been considerably extended and deepened. While earlier investigations were generally content not to make their first observations until some hours after the beginning of illumination, attempts were made in more recent investigations to study as closely as possible from the very beginning of exposure the changes to which growth is subjected.

In 1914 BLAAUW published his investigations on the photo-growth reaction in *Phycomyces* [1]), and VOGT found in 1915 a similar reaction in the coleoptiles of *Avena* [2]); besides two further papers were published by BLAAUW on this reaction in seedlings of *Helianthus* [3]) and in certain roots [4]).

All these investigations were carried out under the influence of the new points of view which BLAAUW and FROSCHEL had opened up in 1909 on the subject of phototropy; hence attention was not confined to the intensity, but a definite amount of light energy was administered. In some cases illumination was continuous throughout the experiment.

While VOGT does not discuss the theoretical bearing of his results, BLAAUW uses his photo-growth reaction as a basis for a discussion of the phenomena observed in phototropy. Formerly it was indeed known that phototropic curvatures arise through growth being changed somehow by unilateral illumination, but since it was not known that a brief omnilateral illumination has an effect on longitudinal growth, it was impossible to obtain any accurate conception of the changes which growth underwent immediately on unilateral

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[1]) A. H. BLAAUW. Licht und Wachstum. I. Zeitsch. f. Botanik. 1914

[2]) E Vogt. Uber den Einflusz des Lichts auf das Wachstum der Koleoptile von Avena sativa. Zeitschrift f. Botanik. 1915.

[3]) A. H. BLAAUW. Licht und Wachstum. II. Zeitschr. f Botanik. 1915.

[4]) A. H. BLAAUW. Licht und Wachstum. III. Mededeelingen van de Landbouw-hoogeschool. Deel XV. 1918.

illumination. This was one of the reasons why phototropy was regarded as a thing apart.

BLAAUW once more defends the old theory of DE CANDOLLE and regards unilateral as a special case of omnilateral illumination; the former would thus have no specific action. If omnilateral illumination gives a photogrowth reaction uniform in all directions, unilateral illumination will only differ in giving an unequal growth reaction on the posterior and anterior sides. Here it is not the difference of light, but the light itself, as energy, which influences the longitudinal growth of every cell, but since the front is differently lighted from the back, the two sides will show unequal changes in growth. The result of this inequality is a curvature towards the source of light or away from it; this is the phototropic curvature. By these considerations phototropy has been saved from its isolation and has become susceptible of deeper and more exact analysis. A further important point is, that BLAAUW ascribes an influence to the posterior side also, which quite corresponds to that of the anterior. It is not the anterior nor the posterior side alone which actively causes the curvature; both are concerned: it is the difference in the change of growth of the two sides which makes the plant curve phototropically.

The possibility that unilateral illumination might be a special case of omnilateral, i. e. that every longitudinal strip of the plant might receive a photo-growth induction independently of the rest of the circumference and might execute a photo-growth reaction, suggested an investigation of the question, whether this could throw any light on various phototropic phenomena described in the literature. I found that the photo-growth reaction gives us the means of explaining satisfactorily many apparently contradictory phenomena. Since phototropism has been most fully examined in *Avena sativa* and since VOGT moreover found a photo-growth reaction here, I have made a study of the literature on this plant. While I was engaged in working up these considerations for a preliminary publication, a paper by BREMEKAMP [1]) appeared, which gave me no reason to change my opinion; I hope to return to this more fully in a later paper.

VOGT illuminated coleoptiles of Avena from above with various intensities during periods of various length, but on this account his energy numbers are not comparable with horizontal light. By the first method the plants receive much less light, since the absorbent surface is much smaller. With horizontal illumination we need apply

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1) C. E. B. BREMEKAMP. Eine Theorie des Phototropismus. Recueil des Travaux bot. néerlandais. Vol. XV. 1918.

much less light energy in order to obtain the same reaction, than with light coming vertically from above. Therefore the intensity and the energy numbers must be divided by a certain coefficient.

Now VOGT found that already after a few minutes the rate of growth began to fall off. This led after about 25 minutes to a minimum, while after 30—40 minutes the zero point was again passed. Then an acceleration of growth occurred, leading to a maximum, so that at about 60 minutes after the beginning of illumination the first rate of growth had been reestablished. After that the growth oscil-. lated for a long time, at first with considerable but later with gradually decreasing maxima and minima.

I have now calculated from VOGT's tables [1], how many μ the plants grew less during the first retardation period than if they had continued their growth in the dark. The following figures therefore give, in μ, the total retardation of growth until the zero-point is again reached and the acceleration of growth begins. It should always be remembered that the intensity numbers must be divided by a coefficient before being comparable to those of horizontally incident light.

