Botany. — W. H. - ARISZ: *"Positive and negative phototropy of the apex and base in oat-seedlings (Avena sativa)."* (Communicated by Prof. F. A. F. C. WENT.)

(Communicated in the meeting of September 27, 1913).

(Preliminary communication).

OLTMANNS [1]) has been able to show very convincingly that in the sporangiophores of *Phycomyces* a weak illumination produces positive curvatures and a strong illumination negative ones. BLAAUW [2]) confirmed these results and determined the quantity of light-energy necessary to produce these phenomena. In the case of Phanerogams also in the course of time negative curvatures have been seen, but except in the case of some roots, the communications are very vague and doubtful. OLTMANNS and before him N. J. C. MÜLLER [3]) saw negative curvatures in seedlings of *Lepidium sativum*, while PRINGSHEIM [4]) saw faint inclinations of the apex in those of *Avena*.

Nevertheless very clear negative phototropic curvatures can easily be obtained in seedlings of *Avena sativa* when they are illuminated with only just that quantity of energy necessary to produce the phenomenon. I have endeavoured to show in an earlier paper [5]) that the reaction which occurs after the application of a certain quantity of light (this is true for 1—100 C. M. S. [6]) has a constant strength. The reaction will increase in strength in proportion as the quantity of energy, used for stimulation, is greater.

With a short duration of stimulus the stronger reaction after more powerful stimuli is shown by the earlier occurrence of the curvature: that is to say, *the reaction-time* [7]) *is a function of the*

1) Flora Bd. 83 1897.

2) Recueil d. Trav. Bot. Néerl. Vol. 5 1909.

3) Botanische Unters. 1872.

4) COHN's Beitr. Bd. 9 1909.

5) Proceedings Roy. Acad. Sc. Amsterdam, March 1911.

6) The usual abbreviation for candle-metre seconds.

7) By reaction-time must here be understood the time which elapses from the beginning of stimulation to the moment at which the curvature becomes macroscopically visible.

The lengthening of the reaction-time after weaker stimuli, when the duration of stimulus (t) is very short and constant (energy $i \times t$ *not constant*) is by no means comparable to the lengthening of the reaction-time which BACH (Jahrb. f. wiss. Bot. Bd. 44 1907) and Mrs RUTTEN-PEKELHARING (Rec. Tr. Bot. Néerl. Vol. 7 1910) found by stimulation with weak centrifugal forces during the presentation time ($i \times t$ *constant*). Here the lengthening of the reaction-time is

amount of light-energy used as stimulus. (Thus at 50 C. M. S. the reaction-time is 30 minutes, at 1 C. M. S. it is nearly 2 hours.)

Also the maximum curvature which is reached, is a function of the quantity of light-energy used as stimulus.

The degree of curvature, which is reached after a certain time, gives therefore (within these limits) a measure, by which conclusions as to the magnitude of the stimulus may be drawn.

These experiments have been continued further with greater amounts of light and have yielded the results that might have been expected. The reaction, which follows on stimulation with a definite amount of light-energy, is constant for that quantity of energy, only when the stimulus is applied for a comparatively short time. If the quantity of energy is applied for a longer time, then so-called tone-phenomena occur, which I intend shortly to discuss in greater detail.

If the stimulus is more than 100 C. M. S. the degree of curvature remains about the same. If however it is made considerably more, as for example 1200 C. M. S. at 23° C., then the resulting curvature is notably smaller; this continues up to 6000 C. M. S. when a new phenomenon appears, *the negative curvature,* which reaches a maximum at about 18000 M. C. S. From the paper of VAN DER WOLK [1]) and the recent one of WILSCHKE [2]) it has been shown that with these quantities of light positive curvatures from the base were to be expected and since it further seemed desirable to exclude such an influence, light was prevented from reaching the base. To this end there was placed round each seedling a black copper tube, which

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entirely due to the longer presentation-time with weak centrifugal forces. For this case MAILLEFER (Bull. Soc. Vaud. Vol. 48 1912) has *mathematically* deduced the formula $i\,(t-k) = constant$ (the reaction-time equals the presentation-time + a constant value.) This agrees with BACH's table 34, not with Mrs. RUTTEN—PEKELHARING's table 27.

The lengthening of the reaction-time on stimulation during the whole reaction-time is more complicated, because in that case neither the strength of the stimulus ($i \times t$), nor the duration (t) is *constant.* For this case TRÖNDLE (Jahrb. f. Wiss. Bd. 48 1910) has put forward the *empirical* formula $i\,(t-k) = constant.$

This formula is not supported by the tables which TRÖNDLE adduces as proof. Nor does BACH's table 33 according to TRÖNDLE give true values, whilst BACH's table 32 gives *constant* reaction-times for which $t = k$.

