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Botany. — *On the connection between stimulus and effect in phototropic curvatures of seedlings of Avena sativa.* By W. H. ARISZ. (Communicated by Prof. F. A. F. C. WENT).

At about the same time there appeared in 1908 papers by BLAAUW [1]) and by FRÖSCHEL [2]) on the perception of lightstimuli.

If a seedling of Avena or Lepidium is unilaterally illuminated, then with different intensities of light a just perceptible reaction was found to take place, when the product of the intensity of light and the duration of the stimulus was a constant.

A repetition of these investigations in Professor WENT's laboratory led to some observations of which I here give a preliminary account.

Madame POLOWZOW [3]) showed for aerotropic and geotropic curvatures, that under the microscope a curvature is seen to occur immediately after the stimulation. BLAAUW [4]) discusses to what extent this may also be regarded as probable in the case of phototropic curvatures. He is of opinion, that either the reaction where

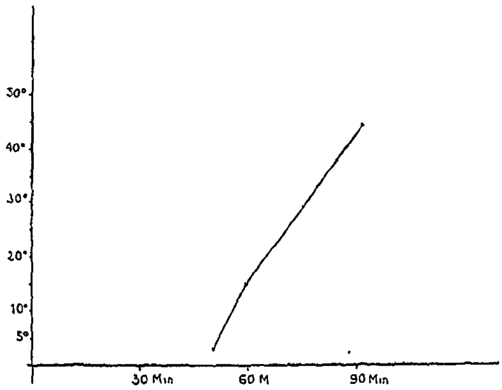


Fig. 1.
Course of the phototropic curvature after BLAAUW.
On the abscissa the time in minutes from the beginning of stimulation, on the ordinate the magnitude of the angle of deviation.

it has become macroscopically visible must just have begun or that at this moment a new stage in the curvature process has been entered upon, and that therefore in any case he is working with a definite point of the reaction.

1) A. H. BLAAUW. Proc. Acad. Sci. Amsterdam, Sept. 1908.

2) P. FRÖSCHEL. Sitzungsberichte der K. Akad. der Wiss. Wien, April 1908.

3) W. POLOWZOW. Untersuchungen über Reizerscheinungen bei den Pflanzen. 1909.

4) A. H. BLAAUW. Die Perzeption des Lichtes. Recueil d Trav. Bot. Néerl. Vol. 5. 1909.

It remains to trace also the course of a phototropic curvature with the microscope in the same way as POLOWZOW did for geotropic curvatures.

In view of the manner of curving, to be described later, the distance between the original position of the tip of the coleoptile and the new position occupied at any moment during the curvature is chosen as the measure of the curvature at that moment. MAILLEFER [1]) and POLOWZOW also took this distance as a measure of the curvature. In the eye-piece there was a net-micrometer, so that it was possible to make under the low power a drawing on squared paper of the whole apex.

By comparing these drawings, made every 5 or 10 minutes, it was possible to trace the origin of a slight alteration in shape. Nutations gave a good deal of trouble, though all specimens in which these occurred were absolutely rejected. Since the nutation movements are sharply distinguished from a phototropic curvature by the change of position of the whole apex with respect to the base, it was fairly easy to recognise them.

In the following curves the abscissa is the time and the ordinate the strength of curvature, measured in the afore-mentioned way.

In one case therefore the curvature began after 12 minutes. Are we then to conclude that the curvature begins just at this moment and that the reaction time is therefore 12 minutes? I think not; it seems to me it would appear that we must come to this conclusion after a study of the shape of the apex at the beginning of the curvature. It is found that while this shape is at first almost exactly conical with a somewhat blunted top, the curvature becomes visible as a slight mutual asymmetry of that side of the cone which is turned towards the light and that which is turned away from it. This asymmetry becomes gradually more marked until the apex begins to bend forward and the curvature extends further and further from the apex. There is no indication of the sudden appearance of curvature. In a few cases the shape of the apex favours the perception of even a slight asymmetry, but it is very probable that in such cases a curvature occurred, even before a deviation was traceable.