TABLE I.

Intensity.	Duration of illumination.			
	1 min.	3 min.	15 min.	continuous.
16 M.C.		39		83
64 M.C.	53			
100 M.C.	102	104	90?	
500 M.C.			122	123
1000 M.C.		294	76	147
1500 M.C.			89	

Since in unilateral illumination the front is always more strongly illuminated than the back, the former is retarded more than the latter, if the retardation of growth increases with increasing intensity. Consequently a positive phototropic reaction occurs, provided the difference in growth retardation is sufficient to give a visible curvature. If the retardation of growth diminishes again with increasing intensity, a negative reaction will occur, for in this case the back side is retarded more than the front. It is seen from the table that the first and second columns will give positive curvatures. We cannot

[1] VOGT l.c. Tables 8, 9 and 11.

conclude from the third column whether the numbers increase or decrease, they are not sufficiently certain. If we, however, arrange the first and the second column according to quantities of energy the figures rise, hence, we might expect much higher figures in the third column. Probably we are here beyond the maximum of growth retardation. On the other hand the figures rise again on prolonged continued illumination; this completely agrees with the fact, that illuminations of longer than 25 mins. always give positive curvatures. Now since it is known that phototropic curvature can already be detected after 25 mins. by means of a microscope [1]), a sufficient difference in growth between the two sides must have occurred in this time. If the photo-growth reaction is therefore to be regarded as the basis of phototropic curvature, the numbers, giving the retardation of growth to 30 minutes after the beginning of exposure, must provide a clue [2]). The occurrence of curvatures at the extreme apex within 25—30 mins. can therefore be sufficiently explained by growth retardation alone. There are however further points, which indicate that the acceleration of growth, following the retardation, has nothing to do with the establishment of the curvature.

When the acceleration of growth is over, the growth curve still shows pronounced rises and falls. These are, however, not to be considered as oscillations about a condition of equilibrium, like those of a pendulum coming to rest, but must certainly be regarded as the reactions of zones situated below. Just as in a phototropic curvature the reaction first becomes visible at the extreme apex, the first period of retardation of growth must also represent the reaction of the extreme apex; the photo-growth reaction of the inferior zones will not occur until later. This is therefore quite comparable to the progress of the phototropic curvature from the apex to the regions further below. The magnitude of the later retardations of growth cannot however be deduced from the tables, since the average rate of growth does not remain constant, which is partly attributable to the great period, which itself is moreover influenced by light. [3])

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[1]) E. PRINGSHEIM. Studien zur heliotropischen Stimmung und Präsentationszeit. Zweite Mitteilung. Cohn's Beiträge zur Biologie der Pflanzen. Bd. IX. 1909.

W. H. Arisz. Onderzoekingen over Fototropie, Diss. Utrecht. 1914; Rec. trav. bot. Nèerlandais. Vol. XII. 1915.

[2]) I neglect here the negative curvatures, which after a time may succeed to positive ones; these can be explained in a quite different manner, as I shall show in my detailed paper.

[3]) H. SIERP. Ein Beitrag zur Kenntnis des Einflusses des Lichts auf das Wachstum der Koleoptile von Avena sativa. Zeitschr. f. Botanik. 1918.

We are here concerned with a conduction of the photo-growth reaction; the magnitude of the growth retardation in the lower zones will likewise depend on the energy applied.

The curve, which represents the dependence of -the growth retardation (ordinate) in respect of the energy applied in 5 mins. (abscissa), we call: *growth retardation curve*. From the numbers of table I we cannot very well construct this curve, as there are too few data. There is however every reason for assuming that there is an ascending portion which can bring about positive curvatures and a descending one producing negative ones. Hence somewhere there is a maximum; its existence and position will be determined later by another method. Since the rule of products will apply also to the photo growth reaction within certain limits, there belongs to every amount of energy (x) a definite retardation of growth (y) after a certain time (here $1^1/_2$ hour).

Now in unilateral illumination the front receives the full energy [1]; the back receives much less. If we are on the ascending part of the curve, the retardation of growth on the anterior side (y_a) is greater than that on the posterior side (y_p) and only a positive curvature will occur. Now 20 M.C.S. is the practical threshold value for a readily visible curvature; on applying this amount of energy therefore, there will occur a difference of growth retardation between the front and back, which is just sufficient to produce a curvature which can be readily detected macroscopically. The threshold value of 20 M.C.S. is however only applicable to plants which have been grown in the dark, and have received a quantity of light energy $= 0$. It is different with plants which have had an omnilateral fore-illumination. This can be done by rotating the plants before the source of light, so that successively all sides are illuminated; in this way all parts of the circumference receive an equal amount of light. If subsequently there is a unilateral illumination, the threshold value for a positive curvature is found to be much higher. 1 will now consider some experiments of ARISZ [2] on' the socalled "disposition (German "Stimmung") to light" in oats and in the first place the omnilateral fore-illumination with less than 2000 M.C.S. applied within 3 minutes with an intensity below 25 M.C. The unilateral after-illumination always took place immediately after the omnilateral.