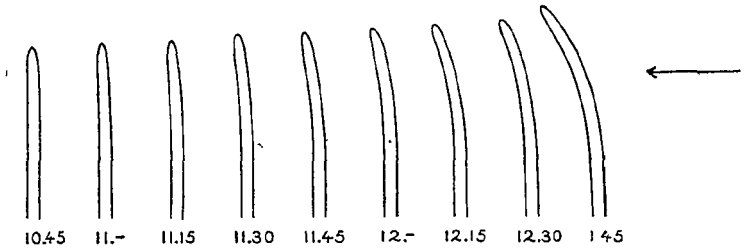
In BACH's tables 34 and Mrs RUTTEN—PEKELHARING's table 27, as has already been pointed out, stimulation was not continued during the whole reaction-time.

[1]) Publications sur la Physiologie végétale, Nimègue 1912.

[2]) Sitzungsberichte K. Akad. Wien, Bd. 122, 1913.

rested on the ground and which could give no occasion for contact curvatures, because it could at no point touch the coleoptile. The phenomena, which are here discussed, are therefore exclusively the result of illuminating the apical zone of 1— 2 mm. length.

The negative curvature can be observed very distinctly, but is much more developed, when after illumination the plant is rotated on a clinostat round a horizontal axis, so that no geotropic influence can counteract the curvature. In the same way as formerly I now also used an intermittent clinostat [1]) in which the positions of rest were separated by 180°. In each of these positions the plant remained for 2 minutes, so that there was enough time to trace the image of the seedling projected on to transparent paper by means of a lens and in this way to obtain a complete survey of the course of the curvature. The drawings were of course made by red light.



Negative curvature of an *Avena sativa* seedling.
At 10.15 the apical zone of 2 mm. was illuminated from the right with an intensity of 340 c. m. s. After stimulation on the intermittent clinostat temp. 25°.

The strength of the curve which is now reached, is found to be by no means inferior to that of a positive curvature, whilst, because only the uppermost zone of the apex is illuminated, there is here also a *conduction of stimulus* towards the basal zones.

Apart from the direction of the curvature a negative curvature is in no single respect distinguishable from a positive one.

Very remarkable and probably of some importance from a theoretical standing-point are the complicated curvatures which occur with illumination of about 9000 C. M. S. applied during 30 seconds.

In this case a positive curvature first takes place, later a negative one is visible and this, although only a length of 1 mm. of the apical zone, is illuminated. *It is evident from this that positive and negative curvatures are perceived and find expression independently of one another.*

[1]) Prof. MOLL in Groningen was so good as to allow me to make use for these experiments in his laboratory of the clinostat of VAN HARREVELD.

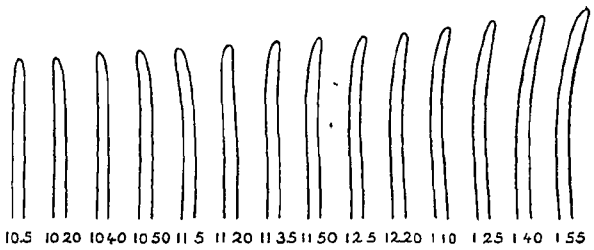


Fig. 2

Course of the curvature of an *Avena sativa* seedling. Illuminated from the left with an intensity of 340 C. M. S at 9.30 during 30 secs. Only an apical zone less than 1 mm. illuminated. Up to 11 8 a *positive* curvature, which afterwards passes into a strong negative one. After illumination on an intermittent clinostat; temp. 25°.

If the stimulus is more than 18000 C. M. S., the negative curvature then decreases again and generally no curvatures at all are observed. The remarkable phenomenon takes place however, that after the very strong stimulus of 400.000 C. M. S. during 4 seconds, weak positive curvatures are seen, which again disappear under the strongest illumination I have been able to apply, namely 1.600.000 C.M.S.

Following these observations of curvatures, which arise after illumination of the apical zone, I am able to give here some results with regard to the sensitiveness of the base.

VAN DER WOLK has stated that positive basal curvatures begin to occur at 20000 C. M. S. and are strong at 60000 C. M. S. VON GUTTENBERG and WILSCHKE have confirmed this. VAN DER WOLK and VON GUTTENBERG surrounded the apex with little caps of tin-foil. WILSCHKE thinks this method is wrong and makes use of a very pretty arrangement, by which the light falling through a slit illuminates a definite zone.

Nevertheless — and WILSCHKE himself shows this in his paper — this method of using little caps is not as he thinks to be dismissed as wholly useless, because the sensitiveness to contact-stimuli is particularly slight with small caps. WILSCHKE's method has the drawback that only very little of the material can be used at a time, and this is probably the reason why the phenomena, which will be described here, have escaped his notice.