The determination of a reaction-time is therefore experimentally impossible, and it is quite conceivable, that the curvature occurs immediately on stimulation.

The passage of a part of the curve which is only visible micro-

[1]) A. MAILLEFER. Etude sur la Réaction géotropique. Bull. Soc. Vaudoise. 1910.

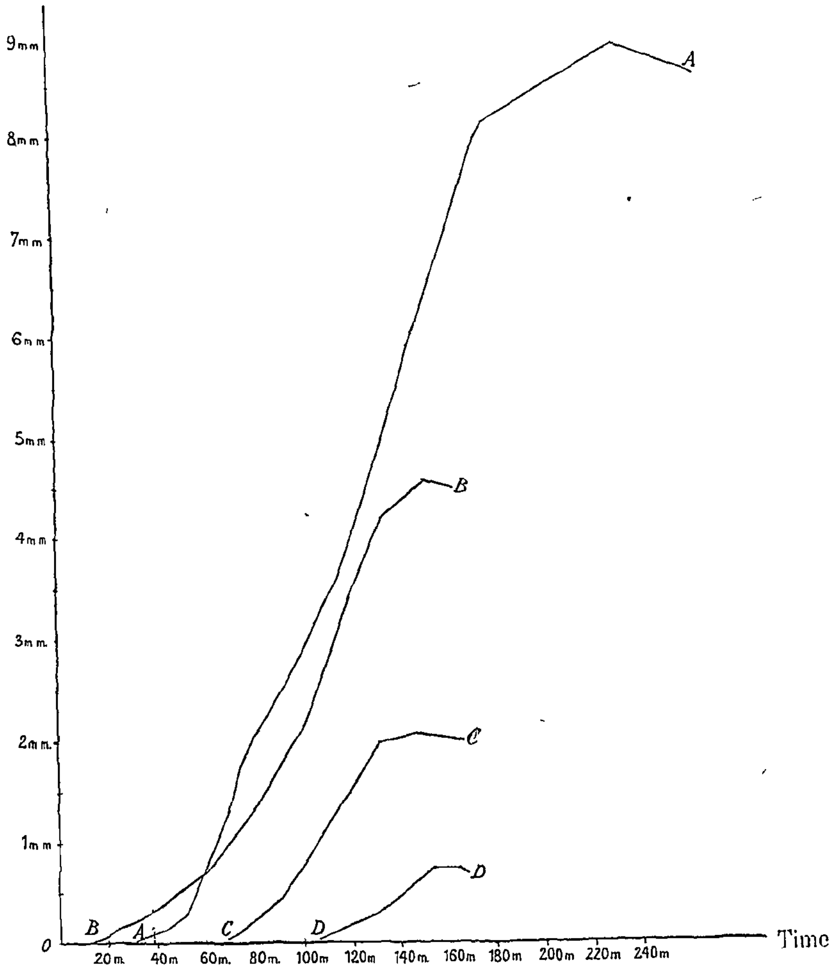


Fig. 2.
Course of the phototropic curvature.
A. stimulated with 800 M.C.S. B. with 112 M.C.S.
C. with ± 20 M.C S. D. with 5 M.C.S.

scopically into a part which can also be perceived macroscopically, takes place more or less gradually.

An obvious break occurs on strong stimulation (see fig. 2 A). BLAAUW's interpretation, that the curvature here enters on a new phase, seems to me very plausible, when we see that just at this moment the parts remote from the apex, which in contradistinction to the apex itself show a considerable increase in length, begin to take part in the curvature.

On comparison of curves obtained in such a way, it became obvious that the maximum curvature seen in plants which were illuminated with different intensities, was not equally great in every case; with weaker light it was considerably less.

It was found that slighter curvatures exist than those observed by BLAAUW and by FRÖSCHEL. This was a quite unexpected result, for although BLAAUW had very cautiously spoken of those curvatures which were only just macroscopically visible, he still believed he was working with a threshold of stimulation.