I find that all the changes, produced by the omnilateral

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[1] Reflection etc. is here left out of account.

[2] ARISZ l.c. Tables 24 and 25. See also ARISZ: Adjustment to light in oats. Proceedings Kon. Ak. v. Wet. A·nsterdam. 1913.

fore-illumination, can be satisfactorily explained by assuming that at every point of the circumference the energy of the unilateral after-illumination is simply added to that of the fore-illumination. The retardation at a given point of the circumference will therefore depend on the total energy received from the two illuminations together. If the energy difference between the anterior and posterior sides is then sufficiently great to give the difference of growth retardation required for a visible curvature, the threshold value will be reached. I have nowhere assumed a change in sensitiveness, in contradistinction to BREMEKAMP[1]), who attempts to explain the increase in the threshold value by the hypothesis, that the plant has become less sensitive as a result of the unilateral fore-illumination and thus imagines a change in the perception-basis.

If we apply unilaterally b M. C. S., the front will receive b, and of this the back $\dfrac{b}{m}$ M. C. S.; m is greater than 1, since the back receives less than the front. If we had, however, previously given a M. C. S. omnilaterally, the later front would have received of this $\dfrac{a}{n}$ M. C. S., the later back also $\dfrac{a}{n}$ M. C. S.; a unilateral after-illumination will then supply to the front in addition b M. C. S., altogether therefore $\dfrac{a}{n} + b$ M. C. S.; the back receives altogether $\dfrac{a}{n} + \dfrac{b}{m}$ M. C. S. In both cases the absolute energy difference between the front and back remains constant, i. e. $b - \dfrac{b}{m} = b\,\dfrac{m-1}{m}$ M. C. S. Now the resultant curvature entirely depends on the difference of growth retardation, which corresponds to an energy difference of $b\,\dfrac{m-1}{m}$ M.C.S. If the growth retardation curve were a straight line, there would always correspond to an energy difference of $b\,\dfrac{m-1}{m}$ M.C.S. one and the same difference of growth retardation, whatever place of the abscissa we may consider, the threshold value would then necessarily be constant. If the growth retardation curve is, however, a curve with decreasing slope, the growth retardation difference corresponding to an abscissa difference of $b\,\dfrac{m-1}{m}$ M. C. S. will become the smaller, the gentler

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[1]) BREMEKAMP l.c.

the slope of the curve becomes, i.e. the greater x becomes.

We call the energy on the anterior and posterior sides respectively x_a and x_p, the retardations of growth y_p and y_a.
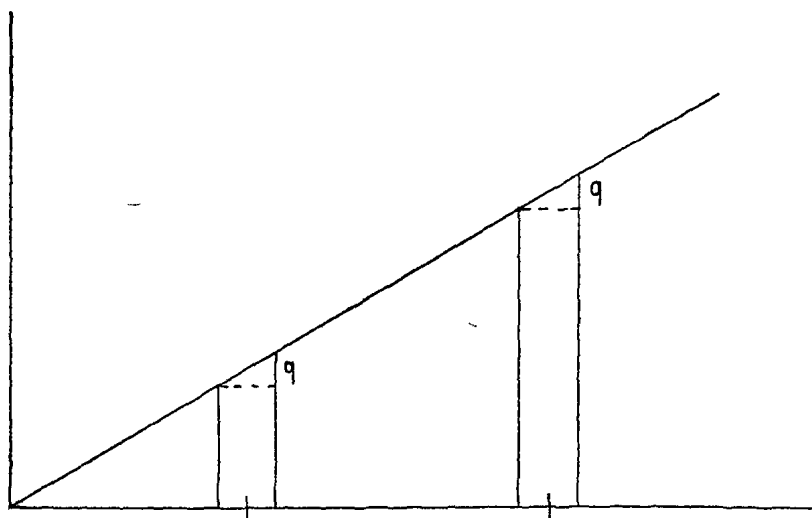
growth retardation

Fig. 1.   energy

In a straight with x_a-x_p constant $= b \dfrac{m-1}{m}$ M.C.S. the difference in growth retardation y_a-y_p is always $= q$ (fig. 1).