I therefore used in my experiments little caps of tin-foil, which were so wide that they could be placed over the coleoptiles without friction. The little caps were completely light-tight and to make this perfectly sure were surrounded above with sealing-wax: this had at the same time the advantage of making them very easy to handle. They were removed immediately after illumination.

Nevertheless experiments were extremely difficult, especially at high temperatures, owing to nutation and contact curvatures. It is found absolutely necessary to use only those plants, which at the beginning of the experiment stood *completely* upright. For this reason about 80 % to 90 % of the cultivated material had to be unquestionably condemned.

It is now found that at 25° C., and it seems very desirable to choose such a high temperature for these experiments, very slight basal curvatures already occur at 100 C. M. S., when the upper 5 m.m. of the plant are covered with a cap. On applying more energy these curvatures increase and are clearly visible, 2 hours after the beginning of the illumination with 300 to 1200 C. M. S. They begin to be macroscopically visible after about half an hour.

If more light is applied in each case with very short duration of stimulus then the results are very uncertain. Sometimes very faint positive curvatures, at other times negative ones occur. The variability of the phenomenon is however so great and the curvatures are so complicated by the fact that sometimes first a positive and then a negative curvature arises, that it has not been possible to fix the amount of energy of which it can be said with certainty that the effect is positive or negative. The complications are probably due in great measure to the fact that the different portions of the base are not all equally sensitive, and various effects are thus superimposed.

A further investigation with only a small zone illuminated might be able to give an explanation of this. It is certain that with the application of 30000 C. M. S. during a short period no strong phototropic curvatures of the base occur. It need cause no surprise that VON GUTTENBERG, VAN DER WOLK and WILSCHKE all give these values since they did not apply this amount of energy as I did in a *short* period of time, but in much longer ones (VON GUTTENBERG, e. g. in an hour). Then the tone-phenomenon also occurs for the base and a large amount of energy applied over a considerable time no longer yields a negative but a positive effect.

To gain an idea of the sensitiveness of the most basal zones, the quantity of light was determined, which applied in a short time so as to eliminate tone, produced positive curvatures when the uppermost 12 mm. of the coleoptile had been covered with a cap. This limit was found to lie at about 400 C. M. S. The curvatures at 500 C. M. S. were the strongest, at more than 800 C. M. S. they were weaker, whilst from 1000 to 2400 C. M. S. even negative ones occurred.

If a comparison is now made of results which have been obtained

by illumination of the apex and of the base, it is found that in order to obtain a positive curvature of the apex a smaller amount of light is sufficient than for one of the base. The negative influence in the base and especially in the most basal zones is however visible with smaller amounts of light.

It is most remarkable that also the negative geotropic curvature, which JOST and R. STOPPEL [1]) found at high centrifugal forces were strongest in the more basal zones. Whether this is due to the greater rate of growth in the basal zones in comparison with the apex can only be decided by future investigations.

The results described point to the possibility of explaining the aberrant results obtained by VON GUTTENBERG and VAN DER WOLK. VAN DER WOLK held that illumination of the base makes the apex more sensitive to an illumination from the opposite side, whilst VON GUTTENBERG observed a smaller reaction of the apex. I also have been able to confirm VON GUTTENBERG's result. He applied 40000 C. M. S. in one hour, obtained therefore a strong positive basal curvature and then concludes from the decreased apical curvature that there is a conduction of stimulus towards the apex. Unfortunately it is impossible to repeat the experiments of VAN DER WOLK, because he did not state what quantity of energy he used for illumination and in what time this was applied. If however this was in a short time, then the assumption is obvious, that he was dealing with a zone in which negative curvatures arose, which superimposed on an apical curvature caused by illumination of the apex from the other side, produced a stronger effect in this direction, thus giving rise to the impression that the apex through the previous illumination of the base had become more sensitive. Experiments carried out in this direction have not led to a conclusive result, although a basal illumination of the base with 20000 C. M. S. and an apical illumination from the opposite side with 15 C. M. S. indeed produce apical curvature sooner and often rather more strongly than in plants without basal illumination [2]). I have not obtained such striking results as those described by VAN DER WOLK, although the possibility is by no means excluded that taking a somewhat different length of the illuminated part and some other amount of energy, applied perhaps during a longer time, the phenomenon may show itself more markedly.

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[1]) Zeitschr. f. Bot. Bd. 4 1913.

[2]) If 120000 C. M. S. in 60 sec. is applied to the base then the apical curvature is noticeably slighter, because in this case a positive basal curvature predominates.