This applies still more to FRÖSCHEL, who attached great value to the smallest product still giving a curvature, as a measure of phototropic sensitiveness, for comparison with that of other plants.

Has the deviation of the apex valued by BLAAUW as still showing curvature, any special value, to which alone the rule of products applies, or would it be found, that to a smaller or greater energy of stimulus there also corresponds a smaller or greater curvature? In general, that a definite quantity of energy causes a definite extent of curvature?

In order to obtain an answer to this question a larger number of experimental data had to be available.

The tedious observation with the microscope was superseded by a much simpler apparatus. A photographic lens, magnifying 2 times, projected the image of the seedlings on a glass plate, upon which a scale of half-millimetre squares had been photographed. The position of the apices was read by means of a simple lens.

The advantage of this arrangement is that in addition to a greater number of plants, the whole coleoptile can always be observed. The deviation of the apex from its original position before the beginning of the curvature, chosen at the moment when this distance is greatest, was taken as the measure of the magnitude of the curvature. Since from the beginning gravity opposes the curvature, there comes a moment when the apex under the influence of phototropism moves no further from the vertical, because phototropism is neutralised by gravity. Although this point will probably give no accurate idea of the sensitiveness, it is here only necessary to have a fixed point of the curvature-proces.

Out of many observations made, I here bring together the following, which hold good for seedlings of an average length of 22.5 m.m. at a temperature of about 17.5 degrees Cent.

The light energy was obtained by various combinations of intensities by stimulation periods of various lengths. (from 2 to 240 sec.)

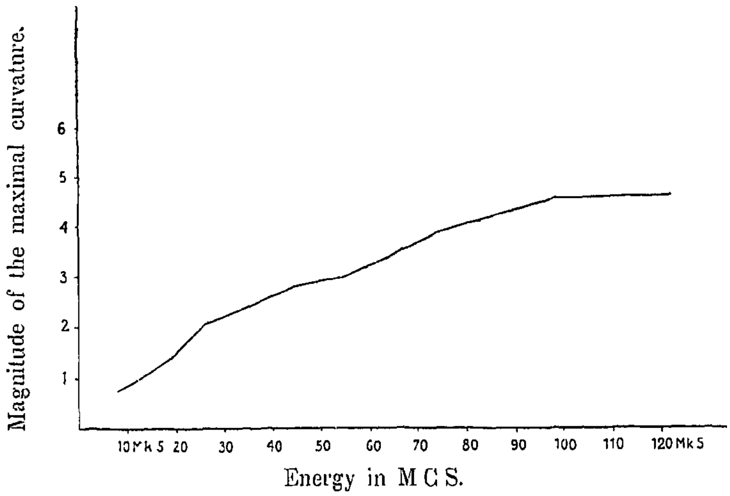
The intensities were determined by a WEBER [1]) Photometer.

[1]) Prof. H. SNELLEN, Director of the Dutch Eye Hospital was kind enough to place this photometer at my disposal.

Light energy in M.C.S. [1])	Magnitude of the maximal curvature in mm.	Number of observations
7.6	0.73	12
12.4	0.96	6
18.1	1.47	10
26.1	2.1	6
44.2	2.8	15
54.0	3.0	7
65.0	3.4	16
75.3	3.9	7
99.0	4.6	13
126.6	4.6	11
144.0	4.3	10
239.0	4.9	10
576.0	3.6	13

These figures are found to be on a smooth curve, which therefore represents the relation of energy and maximal curvature.

Fig. 3.



The curve gives the relation of light energy used as a stimulus and the magnitude of the maximal curvature for plants of ± 22.5 mm. length and a temp. of 17.5° Cent.

[1]) M.C.S. Means the product of the intensity of the light (in Meter candles) and of the length of the exposure.