In a curve with decreasing slope, with x_a-x_p constant $= b \dfrac{m-1}{m}$ M. C. S. the difference in growth retardation y_a-y_p is smaller, according as x_a is larger (fig. 2).

Now x_a will become greater by omnilateral fore-illumination, for $x_a = \dfrac{a}{n} + b$ M.C.S. The absolute energy difference $b \dfrac{m-1}{m}$ M.C.S. or rather the energy of b M C.S. applied unilaterally, will therefore give a smaller difference of growth retardation i. e. a smaller curvature, according as the energy of fore-illumination a is greater. In order nevertheless to obtain a constant difference of growth retardation, giving a just visible curvature, $b \dfrac{m-1}{m}$ and therefore also b will have to be greater.

If the energy of fore-illumination becomes greater, the threshold value will rise, as soon as the curve of growth retardation is a curve with decreasing slope. Here we need not yet assert anything about the further relation between the magnitude of the slope and x.

In our case we can however follow the course of the growth retardation curve more closely by attempting to trace the relationship between threshold value and fore-illumination. If we calculate growth retardation
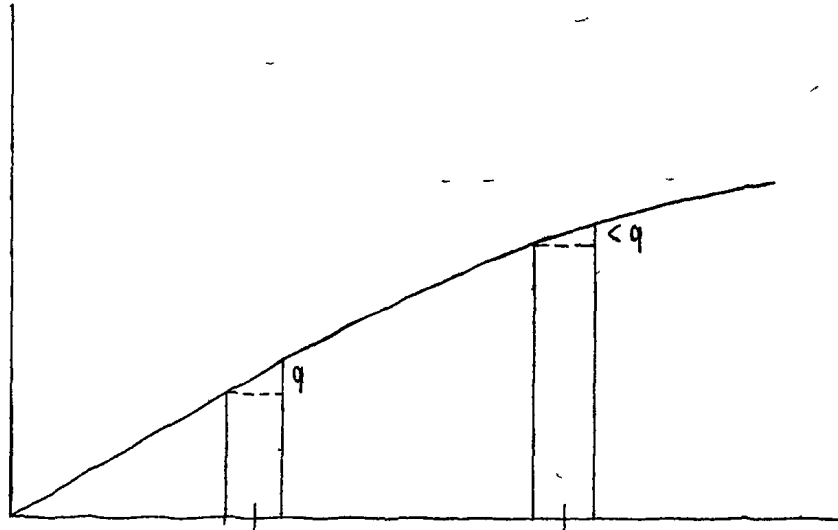

Fig. 2.   energy

from Arisz's tables, mentioned above, the ratio of unilateral after-illumination to omnilateral fore-illumination, we find that, if after-illumination : fore-illumination $= 1 : 11$, there is no curvature;

with this ratio $1 : 10$, 9.9 or 9.2 a few plants give a feeble positive curvature,

, with the ratio $1 : 7.2$ all plants curve positively.

This applies, as was already said above, only to a fore-illumination of less than 2000 M.C.S. given within 3 min. with an intensity below 25 M.C. We must, however, recalculate this for the quantities, which the anterior and posterior sides receive. Since we see, that a feeble positive curvature occurs when the ratio after-illumination : fore-illumination $(b : a)$ has reached a definite magnitude $1 : 9.7$, the ratio of the energy difference $b\dfrac{m-1}{m}$ to the energy of the anterior side $\dfrac{a}{n} + b$ must also be constant, whatever be the values of m and n.

In order to demonstrate this numerically, I propose to make certain assumptions respecting m and n; in principle it does not matter, what values we ascribe to m and n. For m I assume 4; the back is then illuminated with $^{1}/_{4}$ of the intensity of the front, receives therefore in unilateral after-illumination $\dfrac{b}{4}$ M.C.S. Since the omnilateral energy a M.C.S. is distributed uniformly over the whole

circumference, each half, viz. the later anterior or posterior sides, will receive, to begin with, half of the energy, $^1/_2\,a$ M.C.S. Moreover each point, which is turned away from the source of light, receives during rotation a further $^1{}_4$ of the energy of the illuminated side; each half receives therefore altogether $\frac{5}{4} \times \frac{1}{2}a = \frac{5}{8}a$ M.C.S.

Here follows a table, taken from tables 24 and 25 of ARISZ; I have added the numbers representing

$$100 \times \frac{\text{energy difference between front and back}}{\text{energy of front}} \quad \left(= 100 \times \frac{x_a - x_p}{x_a} \right).$$

TABLE II.