Up to 100 M.C.S. there was an increase in the magnitude of the curvature, at first more rapid and then somewhat lower; from 100 M.C.S. to 400 M.C.S. the same magnitude, after which there is a decrease. Below 7 M.C.S. the curvature could not be measured by this method, up to 2 M.C.S. the curvature, as a faint inclination of the apex, was still clearly visible macroscopically. These apical inclinations have been noticed before, e.g. by RUTGERS [1]), who did not however recognise them as phototropic curvatures, because they also arose without previous stimulation. Control-experiment which I made, showed however that when coleoptiles, which showed absolutely no inclination of the apex, were placed in the dark and care was taken that they were previously stimulated neither geotropically nor mechanically by touch or similar agency, they showed no apical inclination, whereby, however (RUTGERS l. c. p. 56) attention was only paid to the curvature at right angles to the plane of nutation.

Below 2 M.C.S. the curvature was so faint, that macroscopically it could not be recognised with certainty. The microscope is likewise inadequate for this. The smallest curvature observed was about $^1/_4$ mm. at 1.4 M.C.S.

No limit can therefore be fixed below which no curvatures arise, but that there are curvatures which at present escape our observation, is highly probable. The suggestion is obvious, and the course of the curve is an argument in favour, that the curve should be continued to point 0. The significance of this is, that every quantity of energy gives rise to a definite degree of curvature.

Each quantity of energy reacts on the plant and is expressed by a curvature of definite maximal strength.

Since the phototropic curvatures with which these observations are concerned, were all to some extent counteracted by gravity, it was desirable to have for comparison experiments, from which the unilateral action of gravity had been eliminated. For this purpose Fitting's intermittent clinostat was used, which makes it possible to place a plant during equal intervals alternately in positions which differ from one another by 180 degrees, so that the action of gravity in one position balances that in the other. In 2 minute periods no appreciable curvature arose in unilluminated plants after 6 hours. Out of every 4 minutes the plants were for 2 minutes in a position in which they could be examined and drawn under the microscope.

[1]) A. A. L. RUTGERS, De invloed der temperatuur op den praesentatietijd bij geotropie. Dissertatie, Utrecht 1910.

The curve below gives the course of a curvature of this kind.

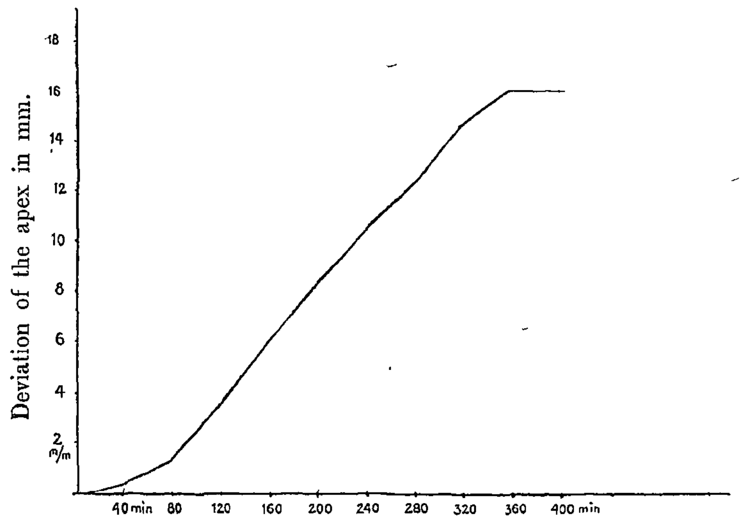


Fig. 4.
Course of the phototropic curvature whilst the unilateral action of gravity is eliminated. Stimulated with 360 M. C. S.

It is clear from this curve that already after 10 minutes, sooner therefore than when gravity is opposing, a curvature becomes visible; this is of course a strong argument in favour of an earlier beginning of the curvature-process. After about 6 hours there comes a moment in which the distance from the vertical no longer increases. In order to facilitate a survey of the curvature I here reproduce figures made from drawings on frosted glass by outlining the image projected by the photographic lens.