Energy of omnilateral fore-illumination in M. C. S.	Energy of the unilateral after-illumination in M. C. S.					
	4×5.5 22	8×5.5 44	5×12 60	10×12 120	5×100 500	10×100 1000
$0 = 0$	75 $+$	75 $++$	75 $++$	75 $++$	75 $++$	75 $++$
$10 \times 5.5 = 55$	29.5 $+$	42.3 $++$	47.9 $++$	58.4 $++$	70.2 $++$	72.5 $++$
$10 \times 12.1 = 121$	17 $+$	27.7 $+$	33.3 $++$	46.2 $++$	65.2 $++$	69.8 $++$
$36 \times 12.1 = 435$	5.6 0	10.4 $+?$	13.6 $+$	23 $+$	48.6 $++$	58.9 $++$
$100 \times 5.5 = 550$	4.5 0	8.5 0	11.1 $+?$	19.4 $+$	44.4 $++$	55.8 $++$
$100 \times 12.1 = 1210$	2.1 0	4.1 0	5.1 0	10.3 $+?$	30 $++$	42.7 $++$

Explanation: $++$ all plants show strong positive curvature.
$+$ all plants show definite positive curvature.
$+?$ a few plants show slight positive curvature.
0 no plants curved.
10×5.5 means: during 10 sec. omnilateral fore-illumination with 5.5 M. C.

$$29.5 = 100 \times \frac{b\frac{m-1}{m}}{\frac{a}{n}+b} = 100 \times \frac{\frac{3}{4} \times 22}{\frac{5}{8} \times 55 + 22}.$$

I here assume $+?$ as the threshold value. We see that for this the quotient $100 \times \dfrac{x_a - x_p}{x_a} = 10.4$, 11.1 and 10.3, and it is therefore sufficiently constant. Then $y_a - y_p$ has become so great that a slight positive curvature occurs. If the curvature can be represented by $f(x_a) - f(x_p)$ and also by $\varphi \left(\dfrac{x_a - x_p}{x_a} \right)$ then f is necessarily $c \log x$ as can be readily shown by a simple mathematical consideration. Since the region of energy, about which the figures supply information, extends from about 300—900 M.C.S. we may say that this portion of the growth retardation curve has a logarithmic course. If the

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quotient $\dfrac{x_a - x_p}{x_a}$ for the threshold value had not been found constant, we should only have been - allowed to conclude, that the growth retardation curve was a curve with decreasing slope, since the threshold value increases with increasing x. In that case also we might perhaps have obtained some further information about the function. I emphasize here that no fundamental significance should be attached to the logarithmic course of this part of the curve between 300 and 900 M.C.S. Moreover the curve from 0—100 M.C.S. is certainly not logarithmic; in a subsequent paper 1 hope to refer to this point in detail.

Arisz regards the omnilateral fore-illumination followed by a unilateral after-illumination as a combination of unilateral illuminations, a short one on the posterior side (fore-illumination) and a longer one on the anterior side (fore-illumination $+$ after-illumination). Since the later posterior side has also received energy during the fore-illumination, a tendency to curve in the opposite direction would have to be overcome. "It need cause no surprise, that the excess which must be given on one of the sides, to obtain an ipsilateral curvature, must be greater in proportion as the tendency to curvature on the other side is stronger." Arisz therefore likewise explains the rise in the threshold value without assuming a change in the sensitiveness. This "tendency to curve in the opposite direction" however, as has been explained above, also exists in plants which have had a purely unilateral illumination, for the curvature depends on the difference of growth retardation between front and back. As in a combined omnilateral fore-illumination and unilateral after-illumination the growth retardation on the posterior side i.e. the "tendency to curve in the opposite direction", becomes relatively greater, the difference in growth retardation and accordingly, also the resulting curvature, becomes smaller (Fig. II). Arisz regards the phototropic induction, and hence also the tendency to curve, as a primary reaction, but since according to the theory of Blaauw, which I have here worked out further, the growth retardation is primary and the tendency to curve secondary, it is better not to employ the latter expression, but to speak of a greater or smaller growth retardation. The unilateral illumination is a special case of the omnilateral and not inversely.

We see therefore, that it is of great importance to ascertain the course of the growth retardation curve. We could not well do this from the figures of table I; moreover the energy numbers had to be divided by a coefficient in order to make them comparable with those for horizontally incident light. We will now try to ascertain the position.

of the maximum of the growth retardation curve in another manner.