If one compares with this a curvature in which gravity opposes, the great difference is at once striking. In this case too, first the becoming asymmetric of the apex, after which the curvature affects more and more basal zones. After about 6 hours the greatest deviation of the apex is reached. If the strength of the curvature is determined at this moment by placing arcs of different radius along the curved part, it is found that the coleoptile is not bent in the arc of a circle but consists of a series of parts with different degrees of curvature. Thus the zone situated fairly close to the apex is most strongly curved, perhaps because it is the zone of most active growth. After these 6 hours the curvature of the uppermost part decreases, so that a slight diminution of the deviation of the apex is observable; it is the beginning of the straightening out. In the more basal parts the curvature still increases continuously. Finally the whole upper part

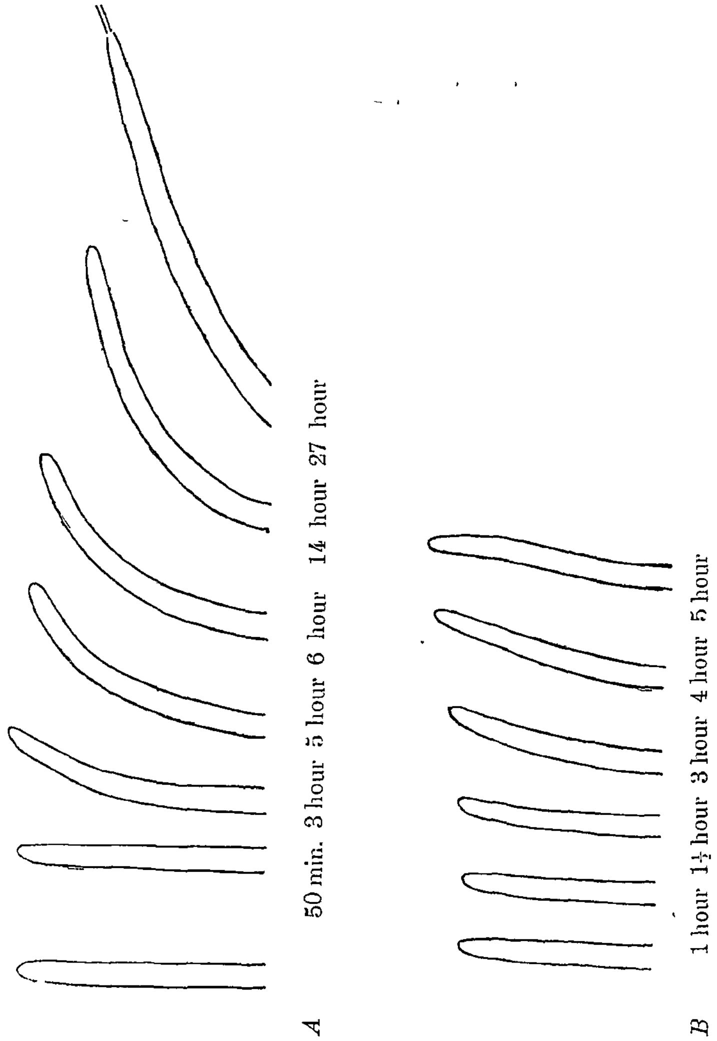


Fig. 5.

A. The course of the curvature whilst the unilateral action of gravity is eliminated.
B. The course of the curvature whilst the unilateral action of gravity is not eliminated.
A and *B* stimulated by the same quantity of light ± 25 M.C.S. (2 ×).

becomes straight and the curvature in the base has become fixed.

Perhaps we possess therefore in this method of observation with an intermittent clinostat a more accurate means of determining the sensitiveness of the plant.

If we once more trace how far the above investigations influence our conception of the process of stimulation, it is clear that the comparability with physico-chemical processes becomes more and more marked. The existence of a threshold of stimulation can no longer be maintained, for not only is each quantity of energy perceived but it is clear now that a reaction will always take place. The time which intervenes between the application of the stimulus and the beginning of the curvature, "the reaction-time" was found to be experimentally undeterminable. Thus the latter can not serve as a measure of sensitiveness.

It is more and more evident that such concepts as "Erregung" and "Erregungshöhe" can be perfectly well dispensed with, because the phenomena do not give the slightest indication of their use.