·A second phenomenon which shows itself in the combination of an omnilateral fore-illumination with a unilateral after-illumination, is that which Clark [1] calls the increase in sensitiveness of the negative reaction. Here also we can find a simple explanation if we suppose the existence of a descending portion in the growth retardation curve. If the front receives in unilateral illumination an amount of light energy just in excess of the maximum, then the back, which receives $\frac{1}{4}$ of this, will still be on the ascending portion. The ordinate of the front is still greater than that of the back, hence a positive curvature occurs. When we now apply more unilateral energy, we shall have to shift the points, representing the back and front energy, along the growth retardation curve, in such a manner that always $x_a = 4\,x_p$. A negative curvature will then only be possible much further on, because of the great distance between x_a and x_p, i.e. x_a will have to pass far beyond the maximum before y_a becomes smaller than y_p; x_p need not yet have passed beyond the maximum When then the negative difference of growth retardation y_a-y_p is great enough to become visible in a curvature, a negative curvature will occur (about 5000 M.C.S. if administered in 5 mins.). This becomes different, however, if x_a and x_p both lie on the descending portion and are less remote from each other; in that case, as soon as x_p has passed the maximum, the possibility of a negative curvature will arise, the front however requires to receive much less than $4x_p$ in order still to render a visible negative curvature possible. By means of an artifice we can arrange that x_a and x_p come near to each other, although both are on the descending portion. This artifice consists in giving an omnilateral fore-illumination with a quantity of light, which is so great, that front and back both receive a quantity of energy corresponding to the maximum of the growth retardation curve. If we then unilaterally apply an amount of energy, which by itself would have given a strongly positive curvature, there will occur a negative curvature, at least if x_a-x_p is so large that y_p-y_a can give a visible effect. Here also the magnitude of the difference of growth retardations, and hence the threshold value for the negative curvature, will depend on the slope of the growth retardation curve, as was the case with the positive curvature. Here some data from tables 25 and 26 of Arisz are appended; I have added the numbers representing the quantities of light in M.C.S. which the front and back receive from omnilateral fore-illumination $+$ unilateral after-illumination.

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[1] O. L. Clark. Uber negativen Phototropismus bei Avena sativa. Zeitsch. f. Botanik. 1913.

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TABLE III.

Energy of unilateral after-illumination in M C. S.	Omnilateral fore-illumination.					
	12.1 M. C. during 180 secs.			25 M. C. during 100 secs.		
	Energy to front in M C. S.	Energy to back in M C S	Reaction.	Energy to front in M C. S.	Energy to back in M. C. S.	Reaction.
44	1405	1372	` 0	1606	1573	0
60	1421	1376	0	1622	1577	0
120	1481	1391	?	1682	1592	0
500	1861	1486	?	2062	1687	?
1000				2562	1812	?

Explanation:

The energy to the front, 1405 M. C. S., is calculated from $\left(\dfrac{a}{n} + b\right) = \left(12.1 \times 180 \times \dfrac{5}{8} + 44\right)$ M. C. S.,

that to the back, 1372 M. C. S, from $\left(\dfrac{a}{n} + \dfrac{b}{m}\right) = \left(12.1 \times 180 \times \dfrac{5}{8} + 11\right)$ M. C. S.

Arisz means by the sign? that "some plants give a feeble positive curvature, but there are always a few which curve negatively"; this has been confirmed by clinostat experiments. He directly connects this phenomenon of "increased sensitiveness to the negative reaction" with the fact, that after 300—600 M.C.S. the strength of the maximal curvature diminishes, and considers it possible that "by combining a quantity of light, which gives a curvature in excess of the greatest maximal strength, with a quantity which is maximal or nearly so, a curvature is obtainable towards the weaker illumination". We may not connect the "decreased sensitiveness to the positive reaction" with the tendency to curve in the opposite direction and as little may we here directly connect the "increased sensitiveness to the negative reaction" with the strength of the maximal curvature, but must explain it from the course of the growth retardation curve. For the maximal curvature will be strongest in that case, where the difference between the ordinates belonging to x_a and $\frac{1}{4} x_a$ is a maximum. The decrease in the amount of this difference is primarily connected with the decrease in slope of the growth retardation curve and it is only the rate at which the curvature diminishes at higher amounts of energy or the change to a negative curvature, which is connected with the question whether or no the growth retardation curve presents a maximum. The growth retardation curve will therefore continue to rise, although the intensity of curvature (i.e. the difference between the ordinates belonging to x_a and $\frac{1}{4} x_a$) is already declining; the maximum will

therefore be situated much higher than 300—600 M. C. S. Now it results from the above table that if the back receives about 1400 M.C.S., negative curvatures may occur. In this neighbourhood therefore the maximum of the growth retardation curve must lie; there may be considerable individual variation; if the maximum lies somewhat higher, a feeble positive reaction will still be possible; if it is at or below 1400 M.C.S., negative curvatures can occur, this depends on the degree of slope of the descending portion. We can also calculate from table II that a negative curvature never occurs, if the back receives less than 1400 M.C.S. Thus 1756 M.C.S. on the front and 1006 M.C.S. on the back still give a strong positive curvature; here the y of 1756 M.C.S. must be greater than the y of 1006 M.C.S. We may therefore place the maximum of the growth retardation curve at about 1400 M.C.S.

With a unilateral illumination the posterior side will not be maximally retarded until the anterior receives $m \times 1400$ M C.S. This amount of energy must of course lie beyond the threshold value for the negative curvature, for otherwise y_p could never become larger than y_a and no negative curvature could occur. From this the value of m can be found approximately.

I shall indicate yet a third method by which the course of the growth retardation curve can be explored. This can be done by assuming the magnitude of the maximal curvature to be proportional to the difference between the front and back growth retardation. If the maximal strengths of curvature are then plotted against the energy values as abscissae, there results a curve of the differences of growth retardation between the anterior and posterior sides. By a simple mathematical calculation, the growth retardation curve of the front can be calculated from the curve of differences, whereby it is assumed again, that the back receives $\frac{1}{4}$ of the energy of the front; here the magnitudes of the growth retardation do not of course represent absolute values. The points of the posterior growth retardations are found by subtracting the curve of differences from the anterior curve; these can also be found by plotting the anterior curve with abscissae four times as great (rule of products). The magnitudes of the maximal curvatures I have deduced from tables 1 and 3 of Arisz; the energy was here always applied in 10 secs. Since the front is exposed to the full energy [1]), we have here again plotted the course of the growth retardation curve. In this way we come to the following result:

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[1]) See footnote p. 61.

from 0—75 M. C. S. the growth retardation curve is more or less rectilinear, then the slope decreases, so that it becomes approximately logarithmic from 300— 700 M. C. S., while a maximum is found at about 1600 M.C.S. This value therefore agrees sufficiently well with that already found.

- Finally I have also succeeded in finding theoretically the further course of the growth retardation curve, which explains both the phenomena attending more prolonged unilateral illumination and those of unilateral preceded by prolonged omnilateral illumination.
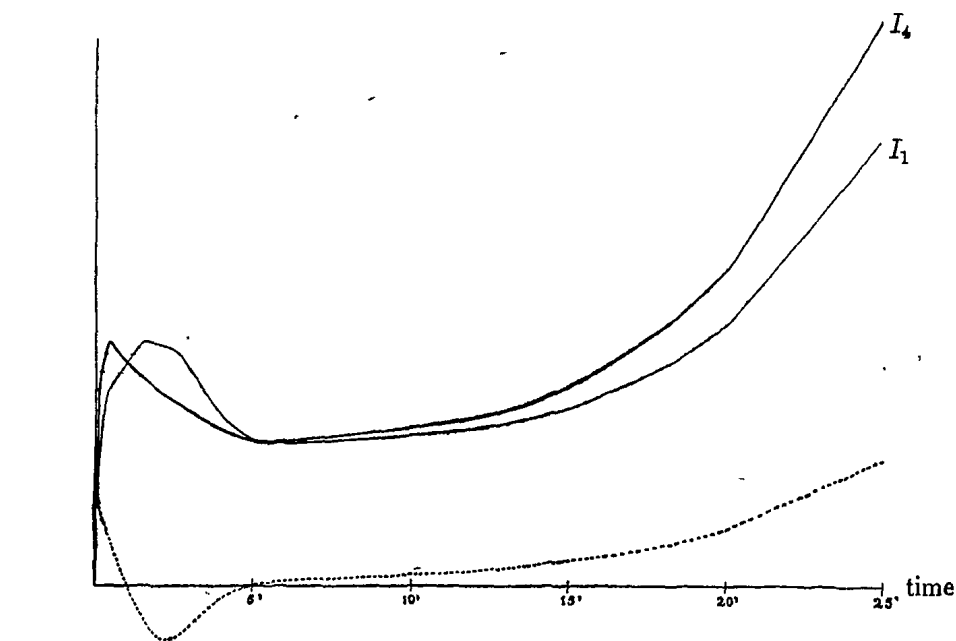
growth retardation

Fig. III.   Diagrammatic representation of
———— the growth retardation curve for an intensity 1.
———— the growth retardation curve for an intensity 4.
.... magnitude of curvature occurring after unilateral illumination with intensity 4.