Similarly the determination of an index or time of relaxation will be found impossible, because it is impossible to show experimentally that no curvature results from the summation of intermittent stimuli.

Since the presentation-time has been conceived as a factor of the quantity of energy, which is just able to traverse the threshold of stimulation, it follows from the above investigations, that when the "Schwelle" is abandoned the presentation-time loses much of its value as a special stimulation period. It remains however, as a time factor of the quantity of energy, which results in a curvature of definite strength.

Henceforth therefore the physiology of stimulation must be investigated by considering the energy which is applied as stimulus and which is determined by the product of the intensity of the operating force and the length of the stimulation period, whilst the reaction can be gauged by the degree of the maximal curvature, at least if the unilateral action of gravity is not eliminated. If the latter be

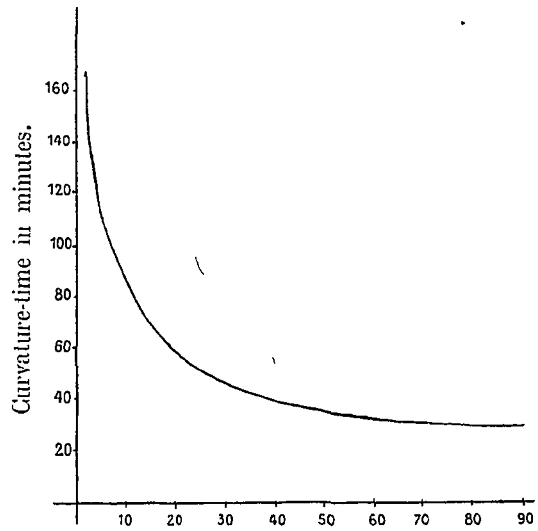


Fig. 6.

Relation between Energy and the time untill the curvature becomes just macroscopically visible.

eliminated the degree of curvature at the moment when straightening out begins, can perhaps serve as measure.

If one wishes to investigate the influence of some external condition on the sensitiveness, one can determine what quantity of energy gives a definite degree of curvature each time this condition is varied; in which case it is very convenient that the moment at which such a curvature becomes visible, is constant.

What was formerly understood by reaction-time but what has now been found to be almost exclusively *curvature-time*, is *constant* for a definite quantity of energy. This curvature-time greatly increases according as the energy of stimulation is smaller, a fact clearly shown by the following curve.

In conclusion I wish heartily to thank Dr. BLAAUW and in particular Professor WENT for their kind interest and advice.

Utrecht. Bot. Laboratory.

Crystallography. — *"On the orientation of crystal-sections."* By J. SCHMUTZER. (Communicated by Prof. C. E. A. WICHMANN).

(Communicated in the meeting of February 25, 1911).

When determining the orientation of a secant-plane from the angles that the traces of three unparallel planes not lying in one zone include together, one generally obtains a biquadratic equation in $\cos 2\varrho$, furnishing as maximum 4 compatible roots. As now angle 2ϱ can be supposed at the same time in two quadrants, it follows that one finds 8 values for ϱ. With these values correspond 8 values of σ. If however three crystal-planes and a definite crystal-section are given, the secant-plane is entirely determined; which value of ϱ and of σ comes in consideration here, can be decided with certainty, if one takes into account the circumstance that a crystal-plane is at the same time the boundary-plane of the mineral substance.

Being admitted a plane (hkl) (cf. fig. 1) the pole of which lies in p, and forming with the plane C ($\perp$ c-axis) a secant-line AB, then the angle $DBE = \alpha < \frac{\pi}{2}$ is filled with mineral-substance, the obtuse angle EBI on the contrary is not. Now one can suppose the projection-globe divided into 8 octants of which 4 are lying above and 4 beneath the projection-plane C, and of which the first two ($BOD = \text{I}$, $DOA = \text{II}$) contain the acute plane-angle DBE. If one fastens s to the coordinates $\varrho = \frown BM$, $\sigma = \frown Ms$, then s lies in the 1st globe-octant, calculated from AB; for a plane P'' $(\bar{h}\bar{k}l)$ s lies in octant III.