Here the growth retardation has not been represented as a function of the energy, but as a function of the time, during which there was illumination with the same intensity. Since unilateral illumination, following an omnilateral illumination of more than 5 minutes' duration, always results in a positive curvature, y_a must again be greater than y_p. This comes about through the renewed rise in the growth retardation curve, if the plant is illuminated for more than 5 minutes. Since the slope increases here, the threshold value for positive curvature must again fall. This latter fact agrees with what CLARK and ARISZ found, namely that the threshold value falls if the plants are submitted to a fore-illumination of more than 5 minutes and less

than 20 minutes. If the fore-illumination is more than 20 minutes, the growth retardation curve has become a straight line, since the threshold value now remains constant; however prolonged the fore-illumination with this intensity is, there is no further change in disposition. *Conversely there will be no question of "disposition", "change of sensitiveness", in a process where the effect increases in a rectilinear manner with increasing strength of stimulus.*

Now since also after unilateral continued illumination (for longer than about 5 mins.) a positive curvature is again obtained [1]), the growth retardation curve, for an intensity m times as great, will run more steeply, i.e. for the same abscissa (time) there will be a greater ordinate (retardation of growth). If we take, however, the growth retardations of different intensities with equal duration of illumination, and plot these against the intensities, the slope of the resulting curve will of course greatly decrease at higher intensities, as a simple consideration will show. With this two facts agree: firstly that the threshold value after prolonged fore-illumination with high intensities comes to lie higher than after prolonged fore-illumination with low intensities; secondly, that prolonged unilateral illumination with a high intensity gives a feebler curvatue than illumination with a low intensity during the same period.

We see therefore that the phototropic curvature is determined by the reactions of the separate longitudinal strips of the front and back respectively. Formerly the curvature was regarded as the direct result of a single condition of stimulation, the phototropic, which was considered to be induced as such. According to the view set out above, the curvature must be regarded as the resultant of the effects arising from the conditions of stimulation, which exist on the side, towards which the ultimate curvature will take place, and on the opposite side. These conditions of stimulation express themselves in photo growth reactions; the difference between the two reactions is expressed by the phototropic curvature.

The cause of that which was formerly called "disposition" lies in the peculiarities of the growth retardation curve. These peculiarities occur to some extent in every process in which the reaction is not directly proportional to the stimulus. A tangent galvanometer also becomes less "sensitive" at greater strengths of current. The "disposition" at a given point of the growth retardation curve, whether we take energy or time as abscissa, depends therefore on the magnitude and the sign ($+$ or $-$) of the angle of slope, and of

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[1]) See footnote 2 p. 60.

the direction in which the latter is changing. We can ascertain the sign by arranging that x_a and x_p approximate closely; then we can see from the curvature whether $y_a - y_p$ is positive (effect: positive curvature) or whether it is negative (effect: negative curvature). In unilateral illumination x_a and x_p lie too far apart and may be on dissimilar parts of the curve, so that the latter is very difficult to draw. According as x_a and x_p approximate more closely, the angle of slope can be found with greater accuracy. Since we have found that the growth retardation curve shows an ascending, then a descending and subsequently again an ascending portion, the "disposition" must therefore have three phases; finally after 20 mins., it is not possible to bring about a "disposition change" by further illumination with this intensity. These three phases have been repeatedly discussed in the literature and explained as processes, involving a change in the perception basis. From the above discussion it is evident, however, that disposition is a concept devoid of specific properties and is simply an expression of peculiarities of the growth retardation curve. Every growth retardation curve has a maximum at about 1400 M.C.S. and a minimum at about 5 minutes. The growth retardation curves of two intensities, which are in the ratio 1 : m and with which 5000 M.C.S. can be applied within 5 minutes, intersect at two points; the first point is the energy threshold for the negative curvature ($\pm$ 5000 M.C.S), the second is the time threshold for the second positive curvature (5 minutes). It will, however, be easier and more accurate to construct the growth retardation curves, both energy curve and time curve, from the numbers for photo growth reactions than from interpolations according to the above mentioned method, which is only qualitative, but not absolutely quantitative. Phototropism retains its value, however, since the study of photogrowth reactions presents difficulties in so far as we are here certainly concerned with the conduction of stimuli, while we only observe the reaction of the whole plant. Since in phototropic curvature the various zones curve, one after the other, we get this conduction of stimuli here separated into its successive phases. The difference in growth retardation will also be more constant as phototropic curvature, than when it is found by examining the photogrowth reactions of two different plants, in one for a quantity of energy 1, in the other for a quantity of energy m. For in unilateral illumination both experiments are carried out on the same plant, one on the front, the other on the back. The difference, the resultant of the two reactions, will thus be less influenced by individual variability.

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